



## HIPPOTAMODON ERYMANTHIUS (SUIDAE, MAMMALIA) FROM MAHMUTGAZI, DENIZLI-ÇAL BASIN, TURKEY

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**Abstract:** The Staatliches Museum für Naturkunde in Karlsruhe houses an interesting collection of Turolian mammals from Mahmutgazi, Turkey, among which is a comprehensive sample of the large suid, *Hippopotamodon erymanthius*. The fossils plot out within the range of metric variation of *H. erymanthius* from Pikermi and Samos, Greece, but lie at the lower end of the range. Like the suids from these sites, the Mahmutgazi specimens lack the first premolar. Overall, the Mahmutgazi sample is metrically and morphologically close to the material from Akkaşdağı, Turkey. The upper and lower third molars and fourth premolars are, on average, smaller than those of *Hippopotamodon major* from Luberon, France (MN 13). Two undescribed fossils of *H. erymanthius* from Pikermi are housed at the SMNK, and are included in this paper in order to fill out the data base for the species at this locality. The chronological position, palaeoecology and sexual dimorphism of the Mahmutgazi suids are discussed.

**Key words:** Suidae, Late Miocene, Turkey, *Hippopotamodon*, biochronology, palaeoecology, sexual dimorphism

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### Introduction

The German-Turkish Lignite Survey, carried out during the 1960's, collected fossils at numerous localities ranging through the Miocene (Sickenberg et al. 1975). Many of the taxa were included in faunal lists, but few of them were described formally. The suids from Mahmutgazi were identified as *Dicoryphochoerus* (Sickenberg and Tobien 1971). During a study visit to Karlsruhe in 2016, the author was enabled to study the suids from Mahmutgazi collected during the survey, which are sufficiently interesting to warrant a paper to themselves. This article complements the revision of the genus *Hippopotamodon* carried out by Pickford (2015). A few suid specimens from Mahmutgazi are housed in the Maden Tetkik ve Arama, Ankara (Pickford and Ertürk 1979, Van der Made et al. 2013), but details about them are scanty.

### Historical background

Previous mentions of suids from Mahmutgazi were made by Sickenberg and Tobien (1971) and Sickenberg et al. (1975) (as *Dicoryphochoerus*), but the material was not described. *Microstonyx major* was listed at the locality by Pickford and Ertürk (1979). Saraç (2003), Liu et al. (2005) and Yakut (2012) briefly discussed the listing but added no details, and the overview of the stratigraphy of the sedimentary basins in southwestern Turkey by Alçiçek

(2010) mentions suids at the site, and correlated it to MN 11–12 (Early to Middle Turolian). Van der Made et al. (2013) included measurements of a tooth from Mahmutgazi in bivariate plots of *Microstonyx major*, but the catalogue number and meristic position were not provided, so it is not possible to discuss their results.

A review of previous literature on Late Miocene suids of Turkey reveals that, apart from a few recent papers dealing with fossils from Yulafli (Geraads et al. 2005), Akkaşdağı (Liu et al. 2005) and Çorakyerler (Geraads 2013), most of the fossils have not been described, nor measurements provided, and this has given rise to a certain degree of uncertainty concerning which taxa occur at which localities. The data base was improved with the publication by Pickford (2015), who provided descriptions, illustrations and measurements for many of the Turkish suid fossils. This description of the Mahmutgazi collection augments the Turkish fossil suid data base, and modifies the taxonomy of the suid from the site (*Hippopotamodon erymanthius* rather than *Hippopotamodon major*).

### Geological and stratigraphic contexts

Mahmutgazi is in the Denizli Basin in southwestern Turkey (Sickenberg et al. 1975, Alçiçek 2010, Alçiçek et al. 2012, Pickford 2015) (Text-fig. 1). There are two localities at Mahmutgazi, (1) at 38°01'24.21"N : 29°24'30.28"E, which corresponds to the locality sampled by the German-Turkish



**Table 1. Faunal lists for Mahmutgazi, Turkey, in the original order published by the authors. See also Alçiçek et al. (2012) who list in addition *Indarctos* and *Hipparion macedonicum*.**

Mahmutgazi faunal list according to Saraç (2003) (NB The large quantity of ?, cf. and aff.)	Mahmutgazi faunal list according to Alçiçek (2010) (NB 1: The record of <i>Dicoryphochoerus</i> is based on specimens of <i>Hippopotamodon erymanthius</i> ; 2: <i>Adcrocuta eximia</i> and <i>Percrocuta eximia</i> are synonyms)
Erinaceinae <i>Parapodemus</i> <i>Huerzelerimus/Castromys</i> <i>Ictitherium robustum</i> <i>Ictitherium</i> cf. <i>tauricum</i> <i>Percrocuta eximia</i> <i>Machairodus aphanistus</i> <i>Orycteropus</i> <i>Hipparion</i> ? <i>Ancylotherium</i> <i>Ceratotherium neumayri</i> <i>Chilotherium schlosseri</i> <i>Dicoryphochoerus</i> <i>Samotherium boissieri</i> <i>Palaeotragus</i> cf. <i>coelophrys</i> ? <i>Helladotherium</i> <i>Gazella</i> cf. <i>capricornis</i> <i>Gazella</i> aff. <i>gaudryi</i> <i>Oioceros wegneri</i> ? <i>Palaeoreas</i> ? <i>Palaeoryx</i> ? <i>Tragocerus</i> <i>Choerolophodon pentelici</i>	<i>Oioceros wegneri</i> <i>Palaeoreas lindermayeri</i> <i>Tragoportax amalthea</i> <i>Tragoportax gaudryi</i> <i>Gazella capricornis</i> <i>Gazella gaudryi</i> <i>Palaeotragus coelophrys</i> <i>Samotherium boissieri</i> <i>Microstonyx erymanthius</i> <sup>1</sup> <i>Dicoryphochoerus</i> <sup>1</sup> <i>Machairodus aphanistus</i> <i>Adcrocuta eximia</i> <sup>2</sup> <i>Protictitherium crassum</i> <i>Ictitherium robustum</i> <i>Ictitherium tauricum</i> <i>Percrocuta eximia</i> <sup>2</sup> <i>Ceratotherium neumayri</i> <i>Chilotherium schlosseri</i> <i>Choerolophodon pentelici</i> <i>Orycteropus</i> <i>Hippotherium</i> <i>Parapodemus</i> <i>Huerzelerimus/Castromys</i>

## Measurements

Measurements were taken with sliding calipers, using the method outlined by Van der Made (1996). Length measurements of worn teeth can be up to 15% less than in unworn teeth, due to interstitial wear. In worn teeth, allowance has been made for this interstitial wear. Breadth measurements are not as badly affected by wear, but it has been noted that tooth germs can be appreciably smaller in all dimensions compared with fully formed teeth. Measurements of tooth germs have not been adjusted, but they should be used with caution in metric analyses because they can give the false impression of the extent of the lower end of the range of metric variation. In the tables of measurements, BL = bucco-lingual breadth, MD = mesio-distal length, lt = left, rt = right.

It is stressed that different authors measure teeth in different ways, and this can contribute to difficulties in the metric analyses that flow from the measurements. The problem is especially evident for the length of the third molars. Van der Made (1996) measures length perpendicular to the anterior side, the method adopted in this paper; Kostopoulos et al. (2001) measure length at the occlusal level, and the cervix, while Harris and White (1979) suggested taking the length at the cervix, which is the least affected by wear. However, when teeth are in situ in jaws, it is often difficult to access the cervix of the teeth for accurate measurements.

## Abbreviations

SMNK – Staatliches Museum für Naturkunde, Karlsruhe

## Systematic Palaeontology

### Family Suidae GRAY, 1821

### Subfamily Suinae GRAY, 1821

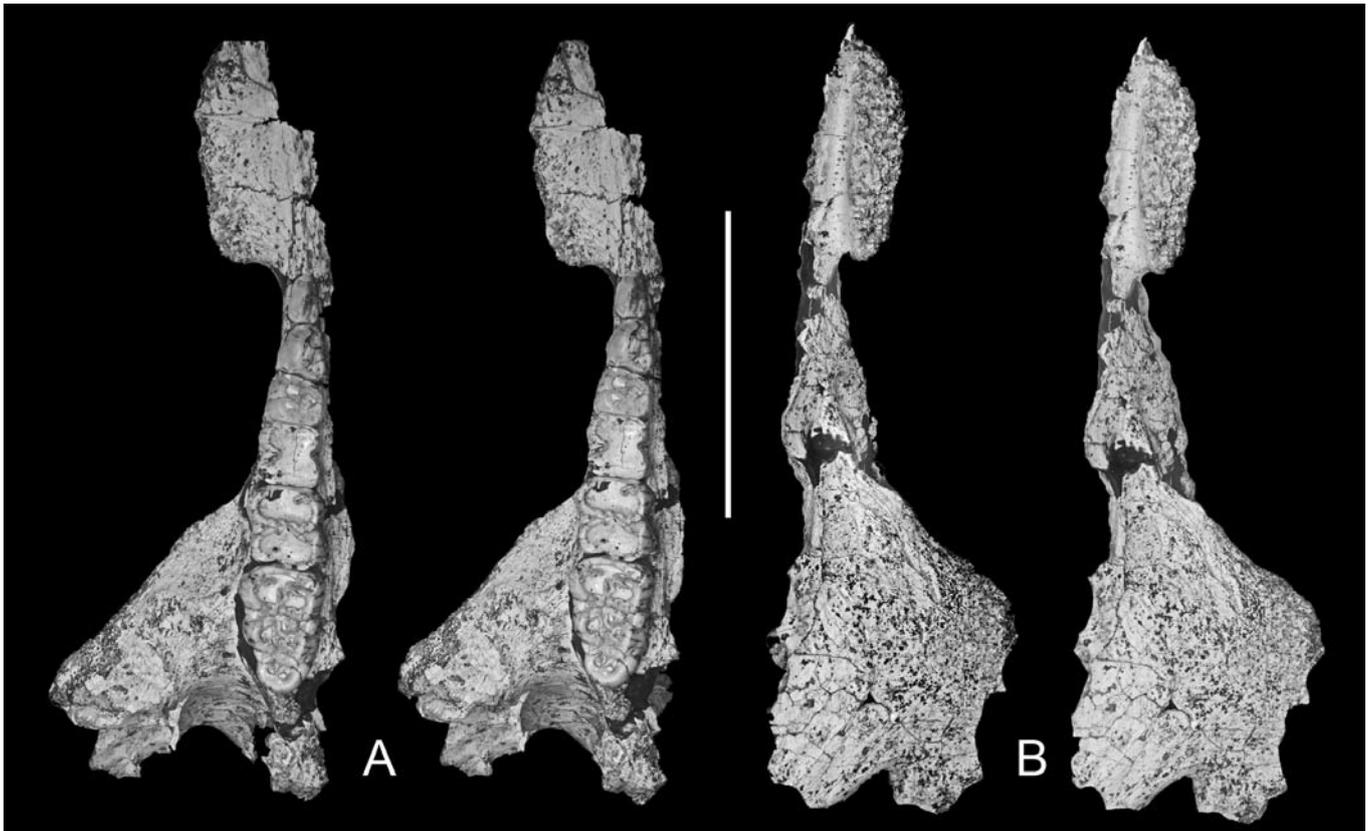
### Genus *Hippopotamodon* LYDEKKER, 1877

Type species. *Hippopotamodon sivalense* LYDEKKER, 1877

**Diagnosis.** Large Suinae in which the males have flaring canines (smaller in Turolian species); molar enamel relatively thin; molars structurally simple with well-developed Fürchenplan; buccal cusps in lower molars noticeably lower crowned than lingual ones; P4/ with posterior accessory cusp almost as large as two main buccal cusps; sagittal cusplets present in central valley between the protocone and the paracone-metacone; p/1 often absent in some Turolian populations; posterior choanae U-shaped, open immediately behind M3/; p/4 with prominent innenhugel and 2-3-4 cusp, anterior cingulum and ac-1 cusp moderately high; diastema between c/1–p/1–p/2 short; broad flat dorsal surface to braincase; the maxillae of males possess a large supracanine flange with a highly rugose dorsal surface, females do not have such a flange (modified from Pickford 1988, 2015).

Other species in the genus:

- Hippopotamodon antiquus* (KAUP, 1833)
- Hippopotamodon major* (GERVAIS, 1850)
- Hippopotamodon etruscus* (MICHELOTTI, 1861)
- Hippopotamodon erymanthius* (ROTH et WAGNER, 1854)
- Hippopotamodon hyotherioides* (SCHLOSSER, 1903)
- Hippopotamodon pilgrimi* (PICKFORD, 1988)
- Hippopotamodon ultimus* (HAN, 1987)



Text-fig. 2. SMNK Ma1 MP8, right maxilla of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) stereo occlusal view, B) stereo dorsal view (scale 10 cm).

**Note.** Pickford (1988) retained two genera for the large Late Miocene suines, *Hippopotamodon* and *Microstonyx*. Whilst there are some morphological differences between the various species included in these “genera”, they are relatively minor, concerning principally the canine, which is rare or absent in many collections. Perusal of the literature reveals that the decision to identify a fossil as *Hippopotamodon* or *Microstonyx* has often boiled down to where it came from (Indo-Pakistan for *Hippopotamodon*; Europe for *Microstonyx*), rather than on morphological evidence. For this reason, in this paper *Hippopotamodon* is employed for these suids, regardless of their provenience. Part of the reason for doing this is that adoption of two genus names gives the impression that there are important biogeographic differences between Europe and Indo-Pakistan during the Vallesian and Turolian, which is probably not the case.

**Species *Hippopotamodon erymanthius***  
(ROTH et WAGNER, 1854)

**Holotype.** Lower jaw illustrated by Roth and Wagner (1854: pl. 5, fig. 1). The whereabouts of the fossil are not known, although a cast is reported to be preserved in the NHMUK, London (Van der Made et al. 2013).

**Type locality.** Pikermi, Greece.

**Diagnosis.** Large species of *Hippopotamodon* in which the length of m/3 ranges between 40.5 and 51.6 mm, and M3/ from 38 to 44 mm. Tendency for P1/ and p/1 to be suppressed. Adult males have a prominent supra-canine flange with rugose lateral and dorsal surfaces.

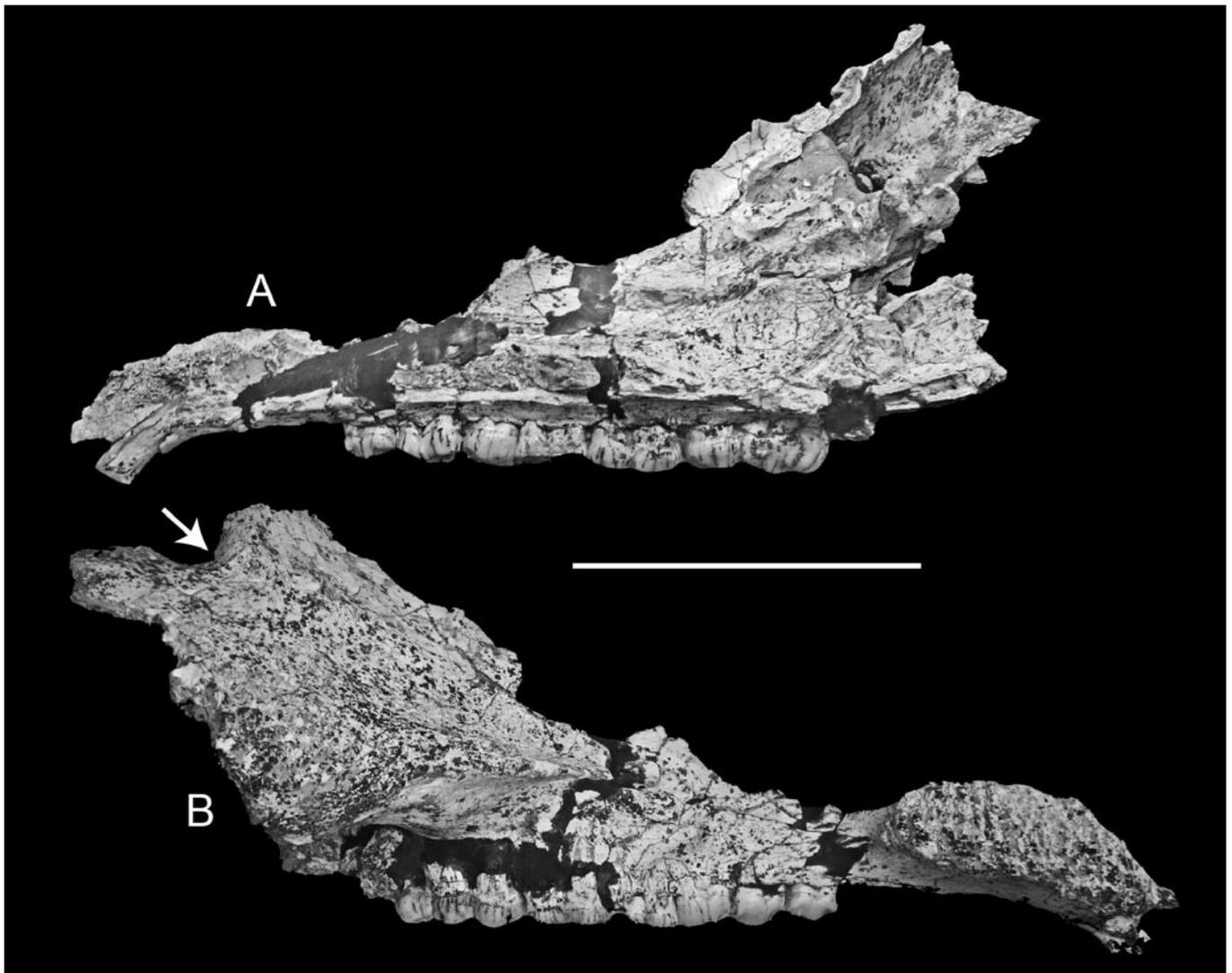
## Description

### Skull

In the Karlsruhe collection of *Hippopotamodon erymanthius* from Mahmutgazi, there is a partial skull, and several mandible fragments, including parts of a juvenile maxilla and mandibles.

The most complete skull fragment in the sample is a right maxilla (Text-figs 2, 3) of a fully adult individual (M1/ deeply worn, M3/ in moderate wear) (SMNK Ma1 MP 8). Almost none of the zygomatic or frontal bones is preserved. There is a large supra-canine flange above and behind the level of the canine, which has highly rugose lateral and dorsal surfaces, which indicate that the specimen is likely to represent a male individual. Dorsally, the rugose part of the canine flange is separated from the facial part of the maxilla by a deep, smooth, groove via which passed the tendons of the snout musculature. The area of the origins of the snout musculature are large, that for the levator rostri occupying a large area of the zygomatic process of the maxilla above the facial crest, beneath which is an extensive zone for the depressor rostri and dilatator nasalis lateralis musculature.

In ventral view, the front of the canine flange ends above the canine, and the rear edge terminates opposite the level of the P2/, forming a right angle with the facial process of the maxilla. There is an alveolar ridge in front of the P2/, which curves slightly laterally as it courses anteriorly, and in the preserved part there is no sign of a P1/ alveolus. The leading edge of the zygomatic arch flares laterally at an angle of about 45°, its anterior root being opposite the front of M2/



Text-fig. 3. SMNK Ma1 MP 8, right maxilla and parts of the zygomatic and frontal bones of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) lingual view, B) lateral view (arrow shows the leading edge of the orbit) (scale 10 cm).

and the maxillary recess lying opposite the rear loph of the M3/. A small part of the anterior edge of the orbit is preserved above and well behind the level of the M3/.

### Mandible

The lower jaw of *Hippopotamodon erymanthius* from Mahmutgazi (SMNK Ma1 Gips 6) shows a long diastema between the canine and the p/2 occupied by a sharp alveolar ridge (Text-fig. 4). There is no sign of the p/1 or of an alveolus for this tooth. There is a short gap between the i/3 and the canine. The rear of the symphysis extends as far back as the level of the front of p/2. The incisor battery is proclive and lies well beneath the occlusal surface of the cheek teeth. The lower canine is short and stubby, and projects laterally and anteriorly only slightly. The left mandible and symphysis from the site (SMNK Ma1 Gips 17) shows essentially the same morphology as the previous specimen (Text-fig. 5).

### Deciduous teeth

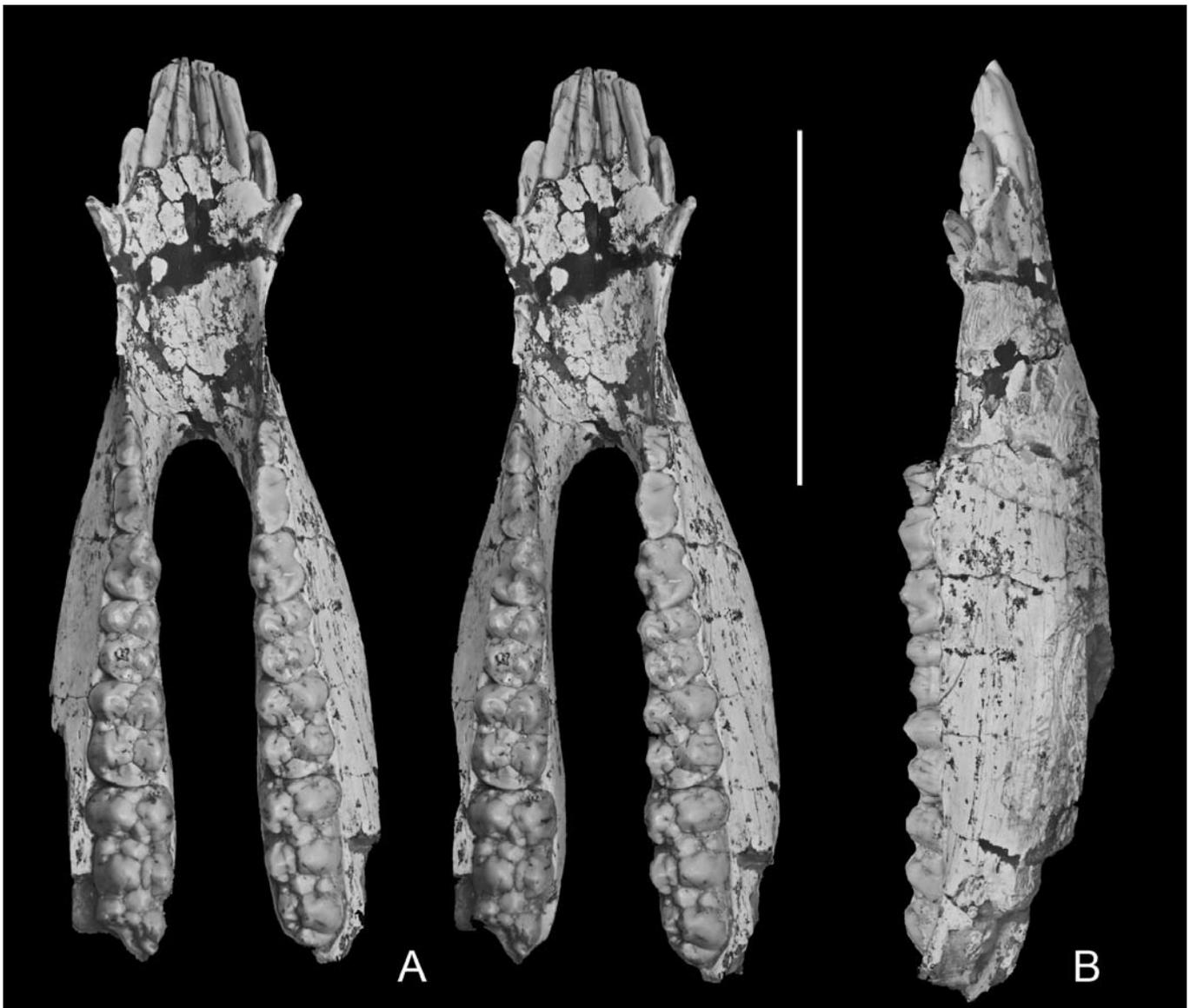
There are two juvenile mandibles and a maxilla in the collection at Karlsruhe. Ma1 MP 5 is a left maxilla containing

D3/–D4/ and M1/ (Text-fig. 6a), and Ma1 Nr 196 is a right mandible containing d/2–d/4, m/1 and a left mandible with d/4–m/1 (Text-fig. 6b).

In occlusal view, the outline of the D3/ is triangular with rounded corners, with a large mesial cusp and a pair of distal cusps forming the rear loph. There are weak mesial distal cingula, as well as small cingular tubercles on the inner face of the mesial cusp. The main cusps are indented by Fürchen.

The D4/ is tetracuspid, like the permanent molars, but the mesial pair of cusps is slightly narrower than the distal pair, which imparts a trapezoidal occlusal outline to the tooth. In the centre-line of the tooth there are small, low, anterior, median and posterior accessory cusplets. The mesial and distal cingula are well formed but do not extend onto the buccal or lingual surface. There is a low tubercle in the lingual end of the median transverse valley. The Fürchen pattern is like that in the permanent molars.

The d/2 is triangular in buccal view with the mesial and distal cusplets about half the height of the main cusp, and it is sectorial in occlusal view. It is narrower mesially than distally. The two roots are splayed apart anteriorly and posteriorly.



Text-fig. 4. SMNK Ma1 Gips 6, mandible of *Hippopotamodon erymanthius* lacking the ascending rami, from Mahmutgazi, Turkey. A) stereo occlusal view, B) right lateral view (scale 10 cm).

The d/3 is a larger version of the d/2.

The d/4 in contrast is molariform, with six cusplets arranged in three lophids, as is usual in artiodactyls. The root arrangement is the usual one found in suids, with splayed mesial and distal roots supporting the anterior and posterior lophids, and a single buccal root under the protoconid of the second lophid.

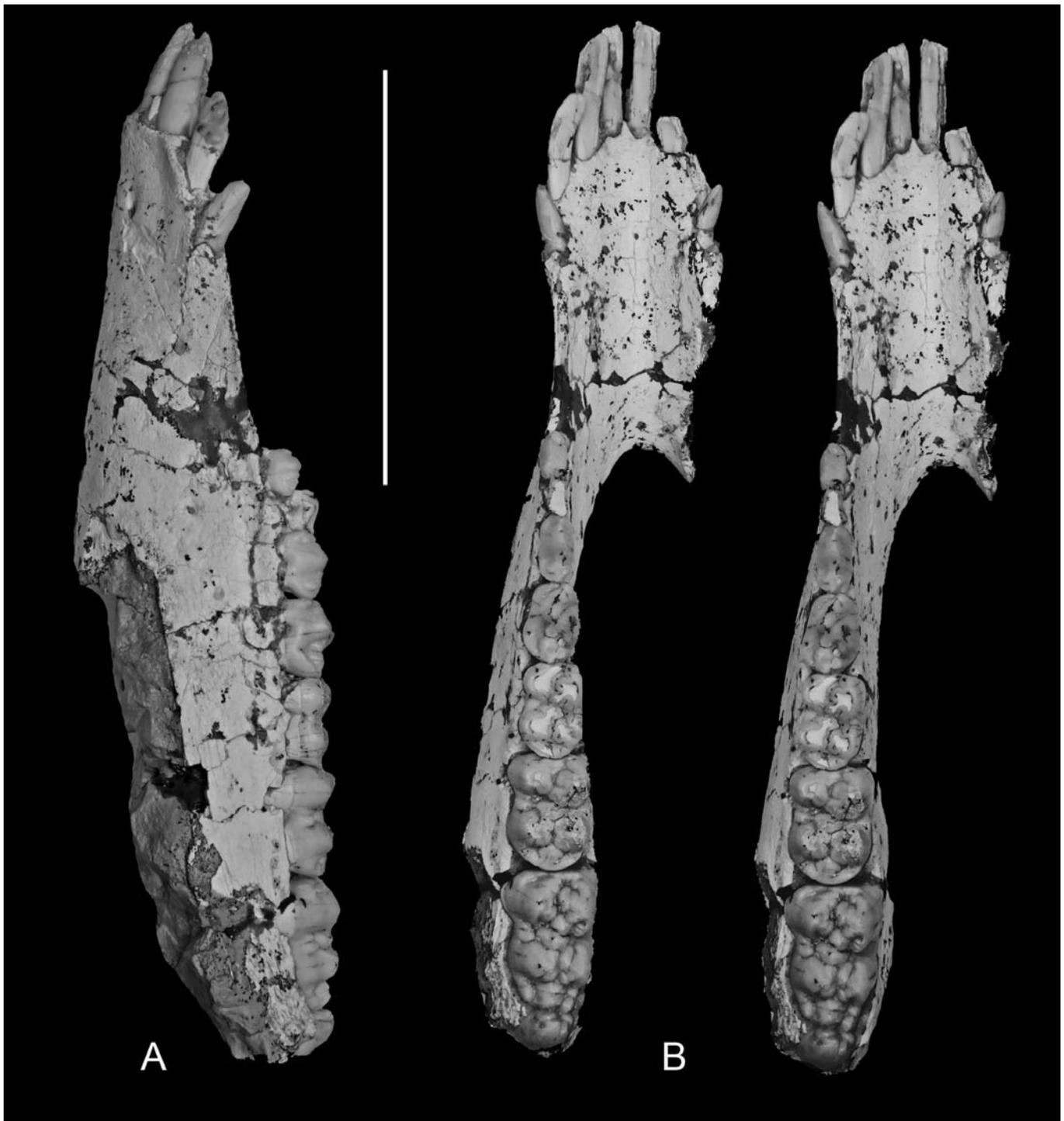
#### Permanent teeth

The upper right central incisor from Mahmutgazi (SMNK Ma1 Nr 176) is unworn and shows a prominent cusplet on the lingual part of the tooth (Text-fig. 7a). This tubercle is an enlarged bead of the lingual cingulum. The cusplet is confluent with the rest of the lingual cingulum and walls off a capacious lingual fossa. The labial side of the crown is bulbous. There is a shallow slit apically, and the distal edge of the crown is beaded, markedly so near the cervix.

SMNK Ma1 MP 6, is a worn right I3/ with a swollen lingual cingulum interrupted distally by a slit (Text-fig. 7b).

The upper premolars and molars of *Hippopotamodon erymanthius* were described by Pickford (2015). The Mahmutgazi specimens are typical of the species (Text-fig. 8). Although the evidence is weak, the only available maxilla suggests that the P1/ was suppressed, which indicates a derived species of the genus. The P2/ has a diminutive disto-lingual tubercle, as in material from Pikermi. The P3/ possesses a thick lingual cingulum, closing off a small mesial fovea, and a capacious distal lingual basin. The rear of the tooth is broad, due to the well-developed disto-lingual cusp. The P4/ is tricuspid, with a pair of sagittal cusplets in the valley between the protocone on the one hand and the paracone-metacone on the other. The incision between the paracone and metacone is relatively shallow, and becomes obsolete in medium wear.

The upper third molars from Mahmutgazi have a short linguallly positioned talon (Text-fig. 9a, b), while the lower third molars have a double-cusped talonid, with the lingual



Text-fig. 5. SMNK Ma1 Gips 17, left mandible and symphysis of *Hippopotamodon erymanthius* lacking the ascending ramus, from Mahmutgazi, Turkey. A) left lateral view, B) stereo occlusal view (note the d/2 between the p/2 and p/3 (scale 10 cm).

cuspid usually smaller and lower than the buccal one (Text-fig. 9c, d, e).

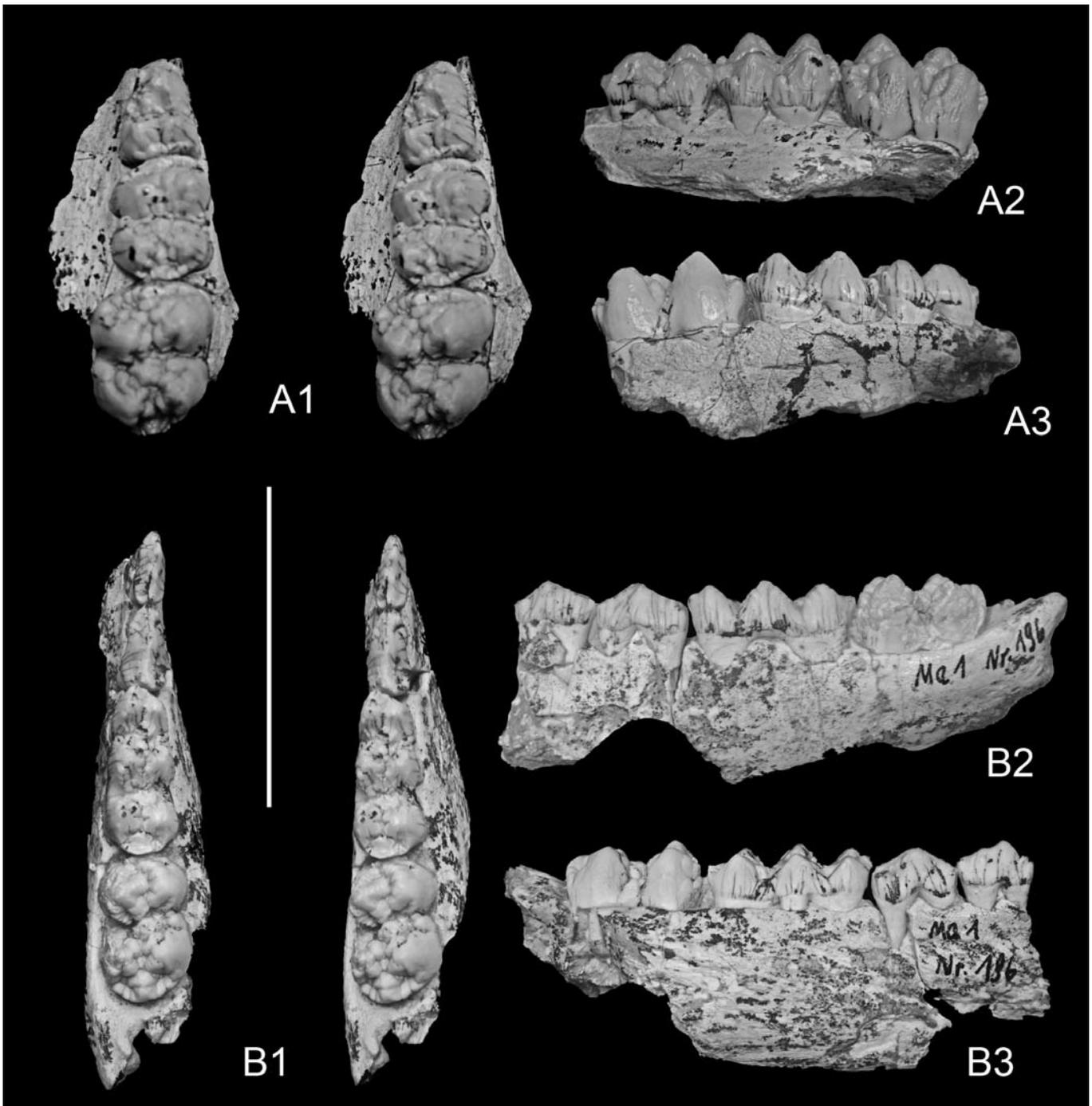
The central and second lower incisors are extremely tall, and even the i/3 is elongated and barely separated from the canine (Text-figs 10, 11). The incisors are arranged such that they comprise a continuous occlusal surface which wears almost flat. The canine extends only slightly above this occlusal surface, and is functionally linked to the same dental battery.

The anterior lower premolars are sectorial with the mesial and distal tubercles about half the height of the main cusp.

The p/4 has a clear inner cusp and a large posterior cusplet (Text-figs 12, 13). The p/1 is absent in all three mandibles that preserve the requisite part of the jaw, which indicates a derived species of the genus (Text-figs 4, 5).

#### Post-cranial bones

The only suid post-cranial element in the Mahmutgazi collection in Karlsruhe is a proximal left radio-ulna (Ma1 Gips 12) (Text-fig. 14). The radius is solidly fused to the ulna, even though the sutures between the bones are clearly visible.

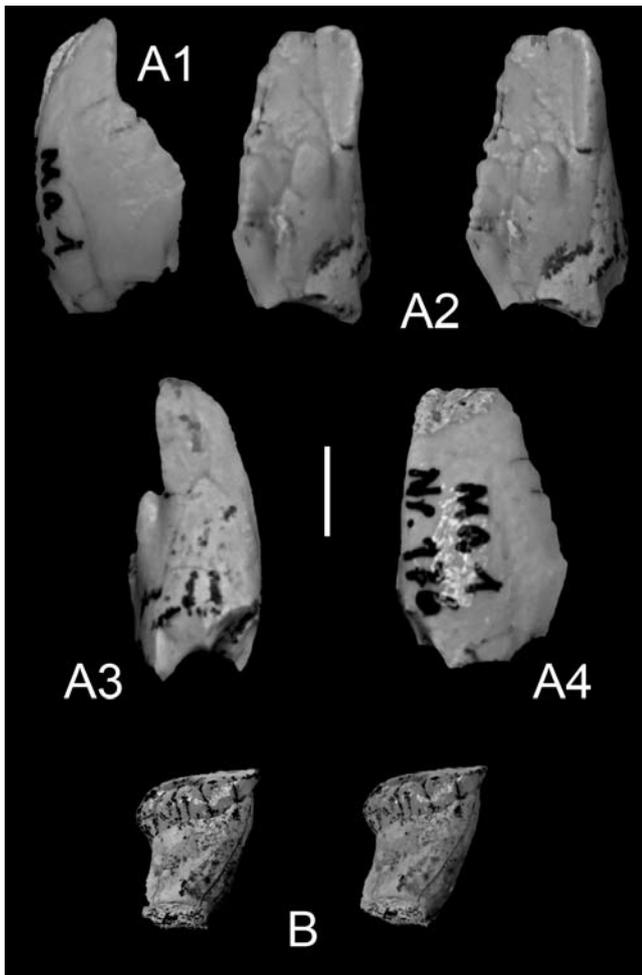


Text-fig. 6. Juvenile specimens of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) Ma1 MP 5, left maxilla containing D3–D4/ and M1/ (A1 – stereo occlusal, A2 – lingual, A3 – buccal views), B) Ma Nr 196, right mandible containing d/2–d/4 and m/1 (B1 – stereo occlusal, B2 – lingual, B3 – buccal views) (scale 5 cm).

The olecranon process is relatively short and medio-laterally robust (broken caudally). In the radius, the articular surface for the distal epiphysis of the humerus shows a broad medial basin, a relatively prominent central groove and a deep but small lateral basin. The articular part of the medial edge of the sigmoid notch in the ulna is expansive. The corresponding part on the lateral side is less expansive. The sigmoid notch extends over more than a semi-circle, all of which indicates an elbow in which joint movements were constrained to the para-sagittal plane.

#### Metric analysis of the teeth of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey

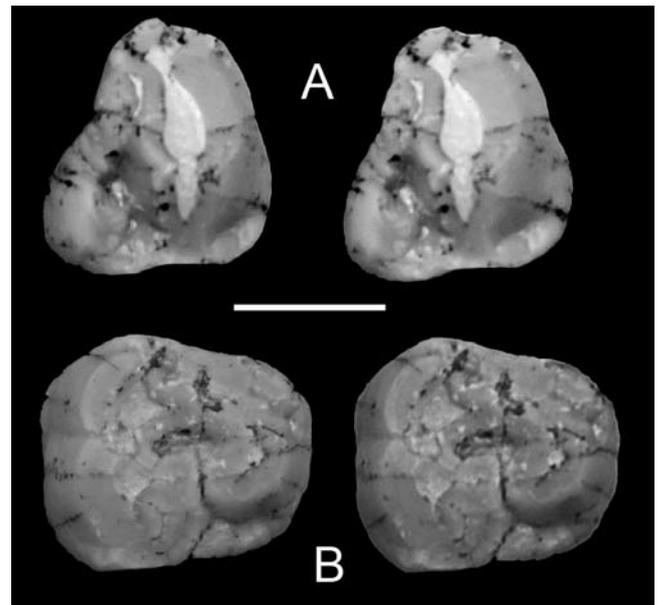
The dimensions of the dental sample of *Hippopotamodon* from Mahmutgazi (Tab. 2) are smaller than any of the specimens from Luberon, France, the type locality of *Hippopotamodon major* (basal MN 13), and are smaller on average than the mean of the Pikermi (MN 12) and Samos (MN 11 + MN 12 or MN 13) samples of *Hippopotamodon erymanthius* (Text-fig. 15). They are similar to the collection from Akkaşdağı, Turkey, (Text-fig. 16) correlated to MN 12 by Liu et al. (2005), and to the large sample from Maragheh



Text-fig. 7. Upper incisors of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) SMNK Ma1 Nr 176, right I1/ (A1 – distal, A2 – stereo lingual, A3 – mesial, A4 – labial views), B) SMNK Ma1 MP6, right I3/, stereo lingual view (scale 10 mm).

(= Maragha) (Iran) correlated to MN 11 by Pickford (2015). Overall the Mahmutgazi specimens are similar in dimensions to the comprehensive sample from Dorn-Dürkheim 1, Germany (Van der Made 1997), which is correlated to MN 11, but are on average smaller than the material from Kalimantsi (Kotopoulos et al. 2001), although there is overlap in the ranges of variation of the fossils from the two localities.

Concerning Turkish samples of *Microstonyx major* (which according to Liu et al. (2005), includes *Microstonyx erymanthius*), the authors wrote that “we usually deal with faunal lists or fragmentary and isolated specimens which preclude a direct comparison with the Akkaşdağı form”. This concern can now be partly addressed (see measurements and descriptions of Turkish suids from many localities published by Pickford (2015)), and it is clear that the cranial and dental suid specimens from Akkaşdağı and Mahmutgazi are metrically closely similar to each other, suggesting similar chronological and/or palaeoecological contexts. The fact that both of these localities have yielded material that is on average smaller than the samples from Pikermi and Samos (Greece) suggests either that the latter two localities are not the same age as Mahmutgazi and Akkaşdağı, or that their palaeoenvironments may have differed, or that they comprise multiple levels (the case for Samos).



Text-fig. 8. Stereo occlusal views of upper premolars of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) SMNK Ma1 Nr 180, left P3/, B) SMNK Ma1 Nr 190, left P4/ (scale 10 mm).

#### Specimens of *Hippopotamodon erymanthius* from Pikermi, Greece, in the SMNK

The SMNK possesses two dentognathic specimens (containing 12 teeth) of *Hippopotamodon erymanthius* from Pikermi, Greece (Tab. 3). This sample augments the large amount of material that has been described from Pikermi (now standing at 358 teeth) (Pickford 2015).

The snout (SMNK MP3) is interesting, as it probably represents a young adult female individual, with no sign of a supra-canine flange, only a bowing out of the maxilla behind the level of the canine (Text-fig. 17). The left and right I2/s are in their crypts, but show the serrated postcrista typical of the genus, and the right P2/–M2/ are fully erupted. The only teeth showing light wear at the apices of the cusps are the M1/ and the P3/.

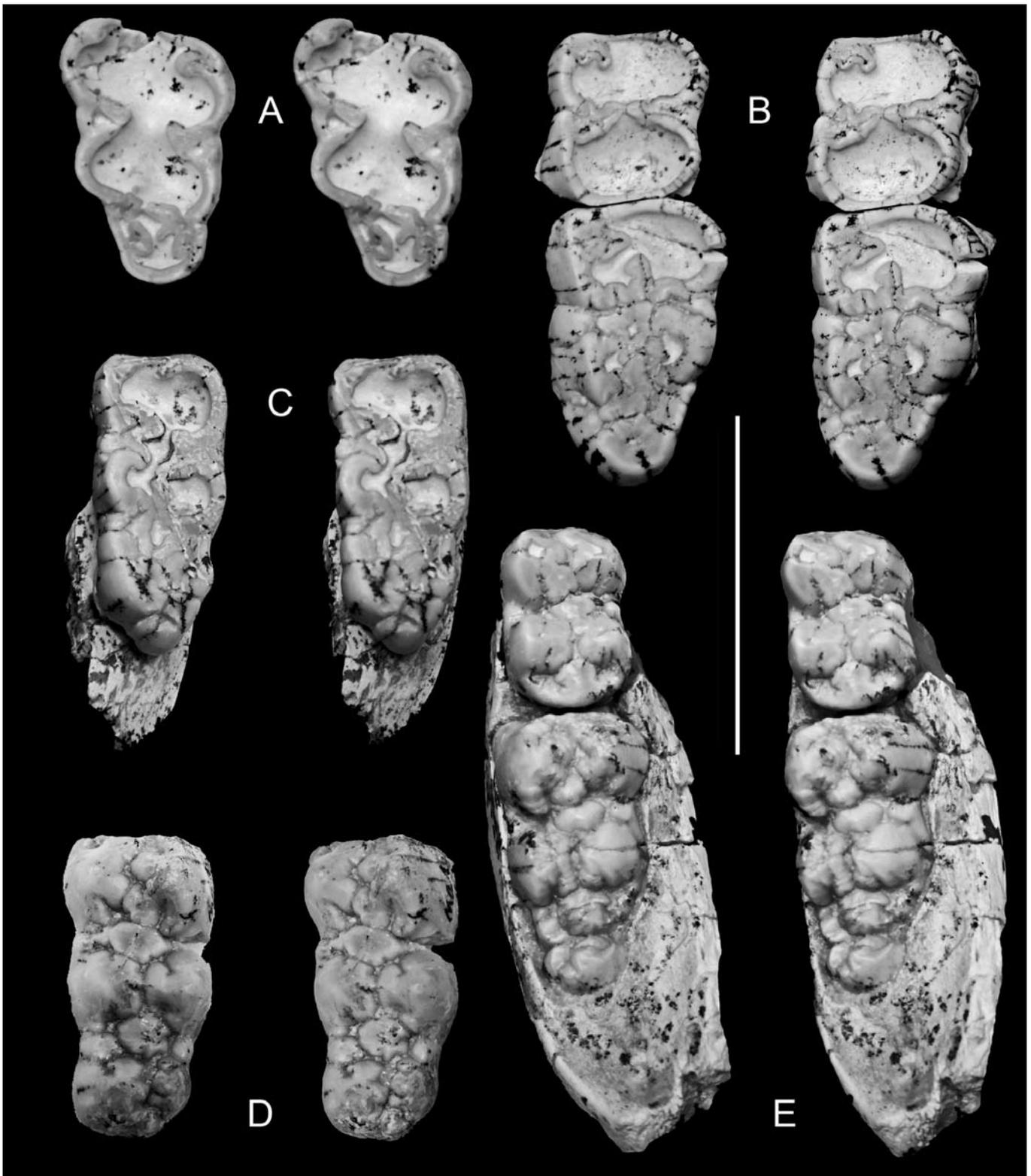
The P4/ shows well-formed sagittal cusplets attached to the buccal cusps and strong mesial and distal cingula (Text-fig. 17b).

The second specimen of *Hippopotamodon erymanthius* in the Karlsruhe collection is a left mandible fragment with moderately worn m1–m/2 and the front lophid of m/3. Measurements of the teeth are provided below (Tab. 3).

#### Sexual dimorphism in *Hippopotamodon erymanthius*

The fossil record of *Hippopotamodon erymanthius* is now comprehensive enough to indicate that the species was sexually dimorphic in the area of the upper canine. There seems to be no bimodality in dental dimensions, save for the fact that males seem to have a slightly larger upper canines than females. The incisors and cheek teeth appear to be metrically unimodal. This finding agrees with the discussion by Liu et al. (2005).

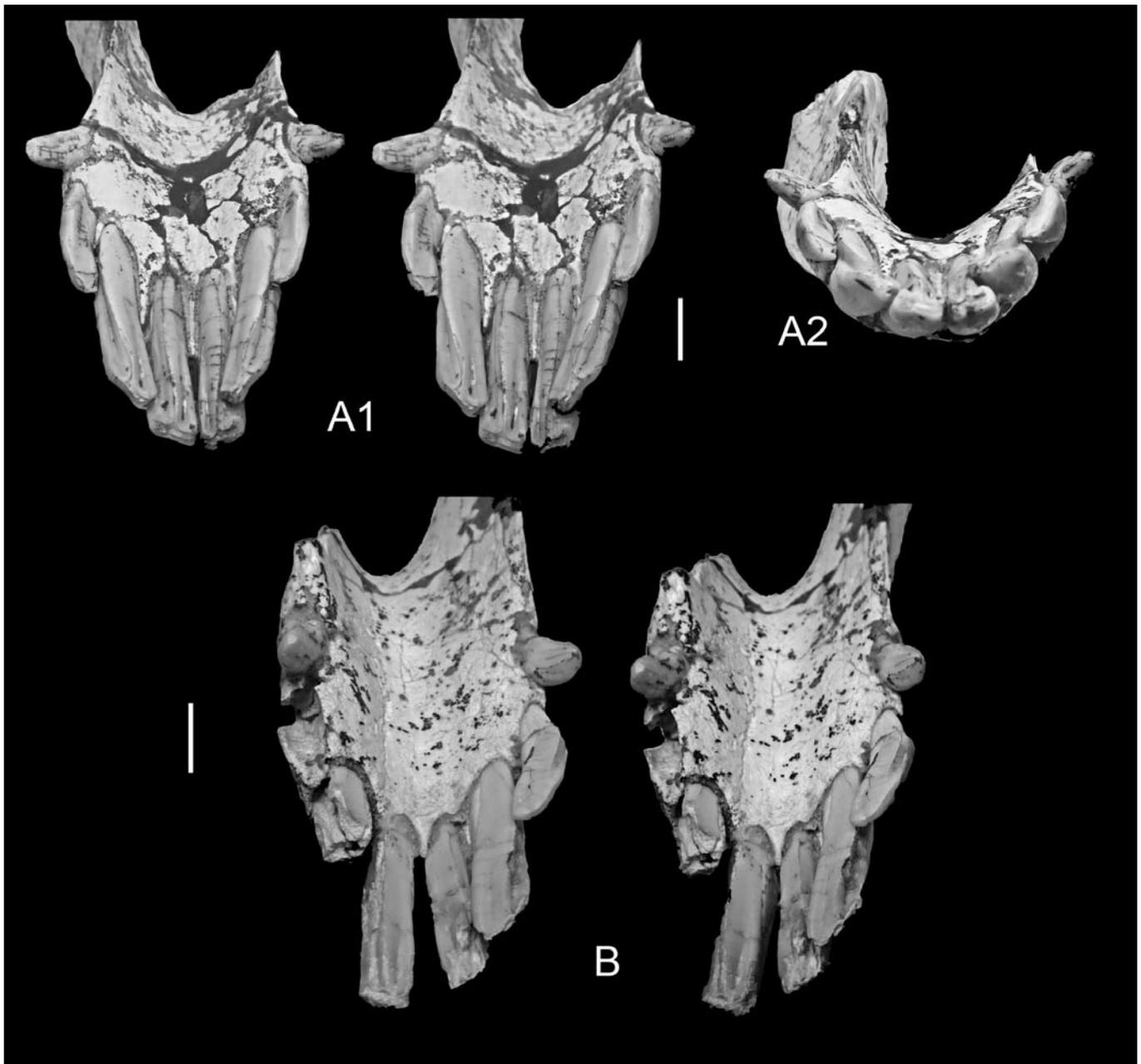
The most obvious sexual character is the supra-canine flange, which is large in males and is adorned with rugose lateral and dorsal surfaces, almost like the rugose surface of



Text-fig. 9. Stereo occlusal views of upper and lower molars of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) Ma1 Nr 181, deeply worn right M3/, B) Ma1 Nr 190, deeply worn left M2/-M3/, C) Ma1 Nr 131, left m/3 in fragment of mandible, D) Ma1 Nr 176, left m/3, E) Ma1 Nr 145, right m/2-m/3 in mandible fragment (scale 5 cm).

cauliflowers. Females show a bowing out of the maxilla behind the upper canine, but there is little or no development of a flange (Liu et al. (2005) thought that females also have supra-canine flanges). In males, the supra-canine flange extends from above the canine backwards to the level of the P2/, corresponding to the diastema between the canine and

P2/. In the Mahmutgazi specimen, the flange is 7 cm long and adds ca. 3 cm to the breadth of the snout on each side. The contrast between males and females is well shown in the Karlsruhe collection by a male specimen from Mahmutgazi and a female individual from Pikermi. The presence of a large supra-canine flange in males suggests that it served as



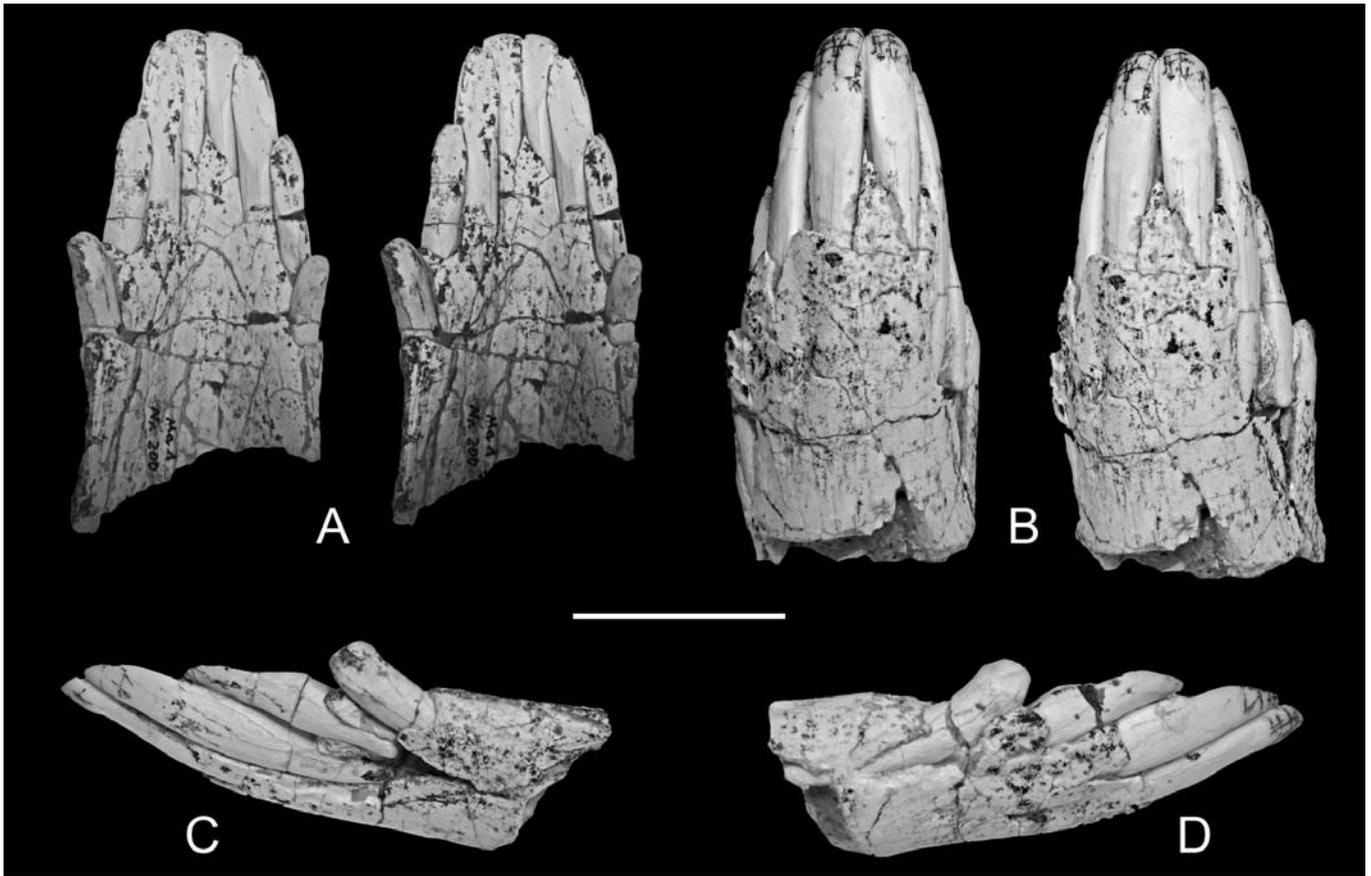
Text-fig. 10. The lower incisor-canine battery of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) SMNK Ma1 Gips 6 (A1 – oblique stereo anterior view, A2 – anterior view); B) SMNK Ma1 Gips 17, oblique stereo anterior view (scales 10 mm).

a weapon during male-on-male combat, or perhaps for protection during such encounters. The canines in *Hippopotamodon erymanthius* are reduced in dimensions and probably played little if any role in intraspecific combat. The canine flanges in contrast are strong in males, and were probably covered in thick skin, perhaps with bristles emerging from them, in which case pushing, shoving and butting the opponent with the side of the snout was probably the main form of combat between males during the rutting period.

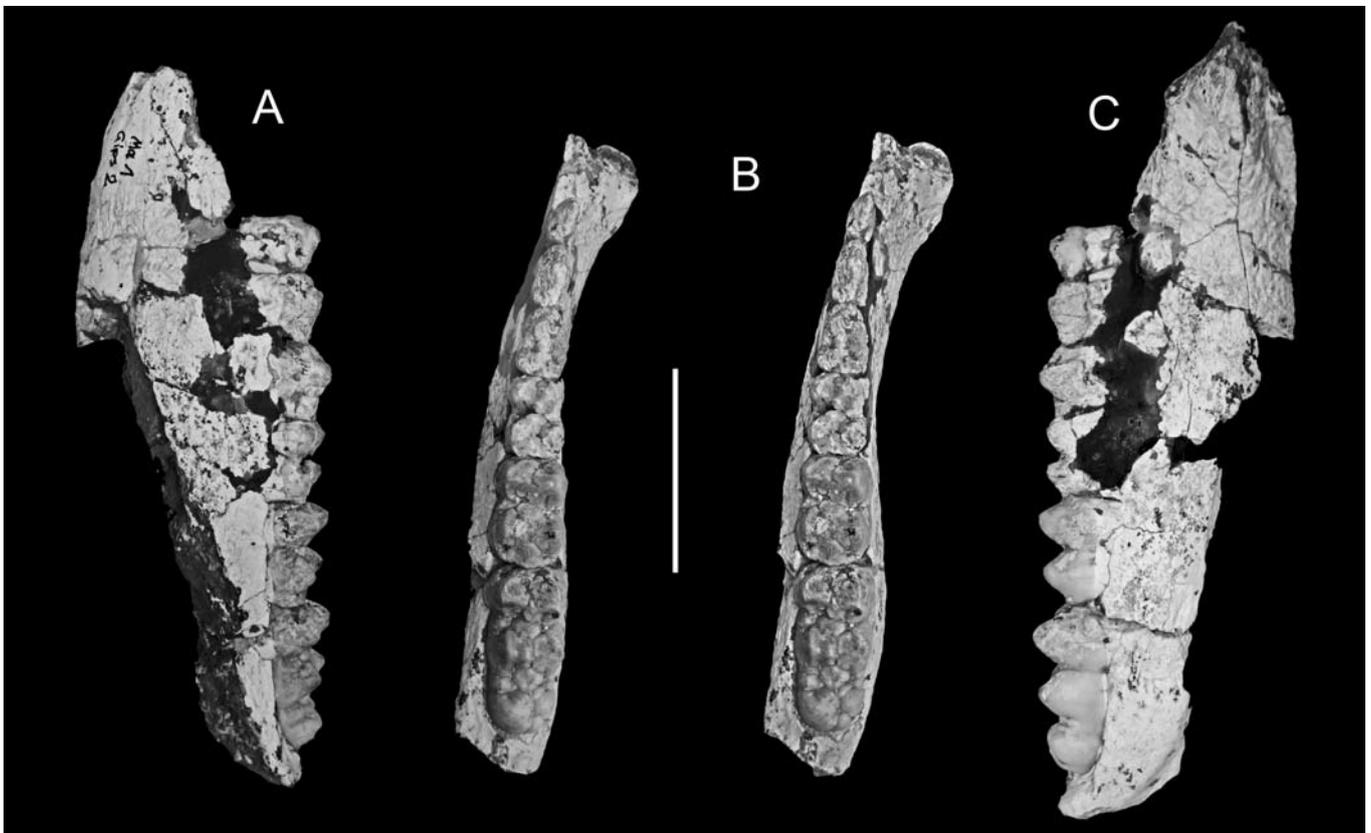
## Discussion

In previous literature, the fossil suids from Mahmutgazi were attributed either to *Dicoryphochoerus* sp. (Sickenberg and Tobien 1971, Yakut 2012) or to *Microstonyx major* (Pickford and

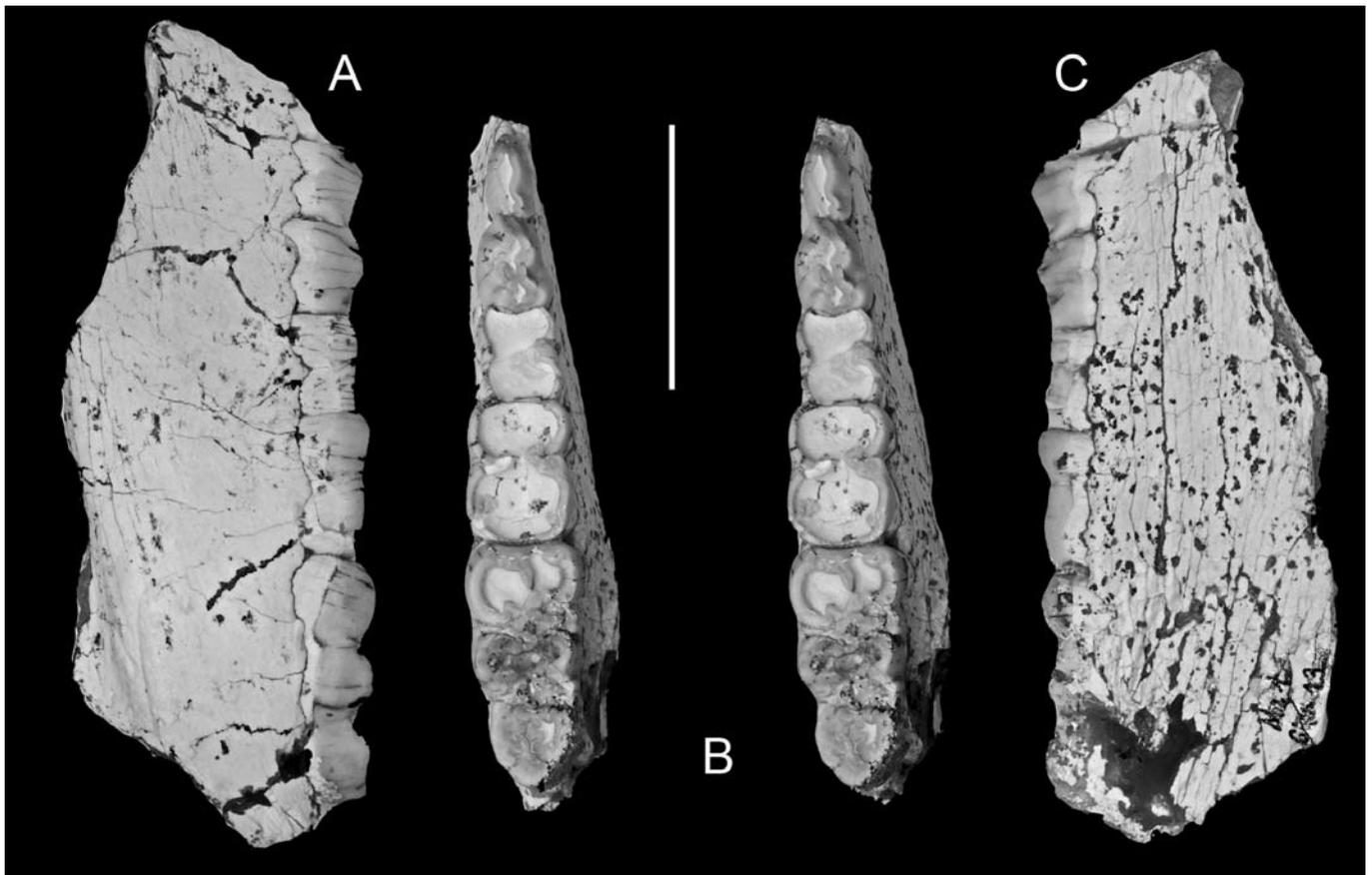
Ertürk 1979, Liu et al. 2005, Van der Made et al. 2013). However, no morphological details or measurements of the teeth have been published, although some unspecified material from the site was included in the bivariate plots by Van der Made et al. (2013). This paper describes a substantial sample of suid dento-gnathic specimens from Mahmutgazi housed in the Staatliches Museum für Naturkunde, Karlsruhe, which is representative enough to reveal that the species present is not the same as *Hippopotamodon major* from Luberon, France, the type locality of that species. The specimens have small, stubby canines, and a male snout has a large supra-canine flange with rugose dorsal and lateral surfaces. There is a long post-canine diastema in the upper and lower tooth rows, but only short gaps between the incisors and the canines. The P1/ and p/1 appear to be suppressed. This conforms with the *Microstonyx* subgroup of the genus *Hippopotamodon* (Pickford 2015).



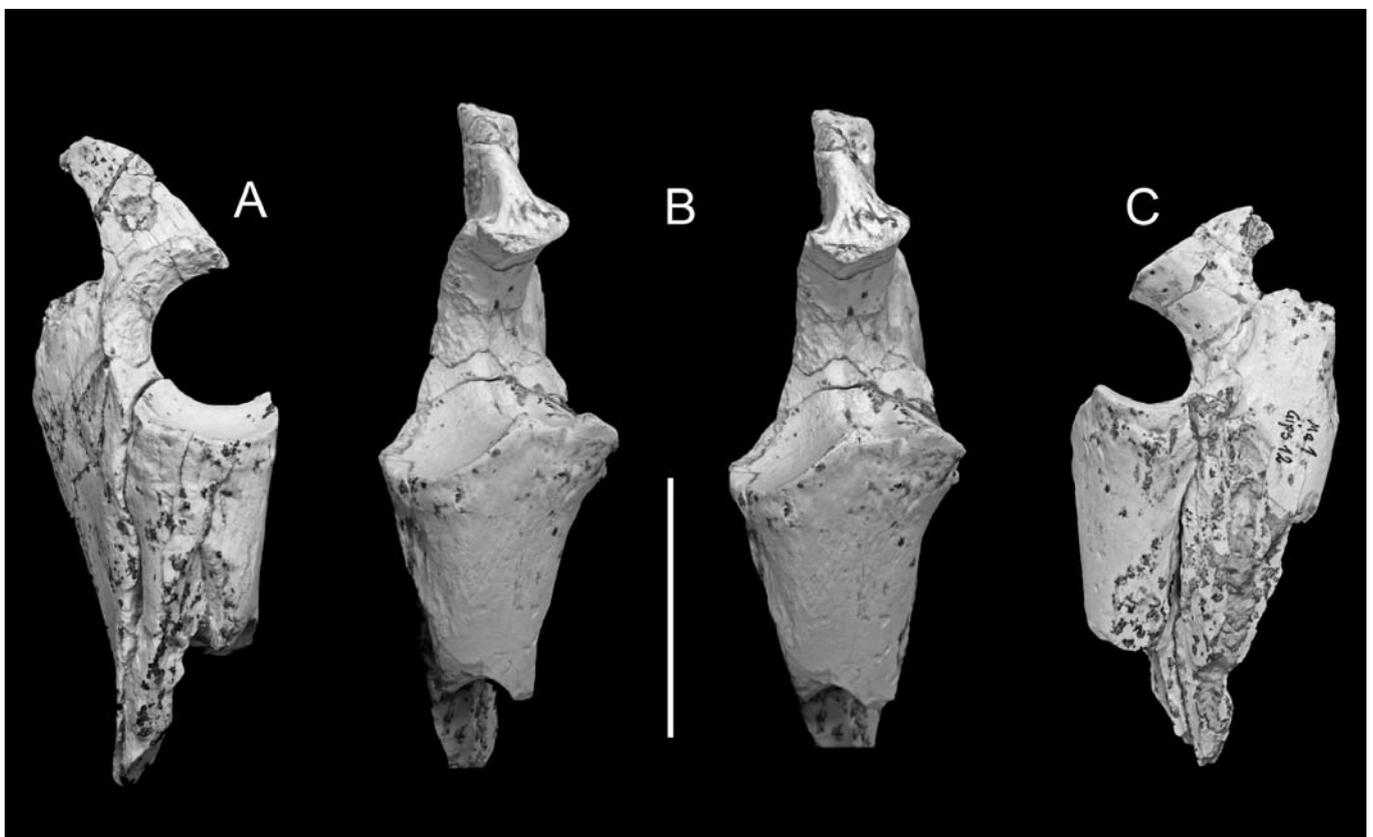
Text-fig. 11. SMNK Ma1 200, mandibular symphysis of *Hippopotamodon erymanthius* with all incisors and canines from Mahmutgazi, Turkey. A) stereo occlusal view, B) stereo ventral view, C) left lateral view, D) right lateral view (scale 5 cm).



Text-fig. 12. Left mandible of *Hippopotamodon erymanthius*, SMNK Ma1 Gips 2, from Mahmutgazi, Turkey, containing lightly worn p/2-m/3. A) buccal view, B) stereo occlusal view, C) lingual view (scale 5 cm).



Text-fig. 13. SMNK Ma1 Gips 13, right mandible of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey, with worn p/3-m/3. A) lingual view, B) stereo occlusal view, C) buccal view. This mandible may represent the same individual as the maxilla Ma1 MP 8 (scale 5 cm).



Text-fig. 14. SMNK Ma1 Gips 12, proximal left radio-ulna of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey. A) medial, B) stereo cranial, C) lateral views (scale 5 cm).

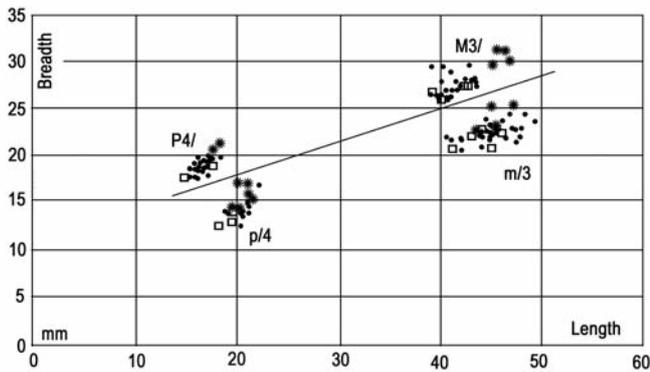
**Table 2. Measurements (in mm) of the teeth of *Hippopotamodon erymanthius* from Mahmutgazi, Turkey (MD: mesio-distal length, BL: bucco-lingual breadth, lt: left, rt: right, CM: male's C1/).**

Catalogue no.	Tooth	MD	BL
SMNK Ma1 Gips 17	c/1 lt	8.4	6.2
SMNK Ma1 Gips 6	c/1 lt	8.5	5.3
SMNK Ma1 Nr 200	c/1 lt	9.3	7.5
SMNK Ma1 Gips 17	c/1 rt	8.1	5.7
SMNK Ma1 Gips 6	c/1 rt	7.5	5.5
SMNK Ma1 Nr 200	c/1 rt	9.2	7.0
SMNK Ma1 MP 8	CM/ rt	10.3	11.5
SMNK Ma1 Gips 17	d/2 lt	11.4	5.0
SMNK Ma1 Nr 196	d/2 rt	12.5	5.1
SMNK Ma1 Nr 196	d/3 rt	14.4	7.5
SMNK Ma1 Nr 193	d/4 lt	--	11.7
SMNK Ma1 Nr 196	d/4 rt	26.8	11.7
SMNK Ma1 MP 5	D3/ lt	17.5	12.6
SMNK Ma1 MP 5	D4/ lt	19.3	15.3
SMNK Ma1 Gips XII	di/2 rt	9.0	5.0
SMNK Ma1 Gips 17	i/1 lt	8.3	12.7
SMNK Ma1 Gips 6	i/1 lt	8.5	13.7
SMNK Ma1 Nr 200	i/1 lt	9.6	11.7
SMNK Ma1 Gips 17	i/1 rt	8.0	12.0
SMNK Ma1 Gips 6	i/1 rt	8.2	13.0
SMNK Ma1 Nr 200	i/1 rt	9.6	11.8
SMNK Ma1 Gips 17	i/2 lt	8.3	12.0
SMNK Ma1 Gips 6	i/2 lt	9.0	13.0
SMNK Ma1 Nr 200	i/2 lt	10.0	12.0
SMNK Ma1 Gips 17	i/2 rt	--	12.0
SMNK Ma1 Gips 6	i/2 rt	8.2	14.5
SMNK Ma1 Nr 200	i/2 rt	9.1	12.0
SMNK Ma1 Gips 17	i/3 lt	8.7	6.7
SMNK Ma1 Gips 6	i/3 lt	10.0	6.3
SMNK Ma1 Nr 200	i/3 lt	--	7.2
SMNK Ma1 Gips 6	i/3 rt	6.0	9.7
SMNK Ma1 Nr 200	i/3 rt	--	6.7
SMNK Ma1 Nr 176	I1/ rt	14.0	9.0
SMNK Ma1 Nr 7	I1/ rt	15.0	9.5
SMNK Ma1 MP 6	I3/ rt	14.3	6.5
SMNK Ma1 Gips 17	m/1 lt	21.7	14.7
SMNK Ma1 Gips 2	m/1 lt	20.5	14.7
SMNK Ma1 Gips 6	m/1 lt	21.3	16.2
SMNK Ma1 Nr 193	m/1 lt	22.3	14.8
SMNK Ma1 Gips 13	m/1 rt	--	15.4
SMNK Ma1 Gips 6	m/1 rt	21.2	16.0
SMNK Ma1 Nr 145	m/1 rt	22.3	14.7
SMNK Ma1 Nr 196	m/1 rt	22.2	14.4
SMNK Ma1 Gips 17	m/2 lt	28.8	19.5
SMNK Ma1 Gips 2	m/2 lt	28.6	19.3
SMNK Ma1 Gips 6	m/2 lt	26.0	20.3
SMNK Ma1 Nr 176	m/2 lt	28.3	20.0
SMNK Ma1 Gips 13	m/2 rt	28.0	21.7

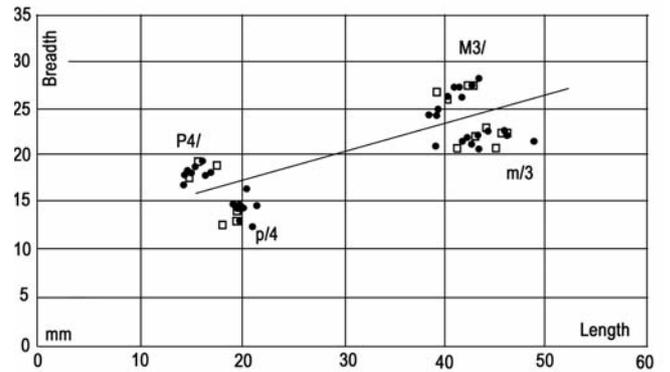
Catalogue no.	Tooth	MD	BL
SMNK Ma1 Gips 6	m/2 rt	26.3	20.2
SMNK Ma1 Nr 145	m/2 rt	27.4	19.0
SMNK Ma1 Gips 17	m/3 lt	43.0	22.2
SMNK Ma1 Gips 2	m/3 lt	41.0	20.8
SMNK Ma1 Gips 6	m/3 lt	44.0	23.0
SMNK Ma1 Nr 131	m/3 lt	45.0	20.9
SMNK Ma1 Nr 176	m/3 lt	45.0	22.4
SMNK Ma1 Gips 13	m/3 rt	46.0	22.5
SMNK Ma1 Gips 14	m/3 rt	--	21.4
SMNK Ma1 Gips 6	m/3 rt	45.2	22.7
SMNK Ma1 Nr 145	m/3 rt	--	22.5
SMNK Ma1 MP 5	M1/ lt	22.2	19.1
SMNK Ma1 MP 7	M1/ lt	--	19.6
SMNK Ma1 Nr 131	M1/ lt	22.3	19.0
SMNK Ma1 MP 8	M1/ rt	--	20.7
SMNK Ma1 MP 7	M2/ lt	--	25.0
SMNK Ma1 Nr 190	M2/ lt	28.0	24.7
SMNK Ma1 MP 8	M2/ rt	--	24.8
SMNK Ma1 MP 7	M3/ lt	40.0	26.0
SMNK Ma1 Nr 190	M3/ lt	42.5	27.5
SMNK Ma1 MP 8	M3/ rt	42.2	27.5
SMNK Ma1 Nr 181	M3/ rt	39.1	26.7
SMNK Ma1 Gips 17	p/2 lt	12.0	6.5
SMNK Ma1 Gips 2	p/2 lt	14.0	7.0
SMNK Ma1 Gips 6	p/2 lt	15.1	7.3
SMNK Ma1 Gips 6	p/2 rt	14.0	7.3
SMNK Ma1 Gips 17	p/3 lt	16.3	8.5
SMNK Ma1 Gips 2	p/3 lt	16.9	9.2
SMNK Ma1 Gips 6	p/3 lt	18.3	9.4
SMNK Ma1 Nr 145	p/3 rt	17.0	8.5
SMNK Ma1 Gips 13	p/3 rt	17.8	9.3
SMNK Ma1 Gips 6	p/3 rt	18.8	9.6
SMNK Ma1 Gips 2	p/4 lt	18.2	12.7
SMNK Ma1 Gips 17	p/4 lt	19.4	13.0
SMNK Ma1 Gips 6	p/4 lt	19.4	14.8
SMNK Ma1 Gips 6	p/4 rt	19.6	14.2
SMNK Ma1 Gips 13	p/4 rt	19.7	14.9
SMNK Ma1 Nr 131	P2/ lt	17.0	9.9
SMNK Ma1 MP 8	P2/ rt	15.8	9.9
SMNK Ma1 MP 7	P3/ lt	16.8	16.0
SMNK Ma1 Nr 131	P3/ lt	17.6	17.6
SMNK Ma1 Nr 180	P3/ lt	17.2	16.0
SMNK Ma1 MP 8	P3/ rt	17.6	16.5
SMNK Ma1 Nr 181	P3/ rt	--	16.0
SMNK Ma1 MP 7	P4/ lt	14.7	17.8
SMNK Ma1 Nr 131	P4/ lt	16.7	--
SMNK Ma1 Nr 190	P4/ lt	16.0	19.4
SMNK Ma1 MP 8	P4/ rt	17.5	19.0

The Mahmutgazi specimens are small within the overall context of *Hippopotamodon* species, with the exception of *Hippopotamodon pilgrimi* from the Chinji levels in Indo-Pakistan (Pickford 2015), which is the smallest of the species attributed to the genus (Pickford 2015) and *Hippopotamodon etruscus* (Michelotti 1861), an endemic island form from Tuscany, Italy (Hürzeler 1982). When compared with *Hippopotamodon erymanthius* from Pikermi, Greece (the type locality), the teeth plot into the lower half of the range of metric

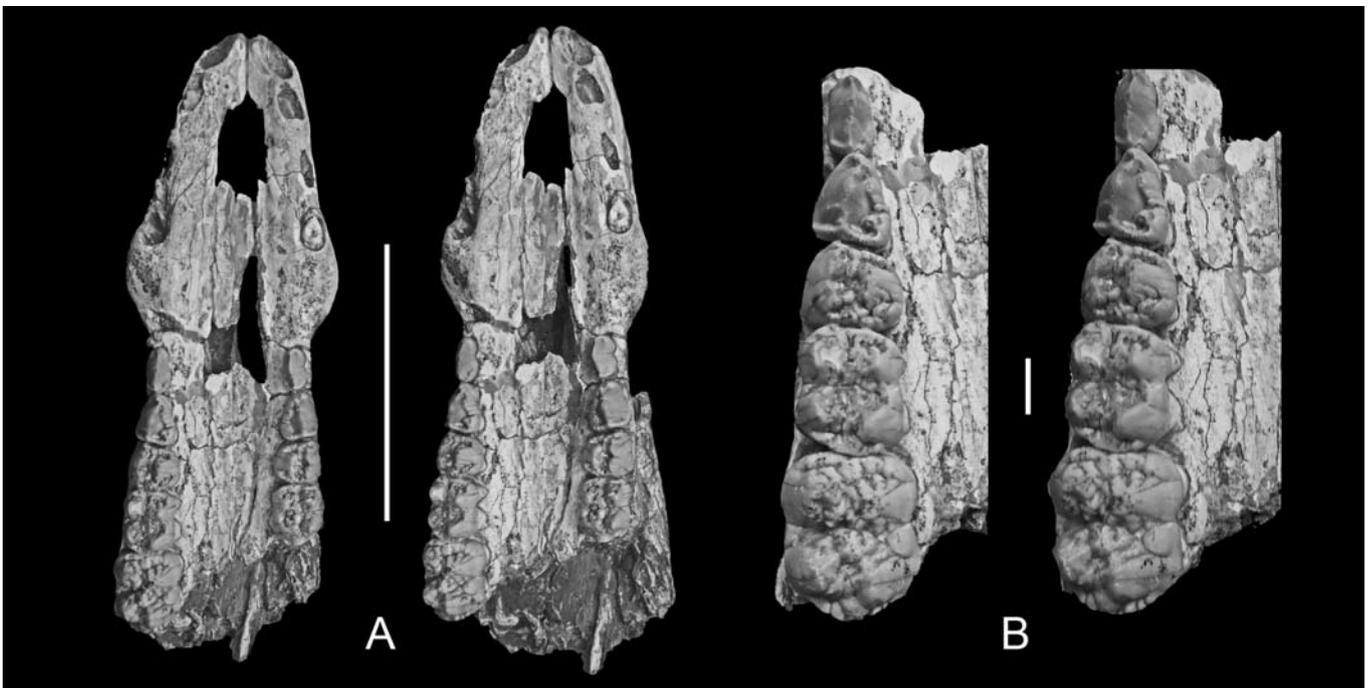
variation. The same applies when the Mahmutgazi sample is compared with that from Samos, Greece. The upper and lower fourth premolars and the third molars are absolutely smaller than the range of metric variation of *Hippopotamodon major* from Luberon (Ventian, basal MN 13) (Morales et al. 2013). From this it is concluded that the species represented at Mahmutgazi is *Hippopotamodon erymanthius*, but that the population comprised relatively small individuals, similar to the sample from Akkaşdağı, Turkey, described by Liu et al. (2005), and



Text-fig. 15. Bivariate plots of upper and lower fourth premolars and third molars of *Hippopotamodon erymanthius* and *Hippopotamodon major* (stars: Luberon, dots: Pikermi and open squares: Mahmutgazi).



Text-fig. 16. Metric comparisons of upper and lower fourth premolars and third molars of *Hippopotamodon erymanthius* from Mahmutgazi (open squares) and Akkaşdağı (dots), Turkey. The two samples are metrically closely similar.



Text-fig. 17. SMNK MP 3, probable female snout of *Hippopotamodon erymanthius* from Pikermi. A) stereo occlusal view of snout, B) close-up stereo occlusal view of right upper cheek tooth row (scales 5 cm and 10 mm).

Table 3. Measurements (in mm) of the teeth of *Hippopotamodon erymanthius* from Pikermi, Greece, housed in the SMNK (MD: mesio-distal length, BL: bucco-lingual breadth, lt: left, rt: right).

Catalogue no.	Tooth	MD	BL
SMNK MP 3	M1/ lt	23.8	19.7
SMNK MP 3	M1/ rt	23.7	20.1
SMNK MP 3	M2/ rt	30.6	25.7
SMNK MP 3	P2/ lt	17.6	9.6
SMNK MP 3	P2/ rt	17.3	9.8
SMNK MP 3	P3/ lt	18.2	16.2
SMNK MP 3	P3/ rt	18.6	18.3
SMNK MP 3	P4/ lt	16.5	19.6
SMNK MP 3	P4/ rt	17.4	19.8
SMNK MP 4	m/1 lt	21.8	15.5
SMNK MP 4	m/2 lt	28.6	20.4
SMNK MP 4	m/3 lt	--	22.6

correlated by them to MN 12. The site of Şerefköy-2 in the Muğla area, southwestern Turkey, yielded material attributed to *Microstonyx erymanthius* by Kaya et al. (2011), a site that the authors correlated to MN 12, but the specimens have not yet been described nor measurements provided, so it is not possible to compare the sample with the Mahmutgazi collection.

Third molars of *Hippopotamodon* from Çorakyerler are large, which is certainly earlier than late MN 12, and the dimensions of *Hippopotamodon* from Dorn-Dürkheim 1 (said to belong to MN 11) (Van der Made (1997) are similar to those from Mahmutgazi. Perhaps comparisons could be made also with Bulgaria, especially Kalimantsi.

The significance of these observations is open to discussion. It could signify a chronological difference between Mahmutgazi and Pikermi, which would accord with correlation of Mahmutgazi to MN 11 (Engesser 1980, Köhler 1987, Pickford,

2015) and Pikermi to MN 12 by several authors (Mein 1990, De Bruijn et al. 1992, Pickford 2015) or, if these two localities are similar in age as implied by the correlation of Akkaşdağı to MN 12, then it could indicate ecological differences between the Mahmutgazi and Akkaşdağı areas on the one hand and the Pikermi area on the other. Samos is a special case, in that sites 1 and 4 are correlated to MN 11, and Samos 5 is correlated to the top of MN 12, or even sometimes near the base of MN 13 (in the sense of Ventian) (De Bruijn et al. 1992), meaning that the relatively large range of metric variation of the suid teeth could be due to the pooling of suids from two or more levels. Because the Pikermi sample has a similar range of metric variation to the combined Samos samples (Samos 1, 4 and 5), it raises the possibility that Pikermi, which is sometimes considered to be a chronologically homogeneous deposit, could contain diverse levels equivalent to MN 12 and MN 13 (Ventian). This suggestion agrees with Schmidt-Kittler's (1975, 1976) conclusion that Pikermi comprised more than one stratigraphic level, the older one positioned in the Vallesian, the other in the Turolian, as well as with the findings of Koufos (2013), who described the Pikermi faunas as being mixed.

Whatever the case, if Mahmutgazi correlates to MN 11, as most authors have suggested, then it would indicate that Akkaşdağı might correlate to MN 11 rather than to MN 12, contrary to the conclusion of Liu et al. (2005). It is interesting to note that Mein (1990) located Mahmutgazi near the top of MN 11, whereas De Bruijn et al. (1992) positioned it a bit lower down, in the middle of MN 11, although in both papers the locality is at the same level as Samos 1 and Samos 4, and well beneath Samos 5 and Pikermi. Schmidt-Kittler (1976), in contrast, correlated Mahmutgazi to the Late Vallesian (equivalent to the older of the two Pikermi faunas that he recognised) on the basis of the presence at the site of *Protictitherium crassum*, *Ictitherium (Palhyaena) hipparionum hipparionum*, *Adcrocuta eximia* and *Machairodus aphanistus*. Peigné (2016) wrote that *Machairodus aphanistus* has never been recorded from MN 12, which tilts the balance towards a correlation of Mahmutgazi to MN 11. Since the introduction of the MN Zonation, Pikermi has generally been correlated to MN 12 (Freudenthal and Martin-Suarez 1999, Gentry et al. 1999, Ginsburg 1999, Heissig 1999, Rummel 1999, Sen 1999, Ziegler 1999), although some authors correlate it to MN 11/12 (Göhlich 1999), and others to MN 12/13 (Hünemann 1999). Further study of all the faunal elements from these localities is required to throw light on the issues. The suids suggest, but do not prove, that Mahmutgazi is probably best correlated to MN 11, mainly on the basis that the specimens are overall smaller than material from Pikermi and Samos, but are derived when compared to material from MN 10 (suppression of P1/ and p/1, for example, although this should not be taken too far because the trait is variable) (Pickford 2015). The other mammals from Mahmutgazi, such as the well-preserved Giraffidae which are still unstudied, could well provide key evidence to resolving the uncertainty. As it is, the described material (carnivores, bovids and suids) indicates a Turolian correlation for Mahmutgazi, with the balance tilting towards MN 11, or the base of MN 12.

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**Annex 1. Distribution of Suinae in the Late Miocene of Turkey in the order published by Pickford and Ertürk (1979) (*H.* – *Hippopotamodon*; *K.* – *Korynochoerus*; *M.* – *Microstonyx*).**

Locality	Taxon
Çoban Pinar	<i>M. major</i>
Muğla	<i>M. major</i>
Salih Pasalar	<i>M. major</i>
Ayas	<i>M. major</i>
Ekçiköy	<i>M. major</i>
Kayadibi	<i>M. major</i>
Gediz	<i>M. major</i>
Konya Hutunsaray Kayadibi	<i>M. major</i>
Konya Hutunsaray Sarisik Inkerli	<i>M. major</i>
Garkin	<i>M. major</i>
Eski Bayirköy	<i>M. major</i>
Çevril	<i>M. major</i>
Kayseri Erkilet	<i>M. major</i>
Dinar Akçaköy	? <i>M. major</i>
Kinik	<i>M. major</i>
Kayseri Urgüp Karain	<i>M. major</i>
Afyon Sandıklı Kinik	<i>M. major</i>
Çorak Yerler	<i>M. major</i>
Taşkınpaşa	<i>M. major</i> or <i>K. palaeochoerus</i>
Küçükçekmece	<i>M. major</i>
Çanakkale	<i>M. major</i>
Silhan	<i>M. major</i>
Küçükyozgat	<i>M. major</i>
Karacahasan	<i>M. major</i>
Mahmutgazi	<i>M. major</i>
Eşme Akçaköy	<i>M. major</i> and <i>H. metei</i>
Yassıören	<i>H. metei</i>

**Annex 3. Distribution of Suinae in the Late Miocene of Turkey in the order published by Pickford (2015). (*H.* – *Hippopotamodon*).**

Locality	Taxon
Akkaşdağı	<i>H. erymanthus</i>
Karain	<i>H. erymanthus</i>
Sinap 49	<i>H. major</i>
Sinap 114	<i>H. antiquus</i>
Sivas	<i>H. erymanthus</i>
Gökdere	<i>H. antiquus</i>
Çoban Pinar	<i>H. erymanthus</i> , <i>H. antiquus</i>
Kavakdere	<i>H. erymanthus</i>
Küçükçekmece	<i>H. major</i>
Yassıören	<i>H. antiquus</i>
Yulafli	<i>H. antiquus</i>
Dinar Akçaköy	<i>H. erymanthus</i>
Karaçay	<i>H. erymanthus</i>
Çevril	<i>H. erymanthus</i>
Çankiri Çorak Yerler	<i>H. erymanthus</i>
Esme Akçaköy	<i>H. erymanthus</i>
Garkin	<i>H. erymanthus</i>
Gülpınar	<i>H. erymanthus</i>
Kayadibi	<i>H. erymanthus</i>
Kinik	<i>H. erymanthus</i>

**Annex 2. Distribution of Suinae in the Late Miocene of Turkey in the order published by Yakut (2012) (*D.* – *Dicroyphochoerus*; *H.* – *Hippopotamodon*; *K.* – *Korynochoerus*; *L.* – *Listriodon*; *M.* – *Microstonyx*; *P.* – *Propotamochoerus*; *S.* – *Sus*).**

Area (Locality)	Taxon	Correlation	Reference
Afyon (Sandıklı-Garkin)	<i>M.</i> , ? <i>K.</i>	Late Miocene (MN 11)	Sickenberg et al. (1975)
Afyon (Sandıklı-Kinik)	<i>M.</i>	Late Miocene (MN 12–13)	Sickenberg et al. (1975)
Ankara (Bala-Yaylaköy)	<i>M. erymanthus</i>	Middle Miocene (MN 9–12)	Saraç (2003)
Ankara (Elmadağ-Karacahasan)	<i>M. erymanthus</i>	Late Miocene (MN 9–12)	Saraç (2003)
Ankara (Ayaş-Pınakaya)	<i>M. erymanthus</i>	Late Miocene	Saraç (2003)
Ankara (Ayaş-Evciköy-Çobanpınar)	cf. <i>P. provincialis</i> , <i>M. major</i>	Late Miocene (MN 11–12)	Van der Made (2003)
Ankara (Kazan-Sarılar-Kavakdere)	<i>M. erymanthus</i>	Late Miocene (MN 12–13)	Van der Made (2003)
Çanakkale (Alçitepe-Keltepeler 1)	<i>M.</i>	Late Miocene (MN 10–12)	Saraç (2003)
Çanakkale (Ayvacık-Külahlıyağı) – Gülpınar	<i>S. erymanthus</i>	Late Miocene (Turolian)	Tuna (1987)
Çanakkale (Lapseki-Arıkaşağı)	<i>S. erymanthus</i>	Late Miocene (Vallesian)	Tuna (1987)
Denizli (Çal-Mahmutgazi)	<i>D.</i>	Late Miocene (MN 11–12)	Sickenberg et al. (1975)
İstanbul (Küçükçekmece)	<i>M. erymanthus</i>	Late Miocene (MN 9–12)	Saraç (2003)
İzmir (Karaburun-Kaynarpınar)	<i>M. major major</i>	Late Miocene (MN 10–11)	Saraç (2003)
Kayseri (Erkilet-Çevril 1)	<i>D.</i>	Late Miocene	Sickenberg et al. (1975)
Konya (Hatunsaray-Kayadibi 1)	<i>D.</i> , <i>M. major</i>	Late Miocene (MN 11)	Sickenberg et al. (1975)
Muğla (Yatağan-Salihpasalar 1)	<i>M.</i>	Late Miocene (MN 12–13)	Saraç (2003)
Nevşehir (Ürgüp-Taşkınpaşa 1)	<i>M. erymanthus</i>	Late Miocene (MN 13)	Saraç (2003)
Nevşehir (Ürgüp-Karain 2)	<i>D.</i>	Late Miocene (MN 11–12)	Sickenberg et al. (1975)
Sivas (Haliminhani 4) Hayranlı	<i>M.</i>	Late Miocene (MN 10–12)	Saraç (2003), Van der Made et al. (2013)
Sivas (Sarıhasan)	<i>M. erymanthus</i>	Late Miocene (MN 10–12)	Saraç (2003)
Sivas (Hafik-Düzyayla)	<i>M. erymanthus</i>	Late Miocene (MN 12)	Saraç (2003)
Uşak (Eşme-Akçaköy 1–6)	<i>L. splendens</i> , <i>D.</i>	Late Miocene (MN 9)	Sickenberg et al. (1975)
Kırıkkale (Keskin-Akkaştepe) Akkaşdağı	<i>M.</i>	Late Miocene (MN 12–13)	Saraç (2003), Liu et al. (2005)