New suoid specimens from Gebel Zelten, Libya

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ABSTRACT

A restricted collection of suoids from Gebel Zelten was made in the 1990's by the Spanish-Libyan Palaeontology Expedition. Dr Dolores Soria filmed the specimens with a video camera and took measurements of the teeth with vernier calipers. This paper uses the images from the video, which, even though somewhat limited in terms of picture quality, are of interest because they represent the first known snout of the gigantic suid *Megalochoerus khinzikebirus*. The images reveal that it is basically an enlarged version of *Libycochoerus massai*, but with relatively small premolars. The sanithere specimens from the site were photographed with an Olympus 1.4 megapixel digital camera, and the image quality is better than from the video camera. These specimens throw light on the degree of sexual dimorphism exhibited by sanitheres, a feature that was previously inferred from isolated teeth, but which can now be confirmed on the basis of the two mandible fragments from Gebel Zelten. This paper is dedicated to the memory of Dr Soria. This paper takes into account a few undescribed suid post-cranial bones from Gebel Zelten housed in the Natural History Museum, London, collected during the 1960's by R. Savage.

Key words: Suoidea, Middle Miocene, Libya, *Megalochoerus*, *Libycochoerus*, *Diamantohyus*, sexual dimorphism.

RESUMEN

Una limitada colección de suoideos procedentes de Gebel Zelten fue hecha a finales de los años 1990 por una expedición paleontológica internacional, con participación española y libia. La Dra. Dolores Soria filmó los ejemplares con una cámara de vídeo y tomó las medidas de los dientes con calibre. En este trabajo se utilizan las imágenes filmadas, que, aunque algo limitadas en términos de calidad fotográfica, son interesantes porque representan las primeras conocidas del rostro del suido gigante *Megalochoerus khinzikebirus*. Las imágenes revelan que básicamente es una versión agrandada de *Libycochoerus massai*, pero con premolares relativamente más pequeños. Los ejemplares de saniterios fueron fotografiados con una cámara digital Olympus de 1,4 megapixeles, y la calidad de las imágenes son mejores que las de la cámara de vídeo. Estos ejemplares arrojan nueva luz sobre el grado de dimorfismo sexual exhibido por los saniterios, un hecho que había sido previamente inferido sólo a partir de dientes aislados, pero que ahora puede ser confirmado en base a dos fragmentos de mandíbula de Gebel Zelten. Este trabajo está dedicado a la memoria de la Dra. Soria. En este trabajo se consideran algunos huesos postcraneales inéditos procedentes de Gebel Zelten, depositados en el Natural History Museum de Londres y recolectados durante los años 1960 por R. Savage.

Palabras clave: Suoidea, Mioceno Medio, Libia, *Megalochoerus*, *Libycochoerus*, *Diamantohyus*, dimorfismo sexual.

Introduction

New collections of suoids from Gebel Zelten, although limited in quantity, are interesting because they contain the first known snout of the giant kubanochoere *Megalochoerus khinzikebirus*, hitherto represented only by a maxilla fragment, a mandible and some isolated teeth. Comparisons can thus be made with *Libycochoerus massai* and *Kubanochoerus gigas* of which more complete material has been described. These three genera are basically similar in snout morphology, but there are differences in position of the incisive foramina and in premolar proportions, the largest species having

relatively and sometimes absolutely smaller anterior premolars than the smaller species.

Four undescribed fossils from Gebel Zelten are attributed to the primitive sanithere *Diamantohyus africanus*. Two mandible fragments are important in that they reveal that the lower canines of sanitheres were strongly dimorphic, with presumed females possessing small rooted canines, and supposed males having extremely hypsodont, ever-growing tushes. An axial first phalanx is important for revealing that the central groove for the keel of the distal metapodial epiphysis is continuous from volar to dorsal aspects, the groove being even better developed than it is in suids, and different from palaeochoerids into which sanitheres were classed by Van der Made. The new material does not resolve the problems concerning the systematic affinities of the sanitheres, some features suggesting that they are the sister group of suids and not palaeochoerids, while others suggest affinities with anthracotheres. Only more complete material will resolve this doubt.

Systematic descriptions

Family Suidae Gray, 1821
Subfamily Kubanochoerinae Gabunia, 1958
Genus *Megalochoerus* Pickford, 1993
Species *Megalochoerus khinzikebirus* (Wilkinson, 1976)

Locality

Gebel Zelten, Libya

Age

Basal Middle Miocene

Material

WUSC 4C33, snout containing the roots of left and right I2/-I3/, canine and left P1/, P2/, and complete right P1/-P3/. (Pl. 1, Fig. 1, 2; Pl. 2, 1-5).
ATH 6C 1, mandible fragment with canine alveolus and m/2.
WUS B10, lower molar (m/1 or m/2).
MD 29, distal end left humerus.

Description

Palatal view

The anterior part of the palate is spatulate (Pl. 1), being narrow at the level of the short diastema between P1/ and P2/, and broadening rapidly anteriorly to its widest point at the canine juga. In front of the juga there is an abrupt but not very great diminution in breadth of the palate. The incisors are arranged in an open U-shaped battery with a gap between the roots of the two central incisors. The incisive foramina are in a very anterior position between the I2/s and the roots of the I1/s and there are two prominent palatal grooves leading posteriorly. The central incisor alveoli are mesio-distally elongated with the long axis of the root oriented almost medio-laterally. The roots of the I2/ and I3/ are almost circular to slightly oval in section. The canines are small, oval in section and the crowns would have pointed ventrally and slightly laterally and anteriorly, but the crowns themselves are missing. The P1/ is just posterior to the canine and located lingually to it. It has two large roots. The P2/ is separated from the P1/ by a short diastema, but P2/ and P3/ touch each other.

Anterior view

The snout is almost semi-circular in section (Pl. 1, fig. 1), with a flat ventral part where the central incisor alveoli dominate the palatal part of the premaxilla, the dorsal part being evenly curved. The nasals are slender, whereas the premaxillae are robust and form a strong V-shaped floor to the nasal cavity. The incisor alveoli lack the external bone so that the internal shape of the roots can be seen. The alveoli are extremely long mesiodistally at gingival level. The distal part of the alveolus slopes gently upwards and sagittally, whereas the mesial edge slopes strongly upwards and laterally at an angle of about 45°. There is a gap between the mesial ends of the roots of the two central incisors with a re-entrant notch in the premaxillae.

Dorsal view

The nasals are long, barrel shaped and terminate anteriorly just behind the extremities of the premaxillae. There is a slight widening of the snout at the

Upper dentition

The upper incisors are missing, but the alveoli are preserved in part (I1/) or entirely (the roots of I2/ and I3/ are present on both sides). The alveoli of the central incisors are mesio-distally elongated (ca 25 mm long) and narrow sharply apically (height ca 30 mm). In palatal view they are oriented almost transversely in the premaxillae. The I2/ alveoli are located distal to the lateral portion of the roots of I1/ and the alveolus for I3/ is slightly lateral and distal to that of the I2/, separated from it by a short gap. The alveoli of I2/ and I3/ open palatally and are not really on the margin of the palate as in other suids. The canine is oval in section and is quite small (ca 23 mm antero-posterior x ca 15 mm labio-lingually) considering the size of the snout.

Disto-lingual to the rear edge of the canine is the P1/ which is two-rooted (Pl. 2, fig. 1). It has a single cusp, the apex of which is over the gap between the two roots. The crown is concave lingually giving it a kidney-shaped occlusal outline. There is a short diastema between the P1/ and the P2/.

The P2/ has a large main cusp and a prominent linguo-distal cusplet separated from the main cusp by a deep valley (Pl. 2, fig. 2). The main cusp is oriented obliquely, with the anterior end in a lingual position and its distal end buccally. There is a cingulum lingually, and a strong waisting in the centre of the tooth on the lingual side, up which runs a low crest. There are two roots.

The P3/ has the same basic structure as the P2/ but it is broader distally and its main and subsidiary cusps are more inflated (Pl. 2, fig. 3). It has two roots and the crown touches the P3/ anteriorly.

Lower dentition

The lower dentition is poorly represented in the new collections. A fragment of mandible has the canine alveolus (table 1) and an m/2. The m/2 falls into the range of metric variation of *Megalochoerus homungous*, and slightly above the range of variation of *M. khinzikebirus*.

An isolated lower molar (WUS B 10) consists of two sand-blasted fragments with a small area of contact that permits reconstruction of an almost complete tooth. The crown was completely formed

Plate 1.—*Megalochoerus khinzikebirus* from Gebel Zelten, base of the Middle Miocene, Libya. (Images processed from a video made by Dr Dolores Soria).
1. WUS 4C 33, snout 1) anterior view, 2) palatal view.

Tooth	Length	Breadth
P1/ WUS 4C 33	22.7	12
P2/ WUS 4C 33	32	19
P3/ WUS 4C 33	33	25.2
Lower canine alveolus ATH 6C 1	39	32.6
m/2 ATH 6C 1	46.6	31.7
m/1 or m/2 WUS B 10	38.2+	24+

Plate 2.—*Megalochoerus khinzikebirus* from Gebel Zelten, base of the Middle Miocene, Libya.
(Images processed from a video made by Dr Dolores Soria).
1. WUS 4C 33, right P1/, occlusal view.
2. WUS 4C 33, right P2/, occlusal view.
3. WUS 4C 33, right P3/, occlusal view.
4. WUS 4C 33, right P1/-P3/, lingual view.
5. WUS 4C 33, right P1/-P3/, buccal view.

posterior fossa as markedly (Pl. 3, fig. 5). The distal articular facet is similar to that of *Sus* and *Libycochoerus massai* (Arambourg, 1963). There is no fenestration in the olecranon fossa, unlike *Sus* in which there is usually such a window. The dimensions of the distal end are provided in table 2.

Discussion

The snout of *Megalochoerus khinzikebirus* was hitherto unknown. In overall shape it resembles that of *Libycochoerus massai* (Pickford, 1986) but it is considerably larger. A significant difference is the position of the incisive foramina, which are located in a very anterior position in this snout, whereas they are positioned further caudally in *L. massai*. In *Kubanochoerus* the incisive foramina are in a distal position in line with the I3/s and rear of I2/s (Qui *et al.*, 1988). Another difference between *M. khinzikebirus* and *L. massai* is that the P1/ is closer to the canine in *Megalochoerus* than it is in *Libycochoerus*. In this feature, *L. massai* resembles *Kubanochoerus*.

The anterior premolars of large kubanochoeres vary a great deal in inter-premolar proportions. The medium sized species *Megalochoerus marymuunguae* has P1/s that are bigger than those of the much larger species *M. khinzikebirus* (Van der Made, 1996). It seems that as the lineage increased in body size, the dimensions of the anterior two premolars were de-emphasized somewhat, so that they ended up being relatively and absolutely smaller in the largest species than they are in the smallest species.

If WUS B 10 is a first molar it falls into the range of metric variation of *M. homungous*, whereas, if it is an m/2, then it falls within the range of variation of *Kubanochoerus gigas* and just below the known range of variation of *M. khinzikebirus* (Pickford, 2001). Given that the lower dentition of the gigantic

but had not erupted at the time of death. It consists of the usual four main bunodont cusps with coarsely wrinkled enamel, and prominent anterior, median and posterior accessory cusplets in the centre line of the tooth. Measurements of the new Gebel Zelten suid teeth are listed in table 1.

Post-cranial skeleton

The only known post-cranial bone of this species is a distal left humerus (D 29, Pl. 3, figs. 1-5) collected by R. Savage in the 1960's and now stored at the Natural History Museum, London. The overall morphology of the humerus is similar to that of other suids such as *Sus scrofa*, but it is considerably larger (table 2). The lateral pillar on the posterior side is relatively taller than in *Sus*, and it is not as curved medio-laterally, thereby not overhanging the

Table 2.—**Dimensions (in mm) of post-cranial bones of Kubanochoerinae from Gebel Zelten, Libya (e = estimated measurement)**

Catalogue Number	Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height	Minimal trochlear diameter	Species
D 29	left humerus	—	—	—	59	85.3	39.8	*L. khinzikebirus*
LBE 520B	left humerus	235	—	—	40.4	61.4	28.8	*L. massai*
LBE 521A	left humerus	—	—	—	39	57.8	26.9	*L. massai*
N 32	right humerus	—	—	—	41	61	27.2	*L. massai*
D 6	left humerus	—	—	—	39	61.8	26.4	*L. massai*
Mt Aimé	left humerus	—	—	—	41	52.5	27	*Sus scrofa*
D 6	left MC III	136	32.6	29	27.8	26.7	—	*L. massai*
CD1	right MC III	123	32	28	26	24.7	—	*L. massai*
L 163	Abaxial metapodial	94.5	—	—	14.6	13.6	—	*L. massai*
R 33	distal tibia	—	—	—	36.6	32	29.2	*L. massai*
E/F 5	left tibia	320e	—	—	41.2	40	32.4e	*L. massai*
P 62	1st phalanx	65	33.7	29	26	19.2e	—	*L. massai*

Breadth of the distal end of the tibia corresponds to talar breadth.

African kubanochoeres is so poorly known, I prefer to attribute this tooth to *M. khinzikebirus*, rather than to any other taxon, although it is possible that it represents a particularly large specimen of *Libycochoerus massai*.

The species *Megalochoerus khinzikebirus* is known from Cheparawa, Kenya, aged 14.5 Ma, (Pickford, 2001) and the larger species *M. homungous* occurs in deposits at Nyakach, Kenya, (Pickford, 1993) aged about 14 Ma. Undescribed material of this species is known from Nachola, Kenya, aged 16 Ma, and Kipsaraman, Kenya, aged 14.5 Ma. The Gebel Zelten specimens attributed to *M. khinzikebirus*, thus suggest an age of between 16 and 14 Ma for the deposits from which they came, the larger specimens favouring the younger end of this time span.

All the Kenyan fossils attributed to *Megalochoerus khinzikebirus* and *M. homungous*, came from deposits that accumulated in well wooded to forested palaeoenvironments. It is likely that Gebel Zelten would have been equally well wooded to forested at the time of deposition. The bunodont nature of the cheek dentitions of these kubanochoeres, which are superficially similar to those of bunodont gomphotheres in terms of their functional morphology, suggests that *Megalochoerus* was probably an omnivore, concentrating on fruits, leafy branches, and tree bark, but avoiding underground food resources and grass. The transversely arranged, massive upper central incisors in particular, suggest that tree bark may have been an important food resource in this lineage.

Body weight estimate

Van der Made (1996b) estimated the body size of listriodonts using the method of Legendre (1986) which uses the size of m/1. This approach employs a dental proxy for estimating body weight on the assumption that there is a close relationship between dental dimensions and body size. For the species *L. khinzikebirus*, the estimate was based on an unspecified tooth since no m/1 was available to Van der Made (1996b, fig. 59). This method provided an estimate of 1104 kg, a figure that was used by Pickford (2001) in his paper on the biochronology of Kubanochoerinae.

An alternative approach for estimating body weight is based on the dimensions of the articular surfaces of the limb bones, since body weight passes through the limbs when the animal is standing and its articular surface must support the body when it is standing, walking and running. In general, because body weight is a function of volume which is the cube of linear dimensions, it is expected that an animal that has articular linear dimensions that are twice as big as those of another animal of comparable body proportions, will weigh eight times as much as it.

The dimensions of the distal humerus of *L. khinzikebirus* suggest that the body weight was considerably lower than 1104 kg. Wild *Sus scrofa* ranges in weight from 35 to 200 kg (average males 90 kg, average females 67 kg) (Duncan, 1974). In this species the breadth of the distal humeral articulation is ca 40 mm, which is similar to the dimensions of the species *Libycochoerus massai* (table 2) for which

Plate 3.—Suid post-cranial bones from Gebel Zelten, base of the Middle Miocene, Libya.
(Scales 10 mm except for tibia, 10 cm).
1-5. D 29, left distal humerus, *Megalochoerus khinzikebirus* (posterior, medial, anterior, lateral and distal views).
6-10. N 32, right distal humerus, *Libycochoerus massai* (posterior, medial, anterior, lateral and distal views).
11-15. E/F 5, left tibia, *Libycochoerus massai* (anterior, medial, posterior, proximal and distal views).
16-17. D 6, left MC III, *Libycochoerus massai* (volar and dorsal views).
18-19. CD 1, right MC III, *Libycochoerus massai* (volar and dorsal views).
20-22. P 62, axial 1st phalanx, *Libycochoerus massai* (dorsal, proximal and lateral views).

Van der Made estimated a body weight of 526 kg on the basis of the size of m/1. The distal humeral articulation in *Megalochoerus khinzikebirus* is 60 mm broad. This figure suggests a body weight for this species of 303 kg if the average male body weight of *Sus scrofa* is upscaled appropriately (1.5^3 x 90), or 675 kg if the maximum body weight of *Sus scrofa* is used (1.5^3 x 200). These estimates fall far short of of the 1104 kg estimate based on tooth dimensions.

Arambourg (1963) already showed that the proportions of the skeleton of *Libycochoerus massai* differed from those of *Sus scrofa*, the metapodials, for example being longer than those of the wild boar whereas the humerus is almost the same size in the two species. The body plan of these two suids was thus not similar and it might be expected that kubanochoeres may have been more heavily built than *Sus scrofa* is, even if the humeral dimensions are comparable. However, since it is expected that there would be a close relationship between body weight and dimensions of articular surfaces in the limbs, the discordance in body weight calculations using dental and skeletal proxies is troubling.

Further research, including estimates based on measurements of the hind limbs is required to settle the matter, but it seems that extrapolation of body weight from dental dimensions may not yield accurate results when applied to suids.

Genus *Libycochoerus* Arambourg, 1961
Species *Libycochoerus massai* Arambourg, 1961

Locality

Gebel Zelten, Libya

Age

Basal Middle Miocene

Material housed in the NHM, London

N 32, right distal humerus (Pl. 3, Figs 6-10).
D 6, left distal humerus.
D 6, left MC III (Pl. 3, Figs 16-17).
CD 1, right MC III (Pl. 3, Figs 18-19).
L 163, lateral metapodial.
E/F 5, complete left tibia (Pl. 3, Figs 11-15).
R 33, distal tibia.

Description

The post-cranial bones atttributed to *Libycochoerus massai* are basically similar in morphology to those of *Sus scrofa* but the proportions between bones are different, as are some relatively minor aspects of the morphology, already noted by Arambourg (1963). The most interesting specimen is a complete tibia E/F 5 (Pl. 3, figs. 11-15) about 320 mm long. The shaft is relatively slender, but the distal end has the morphology typical of suids. An axial first phalanx (P 62, Pl. 3, figs. 20-22) is similar to that of *Sus scrofa*. The anterior articulation shows the characteristic gently curved dorso-volar groove slightly offset from the centre line. The medio-lateral diameter of the proximal end is compatible with the diameter of the distal ends of the axial metapodials attributed to *L. massai* by Arambourg. These bones are appreciably bigger than their homologues in *Sus scrofa* whereas the humerus and tibia are about the same dimensions as those of *Sus*.

Discussion

It is surmised that *Libycochoerus massai* possessed relatively longer metapodials relative to humerus and tibia than occur in *Sus* a feature already noted by Arambourg (1963).

Family Sanitheriidae Simpson, 1945
Genus *Diamantohyus* Stromer, 1922
Species *Diamantohyus africanus*, Stromer, 1922

Locality

Gebel Zelten, Libya

Age

Basal Middle Miocene

Material

2.16.- Right maxilla with wind eroded P4/ - M2/ and detached fragment of M3/ root and surrounding bone. (Pl. 4, fig. 1.1, 1.2, 1.3).
ATH 3B 38.- Mandibular symphysis with alveoli of all the incisors and canines plus that of the right

p/1, and complete left p/1 - p/3 and right p/2 (Pl. 4, fig. 2.1, 2.2, 2.3).

2.Z.- Right mandibular body with canine root in its alveolus, and p/4 - m/3 (Pl. 4, fig. 3.1, 3.2, 3.3, 3.4).

ATH 3B.- Axial first phalanx (Pl. 4, fig. 4).

Descriptions

Specimen 2.16, a right maxilla, is heavily wind eroded, but reveals some interesting morphological details. There is a large sinus above the molar row extending forwards over the P4/ and pinching out above the rear of the P3/. The distal part of this sinus extends into the base of the maxillary part of the zygomatic arch. Above the buccal root of P3/ there is a second sinus-like chamber separated from the floor of the nasal cavity by a sheet of bone, next to which is a smaller vacuity between the buccal and lingual roots of P3/. The portion of palate preserved is flat and there is a palatine foramen opposite the rear root of M2/. The back of the maxillary root of the zygomatic arch is above the middle of M3/, but the anterior part has been sand-blasted away, but it appears to have risen upwards sharply above the P4/.

The cheek teeth are poorly preserved, with large chips of enamel missing buccally and lingually. However, some enamel remains on the occlusal surface, and from them it is possible to determine that the pattern is typical of *Diamantohyus* rather than *Sanitherium*. The P4/ in particular has small sagittal cusplets between protocone and paracone, and to the lingual side of the metacone. There is no hypocone in the P4/, unlike the condition in *Sanitherium* (Pickford, 1984). What little is left of the crowns of M1/ and M2/ is typical of sanitheres, with somewhat selenodont outlines to the protocones and hypocones, and small bucco-lingually compressed paracones and metacones. Measurements of the upper teeth are provided in table 3.

ATH 3B 38, is a mandibular symphysis with alveoli of all the incisors and canines and right p/1, and complete left p/1 - p/3 and right p/2.

The symphysis is solidly fused and extends back to the rear of p/3. It is slenderly built with a long evenly sloping planum alveolare and uniformly curved ventral surface. There is a short diastema (3 mm) between the alveoli of the canine and the p/1. There is a prominent mental foramen low down beneath the centre line of the p/3 which leads into a

Table 3.—**Measurements (in mm) of the upper teeth of specimen 2.16,** *Diamantohyus africanus* **from Gebel Zelten, Libya**

Tooth	Length	Breadth
P4/	8.5	8.2
M1/	9.0	9.6
M2/	11.4	9.8

voluminous mandibular canal. The zone immediately below the premolar row is hollowed out so that the juga of the roots stand out in relief from the mandibular surface, suggesting well developed buccinator musculature.

The three incisor alveoli on each side are close together and diminish is area from i/1 to i/3, that for the i/2 being slightly deeper than that for the i/1, while the one for the i/3 is considerably shallower than that for the i/2. The canine alveoli are small and closed internally, being 7.3 mm deep and only marginally greater in surface area than the incisor alveoli. It is likely that this individual was female. The i/1 root is 9.5 mm deep, that of i/2 is 14 mm, while that of i/3 is only 6.1 mm.

The p/1 has a single root that is comprised of two parts closely fused together throughout their length. The unworn crown is antero-posteriorly elongated with the apex lying in an anterior position above the mesial-most end of the root. The buccal surface is evenly convex, but the lingual surface is hollowed out, with a shallow, small anterior depression and a larger distal one. There is a slight basal swelling on the lingual side, but it does not form a cingulum. The distal end of the tooth overhangs the distal part of the root and is marginally wider than the anterior part of the crown.

The lightly worn p/2 is two rooted, with the distal root somewhat larger than the mesial one. The apex of the tooth is located just anterior of the middle of the tooth, over the rear of the anterior root. There is a low anterior accessory cusplet with a hint of lingual and labial crests descending towards cervix. There is a crest joining this cusplet to the main cusp. This crest curves slightly lingually as it descends anteriorly. The distal crest of the main cusp descends before bifurcating into a small lingual crest and a more swollen buccal one, and between them there is a shallow fovea with wrinkled walls. The buccal crest has a prominent wear facet. The rear of the tooth is appreciably wider than the front half.
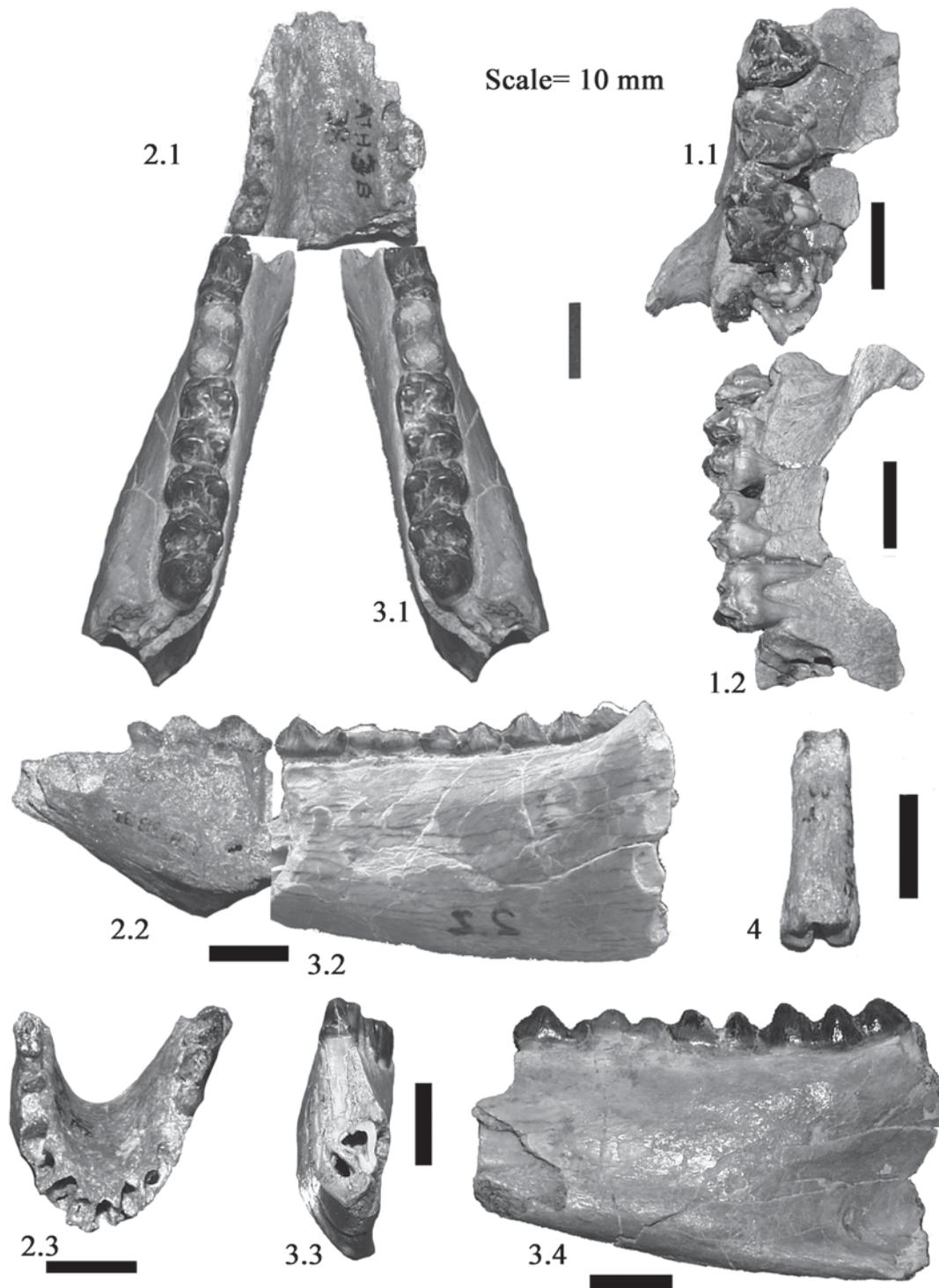
Plate 4.—*Diamantohyus africanus* from Gebel Zelten, base of the Middle Miocene, Libya.
1. 216, right maxilla with sand blasted P4/-M2/. 1.1) occlusal view, 1.2) buccal view.
2. ATH 3B 38, mandibular symphysis with left p/1-p/3 and right p/2. 2.1) occlusal view, 2.2) left lateral view, 2.3) oblique anterior view (note small canine alveolus).
3. 2.Z, right mandible with canine root in its alveolus and p/4-m/3 (and mirror image). 3.1) occlusal view, 3.2) buccal view (reversed), 3.3) section of mandible at front of p/4 showing canine section, 3.4) lingual view.
4. ATH 3B, axial first phalanx, dorsal view.

Table 4.—**Measurements (in mm) of the lower anterior teeth in specimen ATH 3B 38,** *Diamantohyus africanus* **from Gebel Zelten, Libya**

Tooth	Mesio-distal Length	Labio-lingual Breadth
i/1 (alveolus)	2.0	4.0
i/2 (alveolus)	2.3	4.5
i/3 (alveolus)	2.3	3.4
c/f (alveolus)	4.5	3.5
p/1 left	4.7	2.7
p/2 left	6.4	3.4
p/2 right	6.2	3.4
p/3 left	8.4	4.4

The p/3 is lightly touched by wear, and has two roots, the distal one being wider than long. The crown is a larger version of that of the p/2, with all the features exaggerated, but in addition the distal crest from the protoconid bifurcates and then bifurcates again, producing two crests on the lingual side that are directed obliquely backwards. The anterior of these crests swells into a low cusp, almost forming an "innenhugel" (metaconid), which is however, closely applied to the rear of the main cusp and not opposite it as in the p/4. The enamel on the lingual side is wrinkled, especially in the distal fovea and between the two lingual crests. The anterior crest curves lingually and ends in a low but sharp anterior accessory cusplet. On the buccal surface of this crest there is a large flat, but not deep, wear facet. Measurements of the teeth are given in table 4.

Specimen 2.Z is a right mandibular body with canine root in its alveolus, and p/4 - m/3. The mandibular body is robust with an evenly convex ventral border which deepens gradually towards the rear. There is no sign of a mental foramen in the preserved part. The root of the ascending ramus is far back, not hiding the m/3 in lateral view. Lingually there is a well excavated lingual fossa low down below the m/3. In front of it there is a shallower fossa which fades out below the m/2. There is a voluminous mandibular chamber below the roots of m/3 separated from the mandibular canal which runs in a separate canal below it, reaching anteriorly as far as the canine alveolus. All along the buccal side of the jaw there is a prominent bony buccinator ridge immediately below the cheek teeth.

The canine is broken off in its alveolus, but it was evidently an extremely hypsodont, ever-growing tusk-like tooth which extends deeply into the mandible below p/4 and possibly even m/1. Its section is triangular with prominent longitudinal

grooves on the lingual and buccal surfaces, while the distal surface is convex. This individual was evidently male, the specimen being markedly different from ATH 3B 38 which had a tiny canine root with closed alveolus that ends below the p/1.

The p/4 is in medium wear. The main cusp (protoconid) is positioned buccally and it has a prominent offset "innenhugel" (metaconid) lingually and very slightly distally. This pair of cusps forms a wide transverse slightly oblique loph with a shallow valley in its apex. The protoconid has a blunt crest descending anteriorly and lingually towards the anterior accessory cusplet. The latter cusplet has lingual and buccal crests forming a hint of a cingulum. The outer surface of the anterior crest sports a flat, oblique wear facet. The protoconid and the metaconid each have distal crests, and there is a third one between them descending into the distal fovea. Behind this fovea there is a large distal accessory cuspid which is bucco-lingually wide with a shallow but sharp apical valley subdividing it into two parts, a wide buccal portion (hypoconid) and a smaller lingual one (entoconid). Buccally there is a depression in the buccal wall of the crown between the protoconid and the hypoconid. The buccal and lingual enamel is intensely but not deeply wrinkled.

The m/1 is deeply worn to the stage where there are two large dentine lakes separated from each other by a bridge of enamel. The median transverse valley crosses the bridge from buccal to lingual sides. Buccally there is a basal cingulum with wrinkled sides. A remnant of the slit that separates the metastylid from the metaconid is still visible on the lingual side of the tooth.

The m/2 is lightly worn, with small dentine exposures showing only on the two anterior cusps. There are four main cusps, the buccal ones being decidedly bigger than the lingual ones. The antero-buccal cusp (protoconid) has a large anterior crest that leads obliquely forwards to the centre line of the crown and then extends lingually round the front of the antero-lingual cusp (metaconid). There is an anterior cingulum on the antero-buccal corner of the tooth. The distal crest of the protoconid descends obliquely lingually towards the median transverse valley but does not reach it, being separated from the median accessory cusplet by a sharp, narrow slit. This crest is scored by two narrow grooves, thereby forming what Pickford (1984) called the 2/3 cusp, and Van der Made (1998) called 2C (protoendocrista). The antero-lingual cusp (metaconid) has a

low crest leading obliquely anteriorly to terminate in the angle formed by the anterior crest of the protoconid and its lingual extension. The distal crest descends steeply into the median transverse valley, but does not reach its floor, forming a shallow groove down the disto-buccal surface of the cusp. This crest is separated from the metaconid by a shallow groove on its lingual side, thereby creating a separate cusplet (metastylid of Pickford, 1984). The median transverse valley is interrupted centrally by a well formed median accessory cusplet. Buccally it has a low cingular wall which is interrupted opposite the main cusps. The disto-buccal cusp (hypoconid) has anterior and posterior crests that lead obliquely lingually to join the median accessory cusplet and posterior accessory cusplet respectively, imparting a somewhat selenodont outline to the cusp, which is however, still basically bunodont. The distal accessory cusplet is located towards the lingual side of the centre line of the crown. The disto-lingual cusp (entoconid) is small and conical without anterior and posterior crests. The enamel is wrinkled.

The anterior four cusps of the m/3 are similar in layout to the m/2, but distally there is a large talonid comprised of a prominent posterior accessory cusplet (hypoconulid) behind which is a pair of larger cusps with a similar selenodont outline to that observed in the anterior cusp pairs. The metastylid is more clearly expressed than it is in the m/2. The entoconid has anterior and posterior grooves descending from its apex. The talonid loph is slightly narrower than the anterior cusp pairs. In lingual view, the talonid is seen to be distinctly higher than the two anterior lophs giving the occlusal surface of the crown a concave profile. The talonid sits on a well developed root that dips distally. The buccal cingulum is almost continuous from front to back, and the enamel is wrinkled. Measurements of the teeth are provided in table 5.

ATH 3B is an axial first phalanx. The proximal epiphysis has a well developed dorso-ventral groove for the distal crest of the corresponding metapodial. This groove is not vertical but is inclined at an angle of about 10°. There is a marked offset between the levels of the medial and lateral articular surfaces. The diaphysis is flatter in section than is usually the case in suids, more closely recalling the morphology that typifies anthracotheres. There are medial and lateral crests for extensor musculature, especially developed towards the distal end. The distal epiphysis is dorso-ventral-

Table 5.—**Measurements (in mm) of the lower cheek teeth of specimen 2.Z,** *Diamantohyus africanus* **from Gebel Zelten, Libya**

Tooth	Length	Breadth
c/m (in crypt measurement)	6.5	5.8
p/4	9.7	5.7
m/1	10.1	5.9
m/2	11.0	7.1
m/3	18.4	8.0

ly flatter than it usually is in suids, and is thus more similar to anthracotheres. There are prominent medial and lateral fossae for tendinal attachment. The central groove is most marked ventrally and gradually fades out dorsally, but is still present as a shallow depression on the dorsal aspect of the bone. The total length is 21 mm, proximal breadth is 7 mm, proximal height is 6.9 mm, distal breadth 5.7 mm, and distal height 4.8 mm.

Discussion

The maxilla fragment from Gebel Zelten does not reveal much new information, except that the sinus above the molar row is voluminous and extends to the rear wall of the root of the zygomatic arch, and extends forwards to the front of P4/. The zygomatic arch was thus in an very anterior position. It is close to the Nachola specimen (Pickford & Tsujikawa, 2005).

The most intriguing aspect of the two mandibular fragments from Gebel Zelten concerns the canines and incisor battery and the anterior premolars, as these are poorly known in the fossil record. It is now clear that sanitheres were highly sexually dimorphic in canine structure and size, males possessing ever-growing tushes and females having a small, simple canine with a short root. Although the canine tip in the male specimen is broken, it is possible to determine the approximate orientation of the canine in the jaw - it was quite steeply inserted, rather than being splayed markedly laterally. The female canines are slightly divergent and lean anteriorly in lateral view, as judged from the orientation of their alveoli. Similar canine dimorphism was inferred for the Kipsaraman and Namib sanithere collections (Pickford, 2004) on the basis of isolated teeth. The Zelten fossils provide the first *in situ* evidence of canine dimorphism.

The lower incisor battery in sanitheres is evenly curved with large central and second incisor roots, and a much smaller third incisor. The symphysis is solidly fused, unlike those of anthracotheres. An important aspect of the symphysis from Gebel Zelten is that it reveals that the incisor battery was not as procumbent as it is in suids and palaeochoerids As a result the gingival margin of the incisors is at the same level as that of the cheek teeth, unlike in suids, where the gingival margin curves ventrally in front of the canines and in *Doliochoerus* in which the anterior part of the mandible curves ventrally starting at the anterior edge of the p/2. The postcanine diastema in sanitheres is short, confirming that sanitheres were short snouted suiforms. The presence of a well formed p/1 with an incipiently doubled root fused almost to the apex is interesting, as it reveals that in sanitheres there was not a tendency for loss of this tooth, unlike some suid lineages. Colbert (1935) reported that the p/1 in a specimen from Pakistan was two rooted.

The sublingual fossa in the Gebel Zelten mandible comprises two portions, a deeper posterior one with a sharp anterior margin and a shallower extension anteriorly which fades out below the m/2. It is inferred that the deeper, posterior part of the fossa is for insertion of the medial pterygoid muscle, while the shallow extension anteriorly is for insertion of the digastric muscle (Ewer, 1958). This layout differs from the situation in *Doliochoerus* in which the sublingual fossa extends as far forwards as the rear of the symphysis (Ginsburg, 1973), being continuous with the genial fossa. In suids it generally extends forwards as far as the m/1 or further and is sharply triangular in outline. In the bushpig (*Potamochoerus*) the fossa for digastric insertion extends as far anteriorly as the p/3 although the muscle itself extends as far as the symphysis (Ewer, 1958). In neither the suids nor the palaeochoerids is the fossa clearly subdivided into two portions, the area between the insertions for the medial pterygoid and digastric muscles being more in the nature of change in slope rather than a clearly defined boundary. It is inferred that in sanitheres the digastric muscle did not extend as far anteriorly as it did in palaeochoerids and suids.

The axial first phalanx from Gebel Zelten is similar to fossils from Langental, Namibia, attributed to *Diamantohyus africanus* (Pickford, 2004). It differs from suid phalanges by its flatter and more compressed profile in lateral view, its more slender appearance and its overall gracility. In addition, the groove that accepts the keel on the distal epiphysis of the corresponding metapodial, is continuous from volar to dorsal, indicating the presence of a well developed keel on the metapodial. In its proportions and general shape it is closer to phalanges of some anthracotheres. The proximal groove is better developed than it is in suids, and much more complete than is the case in palaeochoeres, doliochoeres and schizochoeres.

Reinterpretation of the skull of *Sanitherium leobense* from Chios, Greece

The sanithere snout from Chios described by Paraskevaidis (1940) is one of the most complete specimens known. The individual from Karungu (Pickford, 1984) lacks the dorsal parts which are preserved in the Greek specimen, even if they are crushed. Because of the crushing that the Chios specimen has suffered there has been difficulty in interpreting it. The Nachola skull was also crushed, but the main features that can be discerned are similar to the Chios specimen (Pickford & Tsujikawa, 2005). The morphology as described by Paraskevaidis is of interest, as it highlights how divergent sanitheres are from other suoids (*Sus*, *Dicotyles*, *Palaeochoerus*) with which he compared the specimen. Yet the Chios fossil seems to have some suidlike characters. Understanding this snout is thus essential for throwing light on sanithere systematics.

Paraskevaidis (1940) provided the following information about the Chios sanithere snout (translated and interpreted with the help of Dr Dolores Soria).

1. The orbit is deep laterally as in primitive suids.

2. The supraorbital foramina are well preserved and are connected to two grooves. They are positioned 6 mm behind the nasal/frontal suture and are separated from each other by 19.5 mm.

3. The supraorbital grooves swing towards each other before separating again, and they terminate above the P3/. They are not deep as in *Sus* and their closest approach is 7.5 mm.

4. The nasals are flat, 32 mm long and 8 mm wide and penetrate between the frontals. The suture is angular as in *Sus*.

5. The maxilla is not prolonged forwards, the snout is short.

6. 15-18 mm above the tooth row there is a crest from the infra-orbital foramen to the front of the cheek bone (root of the zygomatic arch) similar to

the crista pyramidalis in *Sus* and *Palaeocheorus*. Above this crest there is a long furrow for snout musculature.

7. The margin of the premaxilla is steep and does not invade between the nasal and the maxilla, unlike *Sus*.

8. The infra-orbital foramen is doubled, as in *Dicotyles* and is above the rear root of P3/ as in *Dicotyles* (in *Sus* it is over the P4/). It is thus in an anterior position. It is 9 mm above the tooth row.

9. The distance between the two infra-orbital foramina is 23 mm.

10. The palate continues behind M3/. The palatine is 3.5 mm thick and has a long contact with the maxilla. The suture is located between the two palatine foramina which are located at the front of M3/. They are 10.5 mm apart.

11. The palatine grooves run close to the tooth rows.

12. There is a low crest or ridge in the centre line of the palate. The palate is slightly convex from front to back and from side to side.

In summary, according to Paraskevaidis, the snout is short, the supraorbital canals are bow-shaped and not deep, the hind part of the palate is convex ventrally, the infraorbital foramina are located in a forward position, over the P3/ and are fissure-like, and the snout musculature was well developed.

Interpretation of the plates published by Paraskevaidis (1940) is delicate because the specimens appear to be almost black and the various structures described by the author are difficult to make out. Furthermore, it appears that the dorsal part of the skull has been crushed into the maxillary portion, the nasals and frontals coming to lie at an angle between the maxillary processes of the zygomatic arches. Despite this several additional features can be made out which are important for interpreting the systematic position of sanitheres.

Firstly, the orbits are inferred to be in a very anterior position, above the molar row which is similar to the situation in the Karungu and Nachola skulls (Pickford, 1984; Pickford & Tsujikawa, 2005). Secondly, if this interpretation is correct, then the infra-orbital foramina are positioned in line with the rear of the orbits, as in ruminants and horses, but different from suids and palaeochoerids, in which the foramina are in line with the front of the orbits. Thirdly, the upper toothrows are convex ventrally, as was pointed out by Pickford (1984), a morphology that also occurs in the Karungu skull. This confor-

mation is different from the concave profile that occurs in suids and palaeochoerids which is related to the downward curvature of the premaxillae and mandibular symphysis in these taxa. Sanitheres, in contrast did not have downward curvature of the front of the snout, an inference confirmed by the high, straight profile of the gingival level of the mandibular symphysis in the Gebel Zelten specimen and one from Chios described by de Bonis *et al*., (1997). Chewing actions in sanitheres were therefore probably quite different from those in suids.

Material from Chios described by de Bonis *et al*., (1997) reveals that the mandibular condyle is high (ca 25 mm) above the occlusal surface of the tooth row. In lateral view, mandible THY 10 from Chios has a concave occlusal surface, in which the level of p/4-m/2 is below the level of p/3 and m/3. Van der Made (1996, 1998) argued that the curvature of the tooth rows as described by Pickford (1984) was due to post-mortem damage and that, therefore, the character was disputed. The specimen illustrated by de Bonis *et al*., (1997) is not distorted, and confirms that sanitheres, unlike, suids and palaeochoerids, have a convex occlusal arrangement of the upper cheektooth row (concave in the lower tooth row). The arguments put forward by Van der Made (1996, 1998) are thus undermined by the new fossils from Namibia, Gebel Zelten and Chios, and the old ones from Kenya, Chios and Austria, totalling 8 specimens in which the curvature of the tooth row can be evaluated. Not a single specimen shows a suid-like or palaeochoerid-like curvature. Under these circumstances, it is no longer possible to dispute the evidence without recourse to an extraordinary degree of special pleading. Sanitheres simply have too many features that are divergent from palaeochoerids for them to belong to this family as has been proposed on several occasions by Van der Made. They are as divergent from suids but in different ways, which is why Pickford (1984) classed them within their own family.

Systematics

There have been various schools of thought about sanithere systematics. Pilgrim (1926) recognised two groups of sanitheres but placed both of them on the *Sus* lineage separate from other suines such as *Dicoryphochoerus*. *Xenochoerus* was located below the *Phacochoerus-Sus* dichotomy, and *Sanitherium* above it but below the dichotomy

between *Sus* on the one hand and *Hyosus-Porcula-Hippohyus* on the other. Other authors recognised the rather aberrant nature of sanitheres within a suid context and there have been various proposals reflecting this oddness, ranging from inclusion as a subfamily within Suidae (Thenius, 1956; Wilkinson, 1976), or Palaeochoeridae (Thenius, 1979; Van der Made, 1996, 1998; Van der Made & Hussein, 1992) or as a separate family within Suoidea (Pickford, 1984, de Bonis *et al.*, 1997). Thenius (1956) considered that sanitheres were a subfamily of Suidae, in accordance with Simpson (1945), but later (Thenius, 1979) changed his mind and arranged them in Tayassuidae as a new subfamily, Xenochoerinae, but he appears to have excluded *Diamantohyus* and *Sanitherium* from this subfamily. Pickford (1984) classed them in a family (Sanitheriidae) separate from the Suidae, whereas Van der Made (1998) included them within the Palaeochoeridae along with *Palaeochoerus*, *Propalaeochoerus*, *Doliochoerus*, *Schizochoerus* and *Taucanamo*. There are some resemblances between the basic structure of the lower p/4 of *Palaeochoerus* and *Diamantohyus* (or *Sanitherium* as Van der Made preferred to call it) but there are major differences in the molars and anterior premolars, including the presence of metastylids in the molars in *Diamantohyus*, the more exaggerated selenodonty of the buccal cusps, the presence of buccal cingula on the molars, the presence of the "palaeomeryx-fold" in the p/4 and molars, and the doubled talonid in m/3. Sanitheres also possess dm/1 and p/1, whereas suids and palaeochoerids do not replace the first premolar. Van der Made (1998) has argued that these structures could have evolved from a *Palaeochoerus* grundplan, whereas Pickford (1984) stressed the possibility that they could be retained from a more primitive artiodactyl ancestral condition. In the latter case, the *Palaeochoerus* morphology would be derived with respect to that of sanitheres, and not primitive, the position held by Van der Made. The upper dentition is even more divergent from that of palaeochoerids and suids (Pickford, 1984), the premolars being multi-cusped and the molars possessing well developed styles on the ectoloph, with a "palaeomeryx-fold" on the paracone, the buccal cusps being only about one third of the breadth of the crown, and the lingual cusps two thirds of the breadth, and the selenodont aspect of the anterior arms of the buccal cusps among other features. There are usually two lingual roots in sanithere upper molars, as opposed to a single one in palaeochoerids. The upper dM3/ has four cusps, unlike all other suoids, in which this tooth is always tricuspid.

In support of Pickford's view are several features of the skull, mandible (de Bonis *et al.*, 1997; Paraskevaidis, 1940; Pickford, 1984, 2004; Pickford & Tsujikawa, 2005) and post-cranium (Pickford, 2004). Some of the cranial features were already pointed out by Pickford (1984) and include orbits in a very anterior position (the leading edge is above the P4/), the presence of a large facial fossa, nasals much narrower than the palate, premaxilla not invaginating between the maxilla and the nasals, convexly curved maxillary tooth row, convexly curved ventral edge of the mandible, short and steep mandibular symphysis with steeply inclined incisor battery, gingival level of the incisors on the same level as that of the cheek teeth (ie not curving ventrally), a very anteriorly positioned root of the zygomatic arch, the zygoma departing from the face at a shallow angle, and the presence of a depression on the ventral border of the zygoma, the presence of a sagittal crest (Pickford, 1984; Pickford & Tsujikawa, 2005) which extends as far anteriorly as the middle of the zygomatic arch, if not even further, absence of pneumatisation of the roof of the brain case, short paroccipital process, low external auditory meatus, bullae with a vertical orientation and a short auditory canal. Where the morphology in *Palaeochoerus* is known, it resembles more that of suids than that of sanitheres. Unlike suids and palaeochoerids (eg *Doliochoerus*, Deschaseaux, 1959), but similar to extant peccaries, the infra-orbital foramen in sanitheres is doubled (Paraskevaidis, 1940) with foramina leading distally and anteriorly.

There can be little doubt that sanitheres were short-snouted suoids, as was pointed out by Paraskevaidis (1940). The mandibular symphysis from Gebel Zelten confirms this, the incisors being more vertically implanted in a shorter, more upright symphysis than that which occurs in the palaeochoerid *Doliochoerus*, for example, in which the symphysis is more suid-like, being more elongated, and more inclined with procumbent incisors (Deschaseaux, 1959). In sanitheres in addition, the gingival level of the lower incisor row does not descend anteriorly as it does in suids and palaeochoerids (as well as in extant tayassuids, Pearson, (1927)), but is at the same level as the cheek teeth, not only in *Diamantohyus* from Gebel Zelten, but also in *Sanitherium* from Chios (de Bonis *et al.*, 1997).

The lower incisors of sanitheres are much lower crowned than those of suids and palaeochoerids (Pickford, 1997, 2004; de Bonis *et al*., 1997) and they each have an enlarged basal tubercle on the lingual surface, above which there is a deep scoop that extends right up to the apex of the tooth. Suids and palaeochoerids do not possess basal tubercles but do have long medial crests that run up the lingual surface of the first and second lower incisors reaching the apex, and the incisors are not deeply excavated on the lingual side. The enamel in sanithere incisors is bulbous and thick, and the surface of the teeth is coarsely wrinkled as seen in material from Langental, Namibia, and Chios, Greece. Suid and palaeochoerid incisors have thinner enamel which is smooth. Thus sanithere lower incisors are quite different from those of both suids and palaeochoerids, not only in their structure, but also in their orientation within the mandible and in their position relative to the cheek tooth row.

Newly available post-cranial remains of *Diamantohyus* from Namibia (Pickford 2004; Stromer, 1926), and an axial first phalanx from Gebel Zelten, and specimens from Karungu, Kenya (Pickford, 1984) reveal that the non-suid morphology extends into the post-cranial skeleton. Previously available samples (Pickford, 1984) were too limited to show much about sanithere post-cranial anatomy, save to reveal that it was basically suoid.

The metapodials and phalanges from Namibia are relatively elongated and gracile, and dorso-ventrally compressed as in some anthracotheres, and quite different from the stocky, solid-looking metapodials and phalanges of suids and palaeochoerids. The distal end of the metapodials and the proximal epiphysis of the axial first phalanges show well developed central keel and groove respectively, unlike the genera put into Palaeochoeridae by Van der Made (1998) (with the exception of *Sanitherium* of course), which have a weak or non-existent keel dorsally. The volar part of the keel in sanitheres is even more marked than it is in suids, and it extends proximally onto the diaphysis where it blends into a diaphyseal ridge. The latter indicates that the metapodial-phalangeal articulation was highly stabilised, much more so than in suids and palaeochoerids.

The Gebel Zelten fossils show that sanitheres were sexually dimorphic in canine morphology, and in this they are suid-like rather than peccary-like. In several aspects of the basicranium sanitheres are suid-like, yet in some features such as orientation and length of the paroccipital process, and the low and short external auditory meatus they are not like them.

The new data, especially the post-cranial evidence, once more distance the sanitheres from the suids and palaeochoerids, but they do not provide a definitive solution to their systematic position (Pickford, 1993). Some dental and post-cranial evidence supports the sister-group relationship with the anthracotheres, as suggested by Pickford (1997), but the fused mandibular symphysis suggests that these resemblances may be homoplasies or plesiomorphies rather than derived morphology shared with anthracotheres. What seems clearer now is that sanitheres are not closely related to doliochoeres (or palaeochoeres) of the *Palaeochoerus*, *Propalaeochoerus* group, as proposed by Van der Made (1998) and Wilkinson (1976). They are even further removed from the *Taucanamo*, *Schizochoerus* group. A sister group relationship with suids as initially hypothesised by Pickford, 1984, is possible, but it is more likely that sanitheres branched off before the dichotomy between suids and palaeochoerids, and perhaps even before the dichotomy between the Old World suoids and the New World peccaries (Tayassuidae *sensu stricto*).

Conclusion

A restricted sample of suoids from the Basal Middle Miocene site at Gebel Zelten, is of interest in that it throws light on the anatomy and systematic position of three poorly known groups, the gigantic species *Megalochoerus khinzikebirus*, the medium sized species *Libycochoerus massai*, and the small species *Diamantohyus africanus*. The snout of *Megalochoerus* is basically similar to that of other kubanochoerine suids including *Libycochoerus* and *Kubanochoerus*, but despite its greater body size, its anterior premolars are smaller than those of the smaller species. It is markedly divergent from snouts of Listriodontinae.

The few specimens of *Diamantohyus africanus* from Gebel Zelten are important because they demonstrate the presence of marked canine dimorphism in the species, which previously had only been inferred from isolated teeth. They also confirm that the species was endowed with relatively short faces, diastemata being short or absent. Furthermore it is possible to observe that the occlusal surface of the dentition did not descend anteriorly as in suids and palaeochoerids.

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