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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Early Miocene Sanitheriidae from the northern Sperrgebiet, Namibia

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Sanitheres are poorly known suiformes of small size that were widespread in the Old World during Early and Middle Miocene times but never very common. Because much of their anatomy is unknown, especially that of the post-cranial skeleton, there has been debate about their classification within the order, with some authors attributing the group to the Suidae, whereas others prefer to class them in a separate family Sanitheriidae or within Palaeochoeridae. The newly available cranial and post-cranial bones from Langental in the Sperrgebiet, Namibia, support those who view the sanitheres as being separate from Suidae and Palaeochoeridae at least at the family level. The lower limbs appear to have been gracile and elongated, suggesting a more cursorial locomotor repertoire than is usual in suids and palaeochoerids.

Introduction

Sanitheres are widespread in the Old World, reaching their greatest distribution during the Middle Miocene (MN 5), going extinct soon afterwards. Despite its enormous geographic spread, the family remains poorly known, and little has so far been reported of its post-cranial skeleton. Enough small suiform material from Langental has now been collected that elements of the post-cranium can be attributed with confidence to each of the two suoid species represented at the site, *Diamantohyus africanus* and *Nguruwe namibensis*. Over 60 postcranial specimens are attributed to *D. africanus*, which reveal that it was a lightly built suoid with elongated metapodials in which the distal keel was continuous onto the dorsal surface of the articulation, gracile phalanges and well developed crests in the limb articulations (distal humerus, distal tibia, proximal talus, cuboid, distal metapodials, proximal 1st phalanges) suggesting that the species was relatively more cursorial than most suids are, underlining the distinctiveness of the sanitheres from the suids at the family level.

Systematic descriptions

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

Holotype : Right maxilla with P3/, M1/-M2/ (Stromer, 1922, p. 332)

Additional material from Namibia :

Craniodental specimens :

From Langental : Fragment of m/3 mentioned by Stromer, (1926, p. 113); SAM PQ N 124, upper incisor; SAM PQN 124, left I1/; SAM PQN 125, right dm/4; SAM PQN 2123, left m/3; SAM No N°, cranial roof (Pl. 4, Fig. 1); LT 160'96, right mandible with mixed dentition; LT 162'96, left mandible with mixed dentition; LT 168'96, left mandible with p/3-m/3; LT 417'96, right m/3 germ; LT 418'96, rear 2/3 of right m/3; LT 420'96, rear 2/3 of left m/3; LT 422'96, cheek tooth fragment; LT 454'96, lower incisor; LT 235'99, damaged right upper molar; LT 1'00, maxilla fragment with left dM3/-dM4/ (Pl. 1, Fig. 1); LT 2'00, anterior two cusps of left m/3; LT 3'00, buccal half of left lower molar; LT 5'00, right mandible with roots of dm/4 and complete m/1 (Pl. 1, Fig. 3); LT 37'03, lower canine (Pl. 1, Fig. 4); LT 45'03, upper premolar, broken; LT 110'03, half right upper molar; LT 176'03, etched upper molar; LT 209'03, talonid of m/3; LT 212'03, right M3/ broken; LT 223'03, mandible fragments with right m/3 and left m/3 and part of m/2 (Pl. 1, Fig. 2); LT 237'03, upper I3/; LT 21'04, left P4/-M3/; LT 157'04 fragmented left maxilla with P3/-M1/ (Pl. 4, Fig. 2); LT 219’04, hind end of skull.

From Fiskus : FS 18'03, fragmentary mandible with ascending ramus, temporal condyle and coronoid process, teeth in bad condition.

Post-cranial skeleton :

From Langental : Proximal McIII, left and right talus, left cuboid described by Stromer, (1926); LT 164'96, right talus (Pl. 7, Fig. 4); LT 165'96, distal end of axial metapodial (Pl. 1, Fig. 10); LT 166'96, proximal end axial 1st phalanx; LT 424'96, cuboid (Pl. 7, Fig. 7); LT 425'96, broken cuboid; LT 427'96, proximal left metacarpal III (Pl. 1, Fig. 7); LT 428'96, cuboid (Pl. 7, Fig. 8); LT 430'96, proximal right metacarpal III (Pl. 1, Fig. 6); LT 431'96, abaxial metapodial (Pl. 7, Fig. 12); LT 432'96, distal end of abaxial metapodial; LT 433'96, eroded axial metapodial (Pl. 7, Fig. 11); LT 434'96, proximal end and shaft of right metatarsal III (Pl. 7, Fig. 10); LT 6'97, distal end of axial metapodial (Pl. 1, Fig. 9); LT 75'97, proximal right metatarsal III; LT 148'98, proximal radius (damaged); LT 154'98, femur head; LT 156'98, axial 1st phalanx (pedal?) (Pl. 7, Fig. 13); LT 157'98, axial 1st phalanx (manual?) (Pl. 7, Fig. 17); LT 158'98, axial 1st phalanx (manual?) (Pl. 7, Fig. 18); LT 160'98, distal end abaxial metapodial; LT 163'98, eroded distal humerus; LT 73'99, half talus; LT 226'99, distal tibia with medullary cavity preserved in

Plate 1. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 5 cm).
1. LT 1'00, left maxilla fragment with dM3/-dM4/, stereo occlusal view.
2. LT 223'03, a) right m/3, stereo occlusal view, b) right mandible, occlusal view.
3. LT 5'00, right mandible with roots dm/4 and complete m/1, a) occlusal view of m/1, b) lateral view.
4. LT 37'03, left lower canine, male, a) labial, b) lingual views.
5. LT 430'00, distal right humerus, a) posterior, b) anterior views.
6. LT 430'96, proximal right McIII, a) dorsal, b) medial, c) proximal views.
7. LT 427'96, proximal left McIII, a) dorsal, b) medial, c) proximal views.
8. LT 74'03, proximal left McIV, a) proximal, b) dorsal, c) medial views.
9. LT 6'97, distal axial metapodial, a) volar, b) dorsal views.
10. LT 165'96, distal axial metapodial, a) volar, b) dorsal views.
11. LT 65'01, distal abaxial metapodial, a) oblique volar view, b) distal, c) lateral views.

calcite (Pl. 7, Fig. 1); LT 238'99, axial 2nd phalanx (Pl. 7, Fig. 20); LT 243'99, abraded distal humerus; LT 6'00, axial 2nd phalanx; LT 9'00, abaxial second phalanx; L 123'00, cuboid; LT 134'00, distal end of humerus; LT 136'00, calcaneum; LT 137'00, calcaneum (Pl. 1, Fig. 3); LT 138'00, calcaneum fragment; LT 430'00 distal right humerus (Pl. 1, Fig. 5); LT 64'01, calcaneum; LT 65'01, distal end of abaxial metapodial (Pl. 1, Fig. 11); LT 77'01, axial 3rd phalanx; LT 6'03, axial 2nd phalanx (Pl. 7, Fig. 21); LT 32'03 left talus (Pl. 7, Fig. 6); LT 33'03, right talus (Pl. 7, Fig. 5); LT 38'03 axial 1st phalanx (?pedal) (Pl. 7, Fig. 14); LT 69'03, 2nd phalanx; LT 74'03, proximal end of left metacarpal IV (Pl. 1, Fig. 8); LT 75'03, 2nd phalanx; LT 121'03, axial 1st phalanx (pedal?) (Pl. 7, Fig. 16); LT 133'03, distal tibia (Pl. 7, Fig. 2); LT 138'03, femur head; LT 155'03, proximal right ulna; LT 159'03, proximal right metatarsal III (Pl. 7, Fig. 9); LT 206'03, abaxial 1st phalanx (Pl. 7, Fig. 15); LT 214'03, abaxial 1st phalanx (Pl. 7, Fig. 19); LT 247'03, axial 3rd phalanx; LT 30'04, calcaneum; LT 32'04, axial terminal phalanx; LT 70'04, navicular (Pl. 6, Fig. 3), LT 81'04, left calcaneum (Pl. 6, Fig. 2); LT 207'04, distal end abaxial metapodial; LT 17'06, third metatarsal lacking distal epiphysis; SAM PQN No N° axial 3rd phalanx.

From Elisabethfeld : EF 19'98, proximal left radio-ulna (Pl. 5, Fig. 3, 4); EF 28'00 and 29'00, distal right humerus and proximal radio-ulna articulated (Pl. 5, Fig. 1, 2).

From Grillental : GT 1'94, abaxial 3rd phalanx (Pl. 7, Fig. 22); GT 8'94, shaft and distal end of right humerus (Pl. 5, Fig. 5); GT 13'03, distal end of axial metapodial; GT 5'04 complete left radius (Pl. 6, Fig. 1); GT 60'04 distal half of axial metapodial (Pl. 6, Fig. 4); GT 70'04, calcaneum; GT 81'04, distal end of abaxial metapodial; GT 195'04, 3rd phalanx; GT 27'06, right radius; GT 29'06, abaxial first phalanx; GT 32'06, abaxial terminal phalanx.

From Fiskus : FS 32'93, associated second and third axial phalanges (Pl. 5, Fig. 6, 7).

Descriptions : Neurocranium. A specimen with no number collected from Langental by Hamilton is part of the braincase of *Diamantohyus africanus* (Plate 4, Fig. 1). The frontals and parietals are preserved from the anterior edge of the orbits as far back as the nuchal area, although the latter is severely wind eroded. The orbital margins are subparallel to each other and are 37.7 mm apart. The supraorbital grooves and foramina are clearly developed, the foramina being 21 mm apart and located slightly in advance of the middle of the orbits. There are two well developed frontal ridges that converge distally and meet anteriorly to the nuchal zone to form a sagittal crest. The specimen has been somewhat distorted so that, looking from above, the parietal part is twisted anticlockwise with respect to the frontal.

The endocranial surface is remarkable for the development of a prominent sagittal groove which swerves towards the right side (left in the image) as it approaches the distal part of the brain case. There is no equivalent groove on the right side distally.

Back of the skull : LT 219'04 is the hinder end of an artiodactyl skull from early Miocene deposits at Langental, Northern Sperrgebiet, Namibia (Pl. 2, 3). The specimen was found in a fist-sized pedogenic carbonate nodule together with the breastbone and other remains of a large bird the size of a goose near the spot where two mandibles and a maxilla of a juvenile individual of *Diamantohyus africanus* were found in 2000. The specimen, which preserves much of the occipital and exoccipital bones, resembles other specimens containing teeth that have already been attributed to the species (Pickford, 2004; Pickford and Tsujikawa, 2005) and it is therefore confidently identified as this species. The main value of the Langental fossil is that it preserves the basioccipital, the right paroccipital process of the exoccipital, the entire squamous occipital and the left petrosal bone *in situ*. The specimen is fractured and the pieces are slightly out of position relative to one another, but not so badly as to impede proper observation and interpretation. Crushing is minimal, unlike the Nachola, Kenya, specimen (Pickford and Tsujikawa, 2005) and the basicranial part is in excellent condition, despite minor fractures and displacement of bones. Thus, for the first time, we are able to observe the detailed osseous anatomy of the back and base of the skull of this species.

The bones neighbouring the occipital (temporal, sphenoid, squamosal) appear to have been unfused suggesting that the individual was juvenile at the time of death, as were the mandible and left maxillae found separately nearby, and it is possible that with these remains we are dealing with a single individual of the species. It is also entirely possible, despite the lengthy lapse of time between Stromer's (1926) work and the present study, that the holotype maxilla of *Diamantohyus africanus* could belong to the same individual, as it represents the right maxilla with mixed dentition in a similar state of maturity to the newly collected specimens. The fact that the tympanic bulla is missing, yet the petrosal bone is *in situ* provides further evidence of the juvenile status of the individual, the bulla probably being cartilaginous at this stage of development, and thus not getting fossilised.

In distal view the occipital is clearly suoid, with a large concave squamous part flaring dorsally from a narrow base just above the two nuchal tubercles that roof the foramen magnum. The central nuchal fossa is bordered by rounded ridges either side that converge ventrally, and separate the nuchal fossa from the lateral occipital fossa on either side. The dorsal extremity of these ridges is swollen into a tuberosity that fills the area of the junction between the nuchal crest and the temporal crest. The dorsal rim of the squamous part of the occipital is roughened and pos-

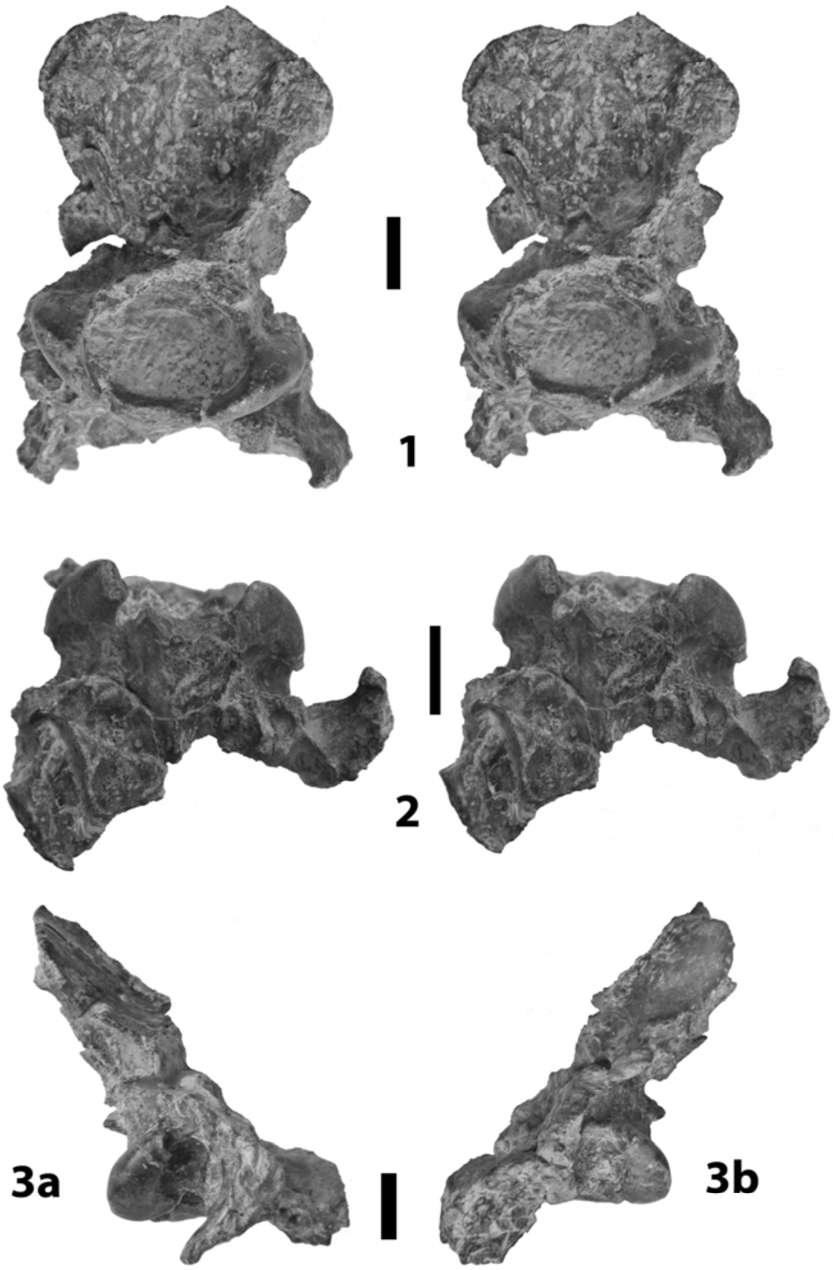

Plate 2. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (Scale : 10 mm).
LT 219'04, hind end of skull. 1 – posterior view, 2 – basal view, 3 – lateral views (3a, right, 3b left) (Stereoscopic pairs).

sesses a low v-shaped fossa on either side that descends into the nuchal fossa.

The foramen magnum is large and the occipital condyles are angled steeply, their dorsal extremity almost reaching the level of the two nuchal tubercles that form the roof of the foramen magnum. Ventrally the occipital condyles are well separated from each other by a ridge forming the distal extremity of the basilar part of the occipital, which is on the same level as the base of the condyles. The ridge between the two dorsal tubercles of the foramen magnum stretches between the two tubercles, but does not rise dorsally as in recent pigs.

The paroccipital process of the exoccipital is short and curves towards the rear. It lies in a line well away from the lateral extremity of the occipital condyle, unlike *Sus* in which it is only slightly lateral to the condyle. The condyles themselves are more dorso-ventrally compressed than are those of *Sus*.

The petrosal bone is in line with the middle of the occipital condyle and is oriented with its long axis almost antero-posterior.

In lateral view, the most striking aspect of the specimen is the posteriorly directed paroccipital proc-

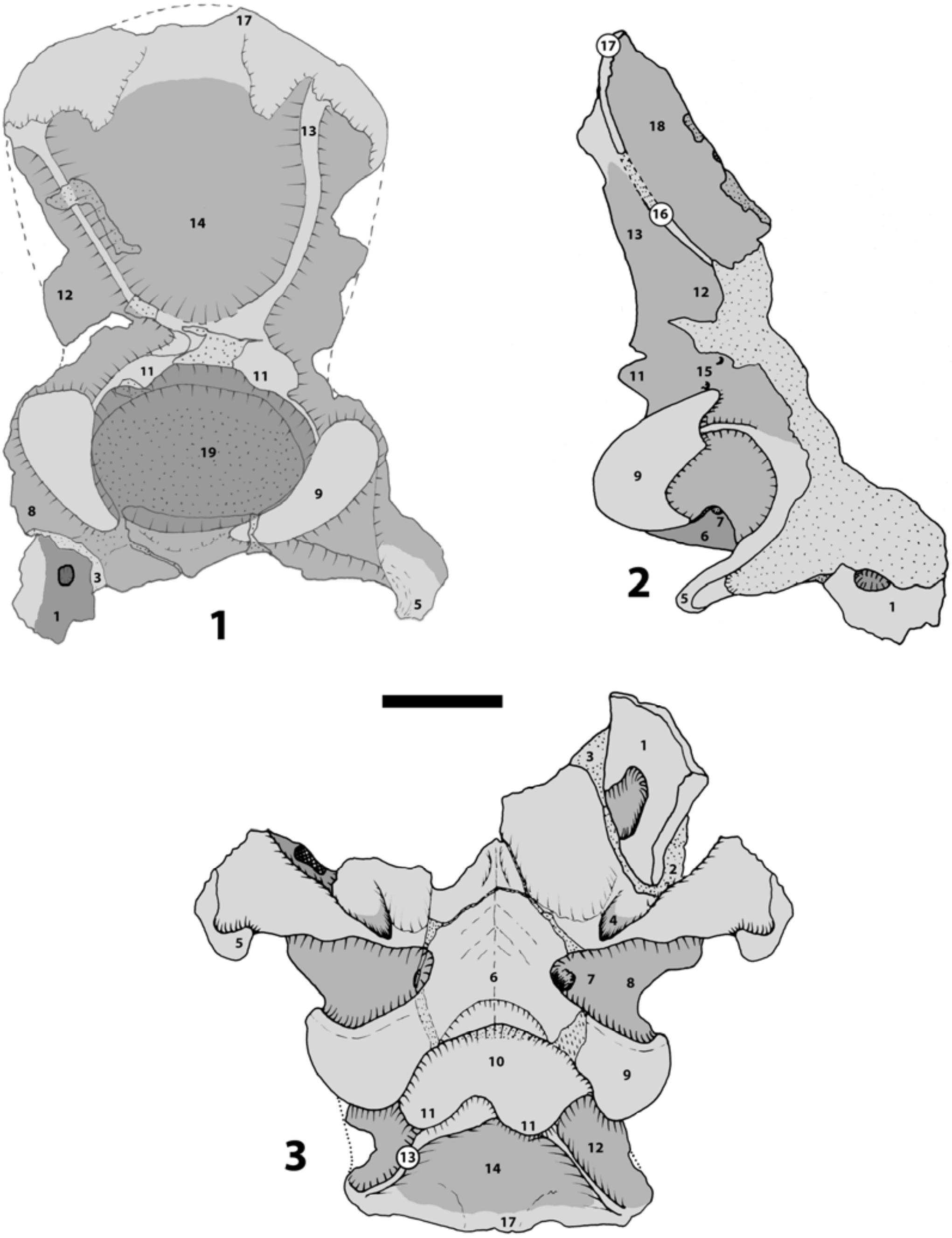

Plate 3. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (Scale : 10 mm).
1. LT 219'04, hind end of skull, interpretive drawings. 1, posterior view; 2, right lateral view; 3, basal view. (1 – petrosal, 2 – foramen lacerum posterior, 3 – foramen lacerum anterior, 4 – hypoglossal foramen, 5 – paroccipital process of the exoccipital, 6 – basilar part of the occipital, 7 – condyloid foramen, 8 – condyloid fossa, 9 – occipital condyle, 10 – roof of foramen magnum, 11 – nuchal tubercle, 12 – lateral nuchal fossa, 13 – nuchal ridge, 14 – nuchal fossa, 15 – nututuve foramina in condyloid fossa, 16 – temporal crest, 17 – nuchal crest, 18 – dorsal surface of parietal bone, 19 – foramen magnum).

ess, which is short, curved, and bears on its antero-lateral surface a shallow fossa. The temporal surface of the occipital is not inflated, unlike the condition in suids, and there is no sign of occipital or temporal sinuses. Because of this the temporal surface of the occipital is deeply concave and inclined antero-ventrally. The well-developed temporal crest separates the expansive area for the temporal musculature from the smaller, but still important fossa for the lateral muscles of the neck. The base of the lateral fossa, just above the antero-dorsal extremity of the occipital condyles, shows two nutritive foramina, one above the other. In this view, the nuchal tubercles above the foramen magnum are clearly evident, as is the concavity between them and the bases of the nuchal ridges.

Visible in medial view is the large circular pocket of the petrosal bone, partly concealed by matrix.

The basilar view is the most interesting as it reveals, for the first time, several details of morphology that could not be studied in previously available specimens. The basilar part of the occipital has a low central ridge from which weak v-shaped ridges diverge distally, but no sign of basilar tubercles, perhaps due to its juvenile status. At its distal end, there is a shallow, dorsally sloping fossa that ends at the edge of the foramen magnum. Between the occipital condyles and the basal part of the paroccipital process there are deep condyloid fossae, which are much more expansive than the comparable region in *Sus*, so much so that in *Diamantohyus* the condyles and the root of the paroccipital process are separated from each other by a wide gap, whereas in *Sus*, the gap is short, and the depression subtle. In the internal end of each condyloid fossa there is a prominent condyloid foramen, well preserved on the left side but partly concealed by displaced bone on the right. This conformation is similar to the situation in the anthracothere *Brachyodus*.

At the medial side of the root of the paroccipital process there is a low depression, at the distal end of which is the hypoglossal foramen, in a position similar to that of *Sus*. This foramen appears to be directed dorso-distally rather than directly dorsally. The small depression that houses the hypoglossal foramen is walled off medially by a low but sharp crest of bone, from a more expansive but shallow fossa in the basioccipital.

The petrosal bone is vertically implanted in the vacuity for the tympanic bulla, and its medial pocket is clearly evident. Between it and the basioccipital bone there is a narrow sediment-filled gap representing the foramen lacerum posterior and the foramen lacerum anterior, the two foramina being parts of a single opening in the skull base, as in *Sus*.

The paroccipital process is short and curves to the rear and slightly medially at its extremity. In basilar view it is possible to discern a light ridge of bone running from its apex towards its root and anteriorly towards the squamosal, which is missing in this individual.

<u>Discussion</u> : The back of the skull of *Diamantohyus* shows a mixture of features found in other suiform artiodactyls, some such as the presence of condyloid foramina and antero-ventrally sloping dorsal surface of the temporal bones resembling the condition in anthracotheres such as *Brachyodus*, others such as the form of the squamous part of the occipital bone and the presence of ventrally converging nuchal ridges resembling the situation in suids and palaeochoerids. The post-cranial skeleton described by Pickford (2004) also shows a mixture of anthracothere-like and suid-like features with phalanges resembling those of anthracotheres and the distal metapodials looking more like those of suids. The anatomy of the back of the skull thus reinforces the distinct familial status of the family within the Suiformes.

In terms of nuchal morphology, *Diamantohyus* is clearly linked to palaeochoerids and suids, showing the derived morphology of the expansive nuchal fossa on the squamous occipital flanked by two ventrally converging ridges that separate the central fossa from the lateral nuchal (or occipital) fossae. Basically similar morphology occurs in palaeochoerids and suids, whereas the nuchal area of anthracotheres such as *Brachyodus* and *Libycosaurus* is radically different, with a large central ridge flanked by deep recesses for the nuchal musculature. The short paroccipital process in *Diamantohyus* is like that of palaeochoerids and primitive suids, but it is more posteriorly inclined than in these lineages. It is unlike the elongated and apically swollen paroccipital process of *Brachyodus* or the long slender process that occurs in suines.

The presence of a large condyloid foramen in the condyloid fossa is similar to the condition in *Brachyodus*, but unlike the situation in suids and palaeochoerids in which the condyloid fossa is reduced in dimensions and shows no sign of condyloid foramina. I take this morphology in *Diamantoyhus* to be primitive among suiforms. Similarly primitive is the absence of sinuses in the temporal bones, which thereby slope strongly ventro-anteriorly from the nuchal crest, as in *Brachyodus*, and unlike suids and palaeochoerids. The presence of a strong and tall sagittal crest is also a primitive feature at the level of suiforms.

<u>Maxilla</u> : Only two fragments of maxilla are present in the new collections. LT 1'00 preserves the dM3/-dM4/, a small sliver of the palatal surface and a flaring lateral surface of the maxilla. The root of the zygomatic arch departs from the face at a shallow angle opposite the middle of the dM3/. This a a very anterior position, even for a juvenile suoid, and presages the anterior position that typifies adult sanitheres (Paraskevaidis, 1940; Pickford, 1984). The other specimen, LT 157'04 consists of the last two premolars and the first molar in small fragments of maxilla (Pl. 4, Fig. 2).

<u>Upper dentition</u> : *Deciduous teeth*. The dM3/ in LT 1'00 is trapezoidal in occlusal outline, possessing two anterior cusps and two posterior ones. In suids the occlusal outline of the dM3/ is triangular, since the anterior cusp is single. The buccal cusp in the anterior loph of LT 1'00 is slightly higher than the lingual one and it has two well developed crests descending from its apex anteriorly and posteriorly in a buccal position, the anterior one swinging centrally to join a low cuspid . The lingual cusp of the anterior loph also has two crests, but they depart from the centre of the cusp directly forwards and backwards and are lower in

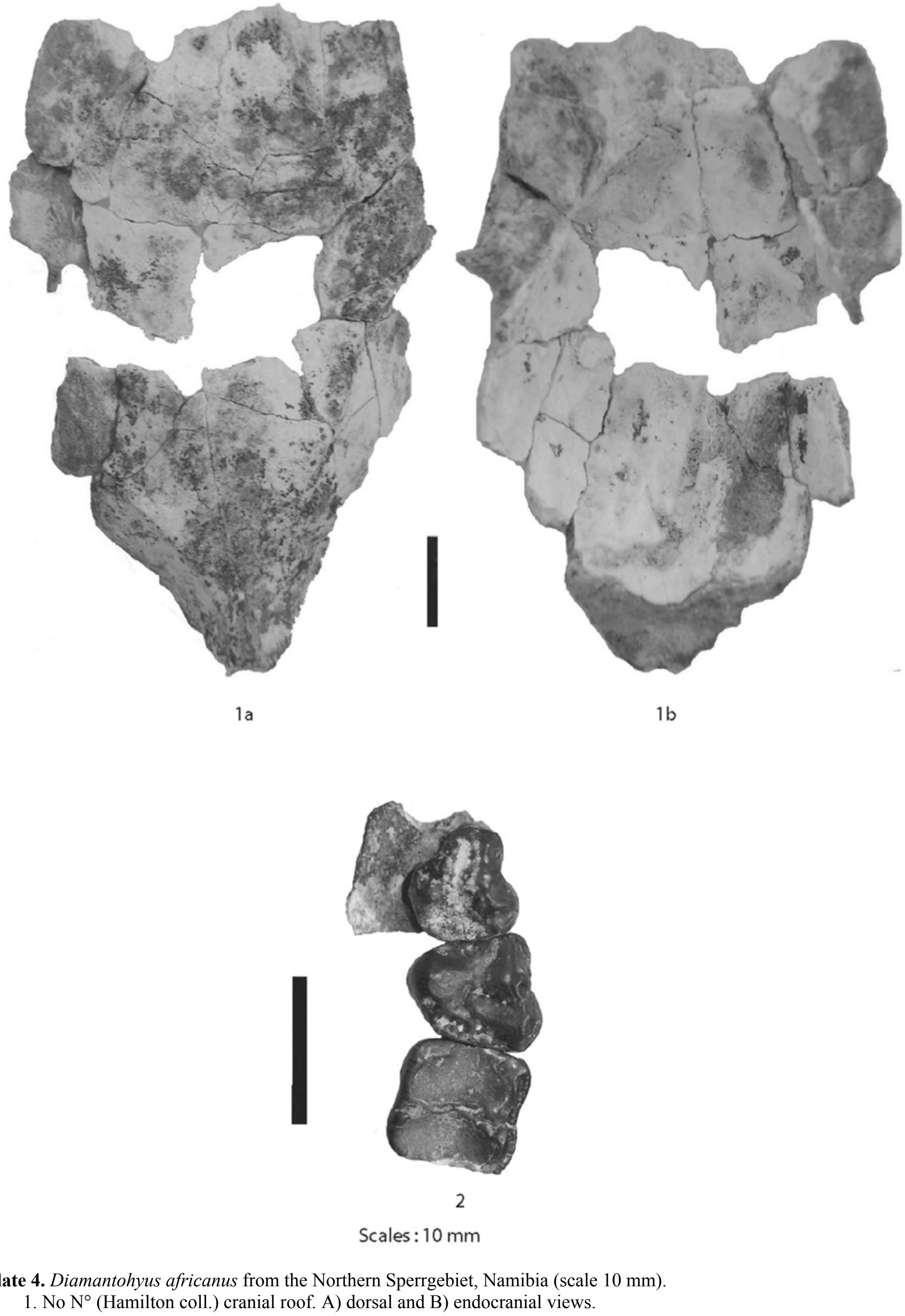

Plate 4. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 10 mm).
1. No N° (Hamilton coll.) cranial roof. A) dorsal and B) endocranial views.
2. LT 157'04, left P3/-M1/, occlusal view.

stature. The rear loph is also comprised of two cusps which are larger than the anterior ones, the rear of the tooth being appreciably broader than the anterior half. Each of the cusps has a crest descending from the anterior part of the apex towards the midline of the tooth, meeting each other low in the centre-line of the tooth. They also have weak crests leading anteriorly into the base of the median transverse valley. The distal crests are also weakly developed. There is a low cingulum in the lingual end of the median transverse valley but none buccally, although abrasion to the outer side of the tooth may be misleading us about this point.

The dM4/ has a slightly trapezoidal occlusal outline, the anterior loph being somewhat narrower than the rear one. It is a four cusped tooth, but in this specimen the rear loph is damaged so that little information can be obtained about cusp morphology. The anterior pair of cusps is in better shape and it is possible to make out that the protocone has a long anterior crest that sweeps obliquely across the front of the tooth to reach almost to the buccal side of the crown. The anterior buccal cusp is missing its buccal surface, but it seems to have possessed an anterior style. The median transverse valley is not obstructed by crests or cusplets, but there does appear to be a low cingulum at its lingual end. In short, the dM4/ looks quite similar to an upper permanent molar, save for its smaller size, thinner enamel and slightly trapezoidal outline.

Permanent upper teeth : Langental has yielded very little of the upper dentition of *D. africanus*. Apart from Stromer's (1922) holotype maxilla, there are two fragmentary upper molars collected in 2003 and two fragments of maxilla found in 2004, as well as an upper central incisor (SAM PQ 124) stored in the South African Museum. LT 237'03 is identified as an upper I3/ of *D. africanus*. It has a broken crown, but what remains is wrinkled in the style of sanithere teeth and the enamel appears to be puffy. The crown was probably originally triangular in lingual outline, but all that is left is the distal half, which sports a well developed wear facet apically. The distal end of the crown overhangs the root by quite a margin. The root is simple with a slight central groove lingually and labially. LT 45'03 is an upper premolar, probably P3/. It has a chip of enamel missing from the buccal side, making it difficult to interpret, but the wrinkled enamel, the presence of several low cusps and a style on the buccal side suggests that this tooth is that of a sanithere.

LT 21'04 is a left upper tooth row from P4/ to M3/ but with the lingual halves of M1/ and M2/ abraded away by sand blasting. The P4/ has a well developed protocone with a long anterior ridge running obliquely across the front of the tooth terminating near the anterior crest of the buccal cusp. In this morphology the front half of the P4/ looks like the front of an upper molar. The buccal anterior cusp is about one third of the breadth of the tooth. The hypocone is absent but there is a low cingular ridge and shelf disto-lingually. The disto-buccal cusp has a prominent crest running lingually. There is an incomplete buccal cingulum. The enamel is wrinkled. The M1/ and M2/ have prominent buccal cingula. The M3/ is quadricuspidate with a large lingually positioned talon. It is in medium wear, and its crown morphology is typical of sanitheres, with long oblique anterior crest on the protocone reaching almost to the buccal edge of the tooth. The hypocone also has a well developed anterior crest reaching obliquely across the crown and extending across the lingual half of the disto-buccal cusp. The lingual roots are not fused unlike Palaeochoeridae. The distal root is trefoil shaped in section comprising the fused buccal and lingual roots attached to the root beneath the talon.

LT 157'04 is a fragmented left maxilla with two premolars and the first molar (Pl. 4, Fig. 2). P3/ and P4/ are in light wear, whereas the M1/ is deeply worn, to the stage where two large transversely oriented dentine lakes have been produced, leaving almost no crown morphology save for the peripheral enamel structures such as cingula. The P3/ is broadly triangular in occlusal view, with a bulbous distal part and a narrower anterior part. The ectoloph is high in the middle and descends anteriorly and posteriorly. There is a buccal rib on the distal part of the ectoloph, as well as a low distal stylar fold. A single lingual cusp is located in the middle of the lingual side of the crown, and is separated from the ectoloph by a valley. The distal shelf is broad but not mesiodistally long. The P4/ is also broadly triangular in occlusal view, but is wider mesially than distally. The ectoloph is comprised of two cusps with buccal ribs descending towards cervix from their apices. There is a large lingual cusp, the protocone, with a prominent preprotocrista that reaches the mesial cingulum internally to the low parastyle. There is a short postprotocrista that descends obliquely onto the distal shelf. The metacone sends a strong crest obliquely mesio-lingually towards the base of the protocone. There is a beaded distal cingulum and a buccal cingulum. The M1/ is deeply worn, but it is possible to observe a well developed buccal cingulum, and a deep transverse valley. The cusp morphology is indeterminate due to the heavy wear.

LT 110'03 is an unworn lingual half of a right upper molar, probably M2/. The protocone is well preserved and has a strong anterior crest leading obliquely across the crown towards the front of the buccal cusp. There is a strong, beaded anterior cingulum, a cingular cusplet in the lingual end of the median valley, and the enamel is coarsely wrinkled. LT 212'03 is 3/4 of an unworn right M3/, lacking the anterior buccal cusp and part of the talon. The two lingual cusps have well developed anterior crests that lead obliquely forwards across the midline of the crown, wrapping across the front of the buccal cusps. This makes the sagittal valley narrow and imparts a

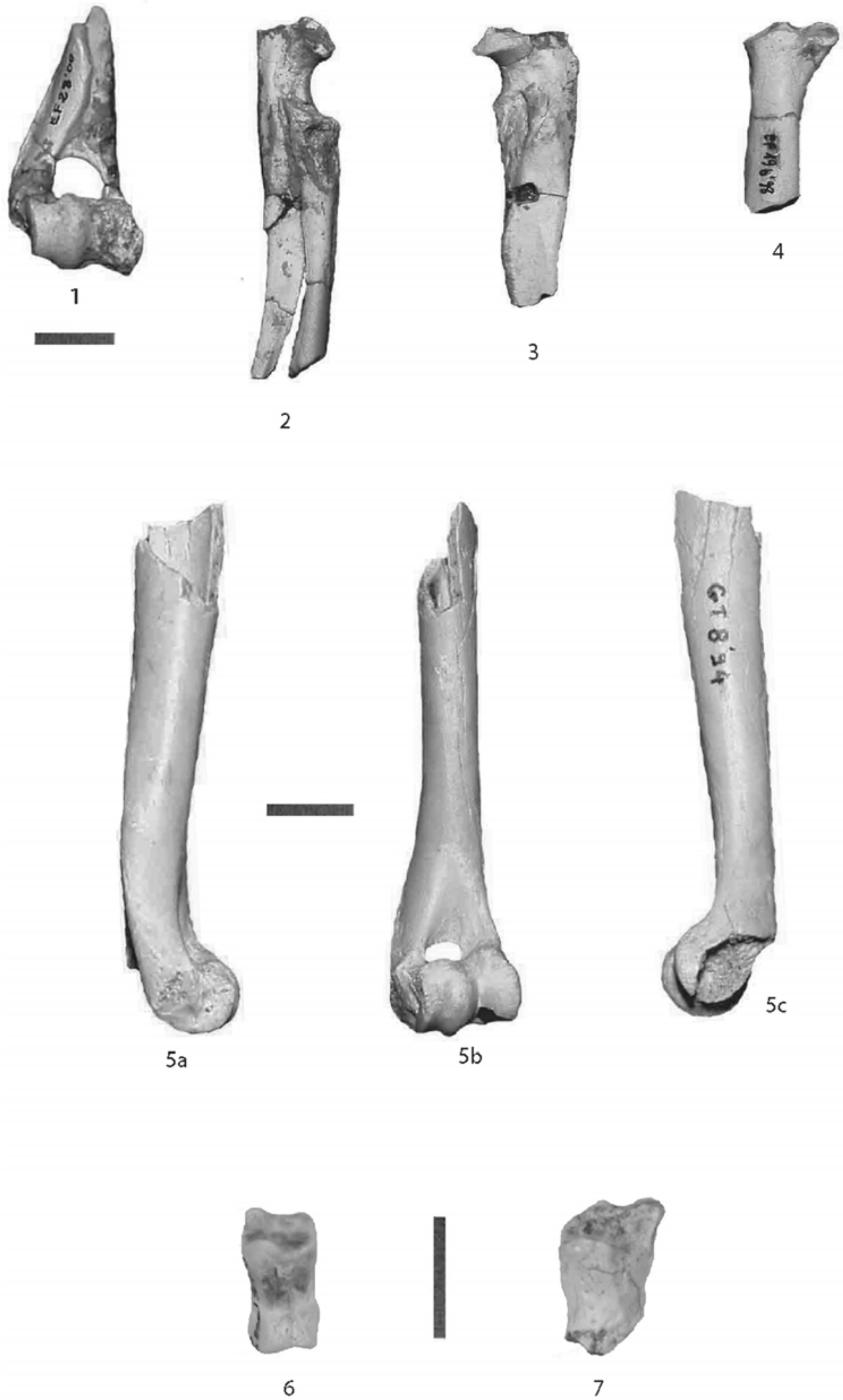

Plate 5. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (1-5 scale 5 cm : 6-7 scale 10 mm).

1. EF 28'00, distal humerus, anterior view.
2. EF 29'00, proximal radio-ulna, oblique lateral view.
3. EF 19'98, distal humerus, anterior view.
4. EF 19'98, proximal ulna, anterior view.
5. GT 8'94, humerus lacking proximal epiphysis, a) lateral, b) anterior, c) medial views.
6. FS 32'93, axial second phalanx, dorsal view.
7. FS 32'93, axial third phalanx, dorsal view.

slight selenodont aspect to the teeth. The posterior buccal cusp is bucco-lingually compressed. The anterior and posterior cingula are well developed and have a beaded morphology. The median transverse valley is closed off lingually by a cingular fold. Measurements (in mm) of the upper dentition are given in Table 1.

Mandible : Pickford, (1997) described most of the available mandibular material from Langental. Since then one new piece has been found (LT 5'00) which is a juvenile specimen with the roots of dm/4 and the fully erupted m/1. The most notable aspect of this jaw is the swollen profile of the buccal side of the body and the depth and extent of the lingual fossa, plus the apparent absence of a strong angle to the base of the jaw, although, being juvenile, this structure might not yet be apparent.

Lower deciduous dentition : The lower milk dentition of *D. africanus* was described by Pickford (1997). No new material has been collected.

Permanent lower dentition : The right lower canine (LT 37'03) attributed to *Diamantohyus africanus* is a sharp triangle in section and very hypsodont. The lingual and labial surfaces are scored by a longitudinal groove. There is thin enamel on the labial and lingual surfaces, but none distally. The lingual surface (8.1 mm) is broader than the buccal one (5.1 mm) which is broader than the distal surface (4.8 mm). About 28 mm of the crown was emergent from the alveolus and the root is ever-growing, suggesting that this individual was male. The wear facet is flat, and was probably vertically oriented, suggesting that the canine was not splayed laterally to any great extent, but was probably slightly off vertical in the jaw.

LT 5'00 has an unworn m/1 in situ. The crown is quadricuspidate, with a well developed, beaded, buccal cingulum. Anterior crests descending from the apices of the buccal cusps wrap around the front end of the lingual cusps, crossing the midline of the tooth, but not reaching the lingual border. The distal crests of the buccal cusps are weaker and that from the anterior buccal cusp does not block the median transverse valley. There is a low posterior accessory cusplet bordered by cingula. The enamel is coarsely wrinkled on the buccal cusps but is smoother lingually. LT 223'02 is a fragmented mandible with both m/3s and part of the m/2. The m/3 has five cusps. The two anterior lophs resemble m/1 and m/2 but are bigger, and the talonid is comprised of a single large cusp in the midline of the crown. There is no sign of the bifid morphology of the talonid that is usually developed in sanithere teeth. The buccal cingulum is remarkably strongly developed and is coarsely beaded. The distal root in both m/3s is aberrant, in that it is offset buccally and forms a sharp crest that invades the enamel upwards. It is also confluent downwards with the posterior root pair below the second loph of the tooth, and this might be related to the lack of bifid morphology in the talonid. Measurements (in mm) of the lower dentition are given in Table 2.

Humerus : LT 134'00, a right distal humerus, is the best preserved of the sanithere humeri from Langental. It has a trochlea that is slightly smaller in diameter than the capitulum. The margins of the capitulum and trochlea are sharp and the central ridge is well developed. The lateral epicondyle is salient but the medial one is almost flat. There are deep anterior and

Table 1. Measurements (mm) of the upper dentition of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Tooth	Mesiodistal length	Buccolingual breadth
SAM PQN 124 Langental	I1/	7.7	4.6
LT 1'00	dM3/ dM4/	8.6 8.2	6.3 7.6
Holotype (Stromer, 1926, p. 113)	P3/ M1/ M2/	8 9.5 11	6 8.5 10
LT 237'03	I3/	4.5	2.3
LT 45'03	P4/	6.0	6.3
LT 110'03	M2/	12e	--
LT 212'03	M3/	13.0	--
LT 21'04	P4/ M1/ M2/ M3/	8.2 -- 11e 13.9	8.4 -- -- 11.2
LT 157'04	P3/ P4/ M1/	7.7 8.2 8.7	7.0 8.5 9.0

Table 2. Measurements (mm) of the lower dentition of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 454'96	i/1	4.2	4.4
LT 2'00	m/3	--	8.3
LT 5'00	m/1	10.6	6.2
LT 223'03	Left m/3 Right m/3	17.9 16.4	8.5 8.3
PQN 125 Langental	right dm/4	11.3	5.2
LT 160'96	dm/3 dm/4 m/1	7.1 12.0 10.4	4.0 -- 6.9
LT 162'96	dm/3 dm/4 m/1 m/2	5.1 11.4 10.6 12.5	3.3 5.1 6.9 8.4
LT 168'96	p/3 p/4 m/1 m/2 m/3	6.7 9.3 9.2 11.0 18.4	3.7 5.6 6.2 7.9 8.5
LT 417'96	m/3	18.7	9.2
LT 2'00	m/3	--	8.3
PQN 2123 Langental	m/3	18.2	8.9

posterior fossae proximal to the articulation with a large window between them immediately below the two distal pillars of the shaft. It appears that movement in the elbow joint was relatively restricted to the parasagittal plane. The lateral pillar is low, almost at the same level as the distal articulation, unlike in *Sus* where the lateral pillar is deep and curves well beyond the level of the articulation. This disposition suggests that in sanitheres the distal articulation is more in line with the diaphysis than it is in suids, in which the distal articulation is markedly offset anteriorly from the axis of the diaphysis. This is confirmed by the observation that the anterior margin of the medial pillar is almost at the same level as the distal articulation, whereas in *Sus* there is a prominent 'step' between the condyle and the diaphysis. The posterior side of the medial pillar is wind abraded, and nothing can be said about its dimensions and shape. A right humerus from Grillental 1, (GT 8'94) has a more complete diaphysis, but its distal end is abraded postero-medially. The shaft is straight in anterior view and slightly curved in medial aspect, especially towards its distal end. Unfortunately the proximal part of the shaft and the head are missing. EF 28'00 + 29'00 is an articulated right elbow joint attributed to *D. africanus*. The distal end of the humerus (EF 28'00) is eroded posteriorly and medially, but the remaining part of the trochlea, and the lateral distal pillar appear to be similar to the Langental specimen. Measurements (in mm) of the humerus are provided in Table 3.

Radio-ulna : The right ulna EF 29'00 is a robust bone with a strong diaphysis. The olecranon is missing, but the sigmoid notch and surrounding bone is well preserved. Proximally there is a well developed lip to the sigmoid notch which articulates with the facet on the lateral distal pillar of the humerus when the forearm is fully extended. The radius is firmly attached, but not fused to the ulna for a distance of about 30 mm below its proximal end. It is abraded anteriorly near its proximal end. The shaft is robust and antero-posteriorly compressed to a small degree. It is also slightly curved in medial view. The second radio-ulna from Elisabethfeld, EF 19'98 is similar to the one described above. However, its radius is not abraded anteriorly, so its proximal end is better preserved. The radius has a large facet for the capitulum of the humerus, a deep facet for the central ridge and a small facet for the rest of the trochlea. The posterior surface of the diaphysis is roughened where it lies attached to the ulna.

LT 155'03, a right ulna lacking the olecranon process is similar to the specimens from Elizabethfeld but it is somewhat larger.

Measurements of the ulna (in mm) are given in Table 4.

GT 5'04 is a complete left radius (Pl. 6, Fig. 1) and GT 27'06 is a slightly damaged right radius. In anterior view the radius is narrow proximally and broadens distinctly distally, as is usual in suiformes. In posterior view the shaft is relatively planar medio-laterally but is curved proximo-distally. It has several shallow grooves and a broad but shallow depression where it articulated with the ulna. The proximal articulation is similar to that in the Elizabethfeld material. There are three curved articular depressions, the central one being the largest, the lateral one the smallest. Distally on the dorsal aspect of the shaft there is a clear, shallow, broad valley for the radial extensor of the wrist. The distal articulation is robust and is dominated by a system of medio-laterally oriented depressions and ridges for articulation with the radial carpal, intermediate carpal and ulnar carpal respectively, rather than the more obliquely oriented system that occurs in suids, anthracotheres and ruminants, for example. The distal epiphysis of GT 5'04 shows several major differences from those of suids. Firstly, the hollow into which the distal end of the ulna fits is reduced in sanitheres, being barely excavated, in contrast to the deeper concavity seen in *Sus*. The facet for the radial carpal is enlarged distally but is barely visible in posterior aspect, whereas in *Sus* it is large and extends well onto the posterior side of the epiphysis. The distal part of the facet for the intermediate carpal bone, which accepts the carpal in the extended wrist position, is smaller medio-laterally than that for the radial carpal, the opposite of the situation in *Sus*. Its posterior part (for accepting the bone when the wrist is in the flexed position) is remarkably medially positioned, and the curved articular surface connecting the two forms a narrow isthmus. The facet for the ulnar carpal is minute as is the depression in which it occurs, a morphology quite divergent from that in *Sus*, in which the facet is clearly expressed and the depression well marked and slightly offset from that for the distal end of the ulna.

The distal radial articulation of the radius is nar-

Table 3. Measurements (in mm) of the humerus of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Distal breadth	Capitulum diameter	Trochlea diameter
LT 134'00	14.0	13.5	11.0
EF 28'00	12.0	--	--
GT 8'94	14.0	--	9.8

Table 4. Measurements in mm of the ulna of *Diamantohyus africanus* from Namibia

Specimen	Breadth at base of sigmoid	a-p diameter at sigmoid
EF 29'00	10.1	8.1
EF 19'98	9.7	10.0
LT 155'03	12.5	11.4

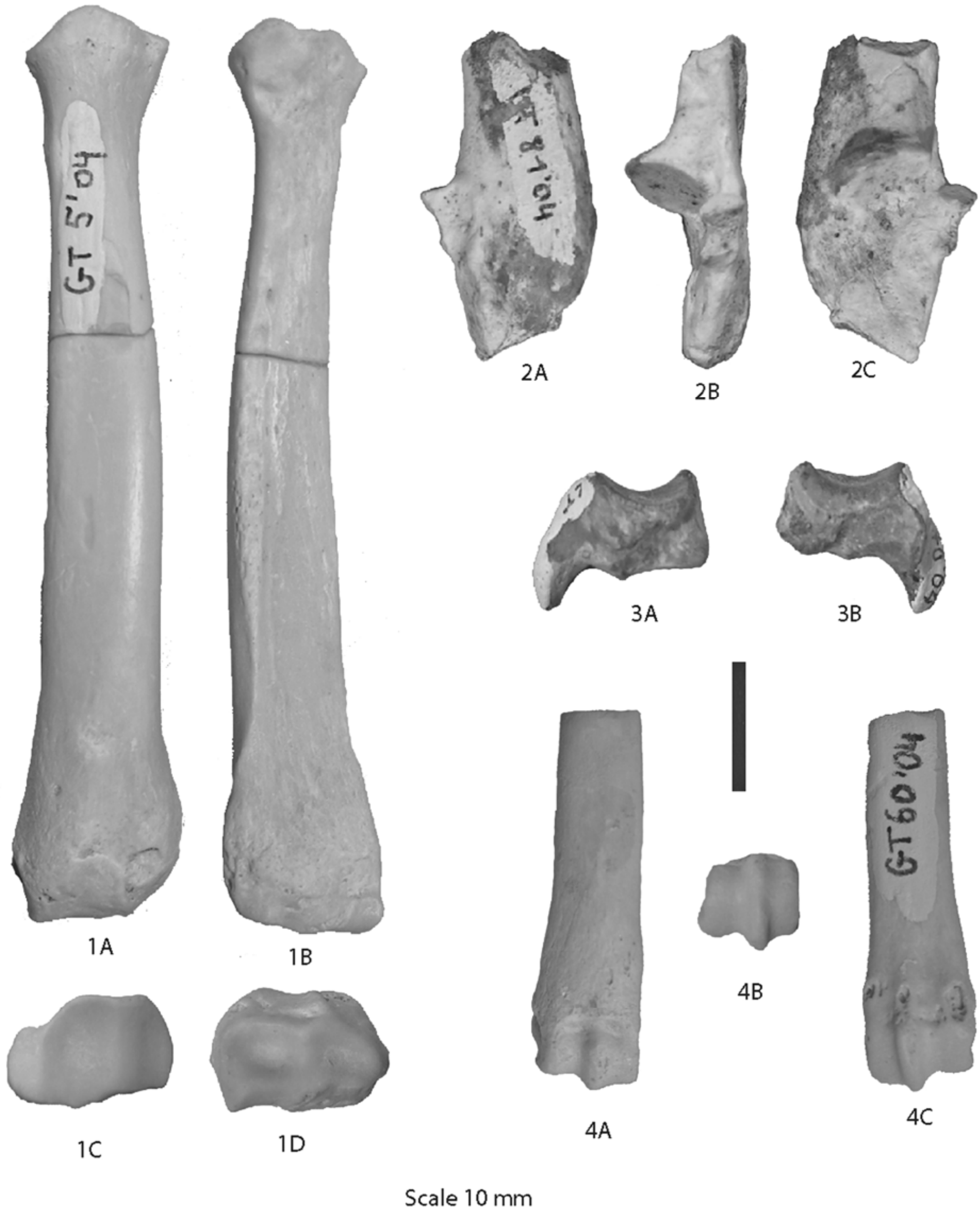

Plate 6. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 10 mm).
1. GT 5'04, Complete radius, A) anterior, B) posterior, C) proximal and D) distal views.
2. LT 81'04, calcaneum, A) lateral, B) distal and C) medial views.
3. LT 70'04, navicular, A) lateral and B) medial view.
4. GT 60'04, distal half of axial metapodial, A) dorsal, B) distal and C) volar views.

rower and less deep (12.6 x 7.3 mm) than the distal part of the shaft (14 x 9.3 mm).

The only radius from Langental is LT 148'98, a damaged specimen from the right side preserving part of the proximal articulation and about half the shaft. In its preserved parts it is similar to GT 5'04.

Measurements (in mm) of the radius of *Diamantohyus africanus* are provided in Table 5.

Metacarpals : LT 424'96, a proximal end of McIII is

Table 5. Measurements (mm) of the radius of *Diamantohyus africanus* from Namibia.

Specimen	Proximo-distal length	medio-laterial breadth of proximal articulation	antero-posterior depth of proximal articulation	medio-lateral breadth of distal articulation	antero-posterior depth of distal articulation
EF 29'00	--	11.5	7.2	--	--
EF 19'98	--	12.6	7.7	--	--
GT 5'04	73.5	12.5	7.8	12.6	7.3
GT 27'06	82.8	14.0	8.7	13.5	9.2
LT 148'98	--	--	6.4	--	--

constructed on the same basic lines as its homologue in *Sus*, but it is considerably smaller. The facet for the third carpal bone is saddle-shaped with a prominent proximally directed projection next to the facets for the 4th metacarpal. The 4th metacarpal, LT 74'03, fits snugly into the re-entrant angle distal to this projection, just as in *Sus*. The facet for the fourth carpal bone is convex with a well developed semi-cylindrical part extending onto the volar process, which is short. On the internal side of the volar process there is a clear facet for contact with the volar process of the McIII. Externally at the proximal end there are two small facets for the McV. The facet for McII has been sand blasted, but there is a wide groove running down the shaft which indicates that this bone was present and probably well developed. Measurements of the metacarpals are presented in Table 6.

Manual phalanges : There are two axial 1st phalanges that are smaller than the rest of the sample, and these are provisionally attributed to the manus. LT 157'98 and LT 158'98 may well belong to a single individual, having similar preservation characters and being medial and lateral axial phalanges. The proximal end is broader than high, has a deep central groove that reaches the dorsal border of the epiphysis, and a wider facet abaxially than axially. The abaxial facet is more proximally positioned than the axial one. The diaphysis is broader than high and is straight in dorsal and lateral views. The phalanges are long considering their breadth and height dimensions, suggesting that the manus was elongated. On the volar side the ridges for the flexors are weakly developed or absent except towards the proximal end. The distal epiphysis is much broader than high, with two articular surfaces separated by a valley on the ventral and dorsal sides. The abaxial facet is slightly smaller than the axial one. Measurements (in mm) of the manual axial 1st phalanges are given in Table 7.

Femur : The only femoral specimens attributed to *D. africanus* are two heads with suoid morphology. LT 154'98 and LT 138'03 are the right size and shape to belong to sanitheres, but they reveal almost nothing about femoral morphology in this group. The antero-posterior diameter of the heads is 10.7 mm and 12.7 mm respectively.

Tibia : There are several distal tibial fragments from Langental that can confidently be assigned to sanitheres. The best preserved is LT 226'99 which is the distal end with part of the shaft and much of the medullary cavity, represented by a calcite infilling that extends over 50 mm beyond the preserved bone. The morphology of the distal articulation is typically suoid with deep grooves for the articular eminences of the talus, and a prominent central ridge between them. The niche for the fibula is weak and there appears to be no facet for it, unlike *Sus* which has a small but distinct one. A significant difference from the distal tibia of suids, however, is the presence of a deep notch for the external proximal articular process of the talus, a morphology comparable to that of anthracotheres. In suids this notch is absent or extremely shallow. In other respects the fossils are merely scaled down versions of their counterparts in *Sus*, but perhaps slightly more gracile. Measurements of the distal tibia (in mm) are given in Table 8.

Calcaneum : There are three calcaneal fragments from Langental attributed to sanitheres on the basis of

Table 6. Measurements (in mm) of metacarpals of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	medio-lateral breadth of proximal end	dorso-volar height of proximal end
LT 424'96 McIII	9.0	8.3
LT 430'96 McIII	8.2	7.4
LT 74'03 McIV	8.2	7.3

Table 7. Measurements (in mm) of manual 1st phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
LT 157'98	22.4	8.7	7.6	7.2	5.4
LT 158'98	21.4	8.0	7.2	5.8	5.1

Table 8. Measurements (in mm) of the tibia of *Diamantohyus africanus* from Namibia.

Specimen	antero-posterior diameter of distal end	medio-lateral diameter of distal end
LT 226'99	12.1	14.2
LT 133'03	12.1	14.0

their diminutive size and suoid morphology. The sustentaculum does not extend right across the bone from anterior to posterior as is usually the case in ruminants and it is separated from the lateral process by a groove. Its articular surface is simple as in suids, not doubled as in anthracotheres, corresponding to the convex posterior articular surface in the talus. The non articular surface of the sustentaculum does not flare at its internal extremity as it does in anthracotheres, and in this respect it is similar to suid calcanea. The tuber calcis is robust with a central groove at its apex, observable in LT 137'00. It is 26.4 mm long measured from the articular surface of the sustentaculum, its minimum medio-lateral diameter is 5.5 mm and its minimum antero-posterior diameter is 9.8 mm. The articular part is typically suiform with a groove at the base of the tuber next to the sustentaculum. The distal process is medio-laterally slender and is strongly curved on the cuboid side so that the apex of the process lies in line with the anterior side of the tuber. The small processes for articulation with the lateral process of the talus and the fibula has two clear facets, one for each bone, but much of the process for the fibula has broken off. The facet for the cuboid is almost flat save for a slight curvature posteriorly. None of the specimens is complete so the total length of the bone cannot be measured, but by extrapolating from LT 81'04 (Pl. 6, Fig. 2) and LT 137'00, a total length of 43.5 mm is estimated.

GT 70'04 from Grillental 6 lacks most of the proximal apophysis, but the tuber is almost complete. There are some depressions on the tuber with impacted bone, suggesting tooth marks made by a small predator, and the bone has been sand blasted. Part of the sustentaculum is preserved and is typically suiform in extent and morphology. Measurements of the calcanea are given in Table 9.

Talus : There are three complete and two fragmentary tali in the Langental sample. They all possess the characteristic suiform distal articulation for the navicular and cuboid that distinguishes tali of suoids from those of ruminants. The proximal articulation has well developed lateral and medial crests with a deep and wide U-shaped valley between them. The external process is less pronounced than the medial one and terminates further proximally. The facet for the sustentaculum of the calcaneum has a low smooth crest on the internal side, but it is otherwise simple and is convex in medio-lateral profile. In dorsal view the talus appears to be bent, as in tragulids, rather than straight as in pecorans, but from the volar side the bone seems to be straight. The cuboid facet is wider than that for the navicular, and is more proximally positioned. Measurements (in mm) of the tali are presented in Table 10.

Cuboid : There are three cuboids in the Langental collection. They are typically suiform, showing no signs of fusion with the navicular. The talar facet is evenly curved and at its proximal side is confluent with the facet for the process of the calcaneum but separated from it by a low angulation. The calcanear facet reaches almost to the anterior border of the bone as in suids, unlike anthracotheres in which it ends closer to the midline of the lateral surface. Distally there is a long process separated by a rounded groove from the body of the bone. Measurements (in mm) of the cuboids are given in Table 11.

Navicular : LT 70'04 is a typical suoid navicular and is attributed to *Diamantohyus* on the basis of its size (Pl. 6, Fig. 3). The distal apophysis is elongated, but

Table 9. Measurements (in mm) of calcanea of *Diamantohyus africanus* from Namibia.

Specimen	Length of tuber calcis	Medio-lateral breadth of tuber	Antero-posterior diameter of tuber	Distance from fibula process to apex of cuboid process
LT 136'00	20++	4.3	9.5	--
LT 137'00	26.4	5.5	9.8	--
LT 138'00	--	5.1	9.8	--
LT 64'01	20++	5.3	9.4	--
LT 30'04	25	5.2	10.7	--
LT 81'04	--	5.0	8.9	14.1
GT 70'04	23.0	5.6	9.4	--

Table 10. Measurements of tali of *Diamantohyus africanus* from Namibia.

Specimen	Internal length	External length	Proximal breadth	Distal breadth
LT 164'96 rt	18.3	--	9.2	10.0
LT 73'99	--	--	9.2	--
LT 32'03 lt	20.1	21.4	9.7	9.7+
LT 33'03 rt	19.3	20.7	9.7	10.8

Table 11. Measurements of cuboids of *Diamantohyus africanus* from Namibia.

Specimen	Proximal antero-posterior diameter	Proximal medio-lateral diameter	Distal antero-posterior diameter	Distal medio-lateral diameter	Anterior length	Posterior length
LT 428'96	10.9	7.3	11.2	7.0	10.8	15.5
LT 424'96	10.6	7.2	11.4	7.9	11.8	14.5
LT 425'96	--	8.0	--	--	10.5	--
LT 123'00	10.6	8.0	10e	--	10.1	13.0

apart from this the bone looks like other suoid naviculars. The dimensions (in mm) are given in Table 12.

Metatarsals : LT 431'96 is a complete right MtII. The proximal end has a small facet where it fits into a niche in the MtIII, and there is another small facet proximally for contact with cuboid. It is a long slender bone, much more gracile than the corresponding bone in *Sus*. Its shaft is medio-laterally slim but in the dorso-volar direction it is deeper. The distal end consists of a swollen half sphere with a sharp volar crest. The internal side has a deep fossa. LT 159'03 and LT 75'97 are right MtIIIs. The niche for the MtII is well developed. The facet for 4th tarsal bone is saddle shaped, as in *Sus*, but there is no facet for the navicular. MtIV is represented by two specimens both from the right side. A sand blasted specimen, LT 433'96, is almost complete. The proximal end is badly damaged, but the length of the bone can be estimated well. LT 434'96 is missing its distal end.

Distal ends of axial metapodials (LT 165'96, LT 432'96, LT 6'97, GT 60'04 (Pl. 6, Fig. 4)) differ from those of suids in having a slightly less developed keel on the dorsal side (even though it is more developed than in Palaeochoeridae such as *Palaeochoerus typus* and *Choeromorus sansaniense*) and a more projecting, almost blade-like keel on the volar side. The volar keel extends proximally well onto the diaphysis without any major interruption. In suids the keel is evenly curved from dorsal to volar aspects, and it terminates before reaching the diaphysis, even though there is sometimes a low ridge on the distal end of the diaphysis. In sanithere metapodials, the volar keel projects further volarly, forming a rounded right angle rather than the arc of a circle as is the case in suids. Thus, the distal metapodials of sanitheres differ from those of suids and palaeochoerids (or Old World tayassuids) even though they are unquestionably suiform in overall morphology. Measurements of the metatarsals and distal metapodials are given in Table 13.

Pedal phalanges : Three complete and one partial axial 1st phalanges are attributed to the feet of *D. africanus* on the basis of the fact that they are slightly larger and more robust than those identified as manual phalanges. In overall morphology LT 166'96, LT 156'98, LT 38'03, and LT 121'03 are similar to the manual phalanges described above, and the same description applies equally to them.

Two abaxial 1st phalanges in the sample from Langental are more slender, more curved in dorsal

Table 12. Measurements (in mm) of the navicular of *Diamantohyus africanus* from Namibia.

Specimen	Proximal antero-posterior diameter	Proximal medio-lateral diameter	Distal antero-posterior diameter	Distal medio-lateral diameter	Anterior length	Posterior length
LT 70'04	9.7	8.0	12.9	6.5	6.3	11.4

Table 13. Measurements (mm) of metatarsals of *Diamantohyus africanus* from the Sperrgebiet, Namibia.

Specimen	Length	Proximal medio-lateral diameter	Proximal dorso-volar diameter	Distal medio-lateral diameter	Distal dorso-volar diameter
LT 431'96 MtII	48.0	3.2	6.6	4.6	5.7
LT 159'03 MtIII	--	8.1	10.6	--	--
LT 75'97 MtIII	--	8.2	10.3	--	--
LT 433'96 MtIV	40.3	4.6e	6e	7.7e	6.4e
LT 434'96 MtIV	--	6.3e	8.1e	--	--
LT 165'96 distal axial metapodial	--	--	--	8.2	7.3
LT 6'97 distal axial metapodial	--	--	--	7.6	8.7
LT 432'96 distal axial metapodial	--	--	--	7.1e	--
GT 60'04 distal axial metapodial	--	--	--	7.6	7.7
LT 65'01 distal abaxial metapodial	--	--	--	4.6	6.5
LT 160'98 distal abaxial metapodial	--	--	--	4.9	6.1
LT 207'04 distal abaxial metapodial	--	--	--	5.1	6.4
GT 81'04 distal abaxial metapodial	--	--	--	4.5	--

view and slightly shorter than the axial phalanges. In LT 206'03, the proximal articular facet has a less well developed groove and a prominent lateral process pointing proximally. The distal articulation consists of two curved surfaces separated by a v-shaped valley. LT 214'03 is less well preserved but is similar in overall morphology, the slight differences possibly being related to the position within the foot or hand.

Axial 3rd phalanges, LT 77'01, LT 247'03 and LT 32'04, are characteristically suoid, with an angled basal surface to the wedge and a strongly angled proximal articulation. They are considerably smaller than the 3rd phalanx attributed to *Nguruwe namibensis*. The length of LT 77'01 is 12.4 mm and the proximal breadth and height are 4.9 mm and 5.8 mm respectively while the homologous measurements of LT 247'03 are ca 12.5 mm long, 5.3 mm broad and 8.2 mm high. LT 32'04 is 12.3+ mm long, and its proximal end is 5.3 mm wide. Its dorso-volar measurement cannot be taken as the dorsal process has broken off.

GT 1'94 is a third phalanx with an obliquely angled proximal articulation which has a low central ridge. The wedge of the phalanx has lateral flanges near its distal end, extending beyond the main part of the wedge and slightly expanding the distal part of the volar surface. There are prominent medial and lateral nutritive foramina near the proximal end and an additional foramen externally on the distal end. The specimen is 13+ mm long (distal extremity broken off near the tip) and is 5.6 mm broad and 6.6 mm high at its proximal end. Judging from its obliquity this specimen is probably an abaxial 3rd phalanx.

A similar specimen from Grillental 6 is GT 195'04. Its length is 11.2 and the proximal height and breadth are 5.4 and 4.1 mm respectively. This specimen is smaller than GT 1'04 and may be from the manus rather than the pes. A third specimen from Langental collected by R.W. Hamilton is 15.5 mm long, and its proximal and is 7.1 mm high and 5.2 mm broad. Measurements of the axial 1st pedal phalanges (in mm) are provided in Table 14.

Measurements (in mm) of abaxial 1st phalanges of unknown position are provided in Table 15.

An interesting specimen from Fiskus consists of associated axial 2nd and 3rd phalanges. The second phalanx has a more upright proximal facet than is usual is suids, the central ridge being almost vertical. The distal articulation is angled as in suids but the central valley is almost vertical. What this means is that the phalanges rotated parasagitally rather than having an oblique component of rotation as occurs in suids. Measurements of the Fiskus phalanges (in mm) are given in Table 16.

Table 14. Measurements (in mm) of phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
LT 166'96	--	9.0	7.2	--	--
LT 156'98	25.9	8.8	8.3	6.5	5.2
LT 38'03	24.4	9.0	8.0	6.3	4.8
LT 121'03	25.0	6.6	5.0	8.0	8.0

Table 15. Measurements (mm) of abaxial 1st phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
LT 9'00	12.1+	5.0	4.3	--	--
LT 206'03	15.3	5.3	4.5	3.4	3.5
LT 214'03	13.4	5.2	5.9	3.4	3.7
GT 29'06	13.2	5.7	5.4	3.6	3.5

Table 16. Measurements of 2nd and 3rd phalanges of *Diamantohyus africanus* from Namibia.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
FS 32'93 2nd phalanx	11.3	6.3	6.9	5.7	6.2
FS 32'93 3rd phalanx	--	6.6	8.2	--	--
GT 32'06 abaxial 3rd phalanx	8.1	3.2	4.6	--	--

Discussion : Stromer (1922) identified the teeth in the holotype maxilla as P4/, M2/-M3/, but in fact the teeth preserved are the P3/, M1/ and M2/ as he had realised by the 1923 publication. Stromer aligned *Diamantohyus* with *Xenochoerus* from Europe, which is in fact a synonym of *Sanitherium*.

There has been some discussion in the literature regarding the attributions of the sanitheres within the suiformes. The arguments were summarised by Pickford (1984 ; 2004 ; Pickford and Tsujikawa, 2005) who noted some major differences from Suidae to which sanitheres have most often been allocated (Pilgrim, 1926; Wilkinson, 1976). But subsequently Van der Made (1998, 1999) has classed them within Palaeochoeridae as did Thenius (1979) (as Tayassuidae, Xenochoerinae). Whilst having some sympathy with this point of view, I cannot agree with Van der Made on several counts. His schema appears to be based on a combination of primitive characters, on a lack of evidence, and on omission of evidence. The sanitheres are still poorly known, especially their anterior dentition, while the post-cranial skeleton used to be virtually unknown. The new collections from the Sperrgebiet add important new evidence to the debate and swing the balance away from the suid and palaeochoerid hypotheses towards the independent familial status of the group within the suiforms. If we look at the derived features of the dentition, skull, mandible, and now the post-cranial skeleton, it becomes less easy to class the sanitheres within Suidae or Palaeochoeridae without radically altering the definition of these families. Rather than do this, I prefer to accept that the group has a long independent history from the suids and palaeochoerids, and that classing sanitheres as palaeochoeres does not throw light on the early evolution of either the suids or the sanitheres. Indeed, it tends to obscure the relationships of the various groups to each other.

In sanitheres, the doubling of the anterior cusp in the dM3/ broadens the anterior end of the tooth giving it a trapezoidal outline, and represents a significant difference from suids and palaeochoerids, even the most primitive known forms attributed to the Palaeochoerinae by Van der Made (1999) who believes that sanitheres belong in the same subfamily. It is also known that the dm/1 is replaced by a p/1 in sanitheres, whereas in suids and palaeochoerids the first premolar is not replaced. The evidence of the milk dentition serves to underscore the distinctiveness of the sanitheres from the suids, (and indeed all other suoids) and supports Pickford's (1984) attribution of the group to a separate family within the Suiformes, a point accepted by de Bonis *et al*., (1997).

Wilkinson (1976) derived the suid *Hyotherium* and the sanithere *Xenochoerus* from the Stampian suoid *Propalaeochoerus* (which he believed was a suid). Van der Made (1998, figs 4, 5) proposed a comparable evolutionary series for the dentition of sanitheres, beginning with the genus *Palaeochoerus* and progressing through three stages of sanitheres. Whilst there are some similarities between some of the teeth of *Propalaeochoerus* and *Palaeochoerus* and those of sanitheres, there are major differences overall. In palaeochoere lower molars there is no sign of the small cusplet associated with the metaconid in sanithere teeth, called the metastylid by Pickford (1984). Van der Made (1998) labels this cusplet 2D' (metapostconulid) but does not recognise its presence in the early stages of his sanithere series. However, this cusplet is present even in the earliest known fossils of the group, from Langental, Namibia and Napak, Uganda, and in unworn specimens it is separated at its apex from the metaconid indicating that it was not a development from a metapostcristid (2D) as implied by Van der Made's evolutionary series, but was a distinct cusplet from the outset. This cusplet also occurs in the deciduous dentition of sanitheres, especially the dm/4, whereas it is unknown in

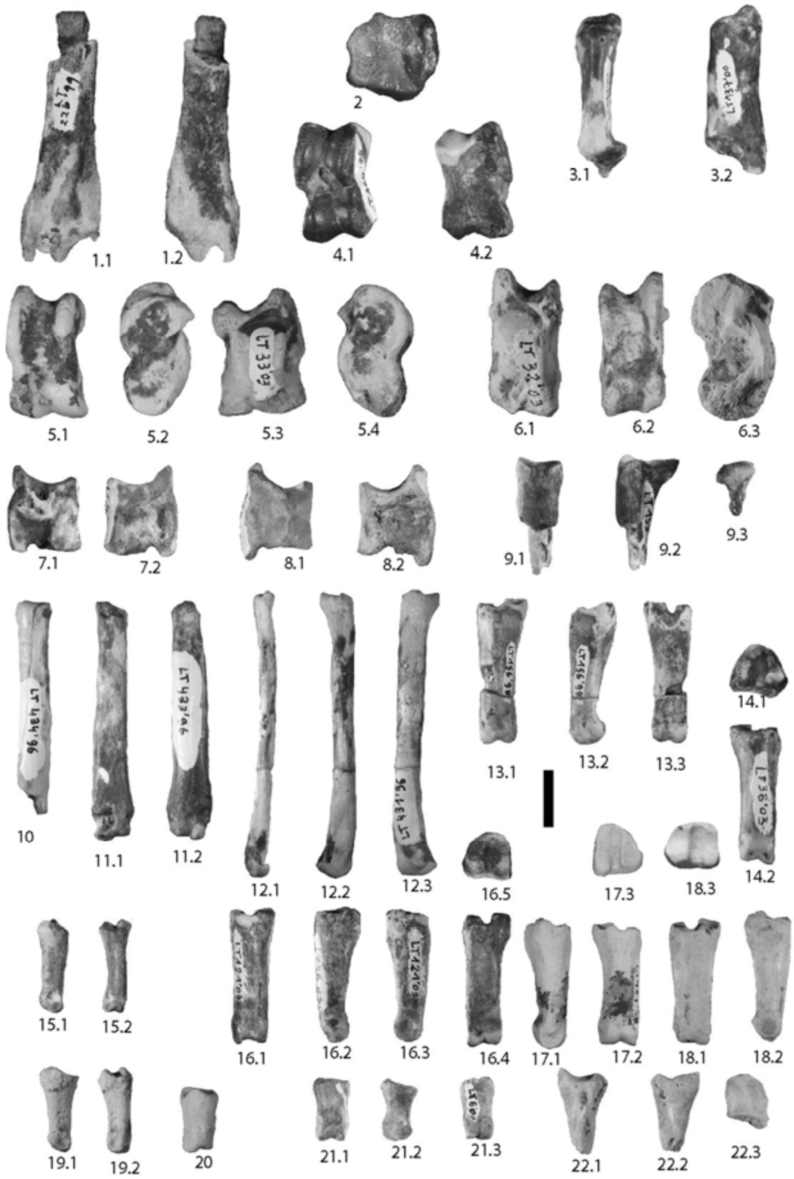

Plate 7. *Diamantohyus africanus* from the Northern Sperrgebiet, Namibia (scale 5 cm).

1. LT 226'99, distal tibia, a) anterior, b) posterior views.
2. LT 133'03, distal tibia, distal view.
3. LT 137'00, calcaneum, a)anterior, b) lateral views.
4. LT 164'96, right talus, a) anterior and b) posterior views.
5. LT 33'03, left talus, a) anterior, b) lateral, c) posterior, d) medial views.
6. LT 32'03, left talus, a) posterior, b) anterior, c) lateral views.
7. LT 424'96, cuboid, a) interior, b) external views.
8. LT 428'96, cuboid, a) external, b) internal views.
9. LT 159'03, proximal right MtIII, a) dorsal, b) internal, c) proximal views.
10. LT 434'96, proximal right MtIV, dorsal view.
11. LT 433'96, proximal right MtIV, a) volar, b) dorsal views.
12. LT 431'96, right MtII, a) volar, b) internal, c) external views.
13. LT 156'98, axial first phalanx, a) lateral, b) dorsal views.
14. LT 38'03, axial first phalanx, a) proximal, b) dorsal views.
15. LT 206'03, abaxial first phalanx, a) lateral, b) dorsal views.
16. LT 121'03, axial first phalanx, a) dorsal, b) lateral, c) medial, d) ventral, e) proximal views.
17. LT 157'98, axial first phalanx, a) lateral, b) dorsal, c) proximal views.
18. LT 158'98, axial first phalanx, a) dorsal, b) lateral, c) proximal views.
19. LT 214'03, abaxial first phalanx, a) lateral, b) dorsal views.
20. LT 238'99, axial second phalanx, dorsal view.
21. LT 6'03, axial second phalanx, a) dorsal, b) lateral, c) volar views.
22. GT 1'94, axial third phalanx, a) internal, b) exterior, c) proximal views.

suid and palaeochoerid deciduous teeth. This cusplet does get larger and more distinct with the passage of time, but it is always closely applied to the metaconid. It occasionally occurs in the p/4, again, a feature unknown in other suoids.

A buccal cingulum is present in all known lower molars of sanitheres, whereas it is usually absent in palaeochoeres and suids. In sanithere p/4s and lower molars a clear enamel fold occurs on the distal surface of the protoconid between two more or less vertical crests. This groove was called the "palaeomeryx-fold" by Pickford (1984) (as a descriptive term not implying any genetic relationship between sanitheres and palaeomerycids). Such a fold has never been observed in suid or palaeochoerid teeth. Similar folds occur in p/3 and p/2 of sanitheres and have never been observed in suids or palaeochoerids.

The talonid in lower third molars of sanitheres is comprised of two cusps forming a transverse pair, whereas in suids and palaeochoerids the distal cusp in the third lower molars is a single cusp located in the centre-line of the crown. Specimens from Kirimun attributed to *Sanitherium* by Ishida and Ishida (1984) have a suid-like talonid in m/3 and the lower molars are bunodont rather than bunoselenodont, and I consider that they belong to the genus *Kenyasus* despite the presence of a buccal cingulum on the m/3 (but not on m/1 and m/2).

The upper cheek teeth of sanitheres are even more divergent from suid and palaeochoerid teeth than the lowers are. It would be difficult, in my opinion, to derive sanithere upper premolar morphology by a simple series of transformations beginning with those of *Palaeochoerus* as envisaged by Van der Made (1998, fig. 5). In the earliest known sanitheres the upper premolars are multicusped with well developed styles on the ectolophs, whereas the premolars of palaeochoerids are simple with no hint of styles. Polycuspy in the premolars of sanitheres is carried through into the deciduous dentition, the dM3/ having two anterior cusps, as opposed to a single cusp in all known suids and palaeochoerids. Sanithere molars are also divergent from those of palaeochoerids in a number of features, including the development of clear styles on the ectolophs and the exaggerated "selenodont" appearance of the lingual cusps.

It is a mistake to describe sanithere premolars as molarised, as was done by Wilkinson, (1976) and Thenius (1979), because they do not resemble molars. The premolars become more complicated by addition of cusps, accentuation of crests which often bifurcate distally in lower premolars and clustering of wrinkles in the distal basins, but the end product of this evolutionary activity is a series of teeth that cannot be confused with molars. Polycuspy and polycristy would be more apt terms to employ in this particular case.

Pickford (1984) discussed cranial features that distanced sanitheres from suids and doliochoeres (or, as they were called at the time - Old World Tayassuidae), and these provide additional weight to the arguments based on dental and post-cranial evidence, that sanitheres should not be classed as suids or palaeochoerids.

In *Diamantohyus* the distal epiphysis of the humerus is more in line with the diaphysis, being only slightly offset anteriorly, quite different from the situation in suids and palaeochoerids, in which the distal epiphysis is well offset anteriorly from the axis of the diaphysis. As a result the humerus in sanitheres is straighter in lateral view than it is in suids. The gracile metapodials and phalanges of sanitheres, which have rather different proportions from those of suids and palaeochoerids, confirm that the sanitheres have a more remote relationship to these families than classing them as palaeochoeres would suggest.

It is a truism that suid post-cranials from the earliest to the latest known forms are mostly rather similar to each other, variations being in the form of elongation or shortening of elements rather than modification of their basic morphology. Thus the post-cranial bones of the extant pig, *Sus scrofa*, look remarkably similar to those of most species of fossil suids, be they from the Pliocene, Miocene or even terminal Oligocene, the main differences being related to size. Some species, such as *Eurolistriodon adelli* had elongated metapodials (Pickford and Moya Sola, 1995), and others such as *Cainochoerus africanus* possessed fused or tightly bound metapodials and sharper crests on the limb bone articulations than is usual in suids (Pickford, 1988), but most of the other known species are basically upscaled or downscaled versions of the corresponding bones in *Sus*. The fact that the post-cranial bones of *Diamantohyus africanus* have different proportions from those observed in *Sus* and most other suids and palaeochoerids, suggests that they are not members of the same family.

Van der Made (1998) listed six major features by which Suidae differ from Palaeochoeridae (in which he included sanitheres). Among these, numbers 5 and 6 relate to the metapodial - phalangeal joint, and are really a single character complex rather than two separate characters. According to Van der Made, "5. Metapodials have a median crest at the distal articulation which clearly continues on the dorsal side in Suidae, but not or not so clear in the Palaeochoeridae. 6. The proximal articulation of the first phalange reflects character 5". Whilst the dorsal keel is low in sanitheres, it is appreciably better developed than it is in palaeochoeres, being intermediate between palaeochoeres and suids. The volar part of the keel is not like that in suids and palaeochoeres. It is better developed in sanitheres than it is in suids, and the groove in the proximal epiphysis of the first axial phalanges is almost as well developed as it is in bovids. Furthermore, the volar part of the distal epiphyseal keel extends proximally and blends into a non-articular crest that reaches well onto the diaphysis, a morphology that does not occur in suids or palaeochoerids. The newly available post-cranial evidence thus strengthens the arguments of Pickford (1984) concerning separate familial status of sanitheres among the Suoidea which were originally based on the cranial, mandibular and dental anatomy. Van der Made (1996, p.41) predicted that "Bones of *Sanitherium* are expected to be similar to those of other Palaeochoeridae, which differ in many characters from bones of Suidae." This prediction is falsified by the fossils from the Northern Sperrgebiet.

Functionally, it appears that, in sanitheres, movements of the postcranial bones were more parasagittally confined than they generally are in suids and palaeochoerids. Furthermore, the distal elements (metapodials, phalanges) are more gracile and relatively more elongated than those of pigs. The presence of volar crests on the distal part of the diaphysis in line with the volar crests of the distal epiphysis reinforces the suggestion that sanitheres were cursorial. This is because such crests tend to occur in lineages which possess highly stabilised joints. For example they occur in springing mammals such as pedetids, and also in cursorial quadrupeds such as equids. There is no evidence to suggest that sanitheres were springing mammals, so we infer that they were cursorial quadrupeds. The indications are that sanitheres were more cursorially adapted than suids.

Biogeography of sanitheres

The record of sanitheres in Africa extends from south Africa (Langental, Grillental, Elisabethfeld (Namibia)); East Africa (Napak, Bukwa (Uganda); Rusinga, Karungu, Chianda, Kalodirr, Buluk, Locherangan, Moruorot, Ombo, Nyakach, Maboko, Kipsaraman (Kenya)); and north Africa (Gebel Zelten, (Libya); Wadi Moghara (Egypt)). In Europe the family is known from Greece (Chios), Turkey (Çiftlikköy) (Besenecker, 1973) and Austria (Leoben) (Pickford, 1984), and its record in the Indian sub-continent includes Bugti, the Sind, Chinji and Kushalghar, Pakistan (Colbert, 1935; Pilgrim, 1926; Van der Made and Hussain, 1992; Von Meyer, 1866).

Sanitheres were thus confined to Africa during the Early Miocene and only spread to Europe and Asia during the Middle Miocene about 16-15 Ma (MN 5) and survived there for a short while before going extinct. They hung on in Africa until about 14 Ma, and then also went extinct there.

Conclusions

The sample of the peculiar extinct suiform artiodactyl *Diamantohyus africanus* has much improved thanks to the discoveries of the Namibia Palaeontology Expedition. Of particular importance are post-cranial bones which were hitherto extremely poorly represented in museum collections (Pickford, 1984). Although there is still a long way to go before we obtain a comprehensive view of skeletal morphology of sanitheres, the sample from the Sperrgebiet now available is an order of magnitude better than previous ones (Table 17). Not surprisingly, like the dental and cranial morphology, the post-cranial bones reveal that sanitheres were not typical suoids, differing markedly from both suids and palaeochoerids into which they had previously been classed by some authors. The metapodials and phalanges in particular reveal that sanitheres had elongated, quite gracile lower limbs unlike the stocky limbs of suids and palaeochoerids. The enhancement of crests, keels and grooves in the articulations suggest that the main movements of the limbs were more constrained to the parasagittal plane than are those of suids and the joints were more stabilised than they are in suids and palaeochoerids. The rectitude of the distal humeral articulation relative to the diaphysis indicates the same thing. The lightness and elongation of the metapodials coupled with the dorso-volar compression of the phalanges suggest that sanitheres were more cursorial than suids, but not as well adapted for this kind of locomotion as bovids are.

The post-cranial skeleton of sanitheres is morphologically more distant from those of palaeochoerids than from those of suids, and it is difficult to subsume the group into the palaeochoerids as suggested recently by Van der Made (1998), unless the definition of this family is radically revised. Whilst we are currently unable to provide a definitive solution to the question of sanithere systematics, it seems clear that they do not fit convincingly in either the suids or the palaeochoerids. As was pointed out more than a century ago, in some features sanithere dental morphology falls between that of suids and anthracotheres (Lydekker, 1879) - the same can now be said for the metapodials and phalanges, which resemble those of medium sized anthracotheres such as *Sivameryx* and *Afromeryx* more than they do to those of suids. A final answer will probably only be possible when a

Table 17. Representation of sanitheres in the Northern Sperrgebiet, Namibia

Locality	Langental	Elisabethfeld	Fiskus	Grillental
Cranio-dental remains	31	--	1	--
Post-cranial remains	56	3	1	11

complete skull is found. In the meantime, it seems safe to maintain separate family status for these enigmatic suoids.

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