MINISTRY OF MINES AND ENERGY

GEOLOGICAL SURVEY OF NAMIBIA

Director : Dr G I C Schneider

MEMOIR 20

GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Obtainable from the Geological Survey of Namibia
Private Bag 13297, Windhoek, Namibia

ISBN 978-99945-68-76-5

Anthracotheriidae from the Early Miocene deposits of the Northern Sperrgebiet, Namibia

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The only anthracothere specimens from the northern Sperrgebiet are a talus previously described as *Brachyodus depereti*, a partial skeleton of a smaller species *Brachyodus aequatorialis*, and a sand blasted neck vertebra from Grillental, and a fragment of upper molar from Langental. These specimens along with those from tropical and northern Africa reveal that the family was pandemic in Africa during the Early Miocene.

Introduction

In 1978 a sand blasted and broken talus of a large anthracothere was collected by G. Corvinus in the Grillental (possibly locality GT 6) and presented to the South African Museum. The specimen was described by Pickford (2003) and attributed to *Brachyodus depereti* on account of its huge dimensions, well above those of the East African species *Brachyodus aequatorialis*. A neck vertebra was found in 2000 by the NPE at the same site. In 2005, a fragment of upper molar was found at Langental and in 2006 a partial skeleton of a smaller anthracothere *Brachyodus aequatorialis* was discovered at Grillental 6. Thus, out of several thousand fossils collected in the Northern Sperrgebiet, there are only a few fragments of anthracotheres. A previous report of *Brachyodus* in the Sperrgebiet (Hamilton and Van Couvering, 1977) was based on a subfossil giraffe talus.

Systematic description

Order Artiodactyla Owen, 1848
Family Anthracotheriidae Gill, 1872
Genus *Brachyodus* Depéret, 1895
Species *Brachyodus depereti* Fourtau, 1918

Material : Wind eroded right talus collected at Greenman's site (Grillental), now housed in the South African Museum, Cape Town. GT 51'00, a sand blasted neck vertebra from GT 6.

Description :

The neck vertebra, GT 51'00, is large, but is so badly damaged that it is merely referred to the species.

The anthracothere talus in the South African Museum is broken into several pieces which were sand blasted, but it has been possible to reconstruct it quite well (Pickford, 2003). It is 136.4 mm long externally which is greater than any of the specimens from East Africa identified as *Brachyodus aequatorialis* MacInnes (1951) (range from 108 to 125 mm) but its proximal breadth (73.2 mm) falls within the range of variation of the equatorial sample (range 70 to 75 mm). It is marginally larger than the biggest of three specimens from Gebel Zelten, Libya housed in the Natural History Museum, London.

Species *Brachyodus aequatorialis* MacInnes, 1951

Material :
LT 21'05, fragment of left upper M1/ from Langental (Pl. 1 (1)); GT 88'06 partial skeleton from Grillental 6.

Description :

The anthracothere tooth from Langental (Plate 1 (1)) is the distal portion of a left upper molar. Preserved are most of the metacone and a sliver of the metaconule and the distal cingulum. The metastyle is a small pinched column and is more lingually positioned than the much larger mesostyle, only the distal part of which is preserved. The bases of these two styles are linked by a short beaded cingulum. A distal cingulum extends across the tooth to the base of the metaconule. The postmetaconule crest is oblique and in distal view its base, which is broken off, would have overlapped part of the metacone. The enamel is wrinkled and thin, as in the teeth of *Brachyodus*. There is an interstitial wear facet on the distal surface of the tooth, indicating that it was not an upper third molar. On the basis of the dimensions of the tooth fragment and the position of the metastyle, it is likely that this tooth is an M1/ of *Brachyodus aequatorialis*.

The partial anthracothere skeleton from Grillental 6 (GT 88'06) consists of much of the skull lacking the muzzle, a scapula, pelvis, talus, phalanx, vertebrae and ribs. In 2006 the skull, talus and phalanx were collected (Pl. 1 (2, 3)), the remainder left in situ because the sediments were sodden after the heavy April rains. The bones are intensely fractured and heavily impregnated with salt, making excavation extremely delicate, especially if the sediments are wet and the salt in solution.

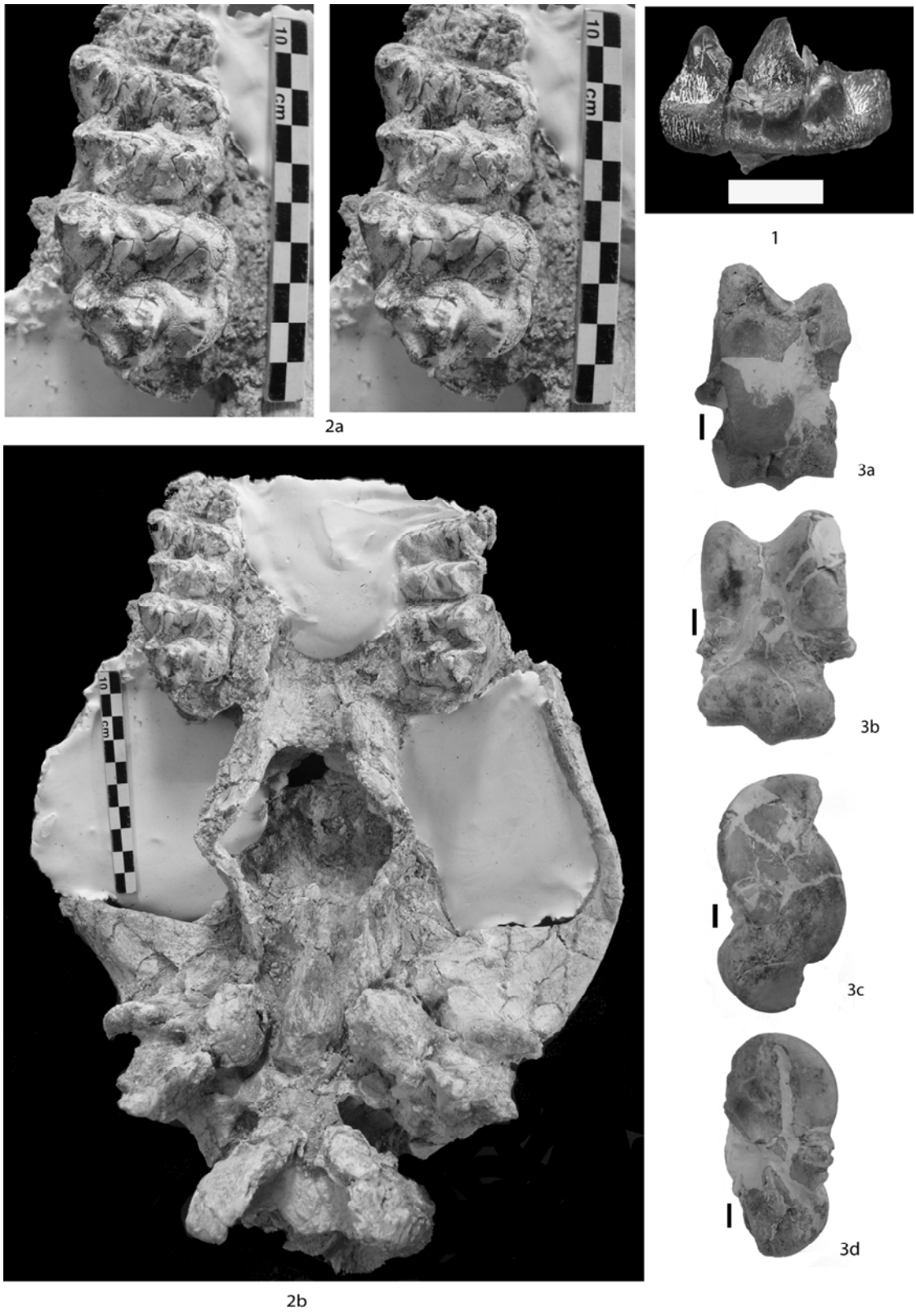

Plate 1.

1. LT 21'05, *Brachyodus* sp. left upper molar fragment from Langental, Namibia, distal view showing interstitial wear facet, the metacone (largely preserved) and the metaconule (only a sliver of which is preserved) (Scale : 10 mm).
2. GT 88'06, from Grillental 6, Namibia, *Brachyodus aequatorialis* skull, a) occlusal stereo view of right M2/-M3/; b) ventral view of basicranium and rear of palate.
3. GT 88'06, from Grillental 6, Namibia, *Brachyodus aequatorialis*, left talus, a) posterior view ; b) anterior view; c) lateral view ; d) medial view (Scale : 10 mm).

The skull was lying in the sediments palate downwards. Erosion had removed most of the snout, but the second and third molars on both sides are preserved, as is most of the basicranium. The top of the braincase is eroded, but much of the sagittal crest and the occiput are preserved. In distal view, the occiput is badly eroded around the foramen magnum, and the occipital condyles are poorly preserved.

The upper molars are pentacuspidate, with large parastyles and mesostyles, and reduced metastyles (Pl. 1 (2a)). The enamel is wrinkled in the usual style of *Brachyodus* teeth and there is a light cover of cementum, especially in the depths of the foveae near the styles. The anterior loph of the molars is appreciably broader than the posterior loph, on account of the presence of a paraconule between the protocone and paracone and the large dimensions of the parastyle. The posterior loph consists of a metacone and metaconule with small metastyle and is separated from the anterior loph by a deep transverse valley, which is blocked off buccally by the mesostyle. There is a prominent lingual cingulum. The pre- and post-cristae of the four main cusps as well as the paraconule are directed obliquely buccally, imparting a selenodont aspect to the tooth. Those on the buccal cusps are more buccally directed than the ones on the lingual cusps, which gives the impression that the outer part of the tooth has been twisted with respect to the lingual half. Measurements are provided in the table.

In ventral view the skull is preserved from the occipital condyles to the front of the second molars (Pl. 1 (2b)). The left zygomatic arch is complete and the right one almost complete. The occipital condyles are large and distally projected, with deep condylar fossae between them and the base of the paroccipital process of the squamosals. The condylar foramina are huge. The basisphenoid is broad distally, becoming slender anteriorly, and possesses two small, almost confluent tubercles near its distal end. The mastoid process is extremely robust and massive basally, and has a large fossa disto-medially on its posterior surface and a crest of bone laterally. The paroccipital processes are robust and elongated, in oblique antero-lateral view forming a tall triangle with a truncated apex. The apex of the paroccipital processes is rounded in section, slightly concave at the end with a low bony nipple projecting ventrally on its medial edge. In lateral view the paroccipital processes project well beneath the level of the occipital condyles and the plane of the molar row. Antero-medially to the base of the paroccipital processes are the tympanic bullae which are large, slightly medio-laterally compressed ovoids with the longest axis of the ovoid almost vertically oriented, but leaning slightly anteriorly. The surfaces of the bullae are not well enough preserved to reveal details of their morphology. The two bullae are in line with the massive, curved post-glenoid process that descends behind the almost flat articular surface for the mandible. The external auditory meatus is at the level of the articulation immediately behind the post-glenoid process. The palatine bones extend distally well behind the M3/s. The pterygoid processes are unusual, forming curved arches that reach almost to the anterior base of the tympanic bullae. They are pierced by a vast fenestra but the Rusinga skull (MacInnes, 1951) appears to have no fenestra, suggesting that in the Grillental skull its presence may be due either to incomplete ossification or to damage. The maxilla has a short projection behind the third molars which bends ventrally to a marked degree. This suggests that *Brachyodus*, like many other anthracotheres was klinorhynch, in contrast to suoids, which are more airorhynch, particularly well expressed in hippopotamids.

In distal view the occipital condyles dominate the base of the skull, and above them there is an extremely robust ridge of bone extending upwards to the flared, flange-like external occipital protuberance, which form extensive almost horizontal nuchal crests. The nuchal area is wedge shaped with a single central ridge of bone extending dorsally to the occipital crest, not concave as it is in *Sus* in which two ridges of bone diverge upwards from the vicinity of the foramen magnum.

In dorsal view the sagittal crest extends anteriorly from the junction between the external occipital protuberance and the central nuchal ridge. Its length

Table 1. Measurements (in mm) of the teeth of *Brachyodus aequatorialis* from Grillental 6 (GT 88'06) and the holotype from Rusinga, Kenya (MacInnes, 1951).

Tooth	Length	Breadth first loph	Breadth second loph
Right M1/	--	--	32.7
Right M2/	35.0	41.4	36.3
Right M3/	37.8	42.7	35.2
Left M2/	34.6	41.5	36.8
Left M3/	39.2	42.9	36.1
Holotype M2/ left	32	35	32.5
Holotype M2/ right	32	36	33
Holotype M3/ left	34	37.5	33
Holotype M3/ right	35	38	34

cannot be estimated due to erosion that has removed most of the top of the skull, but it is possible to determine that the sagittal crest was strong and quite elongated. The temporal fossae are huge, and widest at the distal end of the zygomatic bones, just anterior to the mandibular articulation. At their anterior extremities the zygomatic bones are damaged, but they appear to merge into the maxillary surface at a shallow angle, not far from the outer edge of the molars. Unlike *Sus* the zygomatic arches are shallow in lateral view, are almost horizontal and do not have a flange descending beneath the level of the glenoid fossa. Distally their upper outer edge flares slightly upwards and backwards to form a smooth almost horizontal gutter adjacent to the brain case. Anteriorly this gutter blends into a flat triangular shelf of bone, on the ventral side of which is the glenoid surface.

In lateral view the glenoid cavities are above the plane of the molars, but not as greatly as in *Sus*. The apices of the paroccipital processes in contrast extend well beneath the plane of the molars.

Post-cranial skeleton

The talus of GT 88'06 from Grillental 6 (Pl. 1 (3)) is appreciably smaller and proportionally narrower than the Cape Town specimen attributed to *Brachyodus depereti*. It measures 111.5 mm long externally which falls within the range of variation of *B. aequatorialis* and its proximal end is 59.8 mm broad, which is much narrower than any specimens hitherto attributed to *Brachyodus depereti* (Fourtau, 1918) and slightly narrower than known tali of *Brachyodus aequatorialis* (MacInnes, 1951). There is no proximal extension of the sinovial fossa between the tibial facets, unlike the situation in hippos and *Libycosaurus*. The lateral process is prominent and bears a stop facet for the calcaneum. The calcanear facet is partly eroded by sand blasting so its outline cannot be accurately observed. The facets for the navicular and cuboid are separated by a ridge that is almost in the midline of the bone, the navicular facet being slightly wider than the cuboid one. In anterior view, the navicular facet extends further proximally than the cuboid facet, and thus slightly deeper into the sinovial fossa. The distal half of the talus is slightly skewed with respect to the proximal half. The lateral surface of the distal end possesses a large almost flat articular surface for the calcaneum. The sinovial fossa is blocked off medially by a roughened ridge of bone that extends from the tibial facet towards the navicular one, being separated from the latter by a narrow oblique groove. Laterally the fossa opens via a wide valley between the cuboid facet and the lateral process.

The abaxial first phalanx (GT 88'06) is badly wind eroded, but it is possible to discern the slight curvature of the diaphysis typical of abaxial phalanges, as well as its almost circular section. The distal facet, although heavily abraded shows the steep inclination that it has relative to the long axis of the diaphysis. What remains of the proximal epiphysis is the basal half, which is concave. The proximal plantar tuberosities are eroded but are strongly developed.

Table 2. Measurements (in mm) of the skull of *Brachyodus aequatorialis* from Namibia and Kenya (Rusinga skull after MacInnes, 1951).

Measurement	GT 88'06	Rusinga skull
Zygomatic breadth	268	285
Bicondylar width	94	106
Palatal breadth at M3/	63	61

Discussion

The skull, teeth and post-cranial bones of GT 88'06 are extremely close morphologically to specimens of *Brachyodus aequatorialis* MacInnes, 1951, from East Africa. The teeth of the Namibian fossil are slightly larger than those from Kenya, whereas the skull dimensions are slightly smaller (Tables 1, 2) but I have little hesitation in attributing them to the same species. In its preserved parts the ventral regions of the Grillental specimen are extremely similar to the Rusinga skull, holotype of the species.

Discussion and conclusions

It is most likely, considering its large dimensions, that the Grillental talus housed in the South African Museum belongs to *Brachyodus depereti*, a form that is common in Early and Middle Miocene deposits of Egypt and Libya. It is somewhat larger than tali from East Africa attributed to *Brachyodus aequatorialis* (Table 3). The second talus from Grillental 6 is much smaller than the first one, being comparable morphologically and in dimensions to those of *Brachyodus aequatorialis* from East and North Africa, indicating that there may have been two species of anthracothere in the Northern Sperrgebiet during the early Miocene. Alternatively these anthracotheres may have been somewhat bimodal, with large males and smaller females. In the samples of *Brachyodus* tali from five countries in Africa and Europe, there are usually two size groups, mostly with fewer large specimens than small ones (Table 3). Egypt has yielded 2 large and 5 small tali, Namibia one of each, Kenya, 1 large and 4 small ones, Libya 2 small ones and France 2 large and 12 small ones. The difference in size between the largest and smallest tali in each sample is of the order of 20%, the means would be less divergent than this. The question of strong body size bimodality in *Brachyodus* thus needs to be researched further.

When the few specimens from the Northern Sperrgebiet are added to the pieces from the Orange River Valley (Pickford, 2003), it is clear that large

Table 3. Measurements (in mm) of tali of *Brachyodus* species from Africa and Europe (data for Rusinga specimens are from MacInnes (1951), remainder are by the author).

Specimen	Side	Internal length	External length	Proximal breadth	Distal breadth	Country
No N°	right	105	111.7	62.6	70	Egypt
CGM30822	left	108.8	116	66.3	69.8	Egypt
CGM82978	left	109.5	117	67.3	68	Egypt
CGM30822	left	140.5	123.5	72.2	89	Egypt
CGM30822	right	109	124.3	65.4	74.5	Egypt
CGM30822	left	--	133	--	73	Egypt
CGM30822	right	115.5	142	73.5	70.2	Egypt
FS5893	left	112.7	--	74.1	84.4	France
FS1928	left	91	--	59.4	64.1	France
PO55	right	82.4	92	54	62.6	France
FS6131	right	89.3	98.8	57.2	66	France
FS1748	?	91.3	105	58.5	63.5	France
FS1134	left	90.3	105	56.7	62.6	France
FS5894	left	92.2	105.3	61.7	67.6	France
FS2927	right	98	107.8	61.5	71	France
FS63	right	98.7	107.9	61.1	72.2	France
PO57	right	98.2	110.7	62.4	70.5	France
FS1751	right	93.9	111	61.6	65.6	France
FS58	right	102.4	114	58	64	France
FS2892	left	103.6	118.4	69.4	83.5	France
FS2924	right	103.7	119.6	70.4	77.4	France
Rusinga C	?	98	108	60	75	Kenya
RusInga A	?	103	115	70	70	Kenya
M32834	left	106.8	121.8	67.4	73.8	Kenya
Rusinga B	?	115	125	75	80	Kenya
Rusinga D	?	--	126	--	85	Kenya
B2	left	102.5	120.4	69.0	84.7	Libya
No N°	left	109	133.5	68.4	86	Libya
GT 88'06	left	--	111.5	59.8	--	Namibia
SAM	right	--	136.4	73.2	--	Namibia

anthracotheres occurred in southern Africa, but the rarity of their bones suggests that they were not common there, unlike East and North Africa where they tend to be well represented at most fluvial and lacustrine sites.

Acknowledgements

I thank all the Namibian and French institutions and persons who have helped in making the Namibia Palaeontology Expedition such a success. I particularly wish to thank my Namibian, French and Spanish colleagues who participated in the field work.

References

Fourtau, R.1918. Contributions à l'étude des vertébrés miocènes de l'Egypte. *Min. Finance Egypt Surv. Dept*., pp. i-vii+1-121.

Hamilton, W.R. and Van Couvering, J.A. 1977. Lower Miocene mammals of South West Africa. *Namib. Bull. (Suppl. 2, Transv. Mus. Bull.)*, pp. 9-11.

MacInnes, D.G. 1951. Miocene Anthracotheriidae from East Africa. *Foss. Mamm. Afr.,* **4**, 1-24.

Pickford, M. 2003. Early and Middle Miocene Anthracotheriidae (Mammalia, Artiodactyla) from the Sperrgebiet, Namibia. *Mem. Geol. Surv. Namibia*, **19**, 283-290.