

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

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2008

Suidae from the Early Miocene of the northern Sperrgebiet, Namibia

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Undescribed suid specimens from the northern Sperrgebiet, Namibia, including cranial and mandibular material, throw additional light on the anatomy and affinities of the hitherto poorly known species *Nguruwe namibensis*. This species is smaller than *Nguruwe kijivium* and is likely to be older than it. The few post-cranial elements attributed to *N. namibensis* are typical of suids, and rather divergent from those assigned to sanitheres from the same sites, the bones of which are smaller and more gracile. *Nguruwe* could well be descended from European *Aureliachoerus*.

Introduction

The Namibia Palaeontology Expedition has collected over 40 suid specimens from Langental, Elisabethfeld, Fiskus and Grillental in the northern Sperrgebiet, Namibia. Some of the material was described by Pickford (1997), but material collected since 1994 has not previously been published. It includes several post-cranial bones and additional teeth, a partial skull and some mandibles.

The fossiliferous sediments in the northern Sperrgebiet accumulated in valleys incised into bedrock during the Oligocene low sea stand. The Early Miocene rise in sea level led to choking of the valleys as transient sediment was no longer flushed down into the lower reaches of the valleys, but accumulated within them at Grillental, Elisabethfeld, Langental and elsewhere, partly as fluvial sediments (Grillental, Elisabethfeld, Fiskus), as paludal deposits (Grillental, Elisabethfeld) or as palaeosols developed on fluvio-paludal deposits (Langental).

Systematic description

Family Suidae Gray, 1821

Genus *Nguruwe* Pickford, 1978

Species *Nguruwe namibensis* (Pickford, 1986)

Holotype : SAM PQN 20, fragmented skull and mandible with much of the upper and lower dentition (Pickford, 1986, p. 34) from Langental, Namibia.

Additional material from the Sperrgebiet :

Craniodental specimens :

From Langental : Mandible with m/2-m/3, mandibular symphysis (Stromer, 1926, p. 114); LT 161'96, right mandible with p/2-p/4; LT 163'96, worn lower molar; LT 419'96, left M3/ lacking anterior cusps (Pl. 3.9); LT 421'96, left M3/; LT 8'97, broken right M3/ (Pl. 3.3); LT 149'98, maxilla fragment with left M3/ (Pl. 1.3); LT 150'98, left maxilla with M1/-M2/ (Pl. 1.1); LT 151'98, damaged right I1/ (Pl. 1.4); LT 152'98, half lower i/2; LT 245'98, molar fragments

and lower incisor half; LT 236'99, left mandible fragment with roots of c/1-p/3; LT 237'99, molar fragments including the rear 2/3 of M3/ (Pl. 3.10); LT 240'99, right dI3/ (Pl. 3.1), dM4/ (Pl. 3.5), M1/ (Pl. 3.6); LT 247'99, left P3/ in maxilla fragment (Pl. 1.7); LT 1'00, M3/ (Pl. 1.2); LT 2'00, broken lower molar (Pl. 1.5); LT 4'00, left M3/ missing anterior edge (Pl. 3.8); LT 7'00, upper right M3/; LT 8'00, lower right second incisor; LT 139'00, left M3/ (Pl. 1.6); LT 46'03, half lower i/1; LT 47'03, mandible fragment with half lower premolar; LT 68'03, left M3/ lacking talon; LT 163'03, left I3/ (Pl. 3.2, 3.4); LT 222'03, left mandible with m/2-m/3 (Pl. 3.11); LT 234'03, right lower molar lacking anterior portion; LT 266'03, m/3 fragment (Pl. 3.7); LT 18'04, left M3/ (broken); LT 19'04, left M1/ (same individual as LT 18'04), LT 20'04, left i/2, LT 94'04, left C/ (male?); LT 95'04, upper molar lacking enamel; LT 98'04, upper molar lacking enamel; LT 136'04 left M2/ (same individual as 18'04 and 19'04); LT 137'04, left M3/; LT 153'04, right dM4/; LT 155'04, right M3/; LT 210'04, right m/3; LT 29'05, left upper canine; LT 30'05, left I1/; LT 54'05, mandible with mixed dentition; LT 1'06, right mandible and symphysis with left c/1, right dm/4, m/1 and m/2 in crypt; LT 48'06, left maxilla with P4/-M1/; LT 53'07, mandible with m/1-m/3 (Pl. 6.3); LT 61'07, right i/2 (Pl. 6.4); LT 82'07, various isolated teeth of a single individual (Pl. 6.7); LT 83'07, right M3/; LT 105'07, right dm/4 (Pl. 6.5); LT 107'07, right di/2 (Pl. 6.2); LT 117'07, left M3/; LT 118'07, left M3/; SAM PQN 122, p/3-m/3; SAM PQN 123, maxilla fragment with dM4/ and M1/; SAM PQN 127, associated upper and lower cheek teeth; SAM PQN 128, left mandible with m/2-m/3;

From Elisabethfeld : EF 3'96, left mandible with c/1, p/2-m/3 (Pl. 4.1).

From Fiskus : FS 20'04, left M3/ (Pl. 4.4); SAM PQN 120, left m/2; FS 10'07, crushed palate with cheek dentition.

From Grillental : GT 4'94, edentulous left mandible and symphysis (Pl. 4.2); GT 58'04, left P3/ (broken); GT 100'04, right m/3 (Pl. 4.3); GT 52'05, partial skull; GT 2'06, left p/4; GT 51'06, right mandible

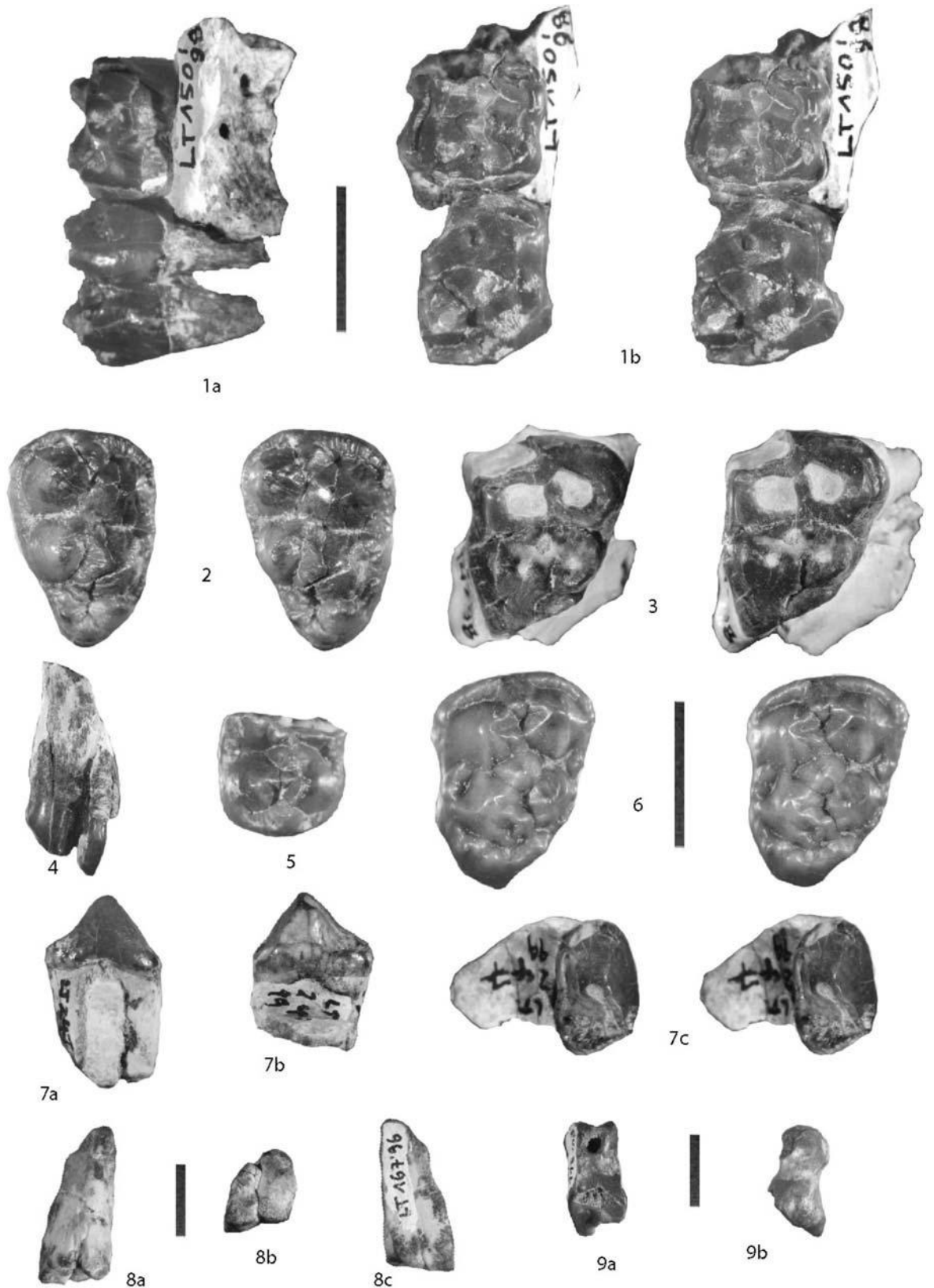


Plate 1. *Nguruwe namibensis* from Langental, Namibia (scale 1 cm).

1. LT 150'98, right maxilla with M1/-M2/, a) lingual, b) stereo occlusal views, 2. LT 1'00, right M3/, stereo occlusal view, 3. LT 149'98, left maxilla fragment with M3/, stereo occlusal view, 4. LT 151'98, upper central incisor (broken), anterior view, 5. LT 2'00, broken lower molar, occlusal view, 6. LT 139'00, left M3/, stereo occlusal view, 7. LT 247'99, maxilla fragment with left P3/, a) buccal, b) lingual, c) stereo occlusal view, 8. LT 167'96, third phalanx, a) dorsal, b) proximal, c) plantar views, 9. LT 118'03, second phalanx, a) dorsal, b) lateral views.

fragment with m/2-m/3; GT 25'07, mandible with m/1-m/3 (Pl. 6.12).

Post-cranial material :

From Langental : Proximal McIII (Stromer, 1926, p. 114); LT 167'96, axial 3rd phalanx (Pl. 1.8); LT 7'97, axial 1st phalanx (Pl. 3.13); LT 74'99, abaxial 1st phalanx (Pl. 3.12); LT 118'03, axial 2nd phalanx (Pl. 1.9); LT 200'04, axial 2nd phalanx. SAM PQN No number, right talus.

From Fiskus : FS 4'03, axial 1st phalanx (Pl. 4.5).

From Grillental : GT 58'96 (GT 6), abaxial 1st phalanx (Pl. 4.6); GT 52'05, (GT 6) rear half of a skull (Pl. 2).

Description : Skull : GT 52'05 is the rear half of a skull in good condition save for minor crushing and displacement of bones (Pl. 2). In the palate the right P4/-M3/ and the left M2/-M3/ are preserved.

Palatal view. The posterior choanae are curved and reach anteriorly as far as the talon of the upper third molars. The palatine foramina are located opposite the front of M2/ and the lingual sides of the M3/s are 22.2 mm apart. The maxillary tuberosity behind the third molar is scored by a prominent groove which is directed laterally and upwards into the temporal fossa. The lateral side of this groove is overhung by a well developed flange. The rear of the zygomatic process of the maxilla is positioned on a level with the middle of the M3/, the anterior part has been eroded away. The anterior end of the base of the zygomatic arch, opposite the M2/ and M3/, possesses a prominent but shallow fossa with a slightly roughened surface, representing the origin of the masseter. Behind this fossa the zygomatic arch is slender and the skull is widest immediately to the rear of the M3/. The temporal condyles are concavo-convex with a tall post-condylar process separated from the mastoid crest by a groove. The tympanic bullae are well preserved and are positioned close behind the pterygoid processes of the palatines. The bullae are inflated and are ovoid in palatal view with a prominent posterolateral valley which leads into the stylomastoid foramen. There is an oblique valley (musculo-tubal canal) separating the lateral surface of the bulla from the articular surface of the temporal condyle. The petro-occipital fissure and the foramen ovale are positioned as in recent *Sus*. The jugular foramen is located relatively far back, close to the anterior margin of the condylar fossa, but it emerges into the brain case well in front of the foramen magnum. The jugular apophysis (paroccipital process) is short and directed slightly to the rear, unlike the elongated and forward leaning apophysis in *Sus*. In this orientation, the apophyses of *Nguruwe* terminate in line with the occipital condyles, in a very different position from that in *Sus* in which they terminate in line with the tympanic bullae. This means that there is a vast space between the bullae and the apophyses in *Nguruwe*, and barely

any space between them in *Sus*. The basisphenoid and basilar apophysis of *Nguruwe* are close in morphology to those of *Sus*, save for the posterior position of the jugular foramen. The external auditory meatus opens immediately behind and above the temporal condyle on a level with its midline.

Lateral view. The front of the orbit is located above the molar row, the post-orbital process descending behind the level of the pterygoid process of the palatine. The anterior part of the orbit is eroded, but a small part of the anterior margin reveals the presence of at least one lacrymal foramen at about mid-height above the front of M2/. The frontal apophysis of the zygomatic arch is preserved on both sides, revealing a wide gap between it and the post-orbital process of the frontal. Behind the frontal apophysis of the zygomatic there is a right angled space into which fits the zygomatic apophysis of the temporal bone, as in *Sus*. The temporal fossa is large with well defined temporal ridges separating the squamous part from the dorsal surface of the skull. These ridges or lines converge distally to form a prominent sagittal crest which merges distally into the external occipital protuberance and the nuchal crest. The external auditory meatus is low down, positioned on a level with the middle of the orbit. This is much lower than the position in *Sus*. The supra-auditory process of the zygomatic is thus low, and does not rise steeply distally as it does in *Sus*. In lateral view the tympanic bullae lean anteriorly and almost overlap the pterygoid processes of the palatines. The paroccipital processes lean distally and ventrally, in side view overlapping the occipital condyles, quite unlike their orientation in *Sus*, in which they are more vertical. The processes are short in *Nguruwe* terminating well above the most ventral part of the tympanic bullae, whereas in *Sus*, they are elongated and extend greatly beneath the bullae.

Distal view. The nuchal area in *Nguruwe* is wide dorsally and narrows slightly ventrally, but not to the great extent that typifies *Sus* in which a high relief V-shaped structure is produced above the nuchal tubercles. The occipital condyles are basically similar to those of *Sus*. The paroccipital processes are short and terminate just beneath the ventral margin of the occipital condyles, unlike the greatly elongated processes that occur in *Sus*.

Dorsal view. The braincase has a strongly developed sagittal crest which merges with a strong external occipital protuberance. The supra-orbital foramen is preserved on both sides, and is located on a level with the anterior third of the orbit, unlike in *Sus* in which it is almost anterior to the orbits. There are several accessory nutritive foramina on the dorsal surface of the skull, notably on the orbital margins and near the inter-frontal suture. There is no sign of a foramen on the temporal surface of the parietals or temporals.

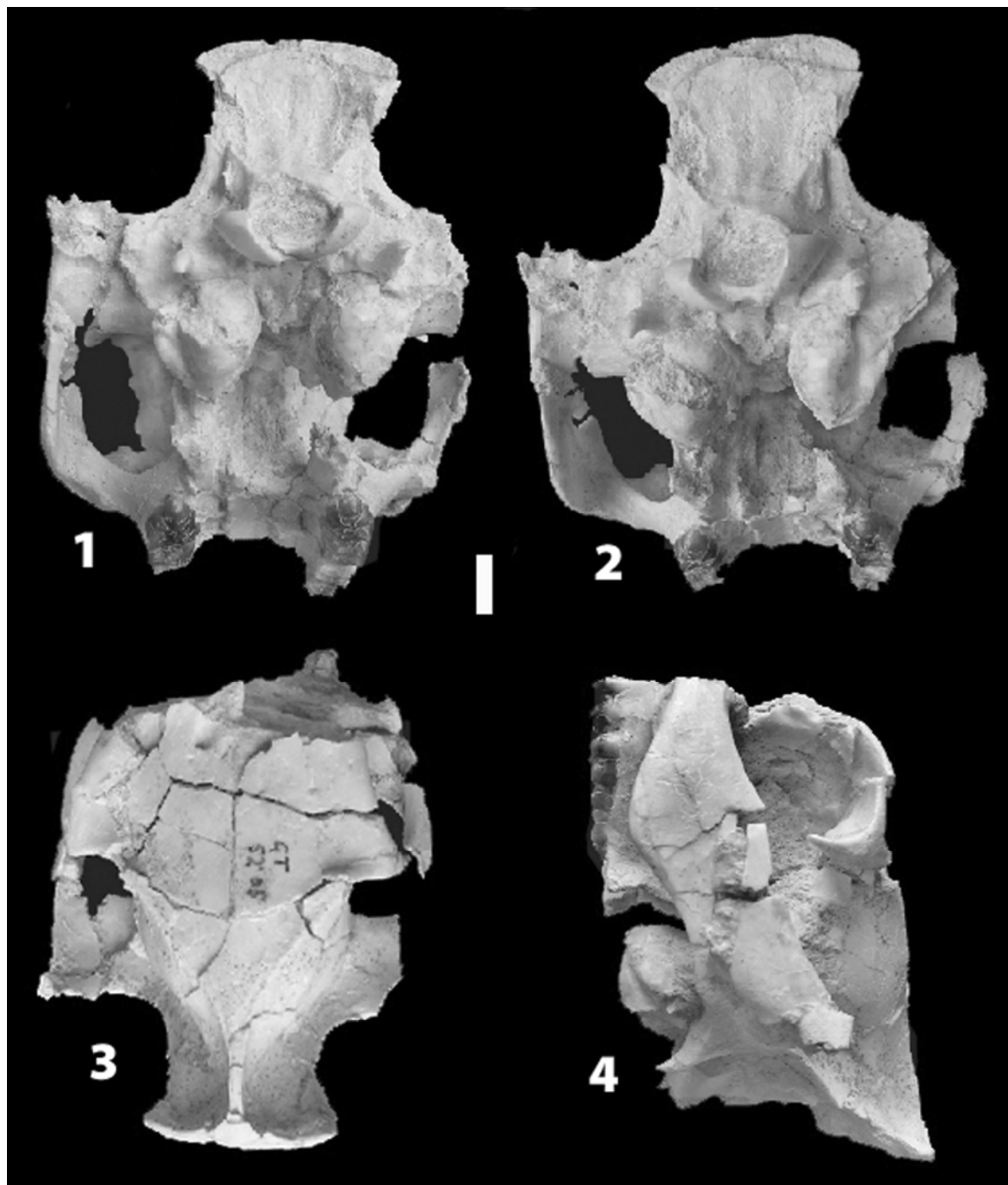


Plate 2. GT 52'05, cranium of *Nguruwe namibensis* from Grillental, Namibia (scale 1 cm).
1. Distal view, 2. Slightly oblique distal view, 3. Dorsal view, 4. Left lateral view.

The nuchal crest is well developed, terminating low down, unlike in *Sus* where it terminates in a higher position.

Upper dentition : The only deciduous upper teeth in the Sperrgebiet sample are LT 240'99, a dI3/ and dM4/ associated with an M1/. The incisiform tooth has a straight root, and its crown is thin enamelled and possesses a small, low distal cusplet. The dM4/ is a smaller version of the M1/ and has thinner enamel

than it.

LT 151'98, is a damaged right upper central incisor. The crown is bulbous anteriorly, but lacks much of the mesial portion due to breakage. There is a large lingual wear facet on the preserved distal part of the crown. The root narrows rapidly towards its apex. LT 163'03, a left upper incisor, has a triangular crown in lingual view, with a small, low distal cusplet near cervix. There is a sloping anterior wear facet on the mesial edge of the crown, but none on

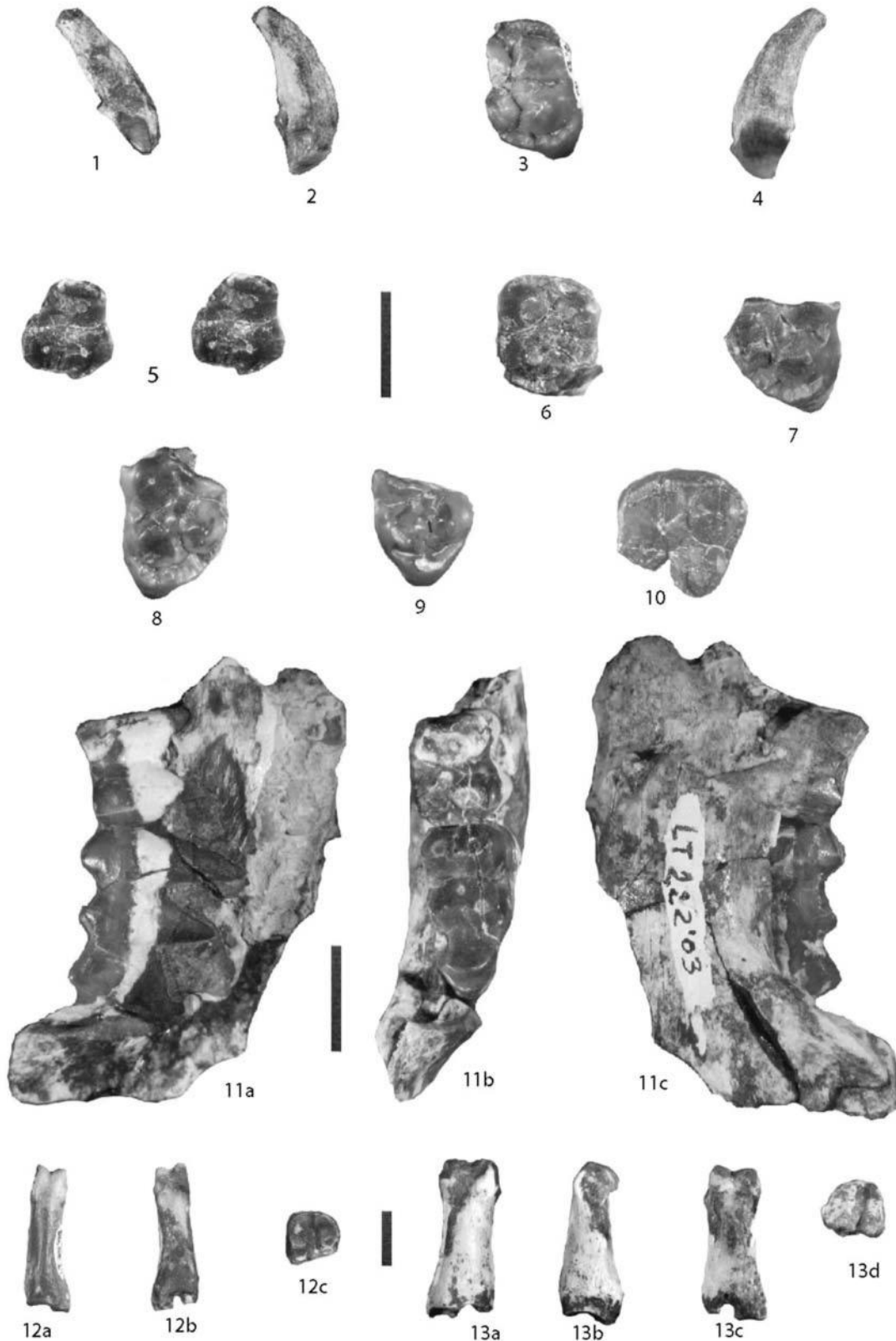


Plate 3. *Nguruwe namibensis* from Langental, Namibia (scale 1 cm).

1. LT 240'99, deciduous I3/, labial view, 2. LT 163'03, left I3/, lingual view, 3. LT 8'97, damaged right M3/, occlusal view, 4. LT 163'03, left I3/, labial view, 5. LT 240'99, left dM4/, stereo occlusal view, 6. LT 240'99, left M1/, occlusal view, 7. LT 266'03, distal half of right M3/, occlusal view, 8. LT 4'00, distal half of left M3/, occlusal view, 9. LT 419'96, distal half of left m/3, occlusal view, 10. LT 237'99, anterior portion of M3/, occlusal view, 11. LT 222'03, left mandible with m/2-m/3, a) lingual, b) occlusal, c) buccal views, 12. LT 74'99, abaxial first phalanx, a) dorsal, b) volar, c) proximal views, 13. LT 7'97, axial first phalanx, a) dorsal, b) lateral, c) volar, d) proximal views.

the distal edge, suggesting that this tooth is a third upper incisor. The root is uniformly curved, extending the curved profile of the crown.

LT 94'04, a left upper canine, possibly of a male individual, is similar in morphology to a specimen from Songhor, attributed to *Nguruwe kijivium* (Pickford, 1986) but is appreciably smaller. The distal crest is well preserved, but the anterior one is missing due to breakage of the specimen. This canine is also similar to those of *Aureliachoerus aurelianensis* of Europe.

LT 247'99 is a left P3/. It has a large conical main cusp with a low anterior cusplet, almost worn away in this specimen, and a larger disto-lingual cusp and distal cingulum separated from the main cusp by a broad, shallow, low valley. The lingual cingulum is complete, low and sharp. There is no buccal cingulum. GT 58'04, from locality GT 6, is the buccal half of a left P3/ similar to the specimen from Langental.

The P4/ in the skull, LT 52'05, is bicuspid with a prominent cingulum that extends continuously across the mesial, lingual and distal sides of the tooth. The buccal cusp is slightly larger than the lingual one, and has well developed antero-posteriorly oriented pre- and post-crista which blend into the mesial and distal cingula respectively. The lingual cusp has oblique pre- and post-crista which terminate at the mesial and distal cingula in the midline of the tooth, thereby interrupting the sagittal valley.

The M1/ in LT 52'05 is deeply worn. The M2/ is heavily worn, showing large dentine lakes on the main cusps as well as the median accessory cusp. The M3/ is in medium wear, with small dentine exposures on the two lingual cusps. The talon is small and is located slightly to the lingual side of the axis of the tooth row, imparting a triangular appearance to the crown. These teeth are morphologically similar to those in the holotype of the species from Langental (Pickford, 1986) but are slightly smaller (Table 1).

LT 150'98 is a broken maxilla with M1/-M2/. The M1/, in medium wear, is quadricuspidate with low, poorly expressed anterior, median and posterior accessory cusplets in the midline of the crown. The buccal cingulum is clear, and sharp. The M2/ is lacking the buccal half of the buccal cusps. Being less worn than the M1/, the anterior, median and posterior accessory cusplets are clearly visible. The four main cusps have weak furchen, and the anterior and posterior cingula are clear, as is a remnant of a cingulum in the lingual end of the median transverse valley.

There are several upper third molars in the Langental sample, and one from Fiskus. They possess four main cusps similar to those of the M2/ but with the addition of a small talon comprising a reduced cusp positioned at the lingual edge of the crown and accompanied by a well developed, beaded posterior cingulum which may or may not extend along the buccal side of the tooth. In LT 7'00, the talon is comprised of a prominent cusplet on the lingual side of

the crown bordered by cingular beads.

An M3/ from Fiskus is important as it reveals the presence of this species at the site. The specimen lacks the mesio-buccal cusp, the other main cusps are bundont and there is a small talon. A poorly preserved suid snout found in 2007, may well represent the same individual (Pl. 6.1). Its canines are buccolingually compressed with a sharp distal crest. A prominent wear facet scores the anterior surface of the crown, and basally, near cervix, one can observe the remnants of a strong anterior crest slightly to the lingual side of the tooth. There is no diastema between the canine and the anterior premolars. The P1/ is two-rooted with the apex of the cusp over the gap between the roots. The P2/ has a small disto-lingual shelf, which is more expansive in the P3/. The buccal wall of the P3/ is comprised of a tall slightly obliquely oriented main cusp and a lower distal cusplet. The P4/ is bicuspid with a diminutive posterior buccal cusp. The molars are similar to other material described above. The palate is poorly preserved but shows the course of the palatine groove as far forwards as the canine.

Measurements (in mm) of the upper dentition of *Nguruwe namibensis* are provided in Table 1.

Mandible : LT 54'05 is a right mandible fragment with the symphysis preserved on the left side as far back as the p/1 and the right ramus as far as the m/3 (Pl. 5). The individual, which retains the deciduous incisors and molars was young when it died. The m/1 was erupted and lightly worn, the m/2 is almost erupted and the m/3 is not fully formed and is still in its crypt. The tip of the permanent canine is just poking out of its alveolus. The symphysis is long and slopes backwards as far as the dm/3, the genial spine being prominently developed. The two genial pits are well preserved above and slightly lateral to the genial spine. The mandible is relatively slender, widening rearwards, especially opposite the molar row. There are mental foramina beneath the dm/2 and dm/4 slightly above mid-height of the ramus. There are very short diastemata between the canine and the p/1, and the p/1 and dm/2, but none between the i/3 and the canine.

All the other mandible fragments from Langental are broken, none of the specimens retaining the inferior margin, but the specimen from Elisabethfeld is complete. LT 161'96 and LT 236'99 reveal that there is no diastema between the lower canine and the p/1. This is confirmed in the Elisabethfeld mandible, EF 3'96, which was described by Pickford (1997). LT 161'96 has a doubled mental foramen in the upper third of the jaw just below the rear of p/1 and front of p/2 and there appears to be another larger foramen below the rear of p/3. A mental foramen is present in a similar position just below the p/1 in LT 236'99. LT 222'03 preserves part of the ascending ramus and its root, which departs from the horizontal ramus near the rear of m/3, not hiding the tooth in lateral view.

Table 1. Measurements (in mm) of the upper teeth of suids from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 151'98	I1/	6.5	4.8
LT 30'05	I1/	5.7	5.1
LT 163'03	I3/	4.7	3.7
PQN 127 Langental	I3/	5.4	3.7
	C1/	7.5	--
	P3/	7.8	6.4
	P4/	6.9	7.8
	P4/	6.8	7.8
	M1/	9.2	9.0
	M1/	--	9.1
	M2/	11.1	10.0
	M2/	11.1	--
	M3/	13.3	9.8
	M3/	13.0	9.9
LT 94'04	Upper Canine	9.3	8.2
LT 29'05	Upper canine	9.2	8.6
LT 247'99	P3/	9.1	5.8
GT 58'04	P3/	8.3	--
LT 150'98	M1/	9.2	9.0
	M2/	11.4	--
LT 240'99	dI3/	3.9	2.8
	dM4/	8.2	7.8
	M1/	9.7	8.6
LT 153'04	dM4/	7.6	8.0
PQN 123 Langental	dM4/	7.5	7.0
	M1/	9.2	8.4
LT 19'04	M1/	9.6	9.5
LT 136'04	M2/	11.7	10.9
LT 421'96	M3/	14.7	11.0
LT 8'97	M3/	13.3	--
LT 149'98	M3/	12.6	9.8
LT 7'00	M3/	15.4	10.5
LT 139'00	M3/	13.9	10.5
LT 18'04	M3/	--	11.0
LT 137'04	M3/	12.5	10.5
LT 155'04	M3/	12.7	9.6
LT 48'06	P4/	6.8	7.8
	M1/	8.9	9.3
LT 82'07	P4/	6.8	7.9
	M3/	12.0e	9.2
LT 83'07	M3/	13.6	--
LT 117'07	M3/	12.3	9.8
LT 118'07	M3/	12.9	9.5
FS 20'04	M3/	13.7	--
FS 10'07	Right C1/	7.8	5.4
	Right P1/	6.7	3.2
	Right P2/	7.7	4.4
	Right P3/	8.8	6.7
	Right P4/	7.7	8.0
	Right M1/	9.8	9.2
	Right M2/	11.5	10.3
	Right M3/	14.2	11.5
	Left C1/	8.0	6.1
	Left P4/	7.6	--
Left M1/	9.4	9.3	
Left M2/	11.3	10.2	
GT 52'05	Left M2/	10.3	10.0
	Left M3/	12.3	10.8
	Right P4/	6.7	8.1
	Right M1/	9.0	9.4
	Right M2/	10.3	10.2
	Right M3/	12.1	10.7

The lower jaw fragment from Grillental 1 consists of the base of the symphysis and much of the left body, with roots of the premolars and first molar. The base of the jaw is preserved, and it resembles

closely that of the Elisabethfeld specimen. The symphysis extends back to the midline of p/3, and there is a well developed genial spine at its ventral base. A second mandibular specimen (GT 51'06) from Gril-

lental 6 is severely damaged, but retains part of the m/2 and a complete m/3. It is similar in all respects to the Elisabethfeld mandible.

Lower dentition : LT 8'00 is a right lower second incisor lacking the apex of the crown. It has a central lingual ridge and a distal scoop near the cervix. In its overall morphology it is close to material from Arrisdrift attributed to *Nguruwe kijivium*. LT 20'04, a left i/2 is in better condition, showing the central lingual ridge and the distal scoop extending from cervix to apex.

EF 3'96, a left mandible in good condition, was described by Pickford (1997). The lower canine has subequal lingual and buccal surfaces and a narrow distal one, while the root appears to be small, suggesting that it represents a female individual. 10 mm of the lower canine is exposed in this mandible. The abraded canine alveolus in LT 161'96 is large and suggests that it was a male individual. The canine root in LT 236'99 is closed apically and is oval in section, probably being female. Thus *Nguruwe namibensis* probably possessed sexually dimorphic lower canines.

The canines in LT 54'05, in contrast, are high crowned and probably represent a male individual. The canine section is scrofic, and there is no enamel on the distal surface of the crown.

The lower premolars of *Nguruwe namibensis* were described by Pickford (1997). The p/1 in specimen LT 54'05 is single cusped, bucco-lingually compressed, almost blade-like, with a disto-lingual hollowing of the lingual surface. The single root has deep grooves buccally and lingually, making it incipiently doubled.

The new lower molars from Langental (LT 222'03; LT 210'04) are slightly larger than those in the Elisabethfeld specimen (Table 2) but they are similar in morphology although they are more worn. The m/3 is a bundont, five cusped tooth. The two anterior lophs comprise four sub-equal cusps with low anterior, median and posterior accessory cusplets. The talonid is a simple cusp that is raised slightly above the level of the rest of the crown. There are weak cingular remnants in the ends of the median and distal transverse valleys on the buccal side. The m/2 in this specimen is deeply worn, and no details of the cusp morphology can be made out, although it is evident that it originally resembled the first two lophs of the m/3. The molars in LT 54'05 are similar to the other material from the Sperrgebiet, but the m/3 is not completely formed, and its dimensions would have been greater when fully mineralised.

LT 234'03 is the rear part of a lower m/2 germ, showing clear development of the median and posterior accessory cusplets. The furchen in all these teeth are weakly expressed.

GT 100'04 from locality GT 1 is a right m/3 lacking the mesio-buccal cusp. It is bunodont with five main cusps. The median transverse valley is rela-

tively wide for *Nguruwe* but is not as open as in *Kenyasus*.

Measurements (in mm) of the lower teeth of *Nguruwe namibensis* are provided in Table 2.

Deciduous lower dentition : The deciduous incisors in LT 54'05 are simple peg-like teeth, slightly compressed labio-lingually with the roots slightly more voluminous than the crown. The di/2 is gently curved from cervix to apex. The di/3s are missing from their alveoli, which are close to those of the di/2s.

The dm/2 is blade-like in occlusal view and triangular in lateral view, similar to the p/1, but has two roots well separated from each other. The disto-lingual hollowing is better defined, and there is a hint of a fine lingual cingulum and a small distal tubercle. The dm/3 has a wider rear half than the dm/2, its crown is bigger and has a better defined distal tubercle. The dm/4 is of the usual artiodactyl type with three lophs arranged on five roots, two lingual and three buccal. The crown is in medium wear and has been chemically etched, so details of the morphology cannot be made out clearly. Nevertheless it is possible to determine that the tooth widens from mesial to distal.

Post-cranial skeleton : Very little of the post-cranial skeleton of *Nguruwe namibensis* is known, in contrast to that of the other small suoid from the site, *Diamantohyus africanus*. From Langental there are six foot bones, and from Fiskus there are additional rare specimens. All of them are morphologically similar to but smaller than material from Arrisdrift which is considered to belong to *Nguruwe kijivium* (Pickford, 1987, 2003). The talus from Langental is too abraded to yield much information, but it has the bent appearance usual in suids. The tibial end is about 12.8 mm wide and the total length is about 26.5 mm. This compares with sanithere tali from the same site which are appreciably smaller, the external length ranging between 20.7 and 21.4 mm, and the proximal breadth 9.2 to 9.7 mm. The axial 1st phalanges (LT 797, FS 4'03) are strong bones with robust diaphyses. The abaxial 1st phalanges (LT 74'99) are more gracile and are slightly curved. The axial 2nd phalanges (LT 118'03 and LT 200'04) are typically suid in morphology and are compatible in size with the 1st phalanges from the site. The 3rd phalanx (LT 167'96) has the volar surface steeply angled relative to the rest of the phalangeal wedge and the inclined proximal articulation typical of suids. Measurements (in mm) of the post-cranial bones are provided in Table 3.

Discussion : Although these few post-cranial bones are not enough to provide a good picture of the morphology of the post-cranial skeleton of the species, it is clear that the bones are larger, more robust, and more typically suid in structure than the material attributed to the other small suoid from the sites (*Diamantohyus africanus*) which has more gracile,

Table 2. Measurements (in mm) of the lower teeth of suids from the Northern Sperrgebiet, Namibia.

Specimen	Tooth	Mesio-distal length	Breadth
LT 105'04	i/1	4.5+	3.5+
LT 8'00	i/2	4.1	4.7
LT 20'04	i/2	4.3	4.6
PQN 127 Langental	i/2	4.0	4.3
	p/3	7.8	4.4
	p/4	8.5	5.4
	p/4	8.6	5.5
	m/1	9.2	7.0
	m/1	9.5	--
	m/2	11.3	8.4
	m/2	11.2	8.4
	m/3	15.7	8.9
EF 3'96	m/3	16.1	8.9
	c/1	5.8	4.0
	p/2	7.1	3.6
	p/3	7.9	4.5
	p/4	8.3	5.4
	m/1	9.1	6.6
	m/2	10.8	8.1
LT 161'96	m/3	14.2	8.5
	p/2	7.0	3.9
	p/3	8.9	4.7
LT 222'03	p/4	8.7	6.2
	m/2	10.9	9.2
LT 243'03	m/3	16.9	9.5
	m/2 broken	--	8.2
LT 136'96	m/2?	11e	8.5
Stromer's material (1926, p. 114)*	m/2	11	7.3
	m/3	16.8	7.3
LT 210'04	m/3	16.6	9.3
LT 54'05	Right di/1	2.4	2.4
	Right di/2	2.2	2.5
	Right p/1	6.1	2.8
	Right dm/2	7.3	3.1
	Right dm/3	7.4	3.2
	Right dm/4	10.7	5.1
	Right m/1	8.5	--
	Right m/2	10.6	8.6
	Right m/3#	14e	7.8e
	Left di/1	2.7	2.5
	Left di/2	2.8	2.2
	Left p/1	6.4	3.0
	LT 1'06 Langental	Right dm/4	11.7
Right m/1		9.7	7.4
PQN 122 Langental	p/3	8.6	4.4
	p/4	7.9	5.4
	m/1	8.6	6.5
	m/2	10.2	8.5
	m/3	17.9	9.2
PQN 128 Langental	m/2	10.7	8.5
	m/3	17.0	8.5
LT 53'07	m/1	8.8	6.7
	m/2	10.5	7.6
	m/3	13.6	8.0
LT 61'07	i/2	3.9	4.1
LT 105'07	dm/4	--	6.0
LT 107'07	di/2	3.0	2.7
GT 100'04	m/3	17.9	9.2e
GT 2'06	left p/4	9.5	6.1
GT 51'06	right m/2	11.4	8.3
	right m/3	15.3	8.3
GT 25'07	m/1	9.0	6.7
	m/2	11.3	8.9
	m/3	18.4	10.1
PQN 120 Fiskus	m/2	12.7	9.2

* The front lobe of Stromer's m/3 is broken. I estimate its original breadth at ca 8.1 mm, based on the figure in Stromer (1926). # The m/3 is incompletely formed, and when completed would have been about 1 mm wider and 2 mm longer.

Table 3. Measurement of suid post-cranial bones from the Northern Sperrgebiet, Namibia.

Specimen	Bone	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
FS 4'03	Axial 1st phalanx	25.6	10.4	12.0	9.4	9.1
LT 7'97	Axial 1st phalanx	27.3	12.0	10.5	9.3	6.8
LT 74'99	Abaxial 1st phalanx	25.8	8.0	7.6	6.1	5.7
GT 58'96	Abaxial 1st phalanx	25.5	7.8	7.4	6.0	5.3
LT 118'03	Axial 2nd phalanx	15.5	9.0	--	8.0	7.7
LT 200'04	Axial 2nd phalanx	14.2	7.1	9.2	6.5	6.8
LT 167'96	Axial 3rd phalanx	20.0	7.3	8.2	--	--

more elongated lower limbs (long axial and abaxial metapodials), with the phalanges being more gracile, and with lower height to breadth indices than those of *Nguruwe*. In this respect the bones attributed to *N. namibensis* are morphologically close to specimens found at Arrisdrift identified as *Nguruwe kijivium*.

The specimens attributed to *Nguruwe namibensis* from Langental and Grillental are similar in dental dimensions. The single mandible from Elisabethfeld, in contrast, has a smaller m/3 than any of the Grillental and Langental specimens, but its m/1 and m/2 are similar in size to those from the latter site. The difference in size between the m/3s is the same order of magnitude as that between *Nguruwe namibensis* on the one hand, and *Nguruwe kijivium* on the other, suggesting that the Elisabethfeld mandible could well represent a separate species, but it could represent a small individual (the canine suggests that it is probably a female). However, in view of the similar sizes of the Langental and Elisabethfeld m/1s and m/2s, I hesitate to formalise this possibility. Additional material may resolve the matter.

Biochronology

In terms of biochronology the dimensions of the Elisabethfeld mandible attributed to *Nguruwe namibensis* suggest that the locality is older than the type site of the species, Langental where most of the specimens are larger (Pl. 4, Pl. 7). In contrast, the similarity in dimensions between specimens from Fiskus, Grillental and Langental indicate that these three sites are likely to be the same age. All the material from the Northern Sperrgebiet is smaller than the

sample from Arrisdrift, Namibia (Pl. 7) attributed to *Nguruwe kijivium*, a species that ranges from 20 -17.2 Ma in East Africa.

It is concluded that the Northern Sperrgebiet sites are earlier than Songhor (Kenya) and Napak (Uganda) which are about 20-19 Ma, and are approximately equivalent to MN 3 in terms of the European Mammal Zonation.

Conclusions

The Elisabethfeld suids (ca 21 Ma) and those from Langental and Grillental (ca 20 Ma) are the oldest known from Africa. The mandible from Elisabethfeld, provisionally attributed to *Nguruwe namibensis* despite its small dimensions, resembles that of *Aureliachoerus* from Europe in several features of the jaw and dentition, including its diminutive size, and it is possible that the two genera are closely related to each other, suggesting that the lineage which gave rise to *Nguruwe* may have originated in Europe. Once suids colonised Africa, they radiated rapidly, with the result that by 18 Ma there were at least three separate genera (*Nguruwe*, *Kenyasus*, *Libycochoerus*).

The available post-cranial bones of *Nguruwe namibensis*, even though they are scarce, are typically suid-like in morphology, the phalanges being short and stocky. The post-cranial bones of *Nguruwe* are morphologically distinct from those of sanitheres from the same localities and are larger. Sanithere bones are more gracile, more elongated and possess sharper crests and keels than those of suids (Pickford, 2004), suggesting that they were more cursorial than suids.

Table 4. Summary of suid specimens from the Northern Sperrgebiet, Namibia.

Locality	Langental	Elisabethfeld	Fiskus	Grillental
Craniodental remains	70	1	2	6
Post-cranial bones	6	--	1	1

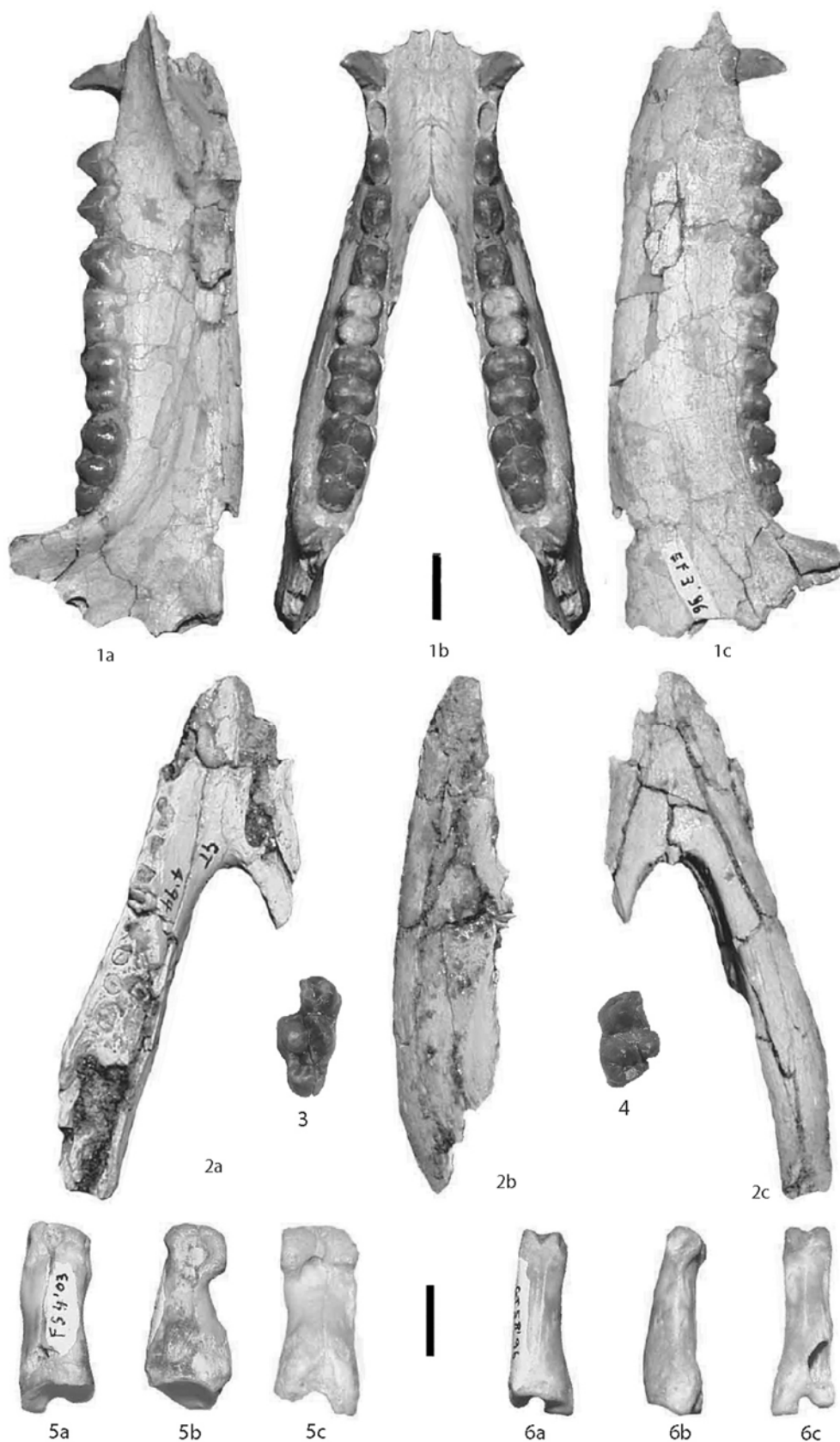


Plate 4. *Nguruwe namibensis* from Elisabethfeld, Namibia (scale 1 cm).

1. EF 3'96, left mandible, a) lingual view, b) occlusal view with mirror image, c) buccal view. 2. GT 4'94, edentulous mandible, a) occlusal, b) lateral, c) ventral views, 3. GT 100'04, right m/3, occlusal view, 4. FS 20'04, left M3/, occlusal view, 5. FS 4'03, axial second phalanx, a) dorsal, b) lateral, c) volar views, 6. GT 58'96, abaxial first phalanx, a) dorsal, b) lateral, c) volar views.

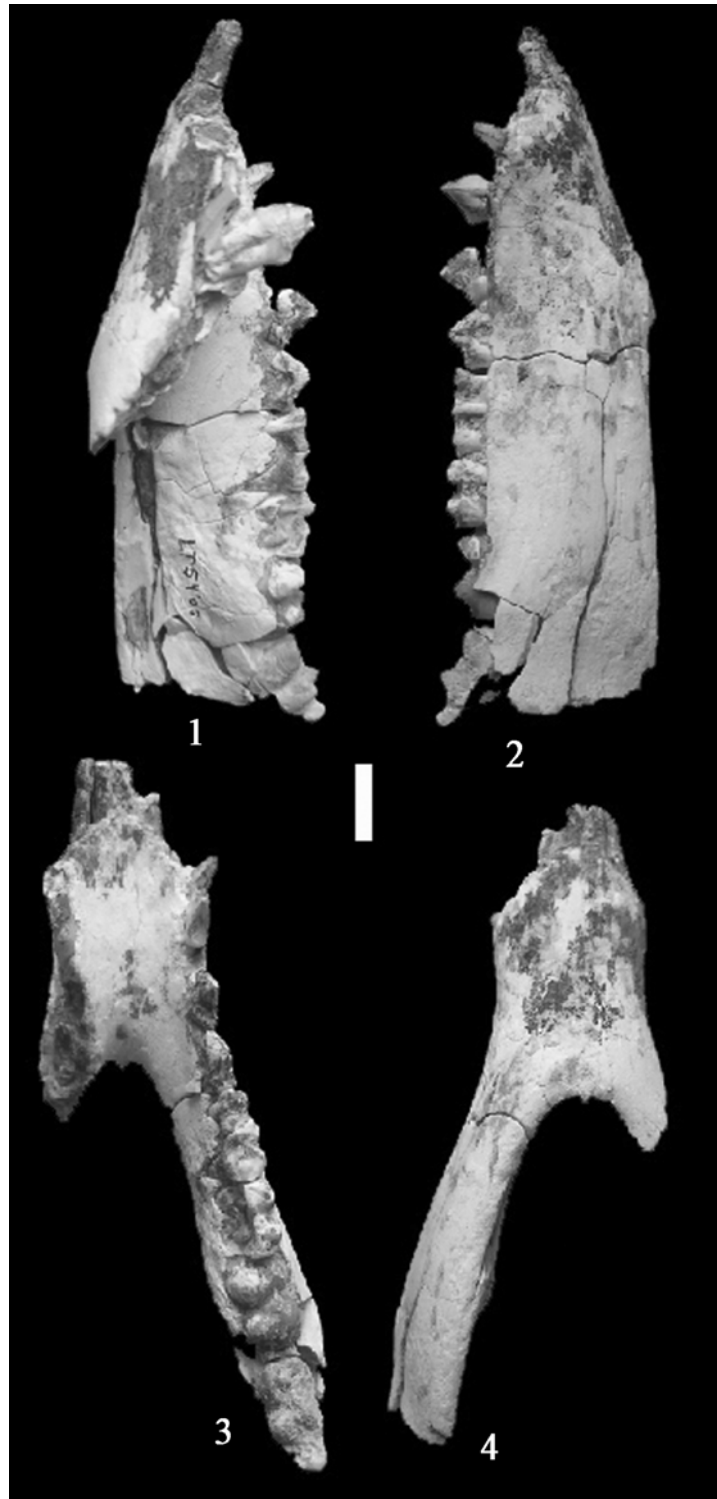


Plate 5. LT 51'05, right mandible of *Nguruwe namibensis* from Langental, Namibia (scale 1 cm). 1. Lingual view, 2. Buccal view, 3. Occlusal view, 4. Ventral view.

A summary of the suid collection from the Northern Sperrgebiet is given in table 4.

Acknowledgements

I thank B. Senut and other members of the Namibia Palaeontology Expedition for all their hard

work in the field and laboratory. Funding for this expedition was provided by the Collège de France, the Muséum national d'Histoire naturelle, Paris, the CNRS, the French Mission of Cooperation in Windhoek, Namdeb, and the Geological Survey of Namibia. Research authorisation was accorded by the Namibian National Monuments Council, and access

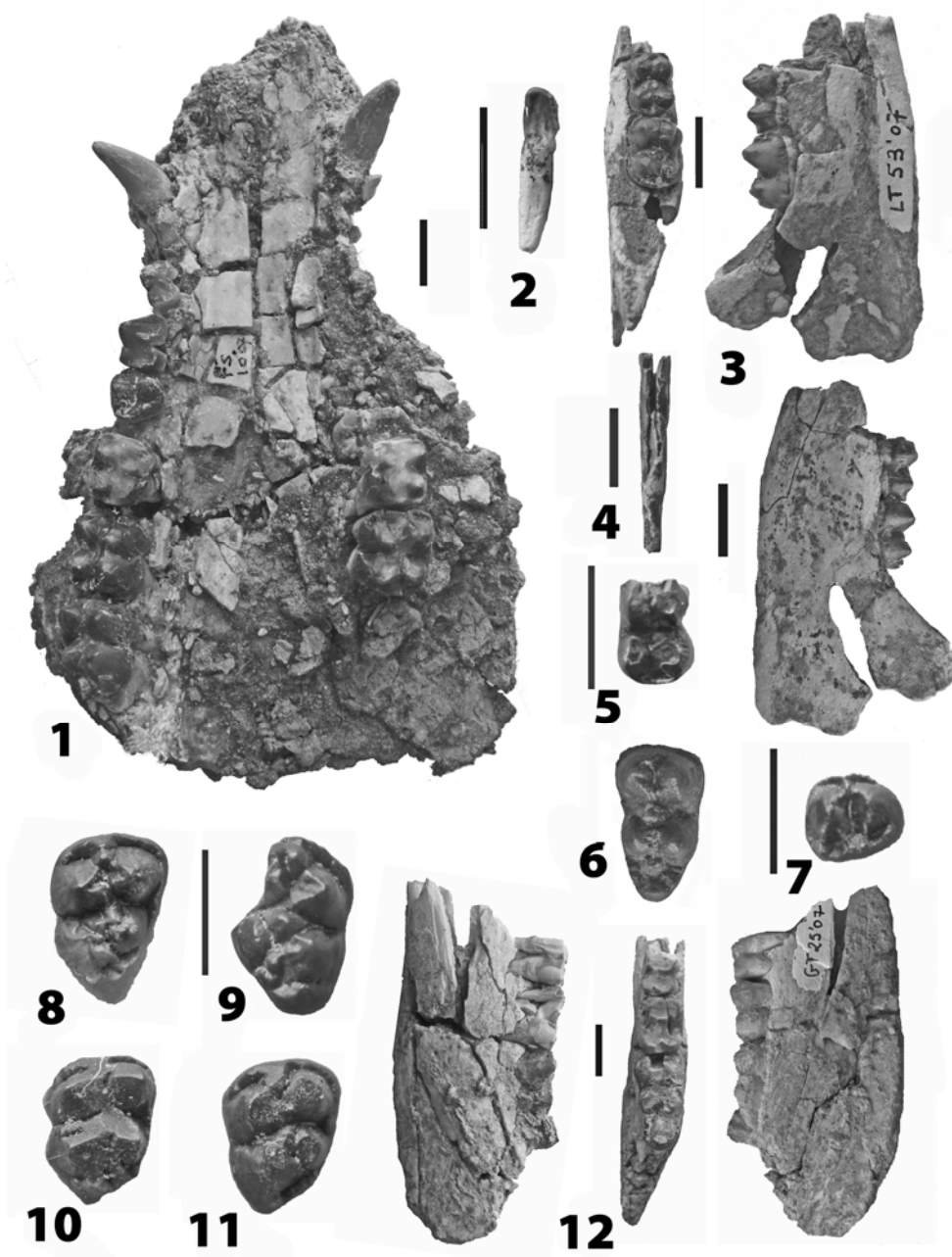


Plate 6. *Nguruwe namibensis* from the Northern Sperrgebiet, Namibia (scales : 1 cm).

FS 10'07, crushed snout with cheek dentition, occlusal view, 2. LT 107'07, right di/2, lingual view, 3. LT 53'07, left mandible with m/1-m/3 (Fig. 6) occlusal, buccal and lingual views, 4. LT 61'07, right i/2, lingual view, 5. LT 105'07, rear 2/3 of right dm/4, occlusal view, 6. LT 53'07, left m/3 from mandible (Fig. 3) occlusal view, 7. LT 82'07, right P4/, occlusal view, 8. LT 82'07, right M3/ occlusal view, 9. LT 83'07, left M3/ occlusal view, 10. LT 118'07, left M3/, occlusal view, 11. LT 117'07, left M3/, occlusal view, 12. GT 25'07, left mandible, buccal, occlusal and lingual views.

to the Sperrgebiet by Namdeb.

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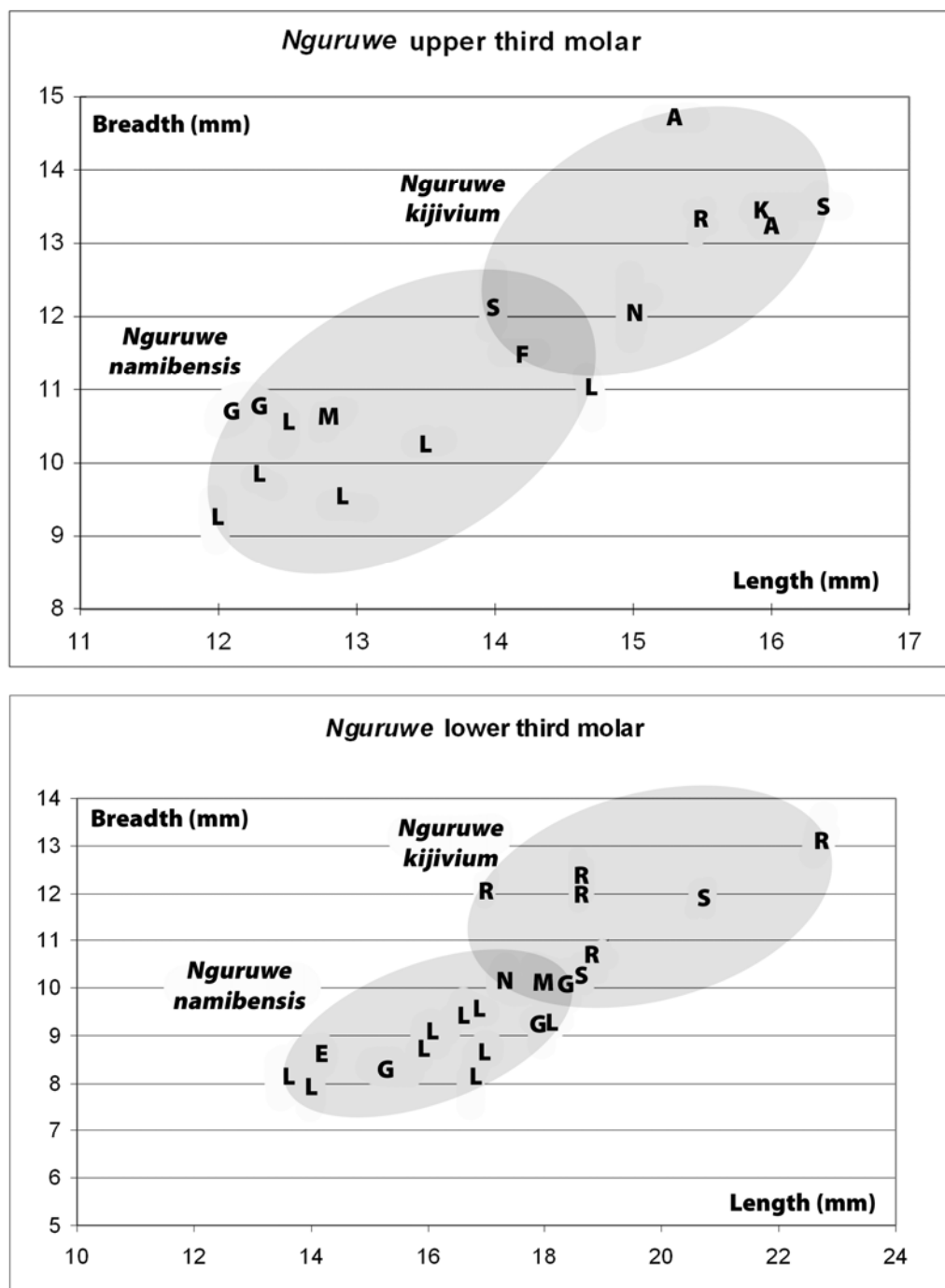


Plate 7. Bivariate plots (in mm) of upper and lower third molars of *Nguruwe namibensis* and *Nguruwe kijivium* from Namibia and East Africa. (A = Arrisdrift; E = Elisabethfeld; F = Fiskus; G = Grillental; K = Koru (Legetet); L = Langental; M = Mfwangano; N = Napak; R = Rusinga; S = Songhor).

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