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**GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND
SOUTHERN NAMIB**

**VOLUME 2:
PALAEOONTOLOGY OF THE ORANGE RIVER VALLEY,
NAMIBIA**

by

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Orangemeryx hendeyi

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by

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Suidae from the Middle Miocene of Arrisdrift, Namibia

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158 craniodental and about 50 postcranial specimens of suids have been excavated from Arrisdrift, southwestern, Namibia. Two species are represented in the sample, *Namachoerus moruoroti* (121 craniodental specimens) and *Nguruwe kijivium* (37 craniodental specimens), both of which also occur in early and basal Middle Miocene sites in East Africa. In East Africa these species have not yet been found in the same localities, *N. kijivium* being confined to Faunal Sets PI and P1/ (ca 20-17.5 Ma), whereas *N. moruoroti* is recorded from Faunal Set PIIIa (17.2-16 Ma). Their co-occurrence at Arrisdrift suggests an age of ca 17.5 Ma for the Namibian site. The Arrisdrift sample of *N. moruoroti* is far more comprehensive than any of the East African collections of the species and throws a great deal of light on the its cranial and dental anatomy. *N. moruoroti* may have descended from the diminutive kubanochoere *Nguruwe namibensis* (ca 21 Ma) by increase in lophodonty, outward bowing of the base of the mandible and slight increase in size. The lineage is not close to Listriodontinae as previously thought, and it did not give rise to *Lopholistriodon*. The sample of *Nguruwe kijivium* from Arrisdrift is the best known of the species, but it is dominated by juvenile specimens. In all material respects the Namibian *Nguruwe kijivium* fossils accord well with samples from East Africa and any doubts about conspecificity that there may have been can now be removed.

Version française abrégée

Introduction

Le site de la base du Miocène moyen d'Arrisdrift dans le sud de la Namibie a livré des restes abondants de deux espèces de suidés : *Namachoerus moruoroti* et *Nguruwe kijivium*.

Le namachoeriné *Namachoerus moruoroti* est connu par plusieurs maxillaires, mandibules et os postcrâniens. Les restes crâniens montrent que c'était un suidé à museau court, dépourvu de diastème aussi bien à la mâchoire supérieure qu'à l'inférieure. Il possédait la denture complète d'euthérien. La mandibule indiquait la présence d'un dimorphisme sexuel portant sur la profondeur mandibulaire bimodale, par contre les canines sont identiques et leur répartition unimodale. *Namachoerus* est bien mieux représenté en Namibie qu'en Afrique de l'Est où il fut décrit pour la première fois. Il s'avère que les suidés lophodontes d'Afrique de l'Est doivent être révisés car on trouve quelques confusions au sein des espèces *Namachoerus moruoroti*, *Lopholistriodon pickfordi*, *Lopholistriodon kidogosana* et *Lo. akatidogus*. Il est maintenant prouvé que *Lo. kidogosana* est un listriodonte qui ne descend pas de *N. moruoroti* comme on le pensait mais bien d'un *Listriodon*. *Namachoerus moruoroti* devait peser entre 14 et 20 kg et sa dentition lophodonte indiquait que c'était probablement un folivore.

Le petit kubanochoeriné, *Nguruwe kijivium*, est bien représenté à Arrisdrift par un museau, des maxillaires, des mandibules, des dents isolées et quelques os. Les fossiles d'Arrisdrift sont voisins par la taille et la morphologie de ceux de la localité type (Napak, Ouganda) ainsi que d'autres localités du Miocène inférieur de l'Afrique de l'Est. La dentition est bunodonte, la formule dentaire est complète, il n'y a aucun diastème, ni maxillaire, ni mandibulaire. Donc, *N. kijivium* était un suidé primitif au museau court qui n'avait probablement pas encore développé la technique du fouissage des suidés ultérieurs à long museau. Son régime consistait probablement en fruits, petites noix, insectes et d'autres nourritures variées trouvées sur le sol. Sa masse corporelle peut être estimée entre 30 et 38 kg.

La présence simultanée de ces deux suidés à Arrisdrift fournit des indications précieuses sur l'âge de la faune. En Afrique de l'Est *N. kijivium* est connu de nombreux dépôts s'étageant de 20 à 17.4 Ma tandis que *Namachoerus moruoroti* n'est connu que de dépôts plus jeunes compris entre 17.2 et 15.5 Ma. La période de recouvrement de ces deux taxa présents à Arrisdrift suggère un âge de 17 à 17.5 Ma pour les dépôts proto-Orange.

Excavations at the basal Middle Miocene site at Arrisdrift, Orange River Valley, southwestern Namibia in 1976 and from 1994 to 2000, have resulted in the collection of some 10,000 fossil vertebrate specimens. Among these there are over 200 suid fossils which form the subject of this paper.

Systematic Descriptions

Family Suidae Gray, 1821

Subfamily Namachoerinae Pickford, 1995

Genus *Namachoerus* Pickford, 1995

Species *Namachoerus moruoroti* (Wilkinson, 1976)

Type species: *Lopholistriodon moruoroti* Wilkinson, 1976.

Distribution: Moruorot (Kenya), Arrisdrift (Namibia). Maboko (Kenya), needs verification.

Descriptions: **Maxilla.** A right maxilla with much of the cheek dentition, AD 557'94, (Pl. 1, Fig. 5-6) was described in detail by Pickford (1995). The important points about this specimen, which led to the erection of the genus *Namachoerus* and the subfamily Namachoerinae, and the removal of this taxon from Listriodontinae, are its small size, the short snout and the lack of diastemata behind the canine and only a short one anterior to it. All listriodonts, including the most primitive, bunodont forms from the base of the Middle Miocene in Europe and Asia, are large suids with elongated snouts and extended diastemata behind the canines. The anterior part of a snout with the incisors and canines, PQ AD 138, (Pl. 2, Fig. 1-4) was described in detail by Pickford (1987). The most important point about this specimen is that it reveals that the upper central incisor is antero-posteriorly elongated, possesses a sharp lingual cingulum, has no lingual ridge and is considerably larger than the second upper incisor. In this specimen the upper incisors are worn, but in other examples, the cutting edge of the central incisor is subdivided by three or four crenulations (Pl. 1, Fig. 7-8), much as in Listriodontinae, but these wear away with moderate abrasion. For example, upper central incisor, AD 570'00, which lacks the mesial corner but is otherwise complete and lightly worn, possesses a crenulated cutting margin of the crown. There is a well developed lingual cingulum, but no lingual pillar.

PQAD 136, a left maxilla with P4/-M3/ (Pl. 2, Fig. 5-6) may be from the same individual as the snout, but there is no contact between the two pieces. The fourth premolar has a well developed anterior loph from the ends of which crests descend distally, forming low walls to a distal fovea. The molars are bilophodont with prominent crests leading anteriorly from the distal loph into the median transverse valley.

A juvenile maxilla with three milk teeth and the first permanent molar, AD 252'96, provides the first useful information about the upper deciduous dentition of *Namachoerus moruoroti*. The dM2/ has an ovoid occlusal outline, narrower mesially than distally. It consists of a single cusp with a sharp distal and labial cingulum. The dM3/ has a rounded triangular occlusal outline and consists of three cusps, one anteriorly surrounded labially, mesially and lingually by a sharp cingulum, and two distally forming a loph which is also bordered labially and lingually by a cingulum. The dM4/ is quadricuspidate and, except for its thinner enamel, looks like a reduced version of the upper first molar. It too possesses a sharp labial cingulum. The upper first molar is bilophodont with strong crests running from the tips of the lingual cusps into the median and posterior transverse valleys. There is a sharp cingulum encircling the crown anteriorly, labially and posteriorly, with remnants on the lingual surface.

Mandible. The mandibles of *Namachoerus moruoroti* (Pl. 1, Fig. 1-4; Pl. 2, Fig. 7-10) differ from those of listriodonts by being short and having no post-canine or precanine diastemata, and their ventral borders are curved (bowed outwards). The rear of the symphysis lies below the third premolar in contrast with listriodonts in which it is relatively further forwards, being below the anterior edge of the second premolar.

AD 61'00, a fragment of left mandible, preserves much of the ascending ramus but lacks the coronoid process. The condyle is located about 16 mm above the occlusal surface of the cheek teeth and is 43 mm above and behind the posterior end of the third molar. The mandibular foramen is 14 mm directly posterior to the m/3. The jaw is 22 mm deep below the third molar measured from the alveolar margin to the base of the body on the lingual side and is 9.5 mm thick. There is a long retromolar space, the ascending ramus not hiding the cheek teeth in lateral view as it swings upwards from the body from just behind and below the posterior end of the third molar.

AD 62'00, a right mandibular body contains lightly worn p/4-m/3. The mandibular foramen lies 16 mm behind the posterior end of the third molar. The root of the ascending ramus emerges from the body below the second loph of the m/3 and swings up well behind the posterior end of the tooth, not hiding any portion of it in lateral view. The mandible is 21.3 mm deep below the m/3 and 20.6 mm below the p/4. At m/3, the jaw is 12 mm thick.

AD 345'00 is a mandible with poorly preserved left m/2-m/3 and the root of the left canine. The interest of the specimen lies in the fact that the symphysis is almost complete and undistorted. The incisor alveoli are abraded labially and reveal that the first and second incisors were long rooted, while the third incisor possessed a short root. There is no diastema, either in front of or behind the canine. In superior aspect the symphysis is slightly spatulate, with only a moderate flare of the body at the level of the canines. The symphysis extends rearwards as far as the third premolar. A large mental foramen

occurs below the p/2 about two thirds of the height of the body. A second, smaller foramen occurs below the p/3. The genial spine is well developed and is bordered by prominent genial fossae. In ventral view the base of the mandible is seen to be markedly curved, the margin swinging sagittally below the third molar to form a voluminous sublingual *fossa*. The ascending ramus departs from the body just behind the m/3. Measurements of the mandibles are given in Table 1.

Table 1: Measurements of the mandible of *Namachoerus moruoroti* from Arrisdrift, Namibia.

Anatomy	Measurement (mm)
Length of the symphysis	31.5
Thickness of the symphysis	11
Breadth of the symphysis at the canines	26.1
Breadth of the symphysis at the p/3	25
Depth of body below p/4	18
Depth of body below m/3	22.1
Thickness of body at m/3	12

Sexual dimorphism in *Namachoerus moruoroti* from Arrisdrift. The depth of the mandibles of *Namachoerus moruoroti* from Arrisdrift is quite variable, with two peaks towards the high end of the range of variation, probably representing males and females respectively. The lower end of the range probably represents young individuals and small females. Measurements (in mm) of the depth of the mandible below the anterior end of the third molar taken from the alveolar margin to the ventral border of the body, are as follows (N = 19).

Dentition: There is no need to redescribe the dental charac-

Table 2: Measurements (in mm) of jaw depth below the third molar of *Namachoerus moruoroti* from Arrisdrift.

Specimen	Jaw depth below m/3
AD 524'94	19.9
AD 549'94	24.6
AD 620'94	24.6
AD 266'95	21.0
AD 344'95	19.6
AD 82'96	23.4
AD 83'96	22.5
AD 142'96	24.6
AD 143'96	25.5
AD 320'96	24.5
AD 946'97	23.9
AD 345'98	22.4
AD 527'98	24.7
AD 528'98	20.2
AD 568'98	18.6 (juvenile)
AD 88'99	22.4
AD 61'00	22.1
AD 62'00	21.7 (young)
AD 345'00	21.9

ters of this species, since a full description was provided by Pickford (1995). A few notes are made about variability in canines, molars and cusp morphology. Appendices I and 2 provide measurements of all the teeth found at Arrisdrift.

Canine variability in *Namachoerus moruoroti* from Arrisdrift. Many taxa of suids possess dimorphic canines in which the females have low crowned, short canines and males have extremely hypsodont, permanently growing tusches. However, in some suids such as the wart hog (*Phacochoerus*), both sexes possess hypsodont canines, but even in these, the females

Table 3: Dental representation of Namachoerinae in Namibia and Kenya
AD = Arrisdrift, MO = Moruorot

	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3	dI1	dI2	dM2	dM3	dM4
Lower																
AD	9	10	2	14	-	2	1	9	12	17	25	2	3	1	2	5
MO	-	-	-	-	-	-	-	1	3	3	2	-	-	-	-	-
Upper																
AD	6	3	-	6	1	2	2	4	8	9	9	1	-	2	1	2
MO	-	-	-	-	-	-	1	1	1	2	1	-	-	-	-	-

tend to possess smaller canines than the males. 13 lower canines and 6 upper canines of *Namachoerus* are known from Arrisdrift. All the lower canines are hypsodont, and a bivariate plot of anteroposterior length against labiolingual breadth does not produce two variation fields, but a single cluster of points. This suggests either a) that the collection only contains male canines, or b) that both male and female canines of *Namachoerus* were hypsodont and that the sexes cannot be differentiated on the basis of the canine dimensions. The latter explanation is probably the correct one.

The six upper canines from Arrisdrift (Pl. 2, Fig. 1-4; Pl. 3, Fig. 2) are morphologically similar to each other and a bivariate plot of greatest diameter versus minimum diameter does not result in a separation into two variation fields. From the above we conclude that *Namachoerus moruoroti* at Arrisdrift did not possess sexually bimodal or dimorphic canines.

Variation in lower third molars of *Namachoerus moruoroti* from Arrisdrift. There are 28 lower third molars in the Arrisdrift sample of *Namachoerus moruoroti*, of which 24 can be measured accurately, the others being broken or warped. Examination of the specimens reveals that most of the variation occurs in the talonid cusp, with the longest teeth corresponding to material with the longest talonids. However, there is a tendency for the longest teeth to be wider on average than the shorter teeth, although there is substantial overlap in the variation of the breadths. It is possible that the longer specimens represent males and the shorter ones females, but the evidence is not clear-cut, since the third molars of suids are not usually sexually bimodal.

Variation in cusp morphology in *Namachoerus moruoroti* from Arrisdrift. There is a relatively wide range of variation in cusp morphology in the molars of *Namachoerus moruoroti* from Arrisdrift. Many of the specimens are extremely lophodont, with very slight development of the anterior, median and posterior accessory cusplets, although all of the molars possess crests that lead onto the centre point of the anterior cingulum and into the centre of the median transverse valley. However, there are several specimens, especially among the smaller individuals, in which accessory cusps are not only present but also form a distinct cusplet rather than a crest. In all other features, several of which are in mandibles, these individuals are close in morphology and size to the fully lophodont specimens, and it is concluded that the differences represent part of the normal range of morphological variation in the species.

What is interesting about this kind of variation is that it throws light on the possible ancestral relationships of the genus. Comparison with early Miocene suids from Africa reveals that the most likely group from which *Namachoerus* evolved was *Nguruwe namibensis*. In particular, the complete

mandible of this species from Elisabethfeld (Pickford, 1997) shows several basic similarities between the two genera, including small size, relatively simple molar cusps without deep furchen, slightly splayed canine orientation, lack of post-canine diastemata and large innenhugel in the lower p/4. If the Elisabethfeld species became a little bit more lophodont and reduced the size of the anterior, median and posterior accessory cusps, then it would closely resemble *Namachoerus*. An additional change would be necessary, the ventral border of the mandible in *Namachoerus* being markedly more bowed outwards than is that of *Nguruwe*.

Discussion: The representation of *Namachoerus* at Arrisdrift is much more comprehensive than it is at any of the East African localities from which it has been reported (Pickford & Wilkinson, 1975; Pickford, 1995; Van der Made, 1996).

The completeness of the Arrisdrift sample permits a critical review of the material from Kenya previously assigned to *Namachoerus* and *Lopholistriodon*. Van der Made (1996) recognised four species of *Lopholistriodon*, of which three (*L. pickfordi* (partim), *L. kidogosana* and *L. akatidogus*) are genuine listriodonts, and one (*L. moruoroti*) has since been assigned to the genus *Namachoerus* Pickford, 1995, in the subfamily Namachoerinae.

Moruorot, Kenya (17.2 Ma): Morphologically and metrically, the small sample of *Namachoerus moruoroti* from Moruorot, the type locality, is extremely similar to the material from Arrisdrift. All the Moruorot teeth plot near the centre of the range of variation of the Arrisdrift fossils and there can be little doubt that the two samples represent the same species.

Maboko and Majiwa, Kenya (ca 15 Ma): The Maboko and Majiwa fossils identified by Van der Made (1996) as *Lopholistriodon moruoroti* are heterogeneous. Some of them do not belong either to Listriodontinae or to Namachoerinae but to a schizochocerine tayassuid (Pickford, 1998). Bivariate plots of the Maboko specimens reveal that some of the specimens fall well outside the range of variation of the Arrisdrift sample, generally because they are considerably narrower. Examination of these fossils, for example KNM MB 15114 (left M3/), KNM MB 10287 (right M2/) and KNM MB 14489 (left M2/), reveals that they are morphologically close to *Lopholistriodon kidogosana* from Ngorora, Kenya. The lophs are perfectly formed with no trace of a mesiodistal sulcus, and the anterior, median and posterior accessory cusps are completely suppressed leaving the wide transverse valleys unobstructed, contrasting with the imperfect lophodonty of *Namachoerus moruoroti*, in which moderately sized accessory cusps and crests lead into the transverse valleys, thereby

partly obstructing them in lateral view. There are several fossils that fall within the range of metric variation of *Namachoerus moruoroti*, but further study of their morphology is required to verify the presence of this species at the site.

Upper incisors From Majiwa which provided the main characters for diagnosing the species *Lopholistriodon pickfordi* are excluded From both Namachoerinae and Listriodontinae because they differ markedly From the 6 upper central incisors in the Arrisdrift collection and From listriodont incisors in general.

West Stephanie, Kenya (17.2 Ma): Van der Made (1996) described a species of *Lopholistriodon* (*L. pickfordi*) From West Stephanie (the type locality), and assigned to the same species material From Majiwa, Nyakach, and Maboko, all sites in Kenya. Among the characters which were used to diagnose this species was the upper central incisor with one lobe, and its slightly larger size compared to *N. moruoroti*. There is also a tendency for the molars to be sublophodont rather than lophodont, although the latter feature does not figure in Van der Made's diagnosis of the species but only in the text. The upper incisors assigned to this species have subsequently been assigned to *Morotochoerus ugandensis* (Pickford, 1998). Bivariate plots of the few cheek teeth assigned to *L. pickfordi* reveal that some of them fall within the upper part of, or above, the range of variation of the Arrisdrift *N. moruoroti* population. Some of the fossils assigned to *L. pickfordi*, especially the specimens from Nyakach, suggest affinities with *Lopholistriodon kidogosana* From Nggora.

Muruyur (Kenya) (15.2 Ma): A few fossils From the Muruyur Formation, Tugen Hills, Kenya, assigned to *Lopholistriodon moruoroti* by Van der Made (1996) differ From this species in several ways. The upper central incisor (KNM MY 25) is single lobed and has a bulbous labial surface and a prominent lingual pillar, quite unlike the corresponding tooth in the Arrisdrift sample of this species. It was re-assigned to the Old World Tayassuidae (Pickford, 1986) by Pickford (1998) in the species *Morotochoerus ugandensis*. An upper third molar From Muruyur (KNM MY 68) possesses a deep mesiodistal sulcus which separates the lingual cusps From the labial ones, unlike the almost continuous crest-like loph that occurs in *Namachoerus*. It too was assigned to *Morotochoerus* by Pickford (1998). Thus the species *N. moruoroti* is not present in available collections From Muruyur.

Subfamily Kubanochoerinae Gabunia, 1958
Genus Nguruwe Pickford, 1986
Species Nguruwe kijivium (Wilkinson, 1976)

Type species: *Hyotherium kijivium* Wilkinson, 1976

Distribution: Napak (Uganda), Rusinga, Songhor, Mfwanganono, Locherangan, Mteitei Valley, Koru, Legetet (Kenya), Ryskop (South Africa), Arrisdrift (Namibia).

Descriptions: Skull. AD 90'99 is a snout with left P2/-M3/ and right P3/-M1/ (Pl. 4, Fig. 1-4). It lacks the tip of the snout anterior to the P1/ and most of the neurocranium is missing.

In anterior view (Pl. 4, Fig. 4) the snout section is rectan-

gular with rounded superior corners. At the level of the first premolars the rectangle is slightly taller than it is broad and its height increases regularly towards the rear, unlike the situation in long-snouted suids in which the dorsal surface of the nasals rises only slightly to the rear. The palate is virtually flat throughout its preserved extent.

In lateral view (Pl. 4, Fig. 3) the angle between the palate and the dorsal surface of the snout is clearly evident. The infraorbital foramen is located above the anterior end of P4/. The anterior root of the zygomatic arch starts as a low crest located above the P4/, immediately above and behind the infraorbital foramen, From where it leads directly backwards to merge with a massive arch that sweeps outwards above the molar row. This anterior crest separates the superior and inferior muscle origins for the snout musculature, but it is not as well defined as it is *Sus* for example which suggests that the snout muscles in *Nguruwe* were relatively poorly defined. The zygomatic arch is thick below the orbit, the anterior margin of which is located above the M2/, which contrasts markedly with the condition in *Sus*, in which the orbit is behind the third upper molar. The ventral border of the zygomatic arch is lowest at the level of M2/ where it is only a few mm above the alveolar margin. The rear edge of the anterior root of the zygomatic arch is located above the midline of the M3/. Damage to the orbital margin makes it difficult to discern the antorbital foramen with certainty, but it could be represented by a hole on the internal rim of the orbit.

In dorsal view (Pl. 4, Fig. 2), the upper surface of the snout is relatively flat from side to side and From in front towards the back. It is marked by two prominent grooves which anteriorly descend the lateral surface of the snout above the P3/, and which posteriorly enter two supraorbital foramina, which in this individual are offset From one another, the left one being forwards of the right one.

In palatal view (Pl. 1, Fig. 1), the lingual edges of the two tooth rows are almost parallel From the P1/ to the M2/ whereupon they converge slightly to the rear. Just to the lingual side of the alveolar process there is a palatine groove which enters the anterior palatine foramen opposite the rear of the first molar. In *Sus* the foramen is at the rear of the M2/. A small part of the roof of the braincase is preserved between the anterior parts of the two orbits. There are no diastemata between the P1/ and the M3/. The overall construction of the Arrisdrift fossil reveals that *Nguruwe kijivium* was a short-snouted suid, with anteriorly positioned orbits and zygomatic arches, no diastemata between the cheek teeth and anteriorly positioned palatine foramina, in stark contrast to long-snouted forms such as *Sus*. As a result of this, the dorsal surface of the snout rises more steeply towards the rear than it does in *Sus*.

PQAD 1795 is an unworn right M3/ (Pl. 3, Fig. 1) which shows the simple bunodont condition of the molars in this species, recalling those of European and Asian *Hyotherium* species. The crown is composed of four main cusps with a very reduced talon and large anterior, median and posterior accessory cusps, thick enamel and shallow furchen.

Upper dentition. (See appendix 4 for measurements). The upper central incisors are relatively short mesiodistally and the labial surface is bulbous, as in material From Songhor and Napak. There is a prominent lingual ridge.

An upper right I3/ AD 239'00, has a prominent main cusp with a distal ridge extending towards a small cusplet which

overhangs the root. There is a strong buccal and lingual cingulum.

The upper P1/ was a two rooted tooth in contact with the second premolar. The P2/ has a prominent main cusp with small anterior and posterior cingula, the distolingual corner of the tooth sporting a small cusp let. The P3/ is a larger version of the second premolar and its distolingual cusp let is more clearly defined and relatively larger. The P4/ is comprised of two large cusps, one labial the other lingual. Wear has removed much of the evidence of the original morphology of the buccal cusp, but indentations in its outline suggest that it may originally have been made up of two cusps closely fused together. There are well developed anterior and posterior cingula which close off the ends of the anteroposterior valley between the two principal cusps. The first molars are heavily worn and little detail can be made out. However, they consist of two lophs separated by the median transverse valley, each loph originally being comprised of two cusps. The second upper molar is also quite deeply worn but the four principal cusps can be distinguished although their morphology has been abraded away. There is no sign of a lingual cingulum. The third upper molar is only slightly worn and consists of four main cusps arranged in two lophs, the posterior one being narrower than the anterior one on account of the reduced size of the hypocone. There is a poorly developed and low distal cingular complex attached to the metacone and a low cingular remnant on the anterolingual corner of the paracone which is confluent with the anterior cingulum. The anterior, median and posterior accessory cusp lets are small.

AD 314'94 is a left maxilla fragment with P4/-M2/ (Pl. 4, Fig. 5-6) less worn than their counterparts in AD 90'99 described above. The specimen is slightly smaller but is otherwise similar in its preserved parts to that specimen.

AD 784'97 is a juvenile left maxilla with dm3/-dm4/ and M1/. The dm3/ has a tricuspid crown with a triangular occlusal outline, comprised of a large anterior cusp with two slightly smaller cusps forming a distal loph. The dm4/ is trapezoidal in occlusal outline, resembling an upper molar save for the thinner enamel and the reduced breadth of the posterior loph due to the small size of the metacone. The M1/ is broken distally but resembles other first molars assigned to the species in being bunodont with narrow transverse median valley and small anterior, median and posterior cusplets.

Mandible and lower dentition. (see appendix 3 for measurements). AD 89a'99 is a juvenile right mandible with dm/3-dm/4 and m/1. AD 313'94 is a juvenile right mandible with the three posterior milk teeth and the first permanent molar (Pl. 3, Fig. 6) and AD 240'98 is a juvenile mandible with both

branches and the symphysis (Pl. 3, Fig. 5). There are other mandibular specimens in the sample from Arrisdrift (Pl. 3, Fig. 3-4) but they are all very similar and can be described together.

The lower incisors in AD 240'98 (Pl. 3, Fig. 5) are still in their crypts, but were excavated for study and then returned. The central lower incisor is more bilaterally symmetrical than the second incisor, but the crowns of the two teeth are almost the same height and the mesial and distal margins are almost parallel to each other. The bases of the crowns are swollen on the lingual surface to produce a prominent boss but not a cingulum. There is a central ridge on the lingual aspect of the crown.

The tip of the unerupted lower canine is visible in AD 301'00. It appears to be scrofic, but no measurements could be taken without damaging the specimen.

The dm/2 is a unicuspid tooth with a swollen distolingual corner and an anterior cingulum. It has two roots. The dm/3 is a larger version of the preceding tooth with a correspondingly enlarged distolingual swelling. The dm/4 has six cusps arranged in three lophs, as is usual in artiodactyls. The cusps are bunodont and the enamel is relatively thin. The furchen are well expressed but not deeply incised. The crown broadens distally. The lower first molar is quadricuspidate and bilophodont with clear anterior, median and posterior accessory cusplets. The median transverse valley is not very wide and the anteroposterior valley is shallow and narrow, all features typical of the genus *Nguruwe*.

Discussion: Unworn lower first and second incisors occur in their crypts in mandible AD 240'98 of *Nguruwe kijivium*. When they are compared with the lower incisors in mandible AD 568'98 of *Namachoerus moruoroti* (Pl. 1, Fig. 1), it is clear that, although somewhat similar in size, their morphology is quite different. In *Nguruwe*, the base of the incisors possess well developed lingual swellings which lead apically to produce lingual pillars whereas those of *Namachoerus* are concave or possess only slight swellings and no lingual pillars. The enamel of the *Nguruwe* incisors is thicker than that of *Namachoerus*. The second incisors of *Namachoerus* possess a scoop shaped distal margin, whereas those of *Nguruwe* are more parallel sided. In both genera, the incisors are tall and possess long roots.

A feature of the Arrisdrift sample of *Nguruwe* is that it is dominated by juvenile specimens. In suid collections the lower third molar is usually the commonest tooth, yet it is unknown at Arrisdrift. Out of 37 specimens from Arrisdrift assigned to *N. kijivium*, 14 are juvenile individuals with milk teeth.

Table 4: Measurements (in mm) of the snout of *Nguruwe kijivium*, AD 90'99.

P1/-M3/	76
Palatal breadth between P2/s	23.7
Palatal breadth between M1/s	24.7
Palatal breadth between M3/s	ca 20
Distance between alveolar border and lowest part of zygomatic root	7
Distance between the inferior margin of infraorbital foramen above alveolar border	7.6
Distance between anteriormost points of the orbits	48
Snout breadth above the infraorbital foramina	34
Breadth of snout at zygomatic arches above M2/	2 x 43.5 = 87
Height of snout above P1/	28
Height of snout above M3/	61
Dorsoventral thickness of zygomatic arch above M2/	20.5

Table 5: Numbers of teeth of *Nguruwe kijivium*.

(RU = Rusinga, SO = Songhor, Nap = Napak, MW = Mfwangano, LC = Locherangan, MV = Mteitei Valley, KO = Koru, LG = Legetet, RK = Ryskop, AD = Arrisdrift)

	I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3	dI1	dI2	dM2	dM3	dM4
Lower																
RU	-	1	-	-	-	-	-	1	1	3	5	-	-	-	-	-
SO	-	-	-	1	1	-	1	2	4	2	6	-	1	1	1	4
Nap	-	1	-	1	-	-	-	-	2	2	1	-	-	-	-	1
MW	-	-	-	-	-	-	-	-	1	4	2	-	-	-	-	1
LC	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	1
MV	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
KO	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
LG	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
AD	5	3	2	-	2	-	-	-	7	3	-	-	1	3	4	7
Upper																
RU	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-
SO	2	1	-	3	3	1	-	2	3	3	2	-	-	2	2	1
Nap	1	-	-	-	-	-	-	-	1	1	2	-	-	-	-	-
MW	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-
KO	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
LG	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
RK	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
AD	2	-	1	-	-	1	3	5	4	2	2	1	-	-	2	2

The Arrisdrift specimens of *Nguruwe kijivium* are morphologically and metrically close to material from the type locality (Napak, Uganda) and other East African localities (Songhor, Mfwangano, Rusinga). There can be little doubt that the same species occurs in both parts of the continent.

Morphologically, the Arrisdrift fossils are close to material of *Nguruwe namibensis* from the early Miocene sediments at Langental and Elisabethfeld in the northern part of the Sperrgebiet, but they differ from these specimens by their superior size. One can postulate a rather direct ancestor-descendant relationship between the two species.

Body weight estimates

Scaling of upper first and second molars against the same teeth in *Sus scrofa*, which has a body weight ranging between 60 and 100 kg (Haltenorth & Diller, 1980), suggests that the mean body weight of *Namachoerus moruoroti* would have been about 14 to 20 kg. Similar scaling of the first and second upper molars of *Nguruwe kijivium* suggest that its mean body weight ranged between 30 and 38 kg.

Biochronology

The known chronological range of *Nguruwe kijivium* in East Africa is from ca 20 Ma to ca 17.5 Ma (Songhor, Kenya and Napak, Uganda to Locherangan and Rusinga, Kenya) (Faunal Sets PI to PII). *Namachoerus moruoroti* is much rarer in Kenya, but is known from the type locality (Moruorot, ca 17.2 Ma) (Faunal Set PIIIa) and has been reported to occur at Maboko and other sites in Western Kenya (ca 15 Ma) (Faunal Set PIIIb), but there is some doubt about the generic status of

the latter fossils, and they may well represent *Lopholistriodon* rather than *Namachoerus*. From the co-occurrence of the two species at Arrisdrift, Pickford (1995) estimated an age of ca 17.5 Ma for the site. The analysis carried out in this paper tends to confirm this estimate, especially since some of the Maboko fossils previously assigned to *Namachoerus moruoroti* have now been removed and the rest need to be re-examined.

Palaeoecology and Palaeoenvironment

Namachoerus moruoroti is a small lophodont suid with wide upper central incisors and thin molar enamel. These are features indicating morphofunctional convergence with listriodonts, tapirs and other folivorous mammals, suggesting a comparable diet of soft leaves. *Nguruwe kijivium* in contrast, has thick enamelled, bunodont cheek teeth and poorly developed "rooting" musculature suggesting that its diet consisted mainly of relatively durable fruits, nuts and other "above ground" resources. There would thus not have been close ecological competition in these two suids which are both small (*Nguruwe kijivium* is slightly larger than *Namachoerus moruoroti*). Previous reconstructions of the palaeoenvironment at Arrisdrift suggest that it was considerably more wooded than it is today, being more akin to the Zambesian region than the present day Namib. The suids provide support for the view that the region was well wooded, perhaps even with forested patches along the river banks, with perennial supplies of leaves for *Namachoerus* and perhaps seasonal supplies of fruits and nuts for *Nguruwe*.

Conclusions

Arrisdrift, a fluvial deposit in the Orange River Valley, south-western Namibia, has yielded two species of suids, the diminutive kubanochoerine, *Nguruwe kijivium*, and the namachoerine, *Namachoerus moruoroti*. Morphometric comparisons with samples from Kenya and Uganda reveal no significant differences between the East African and Namibian material. It has been necessary, however, to remove several specimens from Maboko hitherto assigned to *Namachoerus moruoroti*, because they do not accord with this species either morphologically or metrically. This reduces the known chronological range of the species by eliminating material from Faunal Set PIIIb which indicates an age for Arrisdrift of about 17.5 Ma (latest Early Miocene to basal Middle Miocene). The Arrisdrift suids indicate the presence of well wooded to perhaps even forested conditions at or near the site at the time of deposition.

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Appendix 1: Measurements (in mm) of the teeth of *Namachoerus moruoroti* from Arrisdrift.

Tooth	Length	Breadth		
Lower teeth				
PQ AD 20(d), rt i/1	4.5	4.6	AD 297'99, right m/1	9.4
AD 685'94, right i/1	3.8	4.6	AD 61'00, left m/1	8.6
AD 360'95, left i/1	5.0	4.6	AD 62'00, right m/1	9.6
AD 270'96, left i/1	3.9	4.2	AD 542'94, right m/2	11.6
AD 878'97, right i/1	4.0	5.0	AD 549'94, right m/2	12.1
AD 945'97, right i/1	4.0	4.9	AD 620'94, right m/2	12.6
AD 567'98, left i/1	4.4	4.8	AD 528'95, right m/2	10.2
AD 294'00, left i/1	4.0	4.7	AD 266'95, left m/2	11.6
AD 116'00, right i/1	4.6	4.8	AD 82'96, right m/2	11.3
PQ AD 102, left i/2	4.5	5.0	AD 142'96, left m/2	10.4
PQ AD 1693, left i/2	4.3	4.8	AD 320'96, right m/2	11.0
AD 144'94, right i/2	4.9	5.5	AD 400'96, right m/2	11.0
AD 418'94, left i/2	4.0	4.8	AD 395'97, left m/2	9.9
AD 85'96, left i/2	5.0	4.1	AD 753'97, left m/2	9.4e
AD 440'97, right i/2	4.1	—	AD 783'97, right m/2	11.0
AD 945'97, left i/1	4e	4.8	AD 41'98, left m/2	12.6e
AD 558'97, left i/2	4.7	6.0	AD 527'98, left m/2	9.8
AD 944'97, left i/2	3.3	4.0	AD 567'98, left m/2	11.0
AD 567'98, left i/2	4.5	5.2	AD 88'99, right m/2	11.2
AD 622'98, right i/2	5.0	—	AD 297'99, right m/2	11e
AD 303'00, right i/2	4.6	5.5	AD 62'00, right m/2	12.0
PQ AD 1727, rt i/3	3.8	3.5	AD 61'00, left m/2	11.0
AD 431'99, left i/3	6.3	3.6	PQ AD 135, left m/3	13.9
PQ AD 2583, rt /c	7.0	4.1	PQ AD 636, left m/3	12.5
AD 316'94, right /c	5.8	3.6	PQ AD 2196, rt m/3	14.5
AD 542'94, right /c	6.4	3.9	PQ AD 2927, rt m/3	15.3
AD 620'94, right /c	6.9	4.2	AD 542'94, right m/3	14.3
AD 266'95, left /c	6.5	4.0	AD 549'94, right m/3	15.3
AD 330'95, right /c	8.3	4.8	AD 620'94, right m/3	16.3
AD 82'96, right /c	6.5	4.5	AD 266'95, left m/3	13.5
AD 83'96, right /c	7.6	5.3	AD 344'95, left m/3	14.0e
AD 142'96, left /c	6.8	4.8	AD 528'95, right m/3	14.1
AD 320'96, right /c	7.2	3.2	AD 82'96, right m/3	13.4
AD 527'97, right /c	6.0	4.0	AD 83'96, right m/3	—
AD 567'98, left /c	5.3	3.9	AD 142'96, left m/3	14.0
AD 88'99, right /c	5.4	3.4	AD 143'96, left m/3	14.0
AD 345'00, left /c	6.6	4.0e	AD 320'96, right m/3	12.4
AD 121'98, left /p	5.8	2.9	AD 159'97, left m/3	14.3
AD 142'96, left p/2	3.4	2.3	AD 600'97, left m/3	15.4
AD 683'00, rt p/1 or p/2	3.1	2.4	AD 783'97, right m/3	13.3
AD 142'96, left p/3	6.7	3.9	AD 946'97, left m/3	15.2
AD 549'94, right p/4	8.0	4.6	AD 345'98, right m/3	13.9
AD 82'96, right p/4	7.4	5.2	AD 527'98, left m/3	12.4
AD 320'96, right p/4	7.0	5.0	AD 528'98, left m/3	13.8
AD 142'96, left p/4	7.8	5.0	AD 567'98, left m/3	15e
AD 261'97, left p/4	8.4	5.3	AD 568'98, left m/3	13.7
AD 567'98, left p/4	7.5	5.0	AD 88'99, right m/3	13.5
AD 88'99, right p/4	8.0	4.7	AD 644'99, right m/3	15.4
AD 62'00, right p/4	8.5	5.6	AD 62'00, right m/3	15.0
AD 682'00, right p/4	7.7	5.1	AD 345'00, left m/3	14e
AD 74'94, right m/1	10.0	6.5	PQ AD 1697, rt di/1	3.1
AD 549'94, right m/1	9.1	6.3	AD 689'99, left di/1	3.0
AD 620'94, right m/1	10.6	6.7	AD 263'99, left di/1	3.1
AD 674'94, left m/1	10.5	6.8	PQ AD 1697, rt i/2	3.2
AD 263'95, right m/1	9.5	6.4	AD 944'97, left di/2	3.1
AD 82'96, right m/1	9.4	6.4	AD 524'99, left di/2	3.1
AD 142'96, left m/1	8.7	5.8	AD 121'98, left dm/2	5.5
AD 320'96, right m/1	8.0	6.0	AD 209'94, left dm/3	4.8
AD 395'97, left m/1	9.9	6.7	AD 674'94, left dm/3	5.6
AD 658'97, right m/1	8.5	6.1	AD 2658, left dm/4	12.2
AD 567'98, left m/1	7.5	5.0	AD 674'94, left dm/4	11.8
			AD 418'96, rt dm/4	9.7
			AD 263'95, rt dm/4	10.6
			AD 128'97, left dm/4	10.2
			AD 297'99, rt dm/4	9.7

Appendix 2: Measurements (in mm) of the teeth of *Namachoerus moruoroti* from Arrisdrift.

Upper teeth	Length	Breadth
PQ AD 138, left I1/	10.5	4.5
PQ AD 138, right I1/	10.3	5.1
AD 63'97, left I1/	10e	7.0
AD 526'98, left I1/	10.3	5.9
AD 632'99, right I1/	10.2	5.3
AD 570'00, left I1/	10e	5.6
PQ AD 138, left I2/	5.5	3.5
AD 492'95, right I2/	6.4	4.2
AD 498'95, right I2/	5.5	4.1
PQ AD 49, right C/	9.0	8.0
PQ AD 138, left C/	10.2	8.3
PQ AD 138, right C/	10.2	8.1
PQ AD 3014, left C/	7.5e	5.7
AD 331'95, left C/	8.2	7.7
AD 727'97, right C/	9.6	6.5
AD 144'99, left P1/	4.0	2.8
AD 557'94, right P2/	5.3	4.0
AD 198'95, left P2/	4.2	3.5
AD 557'94, right P3/	7.8	7.0
AD 61'98, right P3/	6.9	6.9
AD 161'96, left P3/	7.4	6.5
PQ AD 136, left P4/	6.2	8.2
AD 554'94, left P4/	5.7	6.8
AD 557'94, right P4/	6.3	8.1
AD 490'99, left P4/	7.1	8.6
PQ AD 136, left M1/	9.1	9.2
PQ AD 2411, left M1/	9.9	9.2
PQ AD 2565, left M1/	9.8	9.3
AD 557'94, right M1/	8.4	8.9
AD 252'96, right M1/	10.1	9.2
AD 827'97, right M1/	10.4	9.2
AD 200'99, left M1/	9.7	9.1
AD 299'99, right M1/	9.7	9.2
PQ AD 136, left M1/	10.8	10.4
PQ AD 1753, left M2/	10.9	10.2
PQ AD 2565, left M2/	10.7	11.3
AD 557'94, right M2/	11.1	10.0
AD 338'96, right M2/	11.0	11.1
AD 433'97, right M2/	10.0	10.4
AD 657'97, right M2/	11.0	11.5
AD 827'97, right M2/	11.4	10.8
AD 100'99, right M2/	11.3	11.2
PQ AD 136, left M3/	11.2	10.0
AD 35'94, left M3/	12.8	10.8
AD 557'94, right M3/	12.0	10.4
AD 345'95, left M3/	11.4	10.0
AD 84'96, left M3/	10.1	9.9
AD 338'96, right M3/	11.0	--
AD 46'97, left M3/	11.3	11.3
AD 433'97, right M3/	11.5	10.0
AD 602'98, right M3/	10.2	10.6
AD 100'99, right M3/	12.8	11.1
AD 251'96, rt dI1/	8.0	3.2
AD 252'96, rt dM2/	5.3	3.8
AD 528'99, left dM2/	5.5	3.6
AD 252'96, rt dM3/	8.0	6.0
AD 252'96, rt dM4/	7.8	8.3
AD 299'99, rt dM4/	7.5	7.1

Appendix 3: Measurements (in mm) of the teeth of *Nguruwe kijivium* from Arrisdrift.

Lower dentition	Length	Breadth
AD 86'96, right i/1	4.7	4.3
AD 240'98, left i/1	4.6	--
AD 240'98, right i/1	4.7	--
AD 523'99, right i/1	4.5	6.0
AD 633'99, right i/1	4.0	5.6
AD 558'97, right i/2	4.8	6.0
AD 240'98, left i/2	4.1	--
AD 240'98, right i/2	5.0	--
AD 529'98, left i/3	4.1	3.6
AD 133'98, left p/1	6.3	3.9
AD 315'99, right p/1	5.8	3.9
PQ AD 631, left m/1	11.4	8.9
AD 313'94, right m/1	12.0	9.7
AD 240'98, right m/1	11.6	9.9
AD 89'99, right m/1	12.2	10.1
AD 301'00, left m/1	12.2	9.3
AD 302'00, left m/1	11.5	8.8
AD 947'97, left m/2	12.0	9.2
AD 240'98, right m/2	14.4	12.0
AD 240'98, left m/2	14.3	11.5
AD 89'99, right m/2	15.2	11.0
AD 247'97, left di/2	3.5	3.5
AD No number, rt I ₃	4.0	4.6
AD 313'94, rt dm/2	7.6	4.1
AD 240'98, lt dm/2	8.6	4.5
AD 240'98, rt dm/2	7.5	3.7
AD 313'94, rt dm/3	9.0	4.5
AD 240'98, rt dm/3	9.1	4.5
AD 89'99, right dm/3	9.0	4.7
AD 240'98, lt dm/3	9.1	4.5
PQ AD 631, left dm/4	--	7.0
AD 313'94, rt dm/4	14.3	7.6
AD 240'98, rt dm/4	13.2	7.8
AD 89'99, right dm/4	14.6	7.9
AD 451'99, rt dm/4	12.9	7.3
AD 230'00, lt dm/4	13.1	7.2
AD 301'00, lt dm/4	14.0	7.3

Appendix 4: Measurements (in mm) of the teeth of *Nguruwe kijivium* from Arrisdrift.

Upper dentition	Length	Breadth
AD 493'95, left I1/	6.4	6.7
AD 342'98, right I1/	7.1	6.5
AD 239'00, right I3/	6.5	4.0
AD 90'99, left P2/	9.8	5.0
AD 90'99, right P3/	9.9	7.6
AD 90'99, left P3/	10.0	7.5
PQ AD 2821, left P4/	8.9	--
AD 314'94, left P4/	8.3	10.3
AD 90'99, right P4/	8.8	10.9
AD 90'99, left P4/	8.4	11.0
AD 24'00, left P4/	8.6	--
AD 314'94, left M1/	11.1	12.5
AD 784'97, left M1/	--	11.6
AD 90'99, right M1/	11.4	13.1
AD 90'99, left M1/	12.0	13.1
AD 314'94, left M2/	14.0	14.3
AD 90'99, left M2/	13.8	15.1
PQ AD 1795, rt M3/	16.0	13.2
AD 90'99, left M3/	15.3	14.7
AD 148'97, rt dI2/	3.6	3.1
AD 711'97, rt dM3/	10.8	6.5
AD 784'97, lt dM3/	9.4	6.3
AD 496'95, rt dM4/	10.0	10.2
AD 784'97, lt dM4/	9.9	9.5

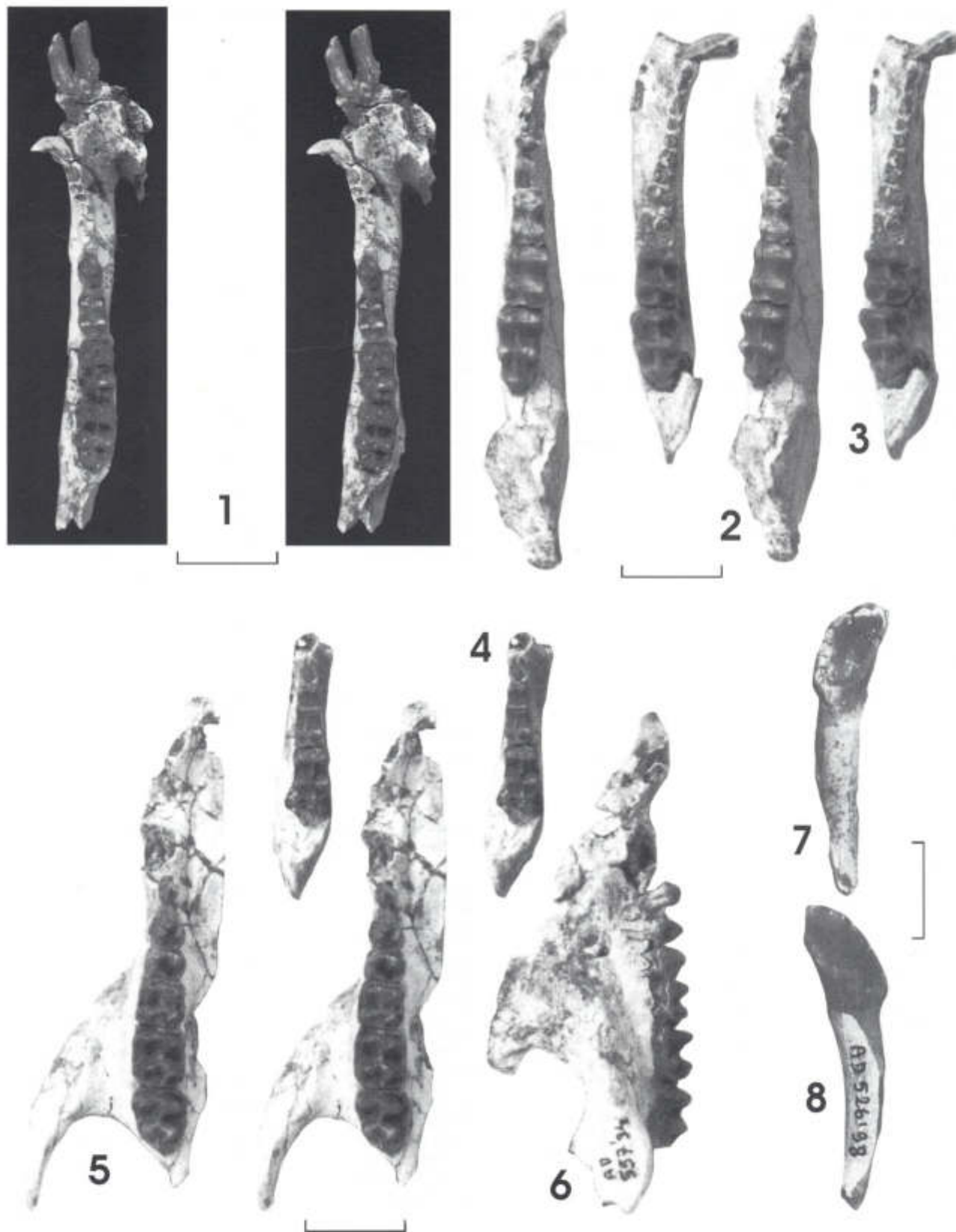


Plate 1: *Namachoerus moruoroti* from Arrisdrift, Namibia (Scale bars = 2 cm except figs 7-8 = 1 cm)

1. AD 568'98, left mandible with i/1-i/2, /c, p/4-m/3, stereo occlusal view.
2. AD 620'95, right mandible with /c, m/1-m/3, stereo occlusal view.
3. AD 542'94, right mandible with /c, m/2-m/3, stereo occlusal view.
4. AD 209'94, left mandible with dm/3-m/1, stereo occlusal view.
- 5-6. AD 557'94, right maxilla with P2/-M3/, stereo occlusal and buccal views.
7. AD 632'99, right I1/, lingual view.
8. AD 526'98, left I1/, lingual view.

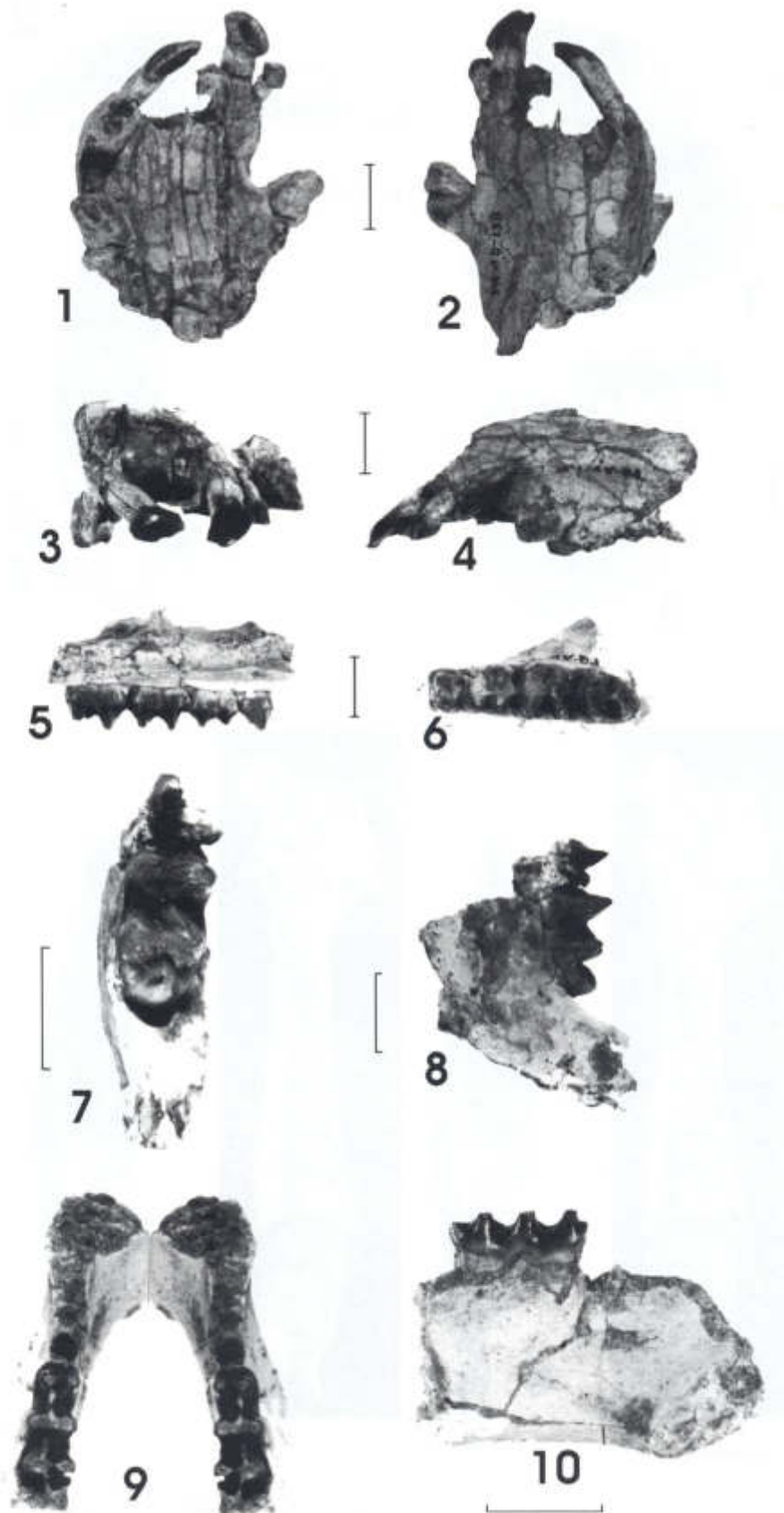


Plate 2: *Namachoerus moruoroti* from Arrisdrift, Namibia. (Scale bars = 1 cm)
1-4. PQAD 138, snout with left I1/-I2/, C/, right I1/, C/, palatal, dorsal anterior and left lateral views.
5-6. PQAD 136, left maxilla with P4/-M3/, lingual and occlusal views.
7-8. PQAD 2927, right mandible with m/3, occlusal and lingual views.
9-10. AD 2658, left mandible with dm/4, occlusal view with mirror image and lingual view.

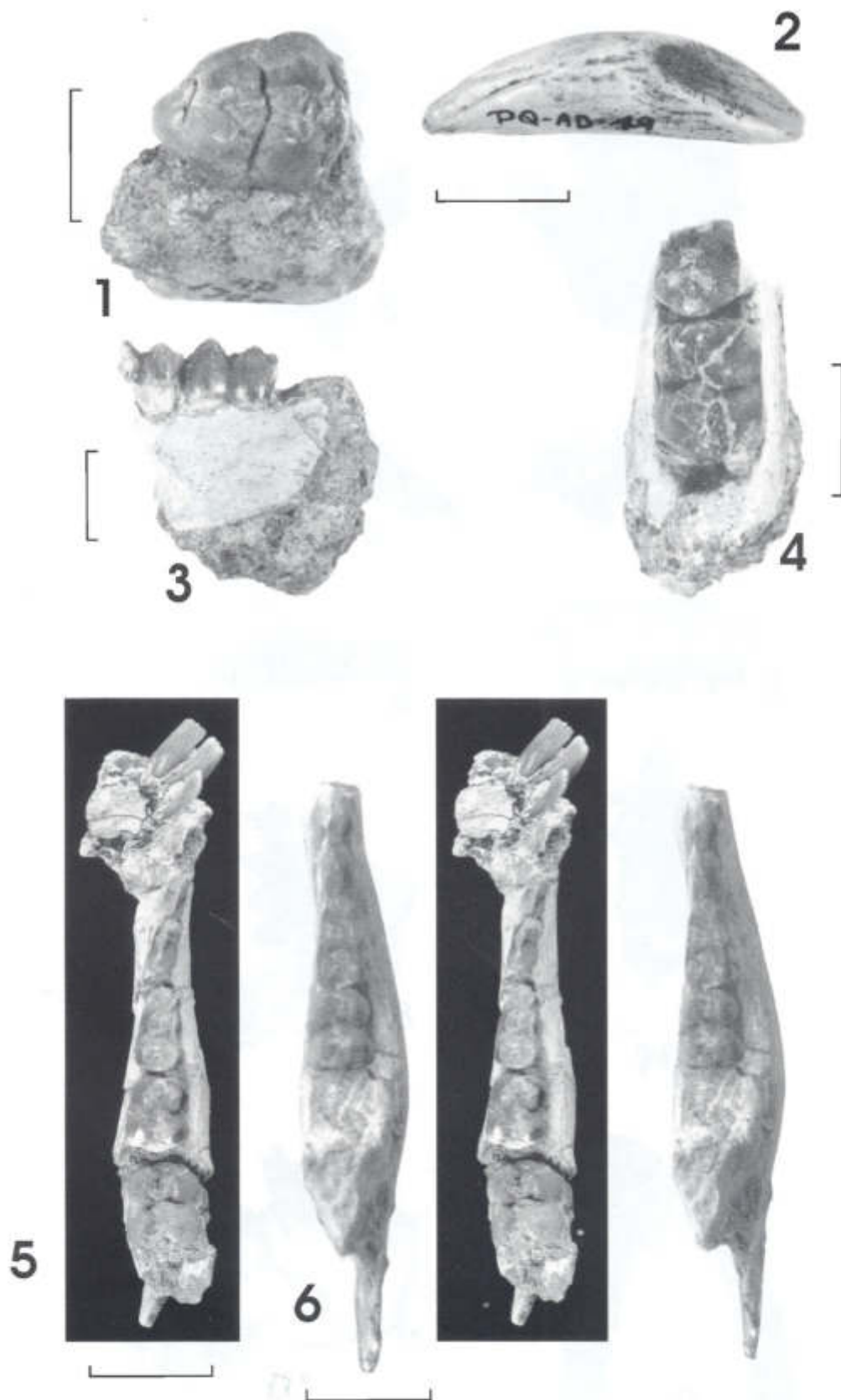


Plate 3: *Ngurube kijivium* (Figs 1, 3-6) and *Namachoerus moriworoti* (Fig. 2) from Arrisdrift, Namibia. (Scale bars = 1 cm for figs 1-4, 2 cm for figs 5-6)

1. PQAD 1795, right M3/, occlusal view.

2. PQAD 49, right upper canine.

3-4. PQAD 631, left mandible with half dm/4-m/1, buccal and occlusal views.

5. AD 240'98, right mandible with left i/1, right i/1-i/2, dm/2-dm/4, m/1-m/2, stereo occlusal view.

6. AD 313'94, right mandible with dm/2-dm/4, m/1, stereo occlusal view.

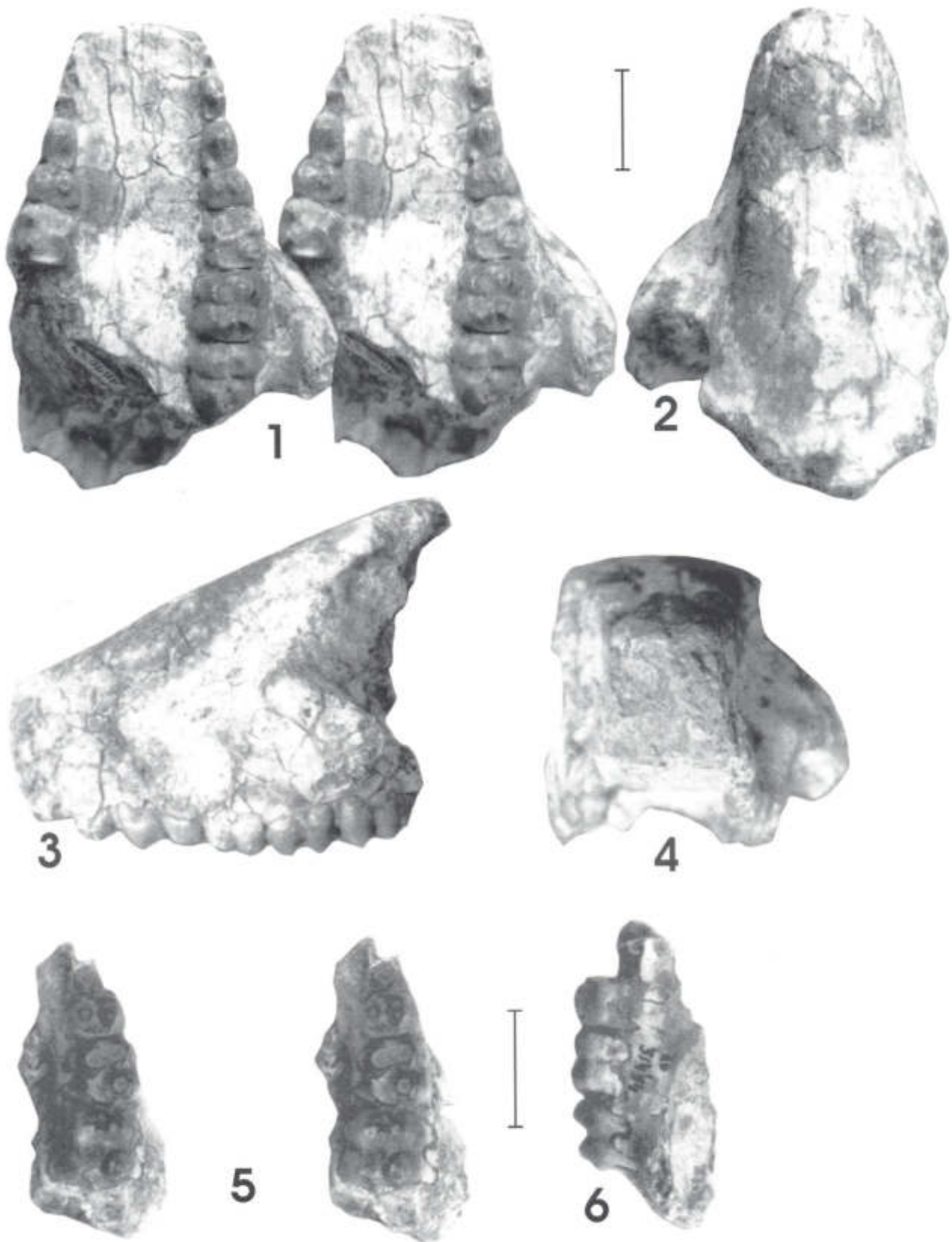


Plate 4: *Nguruwe kijivium* from Arrisdrift, Namibia. (Scale bars = 2 cm)

1-4. AD 90'98, snout with left P2/-M3/ and right P3/-M1/, stereo palatal view, dorsal, left lateral and anterior views.
5-6. AD 314'94, left maxilla with P4/-M2/, stereo occlusal and buccal views.