

GEOLOGICAL SURVEY OF NAMIBIA
MINISTRY OF MINES AND ENERGY



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

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

by

Martin Pickford and Brigitte Senut



Orangemeryx hendeyi

MEMOIR 19
2003

MINISTRY OF MINES AND ENERGY
GEOLOGICAL SURVEY OF NAMIBIA

Director : Dr G I C Schneider

MEMOIR 19

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

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

by

Dr Martin Pickford⁽¹⁾ & Dr Brigitte Senut⁽²⁾

⁽¹⁾Chaire de Paléanthropologie et de Préhistoire, Collège de France, and Laboratoire de Paléontologie,
UMR 8569 du CNRS. 8, rue Buffon, F-75005 Paris, France

⁽²⁾Département Histoire de la Terre du Muséum national d'Histoire naturelle et UMR 8569 CNRS,
8, rue Buffon 75005, Paris.

Typesetting and layout : Estelle Grobler and David Richards

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

ISSN 1018-4325
ISBN 0-86976-609-0

Copyright reserved

2003

A new genus and species of Bovidae (Artiodactyla, Mammalia) from the early Middle Miocene of Arrisdrift, Namibia, and the origins of the family Bovidae

¹Jorge Morales, ¹Dolores Soria, ²Martin Pickford and ¹Manuel Nieto

¹Departamento de Paleobiología Museo Nacional de Ciencias Naturales, CSIC, Jose Gutierrez Abascal, 2. E-28006 Spain
(e-mail: - mcnm166@mncn.csic.es)

²Chaire de Paléanthropologie et de Préhistoire, Collège de France, and Département Histoire de la Terre, UMR 8569 du CNRS, 8, rue Buffon, F-75005, Paris
(e-mail: - pickford@mnhn.fr)

Abundant remains of a small bovid have been unearthed at the basal Middle Miocene locality of Arrisdrift, Orange River Valley, Namibia. Among the more than 10,000 vertebrate fossils excavated at the site only two horn cores have been found. The bovid from Arrisdrift is one of the oldest known species with horn cores. It is here classified as *Namacerus gariensis* nov. gen. nov. sp. *Namacerus* differs from *Eotragus artensis* by its smaller size, greater hypsodonty, and other morphological characters of the dentition. From a phylogenetic point of view the Arrisdrift bovid may well belong to the stem group from which the rest of the bovid lineages were derived. The hypothesis of an African origin for the family Bovidae is strongly supported by the new data. During the Early and basal Middle Miocene Africa possessed a diversity of bovid genera and it was the scene of a major radiation within the family, as indicated by the presence of diverse cranial morphotypes which are primitive with respect to those known from Eurasia.

Version française abrégée

La gisement d'Arrisdrift (17 à 17,5 Ma) a livré les plus anciens bovidés à cornes de l'Afrique, si ce n'est du monde. Le nouveau genre et espèce *Namacerus gariensis*, représenté par de très nombreux restes, dont un neurocrâne, des maxillaires, des mandibules et des éléments du squelette post-cranien, s'avère être un animal de la taille du steenbok actuel (*Raphicerus campestris*), mais avec des proportions corporelles proches de celle des duikers (Cephalophinae). Les chevilles osseuses de *Namacerus* sont des structures coniques simples, légèrement courbes de la base au sommet et placées sur un pédicule ressemblant fortement à celles observées chez *Eotragus artensis* du Miocène moyen d'Europe et d'Asie. Elles sont situées au-dessus des parties latérales des orbites.

En vue dorsale, le neurocrâne est intéressant car il présente une crête temporale double sur chaque côté qui encadre une dépression peu profonde mais clairement visible. Ces crêtes convergent l'une vers l'autre, se rejoignent au niveau du supraoccipital puis divergent pour former une crête nuchale forte. La dentition est typique des bovidés, les dents jugales étant faiblement hypsodontes. La dentition se rapproche plus fortement du type A de Jarman (1974) suggérant que l'animal vivait dans des habitats fermés et était très sélectif dans son comportement alimentaire se focalisant sur des nourritures à apport nutritif élevé. Le degré d'hypsodontie légèrement plus élevé chez *Namacerus* que chez la plupart des bovidés de type A, pourrait indiquer que le premier ajoutait de l'herbe à son régime; mais dans ce cas, il devait choisir les parties les plus nutritives des plantes. Les comparaisons visuelles indiquent que *Namacerus gariensis* avait un poids corporel de 10 à 14 kgs équivalent à celui des bovidés de type B de Jarman.

Les os postcrâniens sont typiques de Pecora, avec des métapodes complètement fusionnés et des corps astragaliens droits. Les extrémités distales des métapodes, ainsi que les premières et les secondes phalanges appartiennent au type A de Köhler (1993).

Namacerus est pour le moment le plus vieux bovidé à cornes connu. Il est bien plus jeune que *Namibiomyx senuti* d'Elisabethfeld en Namibie (ca 21 Ma) qui est plus petit, mais dont la dentition et les os postcrâniens ressemblent à

Namacerus. Il est possible que *Namibiomyx* a donné naissance à *Namacerus* par accroissement de taille et acquisition de cornes si ces dernières étaient effectivement absentes du bovidé d'Elisabethfeld. Le registre fossile en ce qui concerne les chevilles osseuses n'est pas très bon et ce pour plusieurs raisons: ces dernières peuvent être ingérées par des carnivores de taille moyenne et grande cherchant à manger le contenu du neurocrâne; en outre, leur petite taille font qu'elles ont moins de chance d'être conservées que celles des bovidés de grande taille et de taille moyenne. Il faut, en effet, signaler que sur plus de 10 000 restes des vertébrés récoltés à Arrisdrift, seules deux chevilles osseuses ont été trouvées en 1998 et 1999 après plusieurs années de fouilles. En fait, jusqu'à la découverte de ces dernières, on pensait que *Namacerus* ne possédait pas de cornes.

Il semble donc que la famille des Bovidae est née en Afrique au cours du Miocène inférieur (vers 20 à 21 Ma) et plus spécialement en Afrique australe; elle s'est en suite diversifiée et dispersée dans le reste de l'Afrique et en Eurasie au début du Miocène moyen (vers 16 - 17 Ma).

Introduction

Bovidae have been reported to occur at Arrisdrift by Corvinius & Hendey (1978) and the family has featured in several faunal lists published since that time (Pickford, *et al.*, 1996) but few anatomical details have been published. This paper provides a detailed description and interpretation of the Arrisdrift bovid, based on a good sample of craniodental and postcranial remains. No complete skull of this bovid is known, and so far only two horn cores have been discovered at the site. It complements the description of the apparently hornless bovid species from Elisabethfeld, Namibia, described recently (Morales *et al.*, 1995), and confirms the conclusions voiced in that paper that ruminants of bovid grade, albeit possibly without horns, have populated southern Africa since quite deep in the early Miocene (ca 21 Ma). The Arrisdrift species, assigned to a new genus, was about the same size, or was marginally smaller than the extant Steenbok (*Raphicerus campestris*) which has a body weight of about 10-16 kg (Haltenorth & Diller, 1980).

Geological context

Arrisdrift is a fluvialite deposit on the Namibian bank of the Orange River. It was discovered during diamond prospecting operations in 1976, and was first excavated by G. Corvinus from 1976 to 1978. More recently (1994–2000) it has been excavated by the Namibia Palaeontology Expedition. The fossiliferous deposits consist of clays, silts, sands and conglomerates of the Proto-Orange terrace, assigned to the Arrisdrift Gravel Formation by the SACS (1980). These sediments are aged about 17.5 Ma (Pickford, 1995). They accumulated in a shallow channel some 14 metres wide incised into bedrock which locally consists of lightly metamorphosed schists of the Gariiep Group. Detailed descriptions of the deposits appear in Pickford & Senut (2000). None of the fossil material at Arrisdrift is in anatomical connection, virtually all of it having been transported post-mortem. The bovid bones, like many of the others, show various grades of post-mortem modification, including some which are quite fresh, others which are longitudinally cracked (sun cracks?) or polished and abraded. Many of the smaller bones, especially carpals, are lacking. At Arrisdrift there are abundant skeletal remains of two medium to small ruminants (a tragulid (*Dorcatherium* aff. *pigotti*) and the new bovid, *Namacerus gariiepensis*) and there are traces of two other bovid species at the site, one larger than *N. gariiepensis*, based on a single astragalus comparable in size to those of *Walangania africanus* from Kenya and Uganda, and one smaller than it, based on a calcaneum similar in size to that of the Elisabethfeld and Langental bovid *Namibiomyx senuti*.

Systematic description

Order Artiodactyla Owen, 1848

Family Bovidae Gray 1821

Genus *Namacerus* nov.

Type species: *Namacerus gariiepensis* nov. sp.

Derivatio nominis: *Nama* is the name of the dominant tribe in southern Namibia while *cerus* is Greek for horn. *Gariiep* is the Khoi name for the Orange River.

Holotype: AD 435'98, Neurocranium (Pl. 1, Fig. 1).

Type locality: Arrisdrift, Sperrgebiet, Namibia.

Age: Basal Middle Miocene (ca 17.5 Ma) equivalent to Faunal Set PIIIa of East Africa, MN 4a of Europe.

Diagnosis: Bovid of small size, approximating that of the extant Steenbok (*Raphicerus campestris*) and smaller than *Eotragus artenensis* from the early Middle Miocene of Europe. Horn core short, conical and small, inserted vertically above the orbit in lateral view, the cross-section is almost circular, slightly compressed transversely with a hint of a posterior keel. The external side is flatter than the internal surface and shows an incipient angulation (hint of keeling). Strong postcornual *fossa*. The roof of the skull shows the development of doubled temporal crests which enclose a clearly visible depression between them. These crests converge and unite at the level of the supraoccipital suture and then diverge

to form a strong nuchal crest. The occipital is wide, and is inclined to the rear such that the most posterior part of the skull consists of the occipital condyles. The basioccipital is very wide, with moderately developed tubercles for muscle insertions. In posterior view, the mastoid is visible where it forms a lateral sliver of the nuchal region. The tympanic bulla is wide and globose but relatively weakly developed. The tympanohyal vagina is wide and well marked, being delimited by two crests, the anterior one extending far enough to form part of the external wall of the auditory meatus, and partly covering the tympanohyal, the posterior one also surrounding the tympanohyal and separating it from the paroccipital process, but without enclosing it entirely. The external auditory meatus is elongated into an ossified canal, probably almost complete. The petrosal shows a strong development of the *fossa* for the tensor tympanic muscle and the subarcuate *fossa* is clearly delimited. Dentition moderately hypsodont. Lower molars with weak or absent metastylid, absence of palaeomerycid fold, internal wall (metaconid-toconid) smoothly undulating but continuous without incision between the two cuspids; Strong entostylid m/3 with externally positioned hypoconulid. Upper molars with weak styles and columns. Metaconule and protoconule isolated from each other, and separated from the external cusps. Lower premolars simple, not molarised; p/2 with very simple morphology. P2/ shortened. Metapodials short with respect to the rest of the limb bones.

Differential diagnosis: *Namacerus* differs from *Eotragus artenensis* by its smaller size (ca 10% smaller), greater hypsodonty (height of the metaconid: basal width of the metaconid-hypoconid x 100 in the m/3 = 116, in *Eotragus artenensis* ca. 100). In the lower molars it differs by the absence or weakness of the metastylid, absence of incision in the inner wall, linear disposition of the metaconid-endocoid, and hypoconid closer to the other cuspids. In *Namacerus* the upper molars possess external walls with weaker styles and columns, and the union between the lingual and labial cusps is lower. The length of the premolar row relative to the molar row is less than it is in *Eotragus artenensis*. It differs from *Namibiomyx* and *Hispanomyx* by the presence of horn cores. Additionally from *Namibiomyx* it differs by its larger size, greater hypsodonty, shorter premolar row and in the lower molars by the union between the posterior cristid of the hypoconid and the posterior cristid of the endocoid. It differs from *Hispanomyx* by the absence of molarisation in the p/4, the less developed entoconulid in m/3 (very strong in *Hispanomyx*), and the more weakly developed styles on the external walls of the upper molars (well developed in *Hispanomyx*).

Anatomical description: Cranium. The skull (AD 435'98) (Pl. 1, Fig. 1) consists of the brain case with almost completely fused sutures. The parietals, temporals, occipital region, the right tympanic bulla and the left petrosal are preserved. The roof of the skull is notable for the development of doubled temporal crests on each side which enclose a clearly visible depression between them. These crests converge and unite at the level of the supraoccipital suture and then diverge to form a strong nuchal crest. The occipital is wide, especially in comparison with that of *Raphicerus*, but is closer to that of *Gazella* or *Boselaphus*, and is inclined to the rear such that the most posterior part of the skull consists of the occipital con-

dyles. In *Raphicerus* it is the nuchal crest which is the most posterior part of the skull, while in most bovids the nuchal is almost vertically oriented, but in some gazelles and *Boselaphus* the occipital condyles stick out beyond the nuchal crests and thereby approach the condition seen in *Namacerus*. The shape of the foramen magnum and of the occipital condyles is closer to those of Cephalophini, *Gazella* and *Boselaphus* than to that of *Raphicerus*, in particular by the more horizontal orientation of the surface of insertion of the condyles, which are more vertical in *Raphicerus*. The basioccipital is very wide, resembling the situation in Cephalophini, with moderately developed tubercles for muscle insertions. In posterior view, the mastoid is barely visible, being quite different from *Gazella* in which it contributes largely to the nuchal region, and in this respect it is closer to the morphology expressed in Cephalophini. The tympanic bulla is wide and globose but relatively weakly developed when compared with that of most bovids, but the basic structure is the same. The tympanohyal vagina is wide and well marked, being delimited by two crests, the anterior one extending far enough to form part of the external wall of the auditory meatus, and partly covering the tympanohyal, the posterior one also surrounding the tympanohyal and separating it from the paroccipital process, but without enclosing it entirely. This condition is similar to the morphology encountered in most bovids, even though it is clearly more primitive, being not very different from the situation in *Rupicapra rupicapra*, although in this species the tympanic bulla is transversely compressed. It clearly differs from *Gazella*, *Raphicerus*, *Cephalophus*, and other extant bovids by the more distal position of the tympanohyal vagina, which in the extant species is in a more anterior position due to the swelling of the posterior part of the bulla between the tympanohyal and the paroccipital process. In contrast the tympanohyal of *Namacerus* occupies a subcentral position in the bulla. The external auditory meatus is elongated into an ossified canal, probably almost complete. The petrosal of *Namacerus* is close morphologically to that of *Cephalophus*, in dorsal view presenting the same disposition of the elements, but differing by the greater development of the fossa for the tensor tympani muscle, which is noticeably larger and deeper than that of *Cephalophus*. In cranial view the differences between the petrosals of these two genera are minor, the subarcuate fossa being clearly delimited in both.

Fragment of left frontal with a horn core (AD 491 '99) (Pl. 1, Fig. 3). The horn core is short, conical and small, the cross-section is almost circular, being slightly compressed transversely with a hint of a posterior keel. The external side is flatter than the internal one and shows an incipient angulation. The pedicle is high and clearly delimited. The portion of frontal preserved reveals that it was thick and was slightly elevated in the region of the frontal suture. There is a strong postcornual fossa and the supraorbital pit is well developed. The horn core is inserted vertically above the orbit in lateral view. Its dimensions (in mm) are DAP= 13.2; DT= 10.5; H= 21.8. A second fragment of left frontal with a horn core (AD 439'98) (Pl. 1, Fig. 2) shows no significant differences from the former. Its dimensions (in mm) are DAP= 12.6; DT= 9.9; H= 22.2.

Mandible (Pl. 2, Figs 4-8). Similar in size to that of the Steenbok (*Raphicerus campestris*), the mandible of *Namacerus* is more robust, which is related to its more robust dentition.

The ascending ramus is appreciably wider antero-posteriorly, there being a widening of the mandible behind the m/3. The angle of the mandible is well developed and the masseteric fossa is strong. The head of the condylar process is wide (appreciably more than in the Steenbok). The coronoid process is also more strongly developed than in the extant form, and the position of the mandibular foramen is somewhat different - in the Steenbok it extends from the level of m/3 to below it, whereas in the Arrisdrift bovid it is above this level, as in tragulids.

Lower dentition (Table 1). In AD 228'95, (Pl. 2, Fig. 4) the m/3 has the lingual and labial cuspids aligned along an antero-posterior axis. The lingual wall is continuous and smoothly undulating without marked stylids. The metaconid is strongly compressed, the anterior cristid is well developed and high, the posterior cristid is much smaller. The protoconid is high with crescentic cristids which are more developed anteriorly than posteriorly. The anterior cristids of the protoconid and metaconid are strongly united, closing off the lobe anteriorly. There is no sign of a metastylid. The endoconid is less compressed transversely than the metaconid, and there is no posterior cristid. The crescentiform hypoconid possesses two well developed cristids, the anterior one joining the front of the endoconid, and the posterior one reaching the lingual wall, joining a strong cuspid located in the position of the endoconulid. The hypoconulid is slightly displaced to the lingual side, its anterior (lingual) cristid joins the posterior cristid of the hypoconid, and the posterior one, which is smaller, joins the endoconulid, so that the lingual wall is completely closed. There is a basal cingulum on the protoconid, and a strong ectostylid.

The m/2 is basically the same as the first two lobes of m/3, but differs from it by having the anterior cristid of the hypoconid extending further antero-posteriorly, so that the contact with the anterior cristid of the endoconid is less marked. The entoconulid is smaller.

The p/4 has a high mesiolingual cuspid with strongly inclined anterior and posterior cristids, the anterior one joining a stylid and an anterior cuspid (bifurcate anterior wing), the posterior one also joining a stylid and a relatively low posterior cuspid which penetrates the anterior margin of the m/1. The mesio-lingual cuspid is well developed, but there is only a hint of the anterior and posterior cristids. The posterolingual cuspid is oblique with respect to the main axis of the tooth, and the labial notch is smooth.

The p/3 is similar to p/4 except that it only has an oblique cristid which is slightly swollen so as to form an incipient mesiolingual cuspid.

Upper dentition (Table 1; Pl. 2, Figs 1-3). AD 96'95, P2/-P4/ (Pl. 2, Fig. 3). Only the lingual cusp of the P4/ is preserved, but judging from the roots and the alveolus, it must have been subtriangular. The lingual cusp is crescentiform with high and well developed anterior and posterior crests. The lingual cingulum encircles the entire base of the cusp.

P3/ consists of a high and long cusp separated by a deep incision from the anterior style which is strong. There is a prominent lingual cusp which is separated from the posterolingual crest which is well developed and united to the anterior style, thereby forming an anterior lobule separated from the principal one.

P2/ is similar in construction to the P3/ but the lingual cusp

Table 1: Measurements (in mm) of the lower and upper cheek teeth of *Namacerus garipepensis* nov. gen. nov. sp. from Arrisdrift, Namibia. (L = length, W = breadth, row = cheek tooth row, mm = molar row, pp = premolar row).

Specimen	<i>Namacerus</i> lower dentition														
	L row	L pp	Lmm	L m/3	W m/3	L m/2	W m/2	L m/1	W m/1	L p/4	W p/4	L p/3	W p/3	L p/2	W p/2
PQ-AD 105	52	22.2	30	13.3	6.3	9.7	6.5			8.5	4.9	7.9	4	6	
PQ-AD 106						9.9	6.5	9	6.1	8.5	4.1				
PQ-AD 2706				13.6	5.6	9.5	6.1	8.9	5.8						
PQ-AD 2500						9.5	5.5	8.3	5.5	8	4.1	7.7	3.5		
PQ-AD 2220				13.5	6.1	9.1	6.1								
PQ-AD 3090				12.5	5	8.6	5.6								
AD 228'95	52.3	21.2	31.6	13.6	6	9.4	6	8.1	5.5	7.8	4.6	7.6	3.9	5.5	
AD 169'95								9	5.4	8	4.3				
AD 97'95										9.6	4.4				
AD 550'95				13.9	5.7	9.6	6.1								
AD 273'95				14.3	6	9.7	6.1								
AD 68'96						10.1	6	8.7	5.5	8.4	4.3	7.8	4	4.5	
AD 30'97	51	20.5	31	13.5	6	9.4	6	8.2	5.5	8.1	4.4	7.1	3.6	5.3	2.5
AD 425'97				13.4	6.5										
AD 426'97	52.7	21.8	31.3	13	6.5	8	6.2								
AD 427'97	52.4	21.7	30.5	13.3	6.2	9	6.1	8.6	5.9	8	4.3				
AD 27'98			32.3	13.8	5.7	9.9	6.3	9.2	5.9	8.7	4.7	8	4.5		
AD 178'98												7.8	3.8		
AD 189'98			31.2	14	6.2	9.8	6.5	7.9	5.7	8.8	4.9	8.3	4.2		
AD 188'98	57.8	22.3	35.5	15.3	6.2	10	6.5	9	5.7	8.8	4.5	7.8	4	6	
AD 299'98	52.2	22.2	30.8	13.4	5.4	8.5		8.1	5.5	8.9	4.2	8	3.6	6	
AD 433'98			32	13.5	6.1	10.1	6.2	7.9	5.8						
AD 436'98		22				9.8	6.9	8.6	5.5	8.7	4.3				
AD 522'98												7.5	3.6		
AD 692'98				14	6										
AD 585'99	52.1	21.3	30.5	13.7	5.5	9.2	5.7	7.4	5.4	7.8	3.8				
AD 773'99						10.9	6.5								
AD 196'99								8.5	5.1						
Specimen	<i>Namacerus</i> upper dentition														
	L ROW	L PP	LMM	L M3/	W M3/	L M2/	W M2/	L M1/	W M1/	L P4/	W P4/	L P3/	W P3/	L P2/	W P2/
AD 96'95										7.5	8.6	8.6	7	8.5	6.2
AD 76'97				9.3	9.3	9.6	10.6								
AD 284'94				9.2	9.6										

is less prominent.

AD 76'97, M3-2/ (Pl. 2, Fig. 1). The M3/ is broken in the area of the paracone, the mesostyle is moderate to strong, and the metastyle is very strong, joined by a basal cingulum to the mesostyle. The metaconule is smaller than the protocone, and is joined by high crests to the parastyle and mesostyle, although they are not completely fused. The protocone has a high anterior crest which joins the parastyle, and its posterior crest is shorter and narrower and does not contact the posterior crest of the metaconule. The basal cingulum is strongly developed on the lingual cusps. There is a strong ectostyle. The M2/, which is larger than the M3/, possesses a voluminous parastyle, a moderate mesostyle and weak metastyle. The anterior crest of the metaconule is bifurcate and contacts the prolongation of the posterior crest of the protocone, thereby closing off a medial fossette. There is an anterior cingulum but no basal cingulum. The external cusps in both molars are flattened, only the paracone forming a moderate external rib. AD 284'94, a fragment of maxilla with the right M3/ is similar to the preceding specimen but has a weak mesostyle. The parastyle is stronger, and projects moderately anteriorly. The paracone has a moderate external rib. The external wall is quite flat.

Measurements (length x breadth in mm) of the upper teeth of *Namacerus garipepensis* are given in Table 1.

Postcranial skeleton (Pis. 3-4) (Tables 2-4).

Vertebrae. No vertebrae that can be securely identified as

Table 2: Measurements (in mm) of the postcranial bones of *Namacerus garipepensis* nov. gen. nov. sp. from Arrisdrift, Namibia. Scapula, Astragalus & Navicular-cuboid (Abbreviations : AAD= Articular anteroposterior depth; AH= Anterior height; CSAD= Collum Scapulae anteroposterior depth; CSTW= Collum Scapulae transverse width; DTW= Distal transverse width; GAD= Glenoid anteroposterior depth; GTW= Glenoid transverse width; LAD= Lateral anteroposterior depth; MAD= Maximal anteroposterior depth; MH= Maximal height; MTW= Maximal transverse width).

Measurements of *Namacerus* and Steenbok postcranial bones

Scapula	AAD	GAD	GTW	CSAD	CSTW
AD696'94	20.2	16.3	14.3	12.2	7.3
Steenbok	18.8	14.7	13.4	10	6.2
Astragalus	Length	DTW	LAD		
PQAD 1629	21.5	13.1	11.4		
AD 263'97	21.1	12.4	11.5		
AD 30'98	19.8	11.3	11		
AD 531'98	21.2	13.4	11.2		
AD 449'00	21.1	11.8	10.5		
Steenbok	23	13.7	13		
Navicular-cuboid	MAD	MTW	AH	MH	
AD 41'97	14.6	15.7	9.4	15.2	
AD 129'99	15.3	16	10.9	16.2	
Steenbok	19	17.6	11	18.6	

bovid have been collected from Arrisdrift.

Scapula (Table 2). AD 696'94 (Pl. 3, Fig. 2) is a right scapula. The glenoid cavity is roughly circular, the articular surface extending as far as the supraglenoid tubercle, and the contact between this well developed tubercle and the cavity is short and narrow. There is no glenoid notch nor a coracoid process. The caudal border is narrow and there is no infraglenoid tubercle, but a rectangular fossa and laterally a depressed rugose area. The acromion is broken.

AD 696'94 differs from scapulae of *Cephalophus monticola* and *Andegameryx andegaviensis* in which the supraglenoid tubercle is poorly developed and the coronoid process is slim and hook-shaped. The morphology in *Namacerus* is much closer to that in *Gazella dorcas* and to a lesser degree to that of the Steenbok and indicates that the biceps and triceps would have been similar in these species.

Humerus (Table 3). There are four fragments of distal humeri in the sample of which only AD 698'94 is well preserved. AD 402'00a and 402'00b (Pl. 3, Fig. 1) is a left humerus with the articular head unfused but united to the diaphysis by sediment. This specimen is 10% longer than that of the Steenbok. The diaphysis is fractured in several places and is deformed. The deltoid tuberosity and the tricipital line are weakly developed, whereas the epicondylar crest (the insertion for the radial

extensor muscle of the carpus) is strong. In the Steenbok humerus the opposite is true, while *Gazella dorcas* is similar to *Namacerus*, even though the deltoid tuberosity in the Gazelle is stronger.

In the distal epiphysis the medial condyle is well developed proximally, occupying the major part of the coronoid fossa. The trochlear valley is shallow. The capitulum is small and thus the radial fossa is large and is closed laterally. The lateral tuberosity is weak. The weaker development of the capitulum and the relief of its lateral surface indicates that the extensors of the digits were weaker than in the Gazelle and Steenbok, corresponding most closely to morphotype A of Köhler (1993).

In comparing several extant and fossil bovids, we note a tendency to lengthen the axis of the trochlea in a vertical direction thereby enlarging its articular surface both proximally and distally, but above all the medial condyle and the capitulum. *Cephalophus monticola* has the most extreme expression of this tendency, with the articular surface being small and the axis very inclined. The Steenbok, and particularly *Gazella*, represent the opposite extreme. *Namacerus* is somewhat intermediate in morphology. *Hispanomeryx duriensis* is very close morphologically to the Steenbok. *Andegameryx andegaviensis* from Cetina has a distal humerus which is very derived considering its great age, and does not appear to lead to *Namacerus*

Table 3: Measurements (in mm) of the postcranial bones of *Namacerus garipeensis* nov. gen. nov. sp. from Arrisdrift, Namibia. Humerus, Femur & Tibia (Abbreviations : CFAD= Caput Femoris antero-posterior depth; CFTW=Caput Femoris transverse width; DAD= Distal anteroposterior depth; DTW= Distal transverse width; MSAD= Midshaft anteroposterior diameter; MSTW= Midshaft transverse width; PAD= Proximal anteroposterior depth; PTW= Proximal transverse width).

Humerus	Length					DAD	DTW		
AD 698'94						14.9	17.5		
AD 420'00	112					16.3	20.4		
Steenbok	101					16.9	19.8		
Radius	Length	PAD	PTW	MSAD	MSTW	DAD	DTW		
AD 644'97	106	10	17.6	6.6	11.4	11.7	16.4		
AD 158'97	110	10	18	7.6	13	12.1	18.3		
AD 814'97	105	9.9	16.7	6.5	10.6	11.4	17.4		
AD 258'97						11.5	17.8		
AD 458'99	108	10.2	18.3	6.6	12	10.4	17		
AD 111'99	106	8.9	16.8	5.8	12.1	10.8	16.8		
AD 118'00						11	16.7		
PQAD 1458		9.6	17.5						
Steenbok	126.1	10.5	17.1	6.3	10.7	13.7	16.7		
Femur	Length	PAD	PTW	MSAD	MSTW	DAD	DTW	CFAD	CFTW
PQAD 3044			33.2					15.6	18.6
AD 690'94	138	21.4	31.8	11.9	11.2	32.6	26.6	14.2	18.1
AD 217'95		21.2	30.7					14	17.8
AD 610'98	140			11.3	11.2			14	17.8
Steenbok	142.2	18.9	30.7	12.5	12.4	36.5	28.6	14.7	19.4
Tibia	Length	PAD	PTW	MSAD	MSTW	DAD	DTW		
AD 701'94	152.5	28.8	27.7	11.9	12.2	14.8	17.9		
AD 708'94						11.6	16		
AD 547'95	157	29	28.5	11	12.2	14.1	17.4		
AD 549'95						15	18.2		
AD 546'95*	128*		22.4*	8.1*	10.5*	11.5*			
AD 280'96	155	28.6	30			14.5	18.2		
AD 431'98						13.8	17.5		
Steenbok	190	33	30.9	10.3	12.7	15.7	18.6		

* Juvenile

which is a younger form.

Ulna. A proximal ulna (AD 547'97) possibly belongs to *Namacerus* but because of some residual doubt about its identification, we do not describe it.

Radius (Table 3). The following radii are in the sample: PQ AD 1458, left proximal fragment, AD 158'97 (Pl. 4, Fig. 2), AD 814'97, AD 458'99 and AD 111'99 are complete left radii, AD 644'97, complete right radius, AD 258'97 distal half of a right radius, and AD 818a & AD 818b'97, an eroded left radius.

The radius is short (15% shorter than that of the Steenbok) and is robust. The diaphysis widens progressively towards the distal extremity and is quite compressed antero-posteriorly and presents slight lateral torsion.

The proximal end of the radius of *Namacerus* is basically similar in shape to those of the Springbok and *Gazella*: the most elevated part is the facet for the capitulum which is not inclined anteriorly as it is in *Cephalophus monticola*. The posterior margin is horizontal and straight, except for a notch where the lateral facet of the ulna fits. The facet for the medial condyle of the humerus is not much inclined towards the medial side. The lateral tuberosity is very weak.

This morphology is also found in *Andegameryx andegavensis* and *Hispanomeryx duriensis*, but there appears to be a gradient in the anteroposterior development of the humeral facets and in its orientation in a plane which is perpendicular to the sagittal. In these two species the medial facet has a greater anteroposterior diameter than in *Namacerus*, but the facet for the capitulum is small, whereas Steenbok and *Gazella* have the facet for the capitulum very concave and better developed antero-posteriorly, conforming in size to their capituli.

In the distal end of the radius the facet for the scaphoid is low and the crest which separates it from the semilunar facet is low and smooth. These facets are oriented more diagonally towards the medial side, that of the semilunar is very long and that for the pyramidal is narrower. Beside the ulna platform there is a fossa and a narrow platform at the border. The epiphysis is compressed antero-posteriorly. The dorsal groove for the radial extensor of the carpus is wide, shallow and its margins are rounded. The dorsal groove for the extensor of the digits cannot be made out.

The distal epiphysis of the radius in the Steenbok and *Gazella* have different sections from those of *Namacerus*, being narrower and having a greater antero-posterior diameter. The facet for the scaphoid is higher and has a much better developed crest. The semilunar facet is short and is oriented more antero-posteriorly. The distal radius of *Cephalophus* is similar to that of *Gazella* and Steenbok, but has a more compressed section.

Metacarpal (Table 4). The following collection of metacarpals has been studied: PQ AD 1180, (Pl. 3, Fig. 3) left metacarpal lacking the distal epiphysis, PQ AD 571, right proximal metacarpal, PQ AD 503, (Pl. 3, Fig. 6) distal right metacarpal, AD 691'94 and AD 697'94, (Pl. 3, Fig. 4) complete juvenile left metacarpals lacking the pulleys, AD 548'95, (Pl. 3, Fig. 5) complete right metacarpal, and AD 138'96, distal end of a juvenile metacarpal without the pulleys, AD 26'98 and AD 257'99, metacarpals lacking the proximal epiphysis.

The diaphysis of the metacarpal is narrow and very compressed antero-posteriorly. The posterior surface is quite flat. The dorsal groove is only visible in the distal part. The length

is 30% less than that of the Steenbok.

In the proximal surface there is a tendency to possess a more rectangular outline with increase in the size of the unciform facet. *Namacerus*, however, has a triangular outline, and the posterior margin is relatively concave. In the anterior part there is a strong tuberosity on the medial side for insertion of the extensor muscle of the carpus. The groove for the lateral extensor tendon is very short and shallow, being barely visible in several specimens. The distal extremity corresponds basically to type A of Köhler (1993).

In general, the metacarpal of *Namacerus* seems much the same as that of *Cephalophus monticola*, although this species has larger pulleys. *H. duriensis* is similar to *Gazella* and *Raphicerus* in the proximal end, and the distal epiphysis is of type B of Köhler (1993), but with pulleys of type A.

Pelvis. A pelvis from Arrisdrift (AD 303 '97) possibly belongs to a bovid, but because there is some doubt about its identification, it is not described.

Femur (Table 3). PQ AD 3044 and AD 217'95 (left proximal femora), AD 690'94 (Pl. 3, Fig. 7) and AD 610'98 (complete left femora) are the only femora of *Namacerus* known from Arrisdrift.

The general morphology is similar to that of the Steenbok, and its length is virtually the same. The extant form differs in the shape of its head, in proximal view being more rectangular in outline, and with the lateral region wider and longer. In *Namacerus* the morphology corresponds to type A (Köhler, 1993). The distal end is larger in the Steenbok, especially its antero-posterior diameter and the intercondylar fossa is deeper. In the fossils the supracondylar fossa is longer and deeper (for the superficial flexors of the digits and the lateral branch of the gastrocnemius).

Tibia (Table 3). Nine tibiae are taken into account; AD 701'94 and AD 547'95, (Pl. 4, Fig. 1 A-D) complete specimens from the right side, AD 280'96, a complete left tibia, AD 546'95, juvenile left tibia lacking both epiphyses, PQ AD 3024, left proximal tibia, AD 692'94, AD 708'94 and AD 549'95, left distal tibiae (Pl. 4, Fig. 1E), AD 431'98, right distal tibia.

The tibia of *Namacerus* is 18% shorter than that of the Steenbok. There is not much morphological difference between them. In the fossil the tibial crest is longer but the proximal epiphysis is weaker, corresponding to the small size of the distal epiphysis of the femur. The intercondylar eminences are more rounded and because of this the central part of the intercondylar area is shallower. In the distal extremity the medial maleolus and the central anterior process are lower, while the fossae for the astragalus are shallower and shorter. In *Hispanomeryx duriensis* only the distal epiphysis of the tibia is known and it is similar to that of *Namacerus*.

Calcaneum. PQ AD 2432 and AD 572'99 are left and right fragments of calcanei, the former conserving the sustentaculum but broken off at the midpoint of the corpus and the midpoint of the astragalar surface, making it difficult to deduce anything of value. The second specimen consists of the sustentaculum with a small part of the *tuber calcis*. Little can be said about these fragments, except that the remains are typically bovid.

Astragalus (Table 2). Six left astragali have been studied (PQ AD 1629 (Pl. 4, Fig. 4), AD 709'94, AD 263'97, AD 30'98, AD 242'98 and AD 449'00) and one from the right side

Table 4: Measurements (in mm) of the postcranial bones of *Namacerus gariepensis* nov. gen. nov. sp. from Arrisdrift, Namibia. Metacarpal, Metatarsal & Phalanges (Abbreviations) DAD= Distal anteroposterior depth; DTW= Distal transverse width; MSAD= Midshaft anteroposterior diameter; MSTW= Midshaft transverse width; PAD= Proximal anteroposterior depth; PTW= Proximal transverse width).

Metacarpal	Length	PAD	PTW	MSAD	MSTW	DAD	DTW
PQAD 1180		10.5	15.1	6.5	8.8		
PQAD 571		11.1	14.6				
PQAD 503						9.4	16.1
AD 691'94		9.8	13.7	5.3	7.1		
AD 697'94		10.3	14.6	6.2	8.5		
AD 11'95	89.5	10	14.5	6.4	9.1	8.8	15.5
AD 26'98						8.7	15.4
AD 257'99						9.4	15.5
<i>Steenbok</i>	135	10.8	15.8	8	8.8	11	14.3
Metatarsal	Length	PAD	PTW	MSAD	MSTW	DAD	DTW
PQAD 101				9.8	9.9	10.1	17.2
PQAD 2664						11	16.8
AD 942'97	102.4	15.4	13.8	8.8	9.3	11.1	17.3
AD 438'97	109	14.1	13	8.6	8.4		
AD 187'97	101	14.8	12.5				
AD 327'95			13.5	8	8.9		
AD 231'96		14.2	13				
AD 114'96			13.3	8	9		
AD 403'00		17.6	14.5	9.5	9.3		
AD 404'00		14	14.2	9.2	9		
AD 298'00						11	17.3
AD 351'00				8.8	7.5	10	17
<i>Steenbok</i>	148.2	19	16.2	10.3	10	14	17.6
I Phalanx	Length	PAD	PTW	MSAD	MSTW	DAD	DTW
PQAD 21	23.9	9.8	8.9	7	6.2	6.3	7
PQAD 663	25.9	10.5	9	8	6.9	6.5	7.2
AD 114'98	23.6	9.9	9	6.7	6.1	6.2	6.8
<i>Steenbok (ant)</i>	29.6	9.6	7.4	7.5	6	7.1	6.7
<i>Steenbok (post)</i>	31.8	12	9	8.6	7.1	8.1	7.7
II Phalanx	Length	PAD	PTW	MSAD	MSTW	DAD	DTW
PQAD 1182	16.1	9.1	8.1	6.4	7.1	8.1	7.9
AD 517'97	12.2	8	6.7	4.9	5.2	6.2	5.8
AD 518'97	12.2	8.5	7	5.2	5.5	6.9	6.3
AD 194'98	12.5	8	6.6	5.6	5.3	7.7	5.4
AD 181'98	11.1	7.4	6.4	4.8	5	6.2	5.6
<i>Steenbok (ant)</i>	20	10.8	6.8	6.8	4.7	8.4	5.5
<i>Steenbok (post)</i>	22.2	12.4	7	7.5	5.5	9	6

(AD 531'98).

Morphologically the astragali of *Namacerus* are similar to those of *H. duriensis*. They share the presence of a moderate process on the proximal medial condyle, the distal trochlea with asymmetrical condyles separated by a shallow valley, and the stop facets of the posterior surface are very smooth. However, in the *Namacerus* talus the stop facet on the anteromedial border is stronger than that of *Hispanomeryx*. Astragali of *Gazella* and *Raphicerus* have well developed stop facets, especially the posterolateral one which forms a wide and deep fossa. While *Raphicerus* and *Cephalophus* have the distal trochlea similar to that of *Namacerus*, in *Gazella* the condyles are symmetrical and the valley is deep, a morphology also encountered in *Andegameryx*.

Navicular-cuboid (Table 2). Two left (AD 41 '97 (Pl. 4, Fig. 5B-D), AD 129'99 (Pl. 4, Fig. 5A) and one right (AD 826'97) navicular-cuboids have been recovered, the latter specimen lacking the posterior part.

In *Namacerus* the facet for the calcaneum is long and narrow as in *Raphicerus*, the proximal processes are not very high, especially the central one, which is however clearly more elevated than the calcaneal facet. In the posterior surface, the medial border forms a weak crest and the distal lateral pro-

cess is also moderately developed. In the distal surface, the posterior facet for the metatarsal is subtriangular and inclined and the two distal anterior facets are relatively flat.

In its morphology, the navicular-cuboid of *Namacerus* is intermediate between those of *Hispanomeryx duriensis* on the one hand and *Raphicerus* and *Gazella* on the other. The navicular-cuboid of *Gazella* and *Steenbok* present the most derived morphology in the sample that we examined: the proximo-medial and disto-lateral processes being hyperdeveloped vertically and antero-posteriorly. The proximal central process is tiny compared to the medial one. The two distal anterior facets are strongly concavo-convex. *Cephalophus* has the proximal processes as in *Gazella* and *Steenbok*, but the medial border which forms a low but upright and well defined crest, and the distal lateral process are not as well developed. It is also less developed than in *Namacerus*. The navicular-cuboid of *Hispanomeryx* has less developed posterior processes than the Arrisdrift bovid and both share planar distal facets with *Cephalophus*.

Metatarsal (Table 4). 13 metatarsals in the collection give a good idea of the range of variation in *Namacerus*. The material consists of the following specimens;- AD 187'97 and AD 942'97 (Pl. 4, Fig. 3B-E), complete right. metatarsals, AD

438'97 (Pl. 4, Fig. 3A), complete left specimen, AD 327'95, AD 403'00, left, and AD 114'96, AD 404'00, right metatarsals lacking the distal epiphysis, AD 231 '96, right proximal fragment, PQ AD 101, PQ AD 2664, AD 700'94, AD 298'00 and AD 351'00, distal ends of metatarsals.

The metatarsal, like the metacarpal, is 30% shorter than that of the Steenbok. The diaphysis is gracile, square in section, with the posterior surface practically flat. The dorsal groove is wide and shallow especially in the proximal half; distally it is open but is variable in morphology: in AD 942'97, in the distal part there are short processes which overhang the groove but which do not make contact with each other. In this specimen the groove is shallow, differing markedly from that of Cervidae in which it is much deeper.

The proximal surface has a rounded outline, and it does not have a posterior lateral tubercle. The groove for the lateral extensor, as in the metacarpal, is short and weak or absent. The fused Mt II makes a tiny tubercle in all the specimens. However, there is no space for a rudimentary Mt V as in *Andegameryx* and *Orangemeryx*, nor is there any sign of a tubercle. The posterior facet for the navicular cuboid is narrow and rectangular and moderately inclined. The distal end has pulleys which are larger than those of the metacarpal, but of the same type A morphology.

The Steenbok, *Gazella* and *Cephalophus* do not have any tubercle on the proximal surface nor a postero-lateral tuberosity. The two former bovids have the posterior facet for the navicular cuboid much shorter, narrower and inclined. As in the navicular-cuboid, the anterior facets of the metatarsal are strongly concavo-convex. The metatarsal of *H. duriensis* is similar in morphology and size to that of *Namacerus*, but there are some differences. In the proximal end the postero-lateral tuberosity is strong, the pulleys are better developed and the distal end is closer to type B.

Phalanges (Table 4). Eight phalanges have been found as follows:- Phalanx 1. PQ AD 663, PQ AD 21 (Pl. 4, Fig. 6), AD 114'98, Phalanx 2. AD 517'97, AD 518'97, AD 194'98, AD 181'98, AD 299'95 (Pl. 4, Fig. 7).

Both the first and second phalanges are small, short and robust. They correspond to type A of Köhler (1993) being morphologically similar to those of *Andegameryx* and *Orangemeryx*. Phalanges of *Cephalophus*, the Steenbok and *Gazella* are longer and more gracile, and fall into type B. The phalanges of *Hispanomeryx duriensis* have the same length as those of *Namacerus*, but are much more gracile and the characters, especially in the first phalanges, are typical of type B.

Ecology of *Namacerus*

Body proportions and body size: As can be seen from the above descriptions and measurements, *Namacerus* was a small bovid, comparable in size to some extant Neotragini and Cephalophini. Visual comparison suggests that it had a body size similar to that of the Red Duiker, *Cephalophus natalensis*, the body weight of which ranges between 12 and 14 kg. However, metrical comparisons based on the method of Köhler (1993) yield lower figures between 10 and 12 kg depending on which limb bone is considered. Thus an approximate weight of between 10 and 14 kg can be inferred for this species.

In studying limb proportions, comparisons were restricted

to Neotragini and Cephalophini. *Namacerus* is slightly smaller than the Steenbok, *Raphicerus carnpestris*, with the greatest differences residing in the tarsal elements. Whilst their humeri and femora are of the same sizes, the radius (15% shorter), the tibia (18% shorter) and above all the metapodials (30% shorter), not forgetting the phalanges of *Namacerus*, are all considerably shorter than those of the extant Steenbok. The body proportions of the Arrisdrift bovid would have been closer to those of *Cephalophus* and *Silvicapra* than to that of the Steenbok, but would have differed from the Duiker by its longer radius and above all its longer tibia. This would suggest that its locomotor pattern was somewhat different from that of *Cephalophus*. In particular its less parasagittally constrained articulations indicate a greater potential for lateral splaying of the digits. Closer similarity in proportions is found with the Klipspringer (*Oreotragus oreotragus*) although this subsaharan bovid has many limb adaptations to rocky habitats that are not present in *Namacerus*.

Locomotor adaptations: The morphology of the phalanges and metapodials correspond to type A in the classification of Köhler (1993). This morphology is characterised by the possibility of lateral movement and splaying of the digits that is interpreted by Köhler as an adaptation to moist and soft ground.

Dietary adaptations: The morphological traits of *Namacerus* match type A of Jarman's (1974) classification of living antelopes and type A2 of Janis' (1982) modification of his scheme. These species are characterized by their small size - about 10 kg - short limbs, small horns and brachyodont teeth (although *Namacerus* cheek teeth are slightly hypsodont). According to both these authors this kind of species requires a closed habitat in which highly selective browse, concentrated on food items of high nutritive value, forms the basis for their diet. This agrees with the results of the limb bone study presented above. The inferred browsing behaviour of *Namacerus* is consistent with the physiological constraints on grazing in herbivores of small size described by Demment & Van Soest (1985). These authors demonstrated that species lighter than 9.5 kg should be browsers. However, it should be pointed out that the inferred body weight of *Namacerus* - somewhat greater than this limit - and its slightly hypsodont dentition, could mean that its diet included grass, and it would thus conform to Jarman's type B, in which the species feed either entirely on grass or entirely on browse, but are very selective for plant parts high in nutritive value.

The inferred body weight of *Namacerus* - between 10 and 14 kg - is appreciably lower than the 18 kg threshold considered by Janis (1982) to be necessary before horns could evolve in ruminants (Morales *et al.*, 1993).

The oldest known horned bovid of Africa and the origin of the family Bovidae

The origin of the Bovidae is one of the least understood among the families of pecoran ruminants. Recently, Morales *et al.*, (1995) proposed a hornless ancestor to explain the origin of the group. Nevertheless, the transition from hornless to horned bovid is still poorly known, being limited to several isolated remains assigned to *Eotragus artensis* in Spain (Moyà Solà, 1983) and France (Ginsburg & Heintz, 1968) and a recently

erected species *Eotragus noyei* defined on the basis of fragmentary material from the Siwaliks of Pakistan (Solounias *et al.*, 1995). These early bovids possessed small conical horn cores which are similar to the specimens from Arrisdrift.

The moderately brachyodont dentition of *Eotragus artemensis* is structurally close to that of *Namacerus*, although the latter species is slightly more hypsodont and differs from *Eotragus* by the metastylid being almost suppressed and by the continuous lingual wall in the molars. In these two characters *Namacerus* is similar to *Namibiomyx*, *Andegameryx* and *Hispanomeryx* and to many modern bovids. The retention of the primitive condition of these characters by *Eotragus* shows that the early stages in the evolution of the family were complex.

Comparing the skeletal remains of *Namacerus* with those of the Steenbok and *Gazella* we note that even though it shares several characters such as the open dorsal groove and the morphology of the proximal end of the metatarsal, the proximal end of the radius, the distal humerus and the navicular-cuboid, it is a relatively primitive bovid. Despite sharing with *Cephalophus* several features of the metacarpal, distal humerus and proximal radius, and despite *Namacerus* being similar to Steenbok and *Gazella* in other features, in its overall morphology it is more primitive than any of these extant genera.

The cranial anatomy of most of these early bovids is unknown, highlighting the importance of the Arrisdrift material. This reveals that the auditory region is basically similar to that of extant bovids, even though it retains several archaic features. However, the roof of the brain case which possesses doubled temporal crests separated from each other by a narrow depression and which converge and unite before reaching the supraoccipital, differs from the situation in extant bovids. The temporal crests of *Namacerus* show evidence of an incipient doubling of the primitive sagittal crest which, in tragulids and hornless pecorans is simple. This structure of the temporal crests is not strictly homologous to the temporal crests present in the majority of extant bovids which are simple and run parallel to, but well separated from, each other. Nevertheless, in many living forms (*Boselaphus tragocamelus*, *Gazella dorcas*, *Raphicerus campestris*, *Capra hircus* etc.) one can observe a rudimentary V-shaped structure between the temporal crests which, because of its position, would represent the ancestral sagittal crest. Among the known fossil forms are two skulls from Maboko which present a similar morphology to *Namacerus*. The skull M 15544 stored at the Natural History Museum, London, which, by the structure of its horn core is close to *Homoiodorcas tugenium* (Thomas, 1981), also shows a doubled structure of the crests, even though they are less well marked than in the Arrisdrift specimen, the main difference being that the crests meet each other further back on the supraoccipital. Skull M 15543, which was first identified as a bovid by Gentry (1970), and later as a climacoceratid by Thomas (1979, 1984) could well belong to a primitive bovid because the left frontal apophysis, in spite of the reconstruction, reveals a transition between the pedicle and the part that would have been covered by the horn, a defining feature of Bovidae (McCrossin *et al.*, 1998). In this specimen the temporal crests are also incipiently doubled and well marked, and converge over the frontal before diverging gently backwards. This disposition is close to the situation in *Oioceros tanyceras* from Fort Ternan (Gentry, 1970), although in this

species there is no doubling of the sagittal crest which would indicate that this lineage is closer to the Hypsodontinae. The almost circular section of the base of the Maboko horn core, its almost vertical insertion and the tall pedicle support this suggestion. A horn core from Gebel Zelten M 26688, identified by Hamilton (1973) as *Eotragus* sp., could also represent a hypsodontine (high pedicle, vertical insertion of the horn core, almost circular section of the horn core with no signs of compression) despite the presence of an incipient posterior crest. A similar suggestion was made by Van der Made (personal communication) on the basis of the mandible M 26685 identified by Hamilton (1973) as *Gazella* sp. The presence of Hypsodontinae in the early Miocene of Afro-Arabia is confirmed by the attribution to this subfamily of the Negev bovids described by Tchernov *et al.*, (1987) as *Eotragus* cf. *sansaniensis* and *Gazella negevensis*, both of which possess all the characters of the group and which probably represent a single species *Hypsodontus negevensis*.

The new information from Arrisdrift, and the reinterpretation of the Maboko material, indicates that the process of migration of the sagittal crest to become temporal crests occurred progressively by the doubling of the sagittal crest followed by the migration of the outer crest to a more lateral position leaving the inner crest as a relic. This process started in response to a change in the muscular relations of the chewing apparatus, with a change in position of temporal muscles due more to widening of the neurocranium than to a change in hypsodonty or of molarization of the premolar series. Both of the latter tendencies are well expressed in several hornless pecorans (*Dremotherium*, *Sperrgebietomyx*, etc. Morales *et al.*, 1999). This indicates to us that dental hypsodonty occurred prior to both the development of frontal appendices and the appearance of temporal crests. The family Bovidae, as was proposed by Morales *et al.*, (1995), can be characterized by the precocious and advanced grade of hypsodonty - at least in comparison with other ruminants of the same epoch - the bovids, as in other lineages of ruminants, having developed cranial appendages without producing significant changes in cranial morphology. It is likely that during the earliest stages of the evolution of bovids with horns, the brain case retained the original sagittal crest (the Hypsodontinae represent this ancestral condition). This condition can be seen in other ruminants with cranial appendages such as Cervidae and Palaeomerycidae, in which the earliest representatives retain the sagittal crest (*Procerulus*), only later to be transformed into temporal crests without any major changes in dentition being detectable. Widening of the brain case is best explained in terms of important changes in the morphology of cranial appendices which, without doubt, were due to the adaptation of these structures for functions related to behaviour along the lines suggested by Morales *et al.*, (1993).

Several previous scenarios of bovid origins are radically changed by these new observations and interpretations. During the Early and basal Middle Miocene, Africa possessed a relatively high diversity of bovids and bovid-like ruminants and it was the scene of a major radiation within the ruminants, as indicated by the presence of diverse cranial morphotypes which are primitive with respect to those known from Eurasia. From a phylogenetic point of view these African bovids may well be the stem group from which the rest of the bovid lineages were derived. The hypothesis of an African origin for

the family Bovidae is strongly supported by the new data, as is the probability that it is a strictly monophyletic group.

Acknowledgements

The Namibia Palaeontology Expedition is a cooperative project between France and Namibia in which the Geological Survey of Namibia, the Collège de France, Paris, and the Laboratoire de Paléontologie du Muséum National d'Histoire Naturelle, Paris, are partners. The Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, C.S.I.C. of Madrid has actively participated in the field and laboratory studies of this site. Additional support was provided by DGESIC PB98/0691/C03/I and PB98/0513, and the Singer-Polignac Foundation.

References

- Corvinus, G. & Hendey, Q.B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1978** (4), 193-205.
- Demment, M. & Van Soest, P. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *The American Naturalist*, **125**(5), 641-672.
- Gentry, A. 1970. The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In L.S.B. Leakey and R.J.G. Savage (eds) *Fossil Vertebrates of Africa*, **2**, 243-324.
- Ginsburg, L. & Heintz, E. 1968. La plus ancien antilope d'Europe *Eotragus artenensis* du Burdigalien d'Artenay. *Bulltin du Muséum National d'Histoire Naturelle*, **40**, 837-842.
- Haltenorth, T. & Diller, H. 1980. *A field guide to the Mammals of Africa including Madagascar*. London, Collins.
- Hamilton, R. 1973. The Lower Miocene Ruminants of Gebel Zelten, Libya. *Bulletin of the British Museum of Natural History (Geology)*, **21**, 73-150.
- Janis, C. 1982. Evolution of horns in ungulates: ecology and palaeoecology. *Biological Review*, **57**, 261-318.
- Jarman, P. 1974. The social organisation of antelope in relation to their ecology. *Behaviour*, **48**, 213-267.
- Köhler, M. 1993. Skeleton and habitat of Recent and fossil ruminants. *Münchener Geowissenschaftliche Abhandlungen*, **A 25**, 1-88.
- McCrossin, M.L., Benefit, B.R., Gitau, S.N., Palmer, A.K. & Blue, K.T. 1998. Fossil evidence for the origins of terrestriality among old world higher primates. In: Strasser E. et al., (eds) *Primate Locomotion*, pp. 353-396. New York, Plenum Press.
- Morales, J., Pickford, M. & Soria, D. 1993. Pachyostosis in a lower Miocene Giraffoid from Spain, *Lorancameryx pachyostoticus* nov. gen. nov. sp., and its bearing on the evolution of bony appendages in artiodactyls. *Geobios*, **26** (2), 207-230.
- Morales, J., Soria, D. & Pickford, M. 1995. Sur les origines de la famille des Bovidae (Artiodactyla, Mammalia). *Comptes Rendus de l'Académie des Sciences de Paris*, **321**, 1211-1217.
- Morales, J., Soria, D. & Pickford, M. 1999. New stem giraffoid ruminants from the early and middle Miocene of Namibia. *Geodiversitas*, **21**, 229-252
- Moyà Solà, S. 1983. Los Boselaphini (Bovidae, Mammalia) del Neogeno de la península Iberica. *Publicacion Geologica Universidad Autonoma Barcelona*, **18**, 1-236.
- Pickford M. 1995. Suidae (Mammalia, Artiodactyla) from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) moruoroti, and *Nguruwe kijivium*. *Comptes Rendus de l'Académie des Sciences de Paris*, **320**, 319-326.
- Pickford, M. & Senut, B. 2000. Geology and Palaeobiology of the Central and Southern Namib. Vol. 1 - Geology. *Memoir of the Geological Survey of Namibia*, **18**, 1-155.
- Pickford, M., Senut, B., Mein, P., Gommery, D., Morales, J., Soria, D., Nieto, M. & Ward, J. 1996. Preliminary results of new excavations at Arrisdrift, middle Miocene of southern Namibia. *Comptes Rendus de l'Académie des Sciences de Paris*, **322**, 991-996.
- South African Commission of Stratigraphy (SACS), 1980. *Stratigraphy of South Africa*. Kent, L.E. (Comp.): Part 1. *Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophutatswana, Transkei and Venda*. Handbook of the Geological Survey of South Africa, **8**, 690 pp.
- Solounias, N., Barry, J., Bernor, R., Lindsay, E. & Raza, M. 1995. The oldest bovid from the Siwaliks, Pakistan. *Journal of Vertebrate Paléontology*, **15**, 806-814.
- Tchernov, E., Ginsburg, L., Tassy, P. & Goldsmith, N. 1987. Miocene mammals of the Negev (Israel). *Journal of Vertebrate Paléontology*, **7**, 284-310.
- Thomas, H. 1979. Les bovidés miocènes des rifts est-africains: implications paléobiogéographiques. *Bulltin de la Societe géologique de France*, **21**, 295-299.
- Thomas, H. 1981. Les Bovidés miocènes de la Formation Ngorora du Bassin de Baringo (Kenya). *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen*, **84**, 335-409.
- Thomas, H. 1984. Les Giraffoidea et les Bovidae Miocènes de la formation Nyakach (Rift Nyanza, Kenya). *Palaeontographica*. Abt. A, **183**, 64-89.

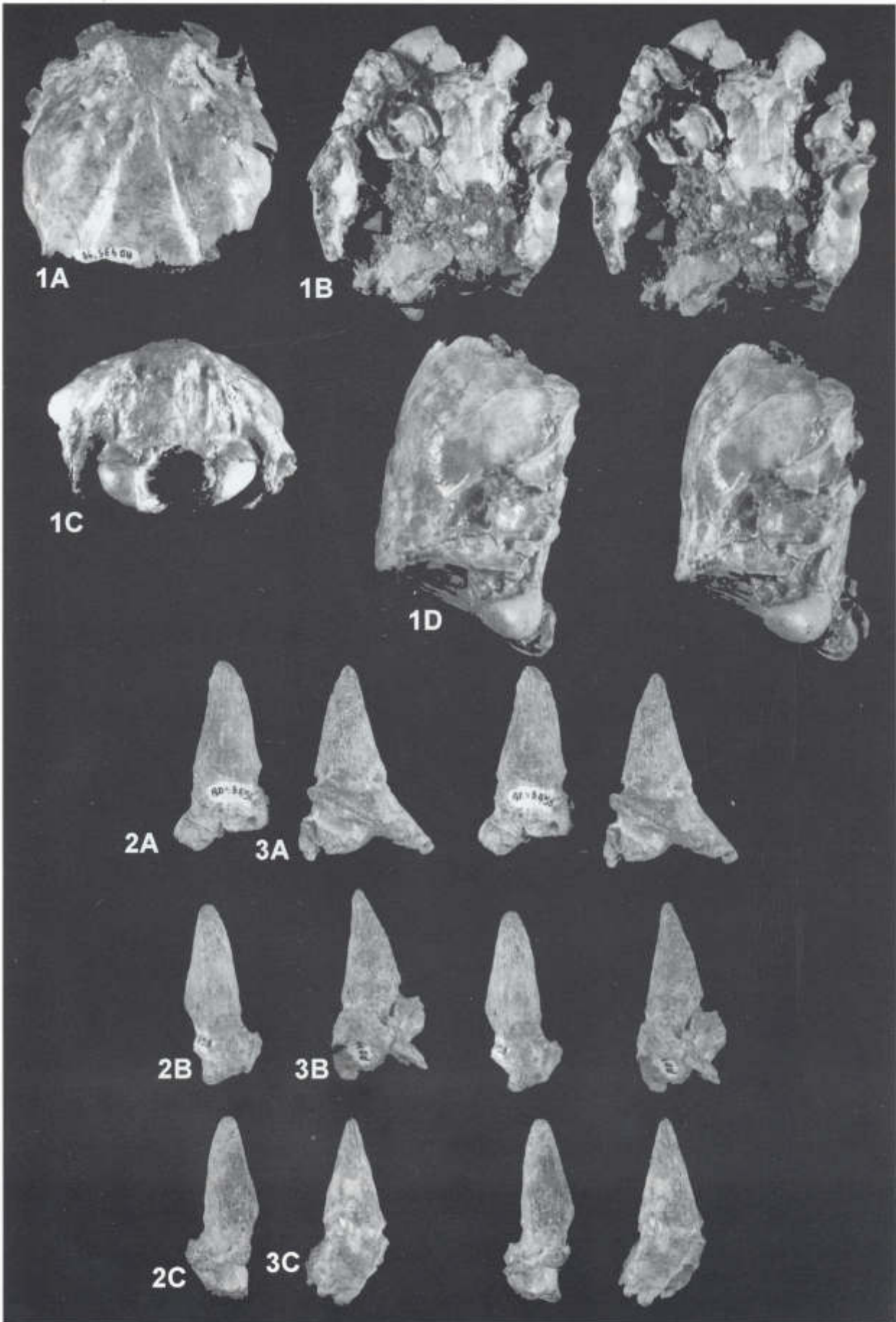


Plate 1: *Namacerus garijensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia, (natural size).
Figure 1. AD 435'98, holotype neurocranium. A, B, D) Stereo views of dorsal, ventral and right lateral; C) caudal view.
Figures 2-3. AD 439'98 (left) and AD 491'99 (right) two left horn cores A, B, C) Stereo views of internal, external and anterior aspects.

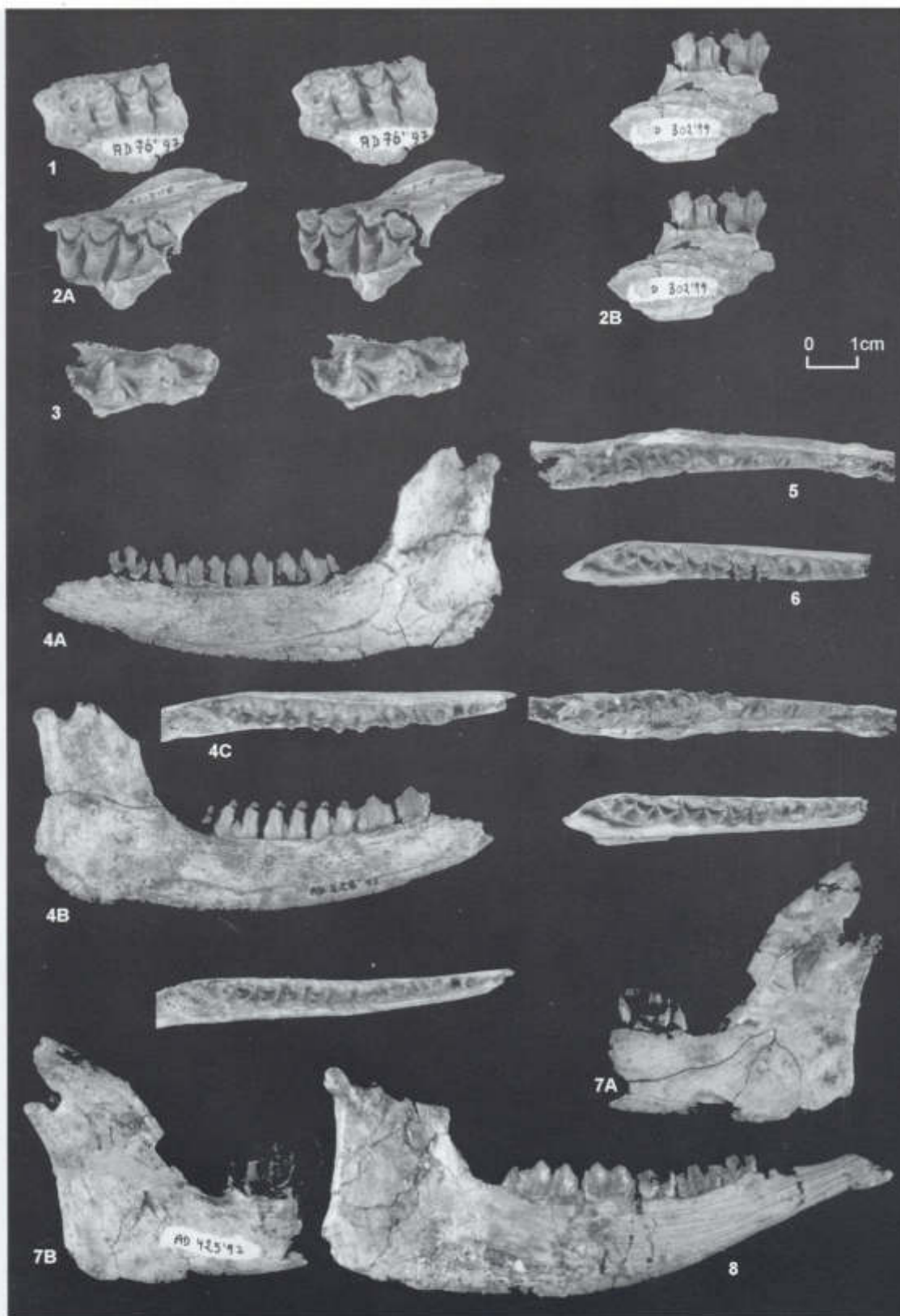


Plate 2: *Namacerus gariopensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia, (scale bar 1 cm).

Figure 1. AD 76'97, right maxilla with M2/-M3/. Stereo occlusal view.

Figure 2. AD 302'99, left maxilla with M2/-M3/. A) Stereo occlusal view; B) Buccal view.

Figure 3. AD 96'95, right maxilla with P2/-P4/. Stereo occlusal view.

Figure 4. AD 228'95, right mandible. A) Lingual; B) Buccal and C) Stereo occlusal views.

Figure 5. AD 30'97, left mandible. Stereo occlusal view.

Figure 6. AD 27'98, right mandible. Stereo occlusal view.

Figure 7. AD 425'97, right mandible. A) Lingual and B) Buccal views.

Figure 8. AD 188'98, left mandible. Lingual view.

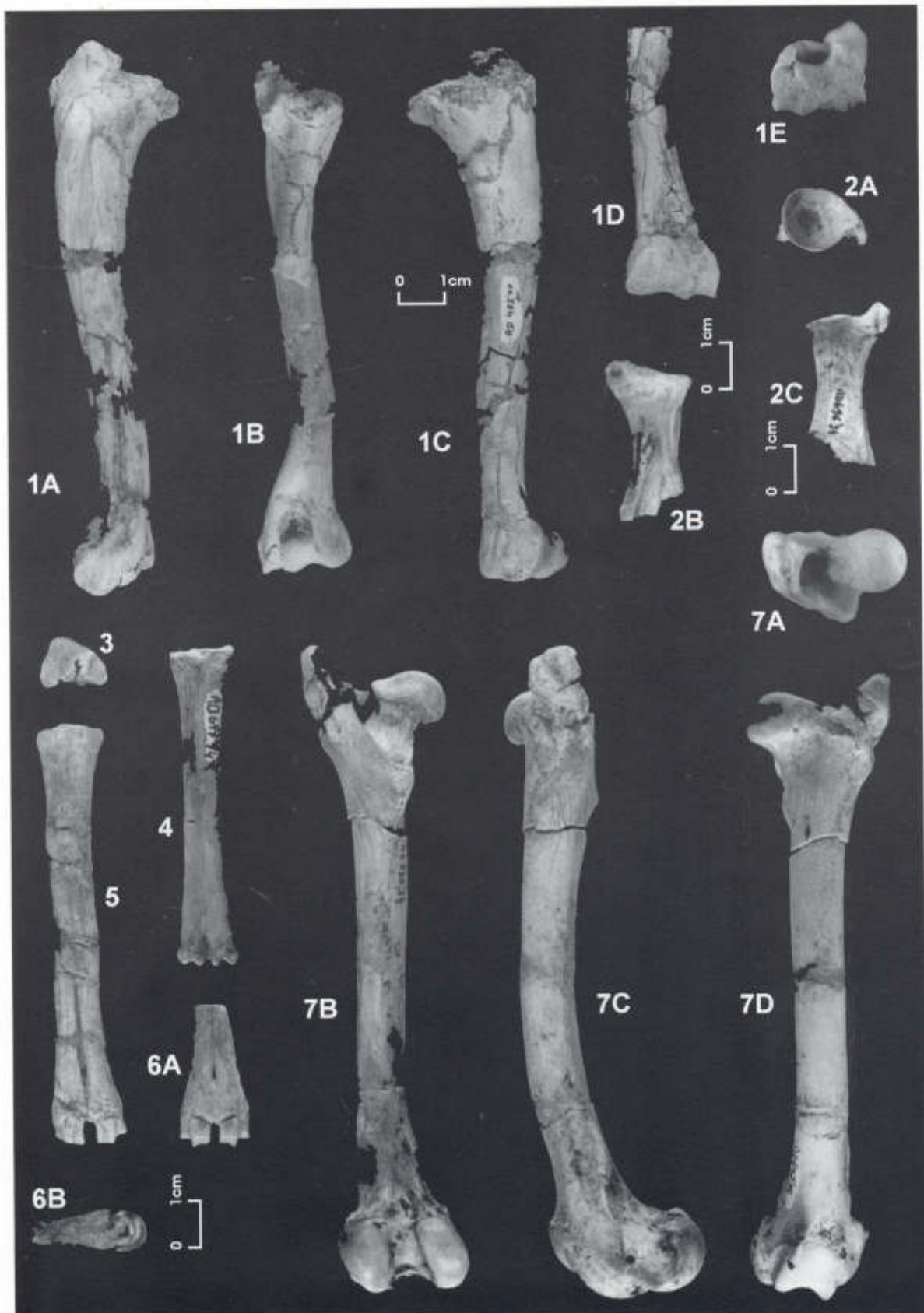


Plate 3: *Namacerus garipepensis*, gen. nov. sp. nov., from Arrisdrift, basal Middle Miocene, Namibia. (Scale bar = 1 cm)

Figure 1. AD 402'00a, left humerus. A) Lateral view; B) Dorsal view; C) Medial view; D) Cranial; E) Distal view.

Figure 2. AD 696'94, right scapula. A) Ventral view; B) Lateral view; C) Medial view.

Figure 3. PQAD 1180, left metacarpal. Proximal view.

Figure 4. AD 697'94, left metacarpal. Palmar view.

Figure 5. AD 548'95, right metacarpal. Dorsal view.

Figure 6. PQAD 503, distal metacarpal. A) External view; B) Palmar view.

Figure 7. AD 690'94, left femur. A) Proximal view; B) Posterior view; C) Lateral view; D) Anterior view



Plate 4: *Namacerus garietpensis*, gen. nov. sp. nov., from Arrisdrif, basal Middle Miocene, Namibia. (Scale bar = 1 cm)

Figure 1. A-D) AD 547'95, right tibia. A) Posterior view; B) Lateral view; C) Anterior view; D) Proximal view; E) AD 549'95, left tibia. Distal view

Figure 2. AD 158'97, left radius. A) Proximal view; B) Palmar view; C) Dorsal view; D) Distal view.

Figure 3. A) AD 438'97, left metatarsal proximal view; B-E) AD 942'97, right metatarsal; B) plantar view; C) Medial view; D) Dorsal view; E) Lateral view.

Figure 4. PQAD 1629, left astragalus. A) Lateral view; B) Plantar view; C) Medial view; D) Dorsal view.

Figure 5. A) AD 129'99, left navicular-cuboid. Proximal view; B-D) AD 41'97, B) Plantar view; C) Lateral view; D) Medial view.

Figure 6. PQAD 21, 1st phalanx. A) Palmar view; B) External view; C) Proximal view.

Figure 7. AD 299'95, 2nd phalanx. A) Proximal view; B) External view; C) Interdigital view.