

GEOLOGICAL SURVEY OF NAMIBIA
MINISTRY OF MINES AND ENERGY



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

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PALAEOONTOLOGY OF THE ORANGE RIVER VALLEY,
NAMIBIA**

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Orangemeryx hendeyi

MEMOIR 19
2003

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Director : Dr G I C Schneider

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by

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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

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2003

Palaeoecological study of Arrisdrift Mammals

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UMR 5125 "Paléoenvironnements et paléobiosphère" du CNRS et UFR des Sciences de la Terre, Université Claude Bernard-Lyon 1, 27-43 boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France.

The Middle Miocene locality of Arrisdrift has yielded 36 species of mammal. Autecological and synecological analyses of this association reveal that it corresponds to an open countryside comprising bushy savanna, traversed by the proto-Orange River which was flanked by a gallery forest.

Version française abrégée

Le gisement miocène moyen ancien d'Arrisdrift a livré 36 espèces de Mammifères. Cette association est analysée des points de vue autécologique et synécologique.

Les trois Insectivores sont de petite taille: *Prochrysochloris* a celle d'une taupe, *Amphechinus rusingensis* est plus petit qu'un hérisson, et *Protenrec* est très petit.

Les trois Macroscelidea sont herbivores: le très abondant *Myohyrax*, hyperhypsodonte, pesait environ 500 g. *Miorhynchocyon gariensis*, bunodonte, avait une masse de 50% plus forte.

Rhinolophus est un Chéiroptère entomophage.

Tous les Rongeurs étaient terrestres. *Protarsomys*, granivore, avait la taille d'une souris. *Megapedetes gariensis*, moins fort que *M. pentadactylus* d'Afrique orientale, atteignait 7 à 8 kg, il était coureur et sauteur; doté de jugales subhypsodontes, il était probablement omnivore. *Megapedetes pickfordi*, aux moeurs probablement identiques, est une forme naine pesant moins de 1 kg. *Paraphiomys*, encore plus petit, est brachyodonte et devait être frugivore-granivore. *Geofossor*, de la taille d'une taupe, était hypogée et mangeur de racines.

Hyainailourus sulzeri était énorme, dépassant 1 m au garrot et 500 kg. *Amphicyon giganteus* atteignait 90 cm et plus de 200 kg. Le Canoidea Amphicyonidae *Ysengrinia ginsburgi* était un peu plus grand qu'un loup. *Namibictis senuti* est un Mustelidae hypercarnivore. *Orangictis* est un Viverridae primitif de taille intermédiaire entre la civette des Indes et la civette commune. *Africanictis meini* est un Stenoplesictidae un peu plus gros que la genette actuelle; *A. hyaenoides*, un peu plus fort, est l'ancêtre probable d'*Ictitherium*. *Diamantofelis* est un félin un peu plus petit qu'un guépard et *Namafelis* avait la taille d'un caracal.

Deinotherium, grand Proboscideen brachyodonte lophodonte, habitait les galeries forestières. *Afromastodon*, comme tous les mastodontes bunodontes, vivait dans la forêt claire et la savane arbustive; les dimensions de ses dernières molaires montrent qu'il était de très grande taille.

Orycteropus minutus ne dépassait pas 3,5 à 4 kg mais était morphologiquement identique à l'oryctérope actuel.

L'hyracoïde *Prohyrax hendeyi* est le mammifère le plus commun d'Arrisdrift; subhypsodonte, il est deux fois plus gros que l'actuel daman du Cap et devait peser 20 kg.

Diceros australis est un très grand rhinocéros brachyodonte et cursorial. Il contraste avec *Chilotheridium pattersoni*, beaucoup plus rare, aquaphile, hippopotamoïde et hypsodonte.

Namachoerus est un suidé au museau court, aux jugales lophodontes, sans doute folivore; sa taille était la moitié de celle d'un sanglier moderne. *Nguruwe kijivium* est un suidé Kuba-

nochoerinae, bunodonte, d'un quart plus petit qu'un sanglier.

Dorcatherium aff. *pigotti* est un petit Tragulidae brachyodonte.

Le grand mammifère le plus abondant est *Orangemeryx*, Giraffoidea Climacoceratidae relativement hypsodonte et à long cou. Ses os canons indiquent une taille et un poids analogues à ceux d'un cerf élaphe actuel.

Namacerus est une antilope un peu plus petite que *Eotragus sansaniensis* du Miocène d'Europe; de taille comparable à celle de l'actuel *Raphicerus campestris*, ce bovidé devait peser de 10 à 14 kg.

Les mammifères d'Arrisdrift témoignent d'une grande biodiversité. De nombreux taxons évoquent une savane buissonneuse plus ou moins boisée. Tous les micromammifères sont terrestres ou souterrains, aucun n'est grimpeur ou arboricole. Il y a peu de macromammifères forestiers. *Chilotheridium*, hippopotamoïde par son allure et ses moeurs, apporté une note humide. L'environnement d'Arrisdrift devait correspondre à une forêt-galerie étendue le long des rives du proto-Orange, dans un pays à géométrie générale très ouverte.

L'étude synécologique a été réalisée à partir de quatre histogrammes représentant respectivement, en pourcentages, le nombre d'espèces présentes regroupées selon leur classification (par ordres), leur masse, leur régime alimentaire et leurs adaptations locomotrices. Les catégorisations sont données tabl. 1, et les histogrammes fig. 1. Elle confirme l'étude autécologique: lors de la formation du gisement, le proto-Orange encadré d'une galerie forestière coulait dans une savane buissonneuse plus ou moins arborée, globalement très ouverte. Cette interprétation est conforme aux résultats déjà acquis par l'étude géologique: Arrisdrift correspond à une forêt-galerie à sous-bois dense sous un climat subtropical chaud semi-aride.

Introduction

The list of Arrisdrift mammals comprising 36 taxa (this volume) is as follows (asterisks mean that Arrisdrift is the type locality).

Autecological study

The comments that follow owe a lot to P. Mein for the micromammals and to M. Pickford for the numerous larger taxa.

The three insectivores are small: *Prochrysochloris* is a hypogeal genus which is not as large as a mole, *Amphechinus rusingensis* is not as large as a hedgehog, *Protenrec* is extremely small.

The two Macroscelidea are herbivores: *Myohyrax*, hyper-

Insectivores

Prochrysochloris miocaenicus
Amphichinus rusingensis
*Protenrec butleri**

Macroscelidea

Myohyrax oswaldi
*Miorhynchocyon garipeensis**

Bats

*Rhinolophus contrarius**

Rodents

Xerini sp. indet.
*Protarsomys lavocati**
*Megapedetes garipeensis**
*Megapedetes pickfordi**
*Paraphiomys orangeus**
Geofossor corvinusae**

Carnivores

Hyainailourus sulzeri
Amphicyon giganteus
*Ysengrinia ginsburgi**
Namibictis senuti**
Orangictis garipeensis**
Africanictis meini**
Africanictis hyaenoides**

Diamantofelis ferox**

Namafelis minor**

Lagomorphs

*Australagomys hendeyi**

Proboscideans

Deinotherium hobleyi
Afromastodon coppensi**

Tubulidentates

Orycteropus minutus

Hyracoids

*Prohyrax hendeyi**

Perissodactyls

*Diceros australis**
Chilotheridium pattersoni

Artiodactyls

Anthracotheriidae indet.

Nguruwe kijivium

Namachoerus moruoroti

Dorcatherium aff. pigotti

Orangemeryx hendeyi**

Namacerus garipeensis**

Pecora indet. sp. 1

Pecora indet. sp. 2

hypsodont, is very abundant at the site, and weighed about 500 g; *Miorhynchocyon garipeensis*, bunodont, was about 500 to 800 g (B. Senut, oral communication).

Rhinolophus is an entomophagous chiropteran.

All the rodents present were terrestrial; *Protarsomys*, granivore, was the size of a mouse; *Megapedetes garipeensis* is smaller than *M. pentadactylus*, its mass was up to 7 or 8 kg, it was a runner and springer, the cheek teeth are subhypsodont and it was an omnivore; *Megapedetes pickfordi* is a pygmy form weighing less than 1 kg, of which the behaviour and ecological requirements were the same as for the preceding species; *Paraphiomys* weighed less than 1 kg, it is brachydont and was probably a frugivore-granivore; *Geofossor* is a burrowing genus about the size of a mole, eating roots.

Hyainailourus sulzeri is a hyaenodontid creodont of very large size: it was taller than 1 m at the shoulder and its M1/ which measures 35.2 x 23 mm (Morales *et al.*, 1998; this volume) indicates a mass in excess of 500 kg. Morales *et al.*, (1998) considered that this enormous carnivore predated *Orangemeryx* as well as rhinocerotids and the occasional proboscideans.

Amphicyon giganteus was the size of *Amphicyon major* from the middle Miocene of Europe, its shoulder height reached 90 cm (this volume); the volume of its cheek teeth (m/1 35.5 x 19 mm, m/2 26.5 x 21.5 mm) and its ursoid aspect permit the estimation of its body weight as much more than 200 kg. J. Morales *et al.*, (1998) suggested that this large carnivore preyed preferentially on *Orangemeryx*, and that it was also a scavenger.

Ysengrinia ginsburgi is another amphicyonid carnivore, its p/4 which measures 15.4 x 8.4 mm means that it was larger than a wolf; the Arrisdrift species is larger than the largest of the European type species, and it preyed on suids and medium sized ruminants (Morales *et al.*, 1998).

Namibictis senuti is a musteline Mustelidae, a hypercarni-

vore (Morales *et al.*, 1998; this volume). *Orangictis* is a primitive viverrine Viverridae, the size of which was intermediate between extant *Viverricula indica* and *Viverra zibetha* (Morales *et al.*, 2001; this volume); its habits were probably close to those of these two species.

Africanictis meini is a Stenoplesictidae a bit larger than the extant *Genetta genetta*, with much the same kind of ecological requirements (Morales *et al.*, 1998; this volume).

Africanictis hyaenoides is another Stenoplesictidae, larger than the previous species, and is possibly the ancestor of *Ichittherium* (this volume).

Diamantofelis ferox is a feline somewhat smaller than a modern cheetah (Morales *et al.*, 1998; this volume).

Namafelis minor is a feline the size of extant caracal.

Deinotherium, which was lophodont, inhabited gallery forests. The dental dimensions of the specimens from Arrisdrift (P4/ = 45.3 x 48 mm, M3/ = 58 x 60 mm, p/4 = 47.5 x 43.2 mm, m/3 = 68 x 53.3 mm; Pickford, this volume) indicate *D. hobleyi* was a very large mammal.

Afromastodon, like all the bunodont mastodonts, lived preferentially in open forest or wooded savannah. The dimensions of its back teeth (M3/ = 190 x 90 mm, m/3 = 190 x 80 mm; Pickford, this volume) show that it was huge.

Orycteropus minutus which was not heavier than 3.5 to 4 kg (Pickford, this volume) is a reduced version of the extant *O. afer* which can weigh as much as 80 kg; the latter is exclusively a consumer of termites, it is nocturnal and digs burrows; it inhabits open savannah, dry regions and open forest.

Prohyrax hendeyi is the most abundant mammal at the site. It is subhypsodont, and was twice the size of extant *Procavia capensis* (the linear dimensions of its skeleton vary between 1.6 and 2.1 times that of the latter), and it is more cursorial (Pickford, 1994 and this volume). Its mass can be estimated as about 20 kg. Extant *Procavia* are hypsodont and eat various plants, dry grass, lichen, bark and fruit; they are rupicole

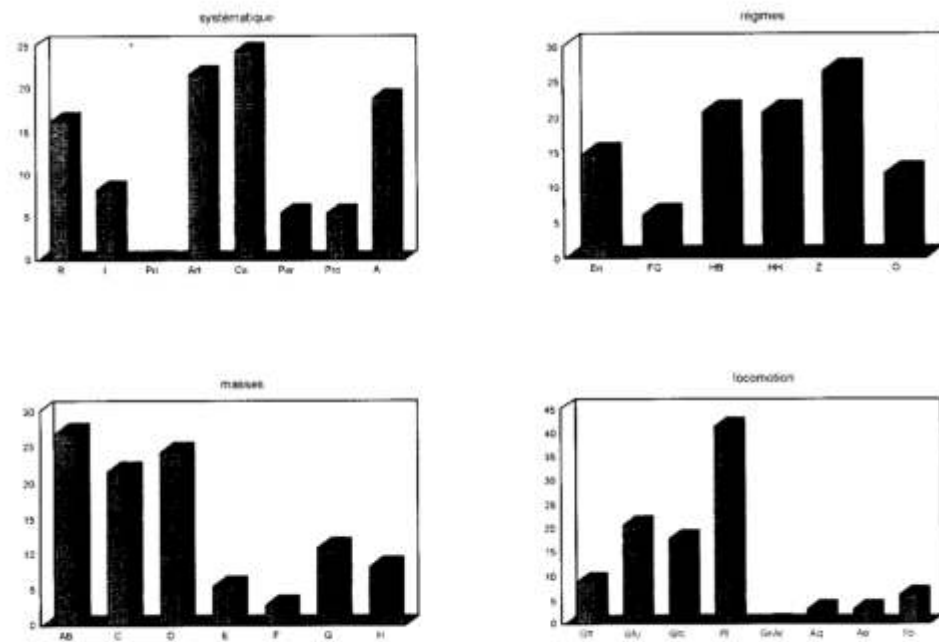


Figure 1: Ecological histograms of basal middle Miocene mammals from Arrisdrift.

and inhabit rocky areas of savannah and arid regions.

Diceros australis is a very large brachyodont, cursorial rhinoceros.

Chilotheridium pattersoni is a small aquaphile hippopotamoid rhinoceros, with hypsodont cheek teeth (Guérin, 2000 and this volume).

Namachoerus moruoroti is a small suid with short muzzle and lophodont cheek teeth (Pickford, 1995 and this volume). The dental dimensions published by M. Pickford, notably those of the P4/ and M3/, show that relative to a mean of sixty extant *Sus scrofa* from western Europe and the Middle East, *N. moruoroti* was about twice as small; it was probably a folivore.

Nguruwe kijivium is a bunodont Kubanochoerinae suid; the dimensions of its teeth show that it was a quarter smaller than extant *Sus scrofa*.

Dorcatherium is a small, brachyodont Tragulidae. *Dorcatherium* aff. *pigotti* from Arrisdrift resembles *Dorcatherium nauti* from the Miocene of Europe and extant *Hyemoschus*, the dimensions of its talus (21 x 11 mm, this volume) reveal that it was the same size.

Orangemeryx hendeyi is a large climacoceratid Giraffoidea with elongated cervical vertebrae and with relatively hypsodont cheek teeth; it is the most abundant large mammal in the site (Morales *et al.*, 1999 and this volume). The anterior and posterior cannon bones are about as long as those of a large deer (*Cervus elaphus*) but are narrower, and the talus is a bit smaller, so the mean body mass must be about the same order of magnitude.

Namacerus is an anti-lope that is smaller than *Eotragus sansaniensis* from the Miocene of Europe, but was more hypsodont; in size it was comparable to the extant anti-lope *Raphicerus campestris*, with a mass of between 10 and 14 kg (this volume).

The Arrisdrift mammals reveal a high biodiversity. Numerous taxa (*Afromastodon*, *Diceros australis*, *Prohyrax*, *Dorcatherium*, *Orangemeryx*, *Namacerus*, the small carnivores,

Table 1: Ecological categorisation of basal middle Miocene mammals from Arrisdrift.

Species	systematic	mass	diet	locomotion
<i>Prochysochloris miocaenicus</i>	I	AB	En	Fo
<i>Amphechinus nuingensis</i>	I	AB	En	PT
<i>Protenac butleri</i>	I	AB	En	PT
<i>Myhyrax coxwoldi</i>	A	C	HH	PT
<i>Protyotheroides</i> sp.	A	C	HH	PT
<i>Macroscelid indet.</i>	A	AB	HB	PT
<i>Rhinohippus conrarians</i>	A	AB	En	Ae
<i>Xerini indet.</i>	R	AB		PT
<i>Protasomys lavocati</i>	R	AB	FG	PT
<i>Megapedetes garipeensis</i>	R	C	O	PT
<i>Megapedetes pickfordi</i>	R	AB	O	PT
<i>Paraphiomys orangeus</i>	R	AB	FG	PT
<i>Geolosaor corvinae</i>	R	AB	HB	Fo
<i>Hyainalourus sulzeri</i>	C	G	Z	GT u
<i>Amphicyon giganteus</i>	C	G	Z	GT c
<i>Ysengrinia ginsburgi</i>	C	D	Z	GT c
<i>Nambictis senuti</i>	C	C	Z	PT
<i>Orangictis garipeensis</i>	C	C	Z	GT u
<i>Africanictis meini</i>	C	C	Z	PT
<i>Africanictis hyaenoides</i>	C	D	Z	GT u
<i>Diamantofelis lerox</i>	C	E	Z	GT c
<i>Namalelis minor</i>	C	D	Z	GT u
<i>Deinotherium hoblayi</i>	Pro	H	HB	GT l
<i>Afromastodon coppensi</i>	Pro	H	HB	GT u
<i>Orycteropus minutus</i>	A	C	En	PT
<i>Austrolagomys hendeyi</i>	A	C	HH	PT
<i>Prohyrax hendeyi</i>	A	D	HH	GT u
<i>Diceros australis</i>	Par	H	HB	GT c
<i>Chilotheridium pattersoni</i>	Per	G	HH	Aq
<i>Nguruwe kijivium</i>	Ar	D	O	GT l
<i>Namachoerus moruoroti</i>	Ar	E	HB	GT l
<i>Antheacotheriidae indet.</i>	Ar	F	O	
<i>Dorcatherium</i> aff. <i>pigotti</i>	Ar	D	HB	GT u
<i>Orangemeryx hendeyi</i>	Ar	G	HH	GT c
<i>Namacerus garipeensis</i>	Ar	D	HH	GT c
<i>Pecora indet 1</i>	Ar	D		
<i>Pecora indet 2</i>	Ar	D		
Total		37	37	34

most of the micromammals) evoke a more or less wooded bushy savannah; all the micromammals are terrestrial or subterranean, none is a climber or arboreal. There are few forest forms (*Deinotherium*, the two suids); *Chilotheridium*, which had hippo-like habits, indicates a more humid environment, compatible with the above indications, perhaps a gallery forest along the banks of the proto-Orange in a generally open

countryside.

Synecological study

The method used is that conceived by T. H. Fleming (1973), and brought up to date by Andrews *et al.*, (1979) and modified by Guérin (1998). A locality is characterised (or a level within a locality) by a group of four histograms expressing as a percentage the number of species present grouped according to zoological classification (taxonomic histogram), size (mass histogram) dietary adaptations (dietary histogram) and locomotor adaptations

- The taxonomic histogram has 8 classes corresponding to Orders: R (Rodents), I (Insectivores), Pri (Primates), Ar (Artiodactyls), C (Carnivores plus Creodonts), Per (Perissodactyls), Pro (Proboscideans), A (others).

- Mass histogram has 7 classes: AB = less than 1 kg ; C = 1 to 10 kg; D = 10 to 45 kg; E = 45 to 100 kg ; F = 100 to 200 kg; G = 200 to 1000 kg ; H = more than 1000 kg.

- Dietary histogram comprises six categories: En = entomophage; FG = trugivores and granivores; HB = brachyodont herbivores; HH = hypsodont herbivores; Z = carnivores (zoophages); 0 = omnivores.

- Locomotor histogram has six classes: GT for large terrestrial mammals, subdivided into f (forest), u (ubiquitous) and c (cursorial); PT for small terrestrial mammals; Gr-Ar for climbers and arboreal forms; Aq for aquatic; Ae aerial; Fo for burrowers.

Table 1 indicates the ecological categorisation of each mammal taxon from Arrisdrift. Figure 1 corresponds to 4 histograms defined above. The following remarks are called for:

- the large number of carnivores, artiodactyls and rodents reveals that the milieu was predominantly open, which confirms the importance of zoophages as well as the limited quantity of large forest forms and arboreal climbers.

- the equivalence of hypsodont and brachyodont herbivores, the elevated number of medium sized species and the strong representation of entomophages and omnivores show that there were forested sectors, which were less extensive than the open regions.

- the large number of large sized species indicates a certain humidity.

The synecological study confirms, therefore, the results of the autecological study: while the Arrisdrift locality was forming, the proto-Orange, flanked by gallery forests, flowed through a bushy savannah which was more or less wooded, but globally quite open. This agrees with the interpretation of Pickford *et al.*, (1996) who considered on the basis of geological features that the palaeoenvironment at Arrisdrift corresponded to a gallery forest with dense understory under a warm subtropical semi-arid climate.

Acknowledgements

I am greatly indebted to Dr. Brigitte Senut and Dr. Martin Pickford for offering me, together with the Miocene Namibian rhinoceros remains, the palaeological conclusion for study and report. Martin Pickford gave me numerous indications on many large mammalian taxa, as did Pierre Mein for all the micromammal genera and species. This work was funded by CNRS and the Singer-Polignac Foundation.

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