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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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The Miocene Rhinocerotidae (Mammalia) of the Northern Sperrgebiet, Namibia

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Three fossiliferous sites in the Northern Sperrgebiet have yielded remains of Rhinocerotidae. At Langental, where *Brachypotherium heinzelini* Hooijer was already recorded in 1971 on the basis of a mandible fragment, the presence of this rhinoceros is confirmed thanks to a well preserved magnum, an isolated upper molar and above all by an almost complete series of upper cheek teeth. At Grillental a IVth metacarpal indicates the presence of *Chilotheridium pattersoni* Hooijer, thereby greatly enlarging the geographic and stratigraphic range of this species, hitherto known from the period 18-11 Ma; two other Rhinocerotidae, one of which is indeterminate, the other most likely *Brachypotherium* cf *heinzelini*, occur at the site. At Fiskus three upper premolars attest to the presence of *Aceratherium acutirostratum* (Deraniyagala), its first discovery in southern Africa, and a poorly preserved pyramidal probably belonging to *Brachypotherium heinzelini*.

Version française abrégée

La Namibia Paleontology Expedition, dirigée par B. Senut et M. Pickford, a découvert et exploité depuis 1991 cinq gisements à rhinocéros miocènes (Pickford and Senut, 2003). Deux d'entre eux, Arrisdrift et Auchas Mine, situés dans la vallée du Fleuve Orange, ont été étudiés en 2003. Trois autres gisements à rhinocéros, Langental, Grillental et Fiskus, se situent dans le Nord du Sperrgebiet et font l'objet de la présente étude.

A Langental, qui date de 20 Ma, une hémimandibule de rhinocéros avait été découverte au début du XXème siècle. Brièvement décrite sans détermination par E. Stromer (1926), elle fut étudiée en 1971 par K. Heissig qui l'identifia comme *Brachypotherium heinzelini* Hooijer. Un magnum complet et en bon état et un fragment très abîmé de métapode ont été recueillis en 1996, le magnum a été étudié et attribué au même brachypothère en 2000 par C. Guérin. Enfin l'essentiel des deux rangées dentaires supérieures d'un crâne en très mauvais état a été découvert en 2003, puis une arrière-molaire supérieure isolée en 2004.

A Grillental qui date de 20 à 19 Ma, un métacarpien IV et une phalange abaxiale de Rhinocerotidae ont été recueillis en 2001, et un gros fragment d'astragale et qu'un trapézoïde complet en 2004.

A Fiskus qui a le même âge une prémolaire de Rhinocerotidae, très usée et en mauvais état, y a été découverte en 1993. En 2004 deux prémolaires supérieures usées mais mieux conservées et un pyramidal en mauvais état ont été recueillis.

Le *Brachypotherium heinzelini* Hooijer, 1963 de Langental

Le genre *Brachypotherium* Roger regroupe de gros rhinocéros hippopotamoïdes au corps en barrique et aux pattes courtes mais puissantes. Les I /2 sont développées en défense; l'ectolophe des jugales supérieures montre une tendance à l'applatissement. Les nasaux sont faibles, il n'y avait pas de cornes. Les moeurs plus ou moins amphibies étaient voisines de celles des hippopotames modernes. Le genre est bien connu dans le Néogène d'Eurasie. Trois espèces ont été décrites dans le Néogène d'Afrique, *B. snowi*, *B. heinzelini* et *B. lewisi*; elles nécessitent une révision (Guérin, 1980 b, 2000).

Brachypotherium heinzelini a été défini en rive droite de la rivière Sinda, Basse Semliki, Congo du NE, il est connu dans une dizaine de gisements d'Afrique orientale et centrale datant de 19 à 4,5 Ma. ce qui constitue une durée énorme. Toutefois sa présence dans divers gisements plus récents que 12 Ma, signalée par divers auteurs et impliquant donc une contemporanéité partielle avec *Brachypotherium lewisi* laisse planer un doute sur la détermination spécifique de ses représentants les plus récents.

Il est représenté à Langental, outre le fragment d'hémimandibule portant la dernière prémolaire et les deux premières molaires déterminé par K. Heissig (1971), par: 7 éléments de deux rangées dentaires supérieures provenant d'un crâne très mal conservé qui n'a pu être recueilli; une M 3/ droite incomplète; un magnum droit en bon état, brièvement décrit par C. Guérin en 2000; un fragment proximal de Mc III droit en très mauvais état de conservation.

Les dimensions des jugales supérieures sont indiquées tabl. 1. Hooijer (1966) donne des dimensions à peu près comparables pour une M /3 de Karungu mais quatre P 4/ de Sinda, Rusinga et Napak sont nettement plus larges que celle de Langental, et une M 2/ de Sinda est incomparablement plus grosse, ce qui laisse planer un doute sur sa détermination: si l'âge de Sinda n'est pas beaucoup plus ancien que 6 Ma, le brachypothère de ce gisement pourrait être rapproché de *B. lewisi*, plus récent et plus grand que *B. heinzelini*. Du point de vue de leur morphologie les caractères à retenir pour les prémolaires (Pl. 1 A) sont l'aplatissement de l'ectolophe et l'absence d'étranglement du protocône, et pour les molaires le profil de l'ectolophe, la présence d'un étranglement du protocône (Guérin, 1980a) et la nette différence de lar-

geur du protolophe et du métalophe.

Les dimensions des molaires inférieures sont données tabl. 2. Celles de la M /2 sont comparables à celles données par D.A. Hooijer (1966) pour une M /2 de Napak II A.

Le magnum (Pl. 1 B) n'avait encore jamais été décrit dans cette espèce.

Les dimensions du Mc III sont compatibles avec celles d'un Mc III de *B. heinzelini* de Rusinga conservé au Musée de Nairobi.

Le *Chilotheridium pattersoni* Hooijer, 1971 de Grillental

Le genre *Chilotheridium* Hooijer, 1971 appartient à la sous-famille des Chilotheriinae qui présente des convergences avec celle des Brachypotheriinae. Toutefois la taille générale est petite, il existait une petite corne dans les deux sexes, les I /2 sont faibles, les jugales sont hypsodontes et la main est tétradactyle. Le genre principal *Chilotherium*, abondant dans le Néogène d'Europe orientale et d'Asie, est absent d'Afrique où il est remplacé par le genre endémique *Chilotheridium*.

Chilotheridium pattersoni a été défini à Turkana Grit près de Loperot, Turkana District, Kénya. Il est connu de 7 gisements (6 d'Afrique orientale et Arrisdrift en Namibie) datant de 18 à 11 Ma.

Il est représenté à Grillental par un Métacarpien IV gauche et une Phalange I abaxiale.

Le Métacarpien IV présente une morphologie (Pl. 1 C et D) et des dimensions (tabl. 3) très proches de celles des Mc IV de Loperot

Le Rhinocerotidae indéterminé et le présumé Brachypothère (? *Brachypotherium* cf. *heinzelini*) de Grillenthal

Un gros fragment (une tranche transversale) d'astragale de Rhinocéros a été recueilli en 2004. Les dimensions et proportions sont incompatibles avec *Ch. pattersoni* ou avec un *Brachypotherium*. Elles pourraient en revanche correspondre à un *Dicerorhinus leakeyi* ou à un *Diceros australis*, mais la pièce n'est pas déterminable au delà de la famille.

En 2004 des éléments d'un squelette de jeune rhinocéros complètement détruit par l'érosion ont été découverts; un trapézoïde gauche complet et l'épiphyse distale non synostosée d'un métapode médian ont pu être recueillis. Le trapézoïde présente une morphologie et des dimensions très proches d'un trapézoïde de *Brachypotherium brachypus* de Sansan

L'*Aceratherium acutirostratum* (Deraniyagala, 1951) de Fiskus

Aceratherium représente le principal sous-ensemble de la sous-famille des Aceratheriinae. Largement répandu dans le Néogène d'Eurasie, il regroupe des rhinocéros tapiroïdes de taille moyenne à grande, sans corne, aux os nasaux courts et grêles; les I /2 sont développées en une puissante paire de défenses; les jugales sont très brachyodontes, les supérieures ont un ectolophe plus ou moins plat. La main est tétradactyle. Deux espèces, *A. acutirostratum* et *A. campbelli* Hamilton, 1973, sont connues en Afrique (Guérin, 1980b, 2000).

L'espèce est définie à Moruaret Hill près de Losodok, Turkana district, Kénya. Elle est connue dans une quinzaine de gisements d'Afrique orientale et centrale datés entre 19,5 et 4,5 Ma.

Elle est représentée à Fiskus par une P 2/ droite, une P 3/ droite et une P 4/ gauche. Les dimensions (tabl. 1) et les caractéristiques morphologiques de ces dents correspondent bien à *A. acutirostratum*:

Le présumé *Brachypotherium heinzelini* de Fiskus

Un pyramidal gauche incomplet et en mauvais état possède des dimensions et proportions compatibles avec *Brachypotherium heinzelini*, connu dans la même région à Langental, dont l'âge est proche.

Conclusion

A Langental la présence de *Brachypotherium heinzelini* est confirmée, et le matériel dentaire permet de préciser certains éléments de la diagnose de l'espèce.

Le petit Chilothériiné *Chilotheridium pattersoni* est reconnu à Grillental, qui constitue désormais le plus ancien gisement de cette espèce. Des restes difficilement déterminables de deux autres Rhinocerotidae existent dans le gisement; parmi eux un trapézoïde correspond sans doute à *Brachypotherium heinzelini*.

Trois prémolaires supérieures isolées de Fiskus correspondent à *Aceratherium acutirostratum*. C'est la première fois que cette espèce bien représentée en Afrique orientale est découverte en Afrique australe. *Brachypotherium* cf. *heinzelini* est également attesté dans le même gisement.

Introduction

Since 1991, the Namibia Palaeontology Expedition, directed by B. Senut and M. Pickford, has discovered and exploited five localities which have yielded Miocene rhinoceroses (Pickford and Senut, 2003). Two of these, Arrisdrift and Auchas Mine, located in the Orange River Valley were studied in 2003. Arrisdrift yielded 112 identifiable remains, most of which belong to the species *Diceros australis* Guérin, 2000, as well as a carpal of *Chilotheridium pattersoni* Hooijer, 1971, a species which was known until then from the Middle Miocene of East Africa. Two specimens of Rhinocerotidae from Auchas Mine could not be identified, even to the generic level (Guérin, 2000, 2003). The three other localities, Langental, Grillental and Fiskus are located in the Northern Sperrgebiet, and form the subject of this study.

In Guérin (2000, 2003) the methods of study were described in detail and an overview of the Neogene Rhinocerotidae of Africa was given. Since then, a new genus and species of Iranotherinae, *Ougan-*

datherium napakense, was recognised in the Early Miocene of Uganda (Guérin and Pickford, 2003). Furthermore the study of an important collection of unpublished specimens from the Neogene of the Tugen Hills in Kenya led to significant advances in the knowledge of several species: one result of this is that the irritating problem of the identification of the postcranial skeleton of certain Miocene medium sized species could finally be resolved (Guérin, in press).

The Localities

Langental: In this locality (ca 20 Ma), which comprises silts infilling a palaeovalley that opens southwards towards the Atlantic, a hemimandible discovered at the beginning of the 20th Century was briefly mentioned by Stromer (1926) and fully described by K. Heissig in 1971 who attributed it to *Brachypotherium heinzelini* Hooijer. A complete, well preserved magnum and a poorly preserved metapodial were recovered in 1996 by the Namibia Palaeontology Expedition. The magnum was attributed to the same species of brachypothere by Guérin (2000). Finally, an almost complete palatal dentition in a very fragmented skull was found in 2003, and an isolated upper molar in 2004.

Grillental: This locality occurs in an old valley infilled with Early Miocene silts and sands. It is aged ca 20-19 Ma. A IVth metacarpal and an abaxial phalanx of a rhinocerotid were collected in 2001, and in 2004 a large fragment of talus as well as a complete trapezoid.

Fiskus: This site is close to Lüderitz dating from ca 20-19 Ma, comprises fluvial silts and clays. A worn and damaged rhinocerotid premolar was found in 1993. In 2004 two better preserved upper premolars and a poorly preserved pyramidal were recovered.

Systematic descriptions

The Langental Brachypothere

Subfamily Brachypotheriinae
Genus *Brachypotherium* Roger, 1904
Species *Brachypotherium heinzelini* Hooijer, 1963

The genus *Brachypotherium* comprises the large hippopotamoid rhinos with barrel-shaped bodies and short, strong feet. The i/2s are tusk-like, the ectoloph of the upper cheek teeth show a tendency to be flattened. The nasals are weak, and there were no horns. The more or less amphibious habits of this rhino were close to those of extant hippopotamids. The genus is well known in the Neogene of Eurasia. Three species have been described in the Neogene of Africa, *B. snowi*, *B. heinzelini*, and *B. lewisi*, which are in need of revision (Guérin, 1980b, 2000).

Original species diagnosis : *Brachypotherium* with P4/ with a buccal cingulum.

Emended species diagnosis (after notes by Hooijer, 1966) : Cheek-teeth brachyodont ; the upper ones are narrowed posteriorly, do not possess an indented protocone and have a reduced antecrochet. Upper premolars with a flattened ectoloph beyond the paracone fold. Lingual cingulum well developed, buccal cingulum unsteady, weak antecrochet not obstructing the medisinus. Upper molars with lingual cingulum present or not. Lower cheek-teeth with a flattened external syncline, with or without buccal cingulum.

Holotype : Upper left P4/.

Other material originally attributed to the species : several dental remains from Sinda and Lake Albert, a talus from Sinda, Congo.

Type locality : Right bank of the Sinda River, opposite Ongoliba Ravine, Lower Semliki, Northeast Congo.

Other localities : other than Sinda (more than 6 Ma), *B. heinzelini* has been recorded at Arongo Uyoma (Early Miocene), Chemeron Formation (Northern Extension) (now known as the Mabaget Formation) (5-4.5 Ma), Cheparawa (Muruyur Formation, 15.5 Ma), Karungu (18 Ma), Rusinga (18 Ma) all in Kenya : Bukwa (between 17.5 and 18.5 Ma) and Napak (19.5 Ma) in Uganda : Karugamania (more than 7 Ma) in Congo.

Material : LT 244'03, 7 upper cheek teeth from a fragmented skull; LT 100'04, incomplete right M3/; hemimandible with p/4-m/2 (Stromer, 1926; Heissig, 1971). A cast of the specimen is housed at the Natural History Museum, London (M 36940); LT 384'96, well preserved right magnum (Guérin, 2000); LT 494'96, poorly preserved proximal end of right Mc III.

Description :

Upper cheek teeth.

Dimensions are provided in Table 1. D.A. Hooijer (1966) gave comparable dimensions for an m/3 from Karungu (Kenya) but four P4/s from Sinda, Rusinga, and Napak are clearly larger than the Langental specimen, while an M2/ from Sinda is much bigger, which suggests that its identification could be incorrect. If the age of Sinda is not much more than 6 Ma, the brachypothere from there could belong to *B. lewisi*, which is younger than *B. heinzelini*.

Left P2/-P3/ : these two teeth are heavily worn; the ectoloph of P2/ is not preserved and that of the P3/ is missing its anterior third. Accurate measurements are not possible. The crochet is the only internal fold. There is no lingual cingulum and the protocone is not indented.

Table 1. Compared dimensions of upper cheek teeth of Miocene rhinocerotids from the Northern Sperrgebiet. (L - length; L abs - greatest length; L anat - anatomical length; DT – breadth ; std. dev. – standard deviation)

Brachypotherium heinzelini **Langental**								**Grillental**	***Aceratherium acutirostratum*** **Fiskus**		
		Left	Right	Left	Right	Left	Right	Right	Right	Right	Left
M 1/	L		49								
	DT										
M 2/	L			49	53						
	DT			57	58.5						
M 3/	L abs.					61.5	63				
	L anat.						54				
	DT						60	64			
P 2/	L								35		
	DT								42		
P 3/	L									42	
	DT									52	
P 4/	L	35									42
	DT	52									60

D. douariensis						***B. snowi***				***O. napakense***			
		n	mean	min.	max.	n	mean	min.	max.	n	mean	min.	max.
M 1/	L	2	60.25	59	61.5	2	61.5	55	68	3	32	37	33.8
	DT	3	61.33	59	64	1	71			2	43.5	43	44
M 2/	L	3	62.83	60	67.5	2	67	63	71	1	45		
	DT	2	68.75	66.5	71	2	76.5	74	79	2	42	45.5	43.8
M 3/	L abs.	1	63							2	43	43.5	43.25
	L anat.	3	57.33	50	64	1	63			2	36	37.5	37.25
	DT	3	61.17	59	64					2	39	39.5	39.25
P 2/	L	3	33.83	32.5	35	2	33	32.5	33.5	2	23.5	24	23.75
	DT	3	41.5	41	42.5	2	42.75	41.5	44	2	25	25.5	25.25
P 3/	L	3	43.67	42	45	2	41.75	41.5	42	2	27	28	27.5
	DT	2	55	53	57	2	60.25	59.5	61	2	33	34	33.5
P 4/	L	2	46.5	46	47	1	49			2	29.5	29.5	29.5
	DT	2	60.75	59	62.5	1	69			2	37.5	38	37.78

Paradiceros mukirii			***D. leakeyi***	***A. campbelli***	***Diceros australis***						
		F. Ternan	**Rusinga**								
							n	mean	min.	max.	std. dev.
M 1/	L		40	58							
	DT		50	68.5							
M 2/	L		48		M 2/	L	4	57.5	54	59	2.38
	DT		56			DT	4	61.5	56.5	64	3.391
M 3/	L abs.		53	54	M 3/	L abs.	4	65.5	64.5	66.5	0.816
	L anat.		43	47.5		L anat.	4	53.5	52	55	1.291
	DT		56.5	49.5		DT	4	61.25	60	62	0.957
P 2/	L	28									
	DT	32.5									
P 3/	L	33.5									
	DT	41.5									
P 4/	L	31.5		48	P 4/	L	3	37.83	32.5	43.5	5.508
	DT	45		63		DT	3	51.83	41	60.5	9.929

Left P4/ (Pl. 1 A) : this tooth is heavily worn. It is appreciably wider at the level of the protoloph than at the metaloph. The ectoloph has a strong paracone fold which is thick but not very projecting; beyond which its profile is more or less flat, slightly undulating; the paracone fold fades into the ectoloph 1 cm from the cervix. The only internal fold is the crochet. The protocone is not indented. There is no lingual cingulum, but the posterior one overhangs the caudal half of the hypocone. There is no trace of a buccal cingulum.

Left and right M2/ : these teeth are well preserved. On the ectoloph, the paracone fold is very thick, in section forming a right angle; behind this fold the profile of the ectoloph deepens progressively lingually before swelling outwards. The crochet is the only internal fold. The protocone is not indented. There are no buccal and lingual cingula, but the anterior one is strong. The posterior cingulum is strong, and encloses a wide but not deep post-fossette.

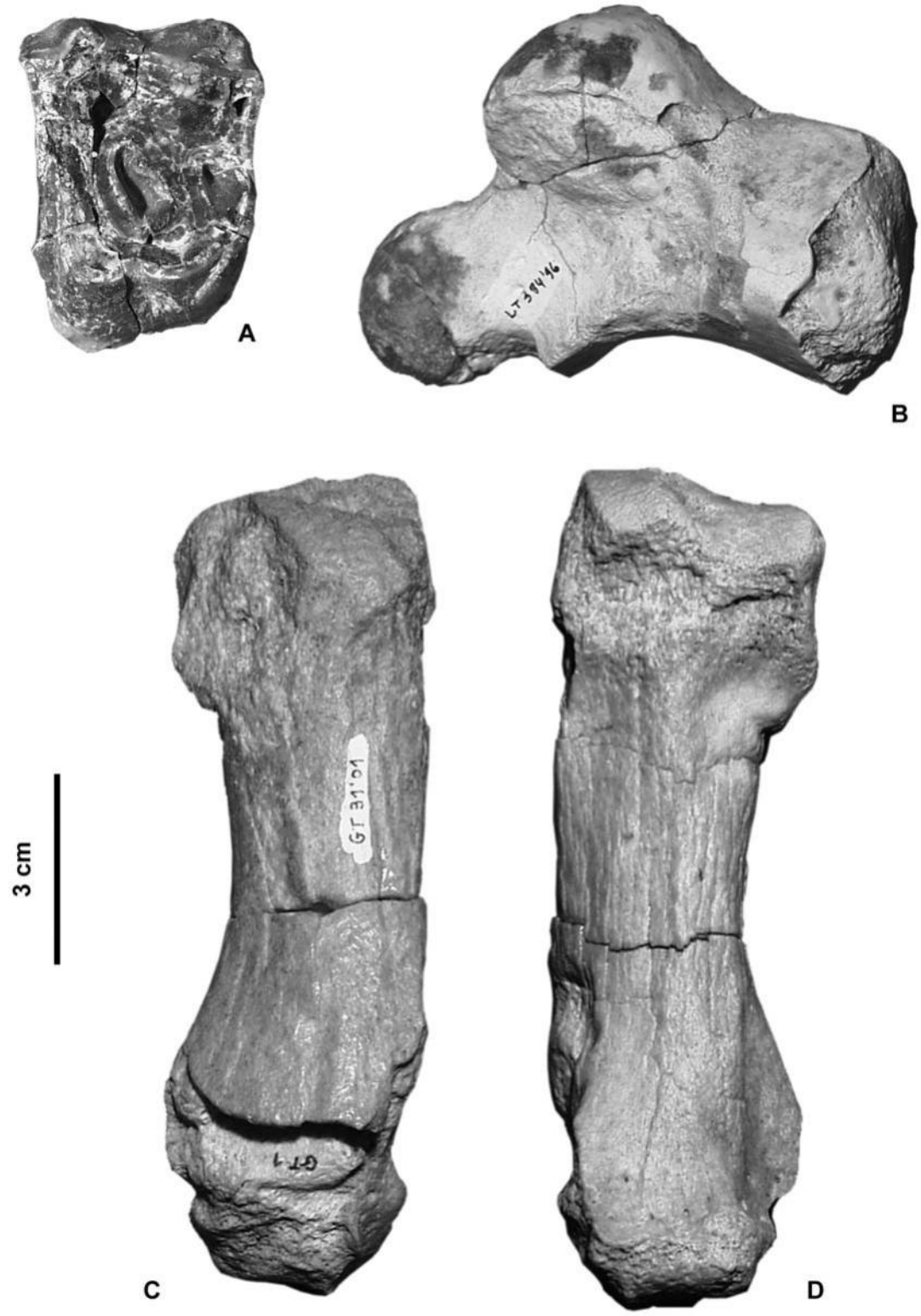

Plate 1

A: *Brachypotherium heinzelini* from Langental, LT 244'03, left P4/, occlusal view.
B: *Brachypotherium heinzelini* from Langental, LT 384'96, right magnum, three quarters oblique anterior view.
C: *Chilotheridium pattersoni* from Grillental, GT 31'01, left Mc IV, posterior view.
D: *Chilotheridium pattersoni* from Grillental, GT 31'01, left Mc IV, anterior view.

Left and right M3/ : these specimens are relatively heavily worn. The left tooth is broken and is reduced at the ectometaloph. Here also the only internal fold is the crochet, and there is no indenting of the protocone. There is no lingual cingulum, but the anterior one is strongly developed and there are traces of a posterior cingulum. The right M3/ discovered in 2004 is incomplete (it is missing the posterior quarter of the ectometaloph) but its medium wear permits additional observations to be made. There is a strong indenting of the protocone, especially on its posterior surface; the crochet is clear and one can see traces of a crista, behind the paracone fold the profile of the ectometaloph is almost straight. The paracone fold is thick and strong and is separated from a strong parastyle by a deep, flat-bottomed groove which extends to the cervix, whereas it does not quite reach cervix in the two M3/s collected in 2003. There is no buccal cingulum, but there is a short lingual one at the end of the transverse valley.

Mandible and lower molars :

The horizontal ramus of the mandible is low and wide; it is 82 mm deep beneath m/2-m/3, and its breadth beneath m/3 is 54 mm.

K. Heissig (1971) identified the three teeth that it contains as the p/4-m/2. He reported its main morphological feature as the strongly flattened external syncline and he also noted the absence of buccal cingulum, reduced to a rudiment on the anterior edge of the lateral surface. He considered that the specimen was Vindobonian, because, for him, earlier brachypotheres did not yet possess these characters.

The dimensions of the lower molars are provided in Table 2. Those of the m/2 are comparable to those published by Hooijer (1966) for an m/2 from Napak IIa.

Magnum :

The anterior surface is wide and low (which is typical of the genus), and possesses a slightly concave anterior margin. In medial view there is no infolding between the facets that correspond to the scaphoid and the Mc II. The posterior tuberosity is relatively short and recurved (Pl. 1 B). Its dimensions are as follows :-

Total length	84.5 mm
Anterior breadth	57 mm
Height of the anterior surface	39 mm
Maximal height	58.5 mm
Sub-articular height	57 mm

Mc III :

The specimen is poorly preserved and consists of the proximal end. On the lateral surface of the epiphysis there is only one crescentic articular facet. The transverse diameter of the proximal epiphysis is greater than 57 mm and the antero-posterior diameter exceeds 49 mm, which are similar to an Mc II of *B. heinzelini* from Rusinga housed at the National Museum of Kenya.

Affinities :

As far as the upper premolars are concerned we note that the diagnosis of *B. heinzelini* is unclear, notably for the cingula and anticrochet. After study there really only remains the flattening of the ectoloph and the absence of indentations on the protocone.

As for the premolars, the diagnosis of the molars by D.A. Hooijer includes features which are highly variable such as the presence of an anticrochet or of buccal and lingual cingula, as well as characters which are more reliable such as the profile of the ectoloph, the presence of indentations on the protocone (Guérin, 1980) and the clear difference between the breadths of the protoloph and metaloph.

Brachypotherium heinzelini lived in eastern, central and southern Africa between 19.5 and 4.5 Ma, which is an extremely long time. However, its presence in various localities younger than 12 Ma, reported by several authors and thus implying a partial overlap with *Brachypotherium lewisi*, indicates that there might be something wrong with the species determination of the younger material.

The *Chilotheridium* from Grillental

Subfamily Chilotheriinae
Genus *Chilotheridium* Hoojier, 1971
Species *Chilotheridium pattersoni* Hooijer, 1971

The subfamily Chilotheriinae show convergences with the Brachypotheriinae, consisting as they do of hippopotamoid rhinos with barrel-shaped bodies and short feet. However, their body size is smaller, there is a small horn in both sexes and the i/2s are weak, the cheek teeth are hypsodont and the hand is tetradactyl. The main genus *Chilotherium* which is abundant in the Neogene of eastern Europe and Asia, is absent in Africa where it is replaced by the genus *Chilotheridium*.

Original diagnosis : Small single nasal horn in both sexes; premaxillaries weak, no upper I; frontals and parietals pneumatised; orbit not placed so near upper contour of skull as in *Chilotherium*; cranium and occiput rather narrow; parietal crests not widely separated; inferior squamosal process not united below; symphyseal portion of mandible narrow, slightly expanding anteriorly. Cheek teeth fully hypsodont as in *Chilotherium* and with the same pattern: uppers with paracone style fading away basally and posterior portion of ectoloph flattened; protocone well set off by folds and flattened internally; anterior fold in metaloph, marking off hypocone; antecrochet prominent basally, curving inward to medisinus entrance; crochet usually well developed, and crista weak or absent; metacone bulge at base of M3/; anterior cin-

Table 2. Compared dimensions of lower cheek teeth of Miocene rhinocerotids from the Northern Sperrgebiet. (L - length; L abs - greatest length; L anat - anatomical length; DT – breadth).

B. heinzelini **Langental**				***Diceros australis*** **Arrisdrift**					
						n	mean	min.	max.
M /1	Length	50		M /1	Length	2	45.75	45	46.5
	Breadth	36			Breadth	1	37.5	37.5	37.5
M /2	Length	60		M /2	Length	3	54.5	50.5	58
	Breadth	38*			Breadth	4	37	33.5	39
M /3	Length			M /3	Length	4	57.62	52.5	60
	Breadth				Breadth	4	36.5	35	39
P /2	Length			P /2	Length	4	31.62	30	33
	Breadth				Breadth	3	20.67	19.5	22
P /3	Length			P /3	Length	5	39.4	38	43
	Breadth				Breadth	4	28.38	27.5	29
P /4	Length	45		P /4	Length	4	42.75	40	46
	Breadth	34.5			Breadth	3	35	32.5	37
L P/3-P/4				L P/3-P/4		1	83	83	83
L M/1-M/3				L M/1-M/3		2	156.75	156.5	157

	Diceros douariensis						***B. snowi***	***Chil. Pattersoni*** **Loperot**				***A. acutir.*** **Karungu**	***P. mukirii*** **Fort Ternan**
		n	mean	min.	max.			n	mean	min.	max.		
M /1	Length	2	48	47	49			2	42	40.5	43.5	39	35
	Breadth	1	30.5					2	30	27	33	30	27
M /2	Length	2	56.75	55.5	58		51.5	3	54.5	50.5	57	47	42
	Breadth	2	33.75	32	35.5		35	3	31	29.5	32.5	32	26
M /3	Length	1	54				58	2	59.5	56	63	54	43.5
	Breadth	1	31.5				36.5	2	30.75	27.5	34	31	25
P /2	Length	1	26				30	4	23.12	20	25	22	24
	Breadth	1	18.5				22	2	16	14	15		14
P /3	Length	1	35.5				36.5	4	33.62	25.5	38.5	32.5	27.5
	Breadth	1	33				26.5	4	21.12	18.5	24	23.5	19.5
P /4	Length	1	43				44.5	4	37.5	34	39	37.5	30.5
	Breadth	1	30				31.5	3	26.17	25.5	27	27.5	24.5
L P/3-P/4		1	80					3	67	53	74.5	66	59
L M/1-M/3		1	155				169	4	152.25	144	159	130	121

Table 3. Compared dimensions of Mc IV of Miocene rhinocerotids from the Northern Sperrgebiet. (DAP - antero-posterior diameter; DT - transverse diameter; dia - diaphysis; max - maximal; dist - distal; prox - proximal; artic – articulation ; std. dev. – standard deviation).

	GRILLENTAL		***Chilotheridium pattersoni***				
	GT 31'01		n	mean	min.	max.	std. dev.
Length	127		3	125.17	121.5	129.5	4.041
DT prox.			2	35.5	34	37	
DAP prox.	41*		2	38	32	44	
DT dia.	29.5		3	26.17	23	30.5	3.884
DAP dia.	21		3	18	17.5	18.5	0.5
DT max. dist.	42		3	42.17	37	47.5	5.252
DT artic. dist.	38.5		3	35.5	33.5	37	1.803
DAP dist.	37*		3	34.33	33	37	2.309

	D. gr. Pachygnathus/neumayri							***A. acutirostratum***
	n	mean	min.	max.	std. dev.	coeff. var.		Rusinga
Length	8	144.81	134	156	9.059	6.26		152.5
DT prox.	8	47.81	43	53	3.535	7.39		
DAP prox.	8	42.12	37	47.5	3.41	8.09		
DT dia.	8	37.69	31.5	41	3.162	8.39		34
DAP dia.	8	24.75	20	29	2.726	11.01		22
DT max. dist.	8	46.69	39	52.5	4.166	8.92		42
DT artic. dist.	8	43.06	37.5	47	3.59	8.34		40
DAP dist.	8	41	37.5	46	2.712	6.62		37

	B. heinzelini					***D. leakeyi***		***O. napakense***			***D. australis***
	n	mean	min.	max.		Rusinga		Right	Left		AD 404'97
Length	2	120	119.5	120.5		165		143.5	143		188*
DT prox.	2	47.25	46.5	48		52		33.5	32.5		55
DAP prox.	2	52	48.5	55.5		46		32	32		51.5
DT dia.	2	37.5	36.5	38.5		34		25	23.5		37.5
DAP dia.	2	24.25	23.5	25		20.5		16	16		27
DT max. dist.	2	52	52	52		50.5		32	32		51
DT artic. dist.	2	46	45	47		46		28	29		45
DAP dist.	2	40.25	38	42.5		40.5		30.5	31		53

gulum strong, internal cingulum weak and usually forming cusp at medisinus entrance. Lower canine (sic*) subtriangular in cross section, depressed dorsoventrally, internal edge sharpened by wear, outer lower edge rounded, and outer upper edge ridged. Scapula low and wide; limb and foot bones not much shortened; radius and ulna, and tibia and fibula not ankylosed; radius with cuneiform facet; lunar without facet for ulna; metacarpal V present, three fifths the length of metacarpal IV; lateral metapodials somewhat divergent posteriorly; femur with small third trochanter; calcaneum without tibia facet; navicular nearly rectangular; cuboid wider than high; metatarsal III with small cuboid facet.

* the tooth described is in fact the i/2 and not the canine.

Holotype : Skull 70-64K, B12, from Loperot.

Other material originally attributed to the species : Hooijer (1971) described a vast hypodigm comprising several specimens of almost all elements of the skeleton.

Type locality : Turkana Grits close to Loperot, Turkana District, Kenya.

Other localities : apart from Loperot (17 Ma), *Ch. pattersoni* is known from Kirimun (15 Ma), Ngorora (12-11 Ma), Ombo (16 Ma), and Rusinga (18 Ma), all in Kenya; Bukwa (ca 18 Ma) Uganda (Hooijer, 1973); Arrisdrift (17 Ma) in Namibia (Guérin, 2000).

Material : GT 31'01, left Mc IV; GT 11'01, abaxial first phalanx.

Description :

Mc IV :

The bone is badly broken proximally and damaged distally. The median transverse section of the diaphysis shows a regularly but weakly convex anterior surface, an almost straight thick medial edge, a thinner and rounded lateral margin and a v-shaped posterior surface with a median crest. The distal epiphysis is strongly enlarged laterally, the enlargement becoming sharp in its upper part (Pl. 1 C, D). The dimensions (Table 3) are similar to those of Mc IVs from Loperot.

Abaxial first phalanx :

This specimen is rolled and incomplete distally

which makes it difficult to identify precisely. Its length is 50 mm, the transverse diameter of the proximal epiphysis is more than or equal to 28 mm and the antero-posterior diameter at the same place is greater than or equal to 23 mm.

Affinities :

Grillental is the oldest known site with *Ch. pattersoni*. The range of the species which is known from eastern and southern Africa was hitherto estimated to extend from 18 to 11 Ma.

The indeterminate rhinocerotid and the presumed brachypothere from Grillental

Rhinocerotidae indet. cf? *Brachypotherium heinzelini*

A large fragment of a rhinoceros astragalus (GT 106'04) has a transverse diameter that is appreciably greater than 86 mm, the greatest height is greater than or equal to 91 mm, and the minimal height is about 67 mm. Few observations are possible on such a fragment. What is left of the fibular facet is oblique and flat, the neck is high, and in lateral view the postero-lateral facet appears very concave.

The dimensions and porportions are incompatible with *Ch. pattersoni* the talus of which is smaller and above all lower, or with *Brachypotherium* which would be as big, but lower. They could correspond however to a *Dicerorhinus leakeyi* or *Diceros australis*, but the specimen is not identifable beyond the family level.

In 2004 elements of a skeleton of a juvenile rhinoceros which have been heavily eroded by wind blown sand, was discovered. A complete left trapezoid and the unfused distal epiphysis of a median metapodial were collected (GT 180'04).

The trapezoid is 50.5 mm long, 38 mm broad and 38.5 mm high, measurements which are close to a trapezoid of *Brachypotherium brachypus* from Sansan (respectively 51.5 x 36 x 36 mm). Breadth and height represent 75 and 76% of the length, the bone from Grillental is thus lower and more massive than that from Sansan. All the lateral surface is articular. On the medial surface, the articulation for the trapezium occupies all the upper margin and half the posterior surface. The anterior surface is swollen, its contour an inverted trapezium showing a weakly convex upper margin, which is slightly oblique. The proximal surface is hollow from anterior to posterior and is convex transversely and curves strongly on the medial side. The distal surface is less concave longitudinally than the proximal one, transversely it is almost flat. The dimensions, proportions and morphology of the anterior, proximal and distal surface approach the Grillental trapezoid to *Brachypotherium*. *B. heinzelini* Hooijer is the only species of the genus known to occur in Africa at the time that the deposits at Grillental accumulated.

The Fiskus acerathere

Subfamily Aceratheriinae
Genus *Aceratherium* Kaup, 1834
Species *Aceratherium acutirostratum* (Deraniyagala, 1951)

The species, originally attributed to a new genus *Turkanatherium*, was transferred to *Aceratherium* by Arambourg (1959) and restudied by Hooijer (1966). *Aceratherium* represents the main sub-group of the subfamily Aceratheriinae. Widespread in the Neogene of Eurasia it contains the tapiroid rhinos of medium to large size, lacking horns, with short slender nasals; the i/2s are developed into a strong pair of tusks, the cheek teeth are very brachyodont, and the uppers have a more or less flat ectoloph. The manus is tetradactyl. Two species *A. acutirostratum* and *A. campbelli* Hamilton, 1973, are known from Africa (Guérin, 1980b, 2000). A.W. Gentry (1987), on the basis of the cranial profile and the large size of the upper cheek teeth, doubted the attribution of these species to *Aceratherium*, but I will not follow him because the genus is relatively polymorphic.

Species diagnosis : emended informally by Hooijer (1963, 1966 and 1968a) :

Holotype : A skull preserved in the Colombo Museum (Sri Lanka).

Type locality : Moruaret Hill (Moruorot) near Losodok (Lothidok), Turkana District, Kenya.

Other localities : Apart from Moruorot (17.2 Ma) *A. acutirostratum* has been recorded in Kenya at Alengerr (14-12 Ma), Chemeron Formation - Northern Extension (now the Mabaget Formation) (basal Pliocene), Karungu (18 Ma), Ngorora Formation (late Middle Miocene), Ombo (18 Ma), Rusinga (18 Ma), and in the Tugen Hills (Cheparawa, 15.5 Ma; Grildain, 13 Ma; Kabarsero, 12.5 Ma; Kipsaraman, 15.5-15 Ma). It is also known from Uganda at Napak (19.5 Ma) and from Congo at Karugamania (more than 7 Ma) and Sinda (more than 6 Ma).

Material : FS 1'04, right P2/; FS 16'93, right P3/; FS 2'04, left P4/.

Description :

P2/ :

Despite its heavy wear the tooth appears to be very brachyodont because of the low lingual opening of the transverse valley. The ectoloph is globally convex with a small paracone fold and weak mesostyle separated from each other by a shallow depression. No internal fold is present. There is no indentation in the protocone. There is no buccal cingulum but there is a continuous lingual one. The dimensions are given in Table 1.

P3/ :

This tooth is deeply worn and poorly preserved. The ectoloph appears to be almost flat, but at this wear stage it resembles not only *Aceratherium* but also *Brachypotherium*. There is a discontinuous lingual cingulum. The dimensions (Table 1) are compatible with *Aceratherium acutirostratum*: a P3/ from Ombo (Kenya) is 42 mm long for a maximal breadth of 56 mm. D.A. Hooijer (1966) gives measurements of 32 and 42 mm respectively for a P3/ from Rusinga.

P4/ :

This specimen is well worn but shows a low lingual opening of the transverse valley, attesting to its brachyodonty. The protoloph and metaloph are almost equal in transverse extent. Behind the paracone fold which is thick but not greatly detached from the external wall, the ectoloph is almost flat, weakly convex. A small sharp metastyle can be seen. There is no internal fold. The protocone is clearly indented on its anterior and posterior surfaces. The lingual cingulum is present only at the lingual end of the transverse valley. The dimensions (Table 1) correspond well with *A. acutirostratum*. A P4/ from Ombo (Kenya) has a maximal diameter of 64 mm, and D.A. Hooijer (1966) indicates a length of 46 mm and a breadth of 60 mm for a P4/ from Lake Albert (Congo).

Affinities :

Despite the dimensions of the Fiskus acerathere being close to those of *A. campbelli* Hamilton (1973), it differs from it by its lower crowned premolars and by the weakness of the paracone fold of the P4/. In contrast, it corresponds closely to *A. acutirostratum*. Even though it is larger, its anatomy, dimensions and proportions recall *A. tetradactylum* and *A. incisivum* from the Middle and Late Miocene of western Europe. It probably had the same lifestyle, similar to that of extant tapirs, inhabiting the banks of water bodies and swampy areas.

A. acutirostratum lived in eastern and central Africa for a considerable period of time, from 19.5 to 4.5 Ma, or about 15 million years if its presence in the Chemeron Formation - Northern Extension is correct. If the latter record is incorrect, then the chronological range would be considerably shorter. The presence of this species at Fiskus is the first evidence of aceratheres in southern Africa.

The presumed brachypothere from Fiskus

A left pyramidal (FS 3'04) is incomplete and in poor condition (it is missing most of the posterior surface). Its upper transverse diameter is more than or equal to 62 mm and its height is about 59 mm. These dimensions and the proportions of the bone are compatible with those of *Brachypotherium heinzelini*, also known at Langental in the same region, which is of similar age.

Conclusions

Five fossil mammal localities excavated since 1991 by the Namibia Palaeontology Expedition have yielded Miocene rhinoceroses : Langental, Grillental, Fiskus, Auchas Mine and Arrisdrift. The rhinos from the last two sites were studied by Guerin (2000, 2003).

At Langental the presence of *Brachypotherium heinzelini*, of which an incomplete hemimandible was collected before the First World War, and identified by K. Heissig (1971), is confirmed thanks to a well preserved magnum, a last upper molar and above all both rows of upper cheek teeth. This confirmation greatly extends the geographic range of this species which was previously restricted to central and eastern Africa.

The small chilotheriine *Chilotheridium pattersoni* is known from Grillental, which is thus the earliest record of the species, hitherto known to range from 18-11 Ma in eastern and southern Africa. Remains of two other rhinos occur at the site but they are difficult to identify. Among these is a trapezoid which could belong to *Brachypotherium heinzelini*.

Three isolated upper premolars from Fiskus correspond to *Aceratherium acutirostratum*. This is the first time that this species has been recorded from southern Africa. *Brachypotherium* cf *heinzelini* is also present at the site.

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