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Miocene Rhinocerotidae of the Orange River Valley, Namibia

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Among the Miocene sites excavated since 1991 by the Namibia Paleontology Expedition, two located in the Orange River Valley have yielded rhinoceros remains: Arrisdrift and Auchas Mine. An atlas vertebra and a mandibular fragment, both encrusted with sediment and thus specifically undeterminable, have been recorded from Auchas Mine. A fine lot of generally well preserved rhino material was found at Arrisdrift among a very diverse Vertebrate fauna. All but one of the 112 rhino pieces constitute a homogeneous sample pertaining to a very large species of cursorial rhino first described in 2000, *Diceros australis* Guérin, of which Arrisdrift is the type locality. The large form from Arrisdrift seems to be the largest of the African Miocene Rhinos; the size and proportions of the metapodials and the other limb bones suggest a strong analogy with *Diceros* gr. *pachygnathus-neumayri* of the Upper Miocene of the Near East; the type of construction of the upper cheek teeth, in particular the fourth premolar, is of Dicerotine kind and presents, as do the dimensions, close resemblances with *Diceros douariensis* of the Upper Miocene of North Africa and Italy; the mandible shows analogies with the Dicerotines, especially the apparently short symphysis. *Diceros australis* is thus by far the oldest known species of the subfamily; the small reduced lower tusks could represent an evolutionary stage prior to the loss of the entire anterior dentition, which is effective in the subfamily since the Upper Middle Miocene. The exception among the Arrisdrift rhino material is an isolated magnum which suggests a small to medium sized short-legged form, probably *Chilotheridium pattersoni*, a species described from Loperot in Kenya, the age of which is about the same as Arrisdrift, i.e. 17 Ma.

Version française abrégée:

La Namibia Paléontology Expedition, dirigée par B. Senut et M. Pickford, a fouillé depuis 1991 les gisements miocènes du Sperrgebiet (Pickford *et al.*, 1995). Quatre gisements à rhinocéros d'âge miocène moyen ont été découverts (Guérin, 2000), dont deux dans la vallée du fleuve Orange: Arrisdrift et Auchas Mine.

1.- Les gisements:

Auchas Mine est un site diamantifère alluvionnaire situé à 50 km en amont d'Oranjemund (Pickford *et al.*, 1995), datant d'environ 18 millions d'années. Parmi les sept espèces de Mammifères recueillies dans la carrière AM 02 se trouvé un rhinocéros indéterminé représenté par un atlas et un fragment de mandibule, tous deux encroûtés de sédiment et indéterminables spécifiquement.

Arrisdrift est un gisement tres riche situé près du fleuve Orange, à 35 km à l'Est d'Oranjemund. Il date d'environ 17 M.A. et a livré de nombreux restes de Vertébrés (Pickford *et al.*, 1996). A une seule exception près, les 112 restes de rhinocéros constituent un matériel homogène appartenant a un très grand rhinocéros coureur décrit pour la première fois en 2000, *Diceros australis* Guérin, dont Arrisdrift est le gisement-type. L'exception est un magnum isolé totalement différent de ceux rapportés à *D. australis*: il évoque *Chilotheridium pattersoni* dont le gisement-type, Loperot au Kénya, est d'âge comparable à Arrisdrift.

2.- Matériel et methodes:

J'ai eu l'occasion d'étudiér une bonne quantité de restes de rhinocéros du Miocène d'Afrique: diverses pièces des trois espèces de *Brachypotherium*, de bons moulages de crânes et de dents de *Paradiceros mukirii*, quelques restes d'*Aceratherium campbelli*, des crânes et mandibules d'*Aceratherium acutirostratum* et de *Dicerorhinus leakeyi*, le type de *Diceros douariensis* et tout le matériel connu de *Chilotheridium pattersoni* de Loperot. Celà ne constitue pas toutefois un ensemble d'échantillons suffisant.

Pour pallier le manque d'éléments post-crâniens en *Aceratherium africains* de taille moyenne j'ai utilisé comme terme de comparaison un regroupement de variables mesurées sur deux espèces miocènes européennes de taille et proportions voisines appartenant à la même lignée, *Aceratherium tetradactyium* et *A. incisivum*; dans les tableaux de mesures l'échantillon correspondant est baptisé Acérathères. On ne connait pas actuellement en Afrique de grande espèce miocene de *Dicerorhinus*, j'ai donc utilisé comme comparaison *Dicerorhinus schieiermacheri* du Miocène supérieur d'Europe. Enfin, pour avoir un bon échantillon de grands *Diceros* miocènes, j'ai regroupé sous le from de *Diceros* gr. *pachygnathus-neumayri* du matériel de *D. pachygnafhus* et *Diceros neumayri*, deux espèces très proches sinon identiques du Miocene de la région méditerranéenne orientale.

3. - *Diceros autralis* Guérin, 2000

La partie la plus interesante du matériel recueilli comprend les fragments d'un crâne et de neuf hémimandibules, trois incisives inférieures, 32 dents jugales isolées, un humérus, quatre radius, trois cubitus, neuf carpiens, cinq métacarpiens, un tibia, treize tarsiens, neuf métacarpiens et plusieurs phalanges.

Trois des fragments d'hémimandibules sont suffisamment importants et comprennent une bonne part de la branche horizontale et de la symphyse, qui était probablement très courte. Le bord postérieur de la symphyse se situé dans tous les cas entre le premier tiers et la moitié de la longueur de la P/2. La brièveté de la symphyse suggère un faible développement sinon une absence d'incisives inférieures, ce qui est un caractère de Dicerotiné. Or nous disposons de deux petites incisives inférieures isolées; ces défenses ne devaient pas être fonctionnelles. Elles constituent par leur faible taille un stade évolutif antérieur.

Parmi les jugales, les plus significatives sont les troisième et quatrième prémolaires supérieures. Toutes présentent un ectolophe doté d'un fort parastyle, et un pli du paracône épais mais peu saillant; il n'y a ni mésostyle ni pli du métacône. Le principal repli interne est un fort crochet, et plusieurs prémolaires possèdent une médifossette fermée. Il existe un fort cingulum lingual continu et crénelé, et le protocône ne montre aucune trace d'etranglement. Une telle morpho logie, tout particulièrement celle de la muraille externe, est très proche de celle observée chez *Diceros douariensis* et *D.* gr. *pachygnathus-neumayri*, et les dimensions sont très voisines. Les rangées dentaires inférieures présentent des longueurs du segment molaire et du segment P /3-P /4 très proches de

celles rélevées chez *D. douariensis* et *D.* gr. *pachygnathus-neumayri*.

Un humérus gauche atteint environ 500 mm de long, soit 10 % de plus que les plus grands spécimens connus de *D.* gr. *pachygnathus-neumayri* et *D. schleiermacheri*, et ses proportions sont différentes.

Le radius dépasse lui aussi les plus grands *D.* gr. *pachygnathus-neumayri* et *D. schleiermacheri*, ce dernier étant par ailleurs plus élancé. Celui de l'*Aceratherium acutirostatum-Dicerorhinus leakeyi* indifférencié de Rusinga, dont les dimensions et proportions sont identiques à celles de notre échantillon d'Acérathères miocènes européens de taille moyenne, est plus petit et présente des proportions différentes. Les radius de *Chilotheridium* et tout particulièrement de *Brachypotherium snowi* sont plus trapus et beaucoup plus courts. Les caractères morphologiques du radius du grand rhinocéros d'Arrisdrift plaident en faveur d'un rapprochement avec la sous-famille des Dicerotinae.

Le plus grand des métacarpiens médians (Mc III) est un peu plus long que les plus grands specimens connus de *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*, mais un peu plus élancé. Ceux de *Brachypotherium snowi* et *B. heinzelini* sont plus courts et plus trapus, et il en est de même pour le petit *Chilotheridium*. Celui des acérathères européens montre plus où moins les mêmes proportions mais est bien plus petit. Un diagramme de Simpson montre que le Mc III d'Arrisdrift n'appartient ni à un Brachypothère, ni à un Acérathère, mais qu'il présente des analogies avec *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*.

Les métacarpiens abaxiaux (Mc II et Mc IV) sont plus longs que ceux des plus grands *Diceros* gr. *pachygnathusneumayri* et *Dicerorhinus schleiermacheri* connus, et nettement plus élancés. Ceux de *Chilotheridium* sont bien plus courts et trapus, ceux des Acérathères sont plus courts et montrent des proportions très différentes.

Le seul tibia recueilli est tres endommagé dans sa partie proximale mais sa longueur peut néanmoins être mesurée. Comme les Mc III il est un peu plus long que les plus grands *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*, et plus élancé. On notera qu'une épiphyse brisée de *Diceros* cf. *douariensis* de Baccinello V3 en Italie présente des dimensions identiques à celles d'Arrisdrift.

Les dimensions et proportions de trois astragales sont proches de *Diceros* gr. *pachygnathus-neumayri*, et different peu de *Dicerorhinus schleiermacheri*. L'astragale de *Brachypotherium snowi* est un peu plus gros mais nettement plus bas, et ces proportions se retrouvént pour *Chilotheridium*. Chez les Acérathères les dimensions sont plus faibles pour des proportions différentes, et il en est de même pour l'échantillon indifférencié *Aceratherium acutirostatum-Dicerorhinus leakeyi*, dont on notera au passage les similitudes avec les Acérathères.

Parmi les cinq calcanéums trois sont adultes et complets. lei encore, les dimensions et proportions sont voisines de *Diceros* gr. *pachygnathus-neumayri* et *D. schleiermacheri*, et n'ont rien à voir avec celles de *Paradiceros*, *Chilotheridium* et des Acérathères.

Le metatarsi en médian (Mt III) est à peu près aussi long que celui des plus grands spécimens connus de *Diceros* gr. *pachygnathus-neumayri* et a sensiblement les mêmes proportions sauf que son diamètre transversal susarticulaire distal est relativement plus faible. Il est significativement plus long que chez *Dicerorhinus schleiermacheri*. Celui de *Chilotheridium* est bien plus court et relativement plus trapu. Celui des Acérathères est plus petit, avec des proportions différentes.

Les métatarsiens abaxiaux (Mt II and Mt IV) sont plus graciles et beaucoup plus longs que ceux de *Diceros* gr. *pachygnathus-neumayri* et *Dicerorhinus schleiermacheri*. Par rapport à *Chilotheridium* et aux Acérathères les différences sont les mêmes que pour le métarsien médian.

Le diagramme des rapports des segments de membres montre lui aussi des similitudes avec *Dicerorhinus schleiermacheri* et *Diceros* gr. *pachygnathus-neumayri*, avec toutefois une particularite notable, la bien plus grande longueur relative des métapodes abaxiaux.

La grande espèce d'Arrisdrift semble être le plus grand des Rhinocéros du Miocène d'Afrique; la taille et les proportions des métapodes et des os longs montrent une grande similitude avec les *Diceros* gr. *pachygnathusneumayri* du Miocène supérieur du Proche-Orient; le type de construction des jugales supérieures est celui des Dicerotinae et montre, comme les dimensions, une forte ressemblance avec *Diceros douariensis* du Miocène supérieur du Maghreb et d'Italie; la mandibule évoque celle des Dicerotinae, notamment par sa symphyse apparemment très courte. Ce sont ces caractères qui nous permettent de I'attribuér au genre *Diceros*. *Diceros australis* est actuellement le plus ancien Dicerotinae connu; les defenses inférieures très réduites pourraient représentér un stade évolutif précédant immédiatement la perte totale de la denture antérieure, perte qui est accomplie au sein de la sous-famille dès la fin du Miocène moyen.

4. cf. *Chilotheridium pattersoni* Hooijer, 1971

L'exception parmi les restes de rhinocéros d'Arrisdrift est un magnum bien conservé. Par sa morpho logie, sa taille et ses proportions ce magnum est totalement différent de ceux recueillis dans le même gisement et attribués à *Diceros australis*.

Bas et très large, doté d'une face antérieure aplatie et oblique, il présente un rapport largeur/hauteur inversé par rapport à *D. australis*, ce qui montre que nous avons affaire à une espèce petite à moyenne aux pattes courtes et fortes, probablement *Chilotheridium*, genre monospécifique dont l'espèce-type a été définie dans le site kényan de Loperot, de même âge qu'Arrisdrift.

Pour 10 spécimens incomplets de *C. pattersoni* de Loperot, D.A. Hooijer (1971) donné une hauteur antérieure légèrement plus forte mais une largeur antérieure un peu plus faible; ces differences ne sont toutefois pas significatives, car elles peuvent résulter d'une variation géographique, mais surtout d'une technique de mesures sans doute quelque peu différente; quoi qu'il en soit les ordres de grandeur sont les mêmes.

Chilotheridium est le seul Chilotheriinae connu jusqu'à present en Afrique. Sa découverte à Arrisdrift accroit très largement son aire de répartition, limitée jusqu'à présent au Kénya et it l'Ouganda. Du point de vue de son extension stratigraphique, il était limité au Miocène moyen (on le connaissait jusqu'ici entre 18 et 11 Ma) mais la toute récente découverte d'un Mc IV gauche dans le gisement namibien de Grillental (20 à 21 Ma) montre que l'espèce remonte à la fin du Miocène inférieur.

History of study

Remains of Miocene mammals were discovered about a century ago in what was at the time German South-West Africa. They were sent to Germany where E. Stromer studied them in 1926, but did not identify the rhinocerotid remains more precisely than "Rhinocerine g. et sp. indet". Several later articles re-examined this old collection, revising certain species and describing new ones, the latest being by R. Hamilton & J.A. Van Couvering (1977), who synthesized previous work and updated the faunal list. In this list the only identified rhinoceros is *Brachypotherium heinzelini*, based on a brief note by K. Heissig (1971) on a hemi-mandib1e from Langental already mentioned by Stromer.

Several sporadic finds occurred later on in Miocene and Quaternary sediments. In 1933, R. Heinz briefly described a skull, mandible and footprints of rhinos discovered near Kolmannskuppe (=Kolmanskop) and Charlottenthal; these remains, preserved at Lüderitz and identified as *Diceros bicornis*, were cited by C. Guérin & G. Demathieu (1993). In 1978 G. Corvinus collected an M3/ of *Ceratotherium* (South African Museum, SAM PQ 2126) in the Upper Grillental. Finally J. Schneider found a complete but eroded metatarsal III of a large *Brachypotherium*, in 1983, 8 km to the SE of Bogenfels (most probably at Glastal 1 or 2 (Pickford & Senut, 1999)); this specimen is preserved in the South African Museum, Cape Town (SAM PQ 2517).

It was from 1991 that the Namibia Palaeontology Expedition, led by B. Senut and M. Pickford, continued excavations in the Miocene deposits of the Sperrgebiet (Pickford *et al.*, 1995; Pickford & Senut, 1999). Five localities yielded rhinoceroses, of which two are in the Orange River Valley, first excavated by Corvinus in 1976¬1978. One of these sites, Arrisdrift, is particularly rich and contains a diverse fauna. In 1998, I was able to examine more than 80 fossils from the site, most of which belong to a new species, *Diceros australis*, which is the oldest known representative of the sub-family, Dicerotinae, to which belong the two extant species of rhinoceros. The results of this study were presented at the congress of the Palaeontological Society of South Africa held at Windhoek in September, 1998, and published a short while later (Guérin, 2000). A second visit to Namibia in May 2001, enabled me to examine the new material found at Arrisdrift since 1998, and thus to complete my study.

Localities

Two localities, of Early and Middle Miocene age, in the Orange River Valley (Arrisdrift and Auchas Mine) were excavated by the Namibia Palaeontology Expedition.

Arrisdrift: This is a very rich site close to the Orange River 35 km east of Oranjemund. It is about 17 Ma and yielded abundant remains of vertebrates (Pickford *et al.*, 1996). Apart from one specimen, all the 112 rhino fossils belong to a homogeneous sample of a large species of cursorial rhinoceros, *Diceros australis*, of which Arrisdrift is the type locality. The exception is a magnum, which is completely different from those attributed to *D. australis*: it is low and wide, evoking the small to medium sized forms with short feet. It could belong to *Chilotheridium pattersoni*, defined at Loperot (Kenya), a site with the same age as Arrisdrift.

Auchas Mine: Auchas Mine is a diamond-bearing deposit located 50 km upstream from Oranjemund (Pickford *et al.*, 1995); it is aged 19 to 20 Ma. Among the 7 mammal species discovered in Pit AM 02 there is an indeterminate rhinoceros, represented by an atlas vertebra and a small fragment of mandible.

Method of study and comparison

Even though the methods used are well known and accurate, there remains a difficulty concerning the elements of comparison: most of the Miocene rhinos of Africa are still poorly known, so I have used several samples from the Miocene of Western Europe and the Near East (Greece and Turkey).

Methods

The methods of study used in this article are the same as those explained by C. Guérin (1980b), notably for the way of measuring, for the statistical treatment of the variables and for the non-quantifiable characters which are useful for discriminating teeth and skeletal remains of Rhinocerotidae. Simpson diagrams (or ratio diagrams) were systematically used to compare proportions of the main elements of the post-cranial skeleton; the reference always being a sample of some 30 adult specimens of extant *Diceros bicornis*.

Miocene Rhinocerotidae of Africa

In the present state of knowledge the family Rhinocerotidae is represented in the Miocene of Africa by 6 lineages corresponding to sub-families. These lineages contain 9 genera and 14 species (Hooijer, 1973, 1978; Guérin, 1980b, 1989, 2000; Prothero *et al.*, 1989). The absolute ages of many of the localities concerned were kindly furnished by M. Pickford.

Aceratheriinae: The aceratheres are medium to large forms, lacking horns, are cursorial and have the aspect of a large tapir. They have 4 metapodials and four functional digits in the front feet. They have a strong pair of lower tusks (the i/2), and their cheek teeth are very brachyodont; the upper cheek teeth have an ectoloph which is more or less flat, without marked folds. They were aquaphile. Two species have been reported from Africa.

- *Aceratherium acutirostratum* (Deraniyagala, 1951) is of medium size. It is known from at least 10 sites: Alengerr Beds (14 to 12 Ma), Chemeron Formation - Northern Extension (5 to 4.5 Ma), Karungu (18 Ma), Moruarot Hill near Losidok (about 17.5 - 17.2 Ma), Ngorora Formation (12 to 11 Ma), Ombo (15 Ma), and Rusinga (18 Ma) in Kenya; Napak (19.5 Ma) in Uganda; Karugamania (more than 7 Ma) and Sinda (more than 6 Ma) in Congo.
- *Aceratherium campbelli* Hamilton, 1973 is large: it is only known from Jebel Zelten (about 17 to 16 Ma) in Libya.

Dicerorhininae: These are two-homed rhinos of medium to large size, with cursorial legs. During the Miocene, the tusks were well developed. The cheek teeth are relatively brachyodont, the uppers (particularly P3/ and P4/) have the ectoloph adorned with two strong vertical folds, corresponding to the paracone and the metacone. The face is long. They live most

often in more or less wooded or bushland zones". One or two species are known in Africa:

- *Dicerorhinus leakeyi* Hooijer, 1966 is medium sized. It is recorded from at least 7 sites: Alengerr Beds (14 to 12 Ma), Chemeron Formation - Northern Extension (about 5 Ma), Karungu (18 Ma), Maboko (15.5 Ma), Ombo (15 Ma), Rusinga (18 Ma) in Kenya and Napak (19.5 Ma) in Uganda. It is noteworthy that in most of the sites that have yielded *D. leakeyi* the species *Aceratherium acutirostratum* also occurs, suggesting that they were sympatric.

- *Dicerorhinus primaevus* Arambourg, 1959, of the Late Miocene of Algeria, the generic position of which is debated (Geraads, 1986).

Up to now, large species of *Dicerorhinus* are not known in the Miocene of Africa, but they exist in Europe, such as *D. schleiermacheri* and several others (Guérin, 1980).

Dicerotinae: This sub-family contains the two extant species of African rhinos, *Diceros bicornis* ("Black" Rhinocéros) and *Ceratotherium simum* ("White" Rhinoceros). The genus *Ceratotherium*, more evolved of the two, with very hypsodont cheek teeth, dates from the end of the Miocene, the species which it contains are grazers living in savanna. The genus *Diceros*, much less specialised, dates from the Middle Miocene and includes large, strongly built, two homed species. The face is short, the mandibular symphysis is short and there is no anterior dentition. The upper cheek teeth are brachyodont, and possess a single well defined vertical fold on the ectoloph, the paracone fold. Its preferred habitat is spiny bushland in arid regions. Miocene forms of *Diceros* existed in the Maghreb, in Southern Spain, in Italy and the Near East (Greece and Turkey). Four species of Dicerotinae are known in the Miocene of Africa:

- *Diceros douariensis* Guérin, 1966: the species is defined at Douaria (9.5 Ma), in Tunisia, it is also present at Djebel Krechem el Artsouma (Late Miocene) in the same country (Geraads, 1989), as well as at Baccinello V3 (zone MN 13) in Italy (Guérin, 1980). Several remains found at Gravitelli (Late Miocene) in Sicily (Italy), as well as at Cenes de la Vega and Los Hornillos (both sites in MN 13) in the Grenada Basin, Spain, most likely belong to *Diceros* but the available material does not permit definite specific identification

- *Diceros australis* Guérin, 2000 is at present only known from Arrisdrift (Namibia) where it was defined. A detailed description is provided below.

- *Paradiceros mukirii* Hooijer, 1968 is a small species discovered at Fort Ternan (about 13 Ma) and perhaps at Maralal, also in Kenya, it is present at Kisegi (14 to 13 Ma) in Uganda, and at Beni Mellal (12.5 Ma) in Morocco (Hooijer, 1968; Guérin, 1976, 1994).

- *Ceratotherium praecox* Hooijer & Patterson, 1972, which is very abundant in the Pliocene of East and South Africa (Guérin, 1999), is also present in the Late Miocene, notably at Lothagam (7.2 to 5.5 Ma), Lukeino (6 to 5.5 Ma) and Mpesida (6.5 to 6 Ma).

Iranotheriinae: These are very large rhinos of Eurasia, heavily constructed with cheek teeth characterised by very marked hypsodonty and the strongly folded enamel. The subfamily is often assimilated into the Elasmotheriinae but I consider that the resemblances are convergences and not due to identity. Two species of Iranotheriinae are known in Africa, one of which remains poorly known:

- *Kenyatherium bishopi* Aguirre & Guérin, 1974 has for the present only been found in Kenya, at Nakali (9.5 Ma) which is the type site, and at Samburu Hills, of similar age (Nakaya *et al.*, 1999).

- *Ougandatherium napakense* Guérin & Pickford, 2003, is known from partial skeletons from Napak, Uganda. It is a small, hypsodont form, with much cementum on the cheek teeth, and long slim metapodials.

Brachypotheriinae: The brachypotheres are large rhinos with a hippo-like appearance, with barrel-shaped bodies and short thick legs. They have strong tusks. The cheek teeth tend towards hypsodonty, the ectoloph becoming flat. They were aquatic, their behaviour being similar to that of hippos. Three species are known in Africa, which, as noted by M. Pickford *et al.* (1993, p. 109) necessitate a revision:

- *Brachypotherium snowi* (Fourtau, 1920) has been found only at Wadi Moghara in Egypt and at Jebel Zelten (17 to 16 Ma) in Libya.

- *Brachypotherium heinzelini* Hooijer, 1963 is known from a dozen sites: Arongo Uyoma (Lower Miocene), Chemeron Formation - Northern Extension (about 5 to 4.5 Ma), Karungu (18 Ma), Rusinga (18 Ma) in Kenya; Napak (19.5 Ma) in Uganda; Karugamania (more than 7 Ma) and Sinda (more than 6 Ma) in Congo; Langental (18 Ma) in Namibia.

- *Brachypotherium lewisi* Hooijer & Patterson, 1972 is known from Kanapoi (4.5 Ma), Lothagam (7.2 to 5.5 Ma), Mpesida (6.5 to 6 Ma), Ngorora (12 to 11 Ma) in Kenya and at Sahabi (6.5 Ma) in Libya.

Chilotheriinae: The chilotheres, even though they have some resemblances to brachypotheres, constitute a separate sub-family. They are single homed, small, almost hippopotamoid forms with short legs (of which the front ones are tetradactyl). The tusks are small, the cheek teeth hypsodont, and they were aquatic. A single species is present in the Miocene of Africa:

- *Chilotheridium pattersoni* Hooijer, 1971 is known from six localities in Kenya and Uganda, listed in the penultimate paragraph of this paper.

Comparative material

For many years, I have had occasion to study a good quantity of Miocene African rhinoceros remains, in particular those stored at the Natural History Museum, London, where there are various specimens of three species of African *Brachypotherium*, good casts of the skull and teeth of *Paradiceros mukirii*, several remains of *Aceratherium campbelli*, skulls and mandibles of *Aceratherium acutirostratum* and *Dicerorhinus leakeyi*. I also had the opportunity to examine all the fossils attributed to *Chilotheridium pattersoni* collected at Loperot when they transited the Netherlands. Finally, the type specimen of *Diceros douariensis* is at the Université Claude Bernard-Lyon I, and the fossils from Baccinello V3 are kept at the Musée de Bâle, Switzerland. My comparative sample, suffers nevertheless from a scarcity of certain limb elements.

Apart from the fact that some species are rare, another reason for this lack is the affirmation of D.A. Hooijer (1966, 1973) who stated that it was impossible to distinguish the post-cranial skeletons of *Dicerorhinus leakeyi* from those of *Aceratherium acutirostratum*, which are generally sympatric

and closely similar in size. Because of this, no-one has tried, and the leg bones of these two species are not separated in the London collections, where, in any case, they are not sufficiently numerous to permit their identification taking into account individual variation. Having been confronted with similar problems at various stages when studying different families of Neogene and Quaternary mammals with several sympatric species, and having resolved them (see for example Guérin, 1980), I am convinced that such a distinction is possible as soon as there is enough material. Thus I believe that the abundant remains preserved in the National Museums of Kenya in Nairobi will permit a resolution of this problem. In the meantime, however, I have overcome the difficulty by using the following comparative terms:

- In the tables the undetermined specimens belonging to *D. leakeyi* and/or *A. acutirostratum* are referred to as IDA;

- Not having limb bones of medium sized African aceratheres, I have used measurements of two species from Europe that I consider to belong to the same lineage, and which have quite similar proportions, even though they are not identical. They are *Aceratherium tetradactylum* from the late Middle Miocene and early Upper Miocene, and *Aceratherium incisivum* from the Upper Miocene. In the tables, the sum of this addition, which does not exceed the limits of a single lineage, is referred to as aceratheres; in the text it is called true aceratheres in order to avoid confusion with a certain number of related genera (*Alicornops* and others), also from the Miocene of Europe, which belong to different lineages and are therefore not considered further here.

- In the absence of large *Dicerorhinus* in the Miocene of Africa, I used *Dicerorhinus schleiermacheri* from the Upper Miocene of Europe.

- Finally, in order to have a good sample of large Miocene *Diceros*, I used remains of *Diceros pachygnathus* from Pikermi in Greece (which are preserved in many museums in Europe) associated with others of *D. neumayri* from Turkey, preserved at the Museum of Münich in Germany. The status of these two species is unsettled, (for some they are synonyms, for others they are distinct but close), and I call the ensemble *Diceros* gr. *pachygnathus-neumayri*.

Systematics and Taxonomy

Sub-family Dicerotinae
Genus *Diceros* Gray, 1821
Species *D. australis* Guérin, 2000

Diagnosis: Very large cursorial dicerotine. Upper cheek teeth brachyodont, with more or less continuous crenulated lingual cingulum, the crochet being the only or the main internal fold. Ectoloph of the premolars with strong parastyle, paracone fold thick and not very projecting, and devoid of mesostyle and metacone fold. Upper molars with the ectoloph bearing a strong paracone fold and a weak vertical median fold, with the protocone having a weak constriction on the anterior surface. Limb bones long but robust. Abaxial metapodials remarkably long in comparison with the axial metapodial.

Locus typicus and Stratum typicum: Detritic fluvial diamondiferous sediments of Arrisdrift, Sperrgebiet, Southern Namibia; early Middle Miocene, ca 17 Ma.

Holotype: Third left metacarpal AD 52'97 (Guérin, 2000, fig. 5. 3 and 4).

Referred specimens: Left demi-mandible AD 300'97; 4th right upper premolar AD 578'98 (Guérin, 2000, fig. 3: 3); Left upper 4th milk molar AD 292'94 (Guérin, 2000, fig. 3: 2); Right 3rd upper molar PQ AD 339 (Guérin, 2000, fig. 3: 4); Left lower 2nd premolar AD 86'98 (Guérin, 2000, fig.3: 6 and 9); Left lower 3rd premolar AD 200'98 (Guérin, 2000, fig.3: 7 and 10); Left lower 3rd milk molar PQ AD 635 (Guérin, 2000, fig. 3: 5 and 8); Left radius PQ AD 3099; Left astragalus AD 619'94 (Guérin, 2000, fig. 1: 2); Right calcaneum AD 50'97 (Guérin, 2000, Fig. 1: 1); Right 3rd metatarsal AD 618'94 (Guérin, 2000, fig. 5: I and 2).

Conservation: all the material is preserved at the Geological Survey of Namibia in Windhoek (Namibia).

Studied material: I small fragment of skull; 9 fragments of mandibles (4 large and 5 small), each bearing part of the corresponding dentition; 3 lower incisors; 16 isolated upper cheek teeth; 16 isolated lower cheek teeth; 3 proximal fragments of scapula; 1 humerus; 4 radii, including a complete one, 3 ulnae including a complete specimen; 9 carpals (3 magnums, 2 pyramidals, 2 semilunars, I trapezoid, 1 pisiform); 5 metacarpals (1 Mc II, 3 Mc III, 1 Mc IV); 1 tibia; 1 large fragment de fibula; 1 patella; 13 tarsals (3 astragali, 5 calcanea, 1 cuboid, 2 naviculars, 1 small cuneiform, 1 external cuneiform); 9 metatarsals (4 Mt II of which 2 are complete, 4 complete or almost complete Mt III, 1 entire Mt IV); 11 phalanges. All these specimens come from Arrisdrift.

Description: Skull. There is a fragment of the back of the skull corresponding to an almost complete occipital crest (the "chignon"). The transversal diameter, calculated by symmetry, is 220 mm; this value, greater than the maximum observed in *D. bicornis*, is close to the mean of extant *C. simum* (Guérin, 1980). The chignon is deeply excavated in its centre, forming a sort of saddle of which the arrow in the sagittal plane reaches 18 mm. The posterior surface (occipital) is excavated just below the large crest, for a height of a dozen cm, into a *fossa* subdivided into two by a vertical median crest; below the *fossa*, the occipital surface becomes vertically convex.

Mandible. Three large fragments of horizontal ramus possess part of the symphysis which was certainly remarkably short, even though none of them preserve the rostral part. The dorso-ventral symphysis diameter has a maximum value of 35 mm. In the three specimens, the posterior border of the symphysis is located at the level of the anterior third or in the middle of the p/2. The brevity of the symphysis suggests that the lower incisors were absent or vestigial, which is the usual case in Dicerotinae. At the break in the demi-mandible AD 505'99, one can see the root of a small i/2, the size and shape of which being similar to the isolated vestigial incisor AD 87'98.

On this hemi-mandible, the horizontal ramus has a weakly convex ventral edge, with an inflexion below the anterior edge of the ascending ramus, and the talon does not project behind the rear of the articular condyle.

In *Diceros douariensis* the symphysis is 100 mm long and 43 mm high, with the posterior margin located between p/2 and p/3; in *D. pachygnathus* the same margin is at the level of the front of p/4. Even though the anterior part of the horizontal ramus of *D. australis* is lower, its posterior part (from the level of m/2) is comparable in size to those of *D. douariensis* (Tabl. 1). The African medium sized Aceratheriinae and Dicerorhininae are much smaller than *D. australis*, and *Paradiceros* is even more so; as for *Chilotheridium pattersoni*, its mandible has very different proportions.

Lower incisors. Three lower incisors were found. Recall that the tusks of rhinos are the i/2 and not canines, contrary to what was written by D.A. Hooijer (1971), who also described an internal margin sharpened by wear in *Chilotheridium* whereas this genus does not have upper incisors!

AD 88'98, unworn and in the shape of a button, has the appearance of a vestigial tooth and could be a dill; its total length is 41.5 mm of which II mm comprise the crown; the transverse diameter at cervix is 9.5 mm for a dorsoventral diameter of II mm.

AD 87'98 is a lower right tusk, only slightly worn (Pl. 1, Fig. 1); the length is 84 mm of which 24 mm is the crown; the transverse diameter at cervix is 19 mm while the dorsoventral measurement is 13.5 mm; The wear surface is oblique and is II mm long and 10 mm wide; the enamel thickness suggests a permanent tooth, an i/2. The transverse section is an asymmetrical flattened ellipse. AD 22'99 is an unworn distal fragment of a similar tusk.

The tusks of *Chilotheridium* are much stronger: according to Hooijer (1971), their transverse sections reach respectively 22 x 17.30 x 18.30 x IS and 40 x 25 mm, with a crown height in worn specimens of between 44 and 55 mm; their shape is different, more asymmetrical (Hooijer, 1971, Pl. 6), and there is a cingulum. Because of their reduced size the Arrisdrift tusks could not have been very effective, whereas in all the other rhinos bearing tusks, they are much larger and were used by their possessors like bayonets.

I consider that the small adult tusks from Arrisdrift represent a stage towards the disappearance of the entire anterior dentition, which occurs in the Dicerotinae between the end of the Middle Miocene and the Upper Miocene. Such a disappearance also occurred in other rhino lineages, including the palaearctic Dicerorhininae in which the tusks are functional until the end of the Miocene, but are reduced into vestigial buttons in *Dicerorhinus megarhinus* from the Ruscinian, before disappearing completely in later forms (Guérin, 1980).

Upper cheek teeth. There are two well preserved dM4/ and the ectoloph of a third specimen; AD 292'94 is lightly worn (Pl. 1, Fig. 2), its maximum height is 38 mm which gives it a hypsodonty index of 81. A strong paracone fold is the only

Table 1: Comparisons of the measurements of the mandible of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

ARRISDRIFT	AD	AD	AD	AD	AD	AD	AD	AD		*Diceros douariensis*		
	556'94	300'97	313'98	437'97	223'97	478'95	356'00	505'99	n	mean	min.	max.
Side	R	L	R	R	R		L	R				
Symphysis-talon distance		462						ca 475	1	396		
Mandible depth below p/2-p/3		67		67,5					1	82,00		
Mandible depth below p/3-p/4		80			77				2	84,50	80	89
Mandible depth below p/4-m/1	87,5	81							2	96,50	95	98
Mandible depth below m/1-m/2	93,5	93						85	2	108,00	106	110
Mandible depth below m/2-m/3	99	102,5	108				Ca 96	87?	1	100,00		
Mandible depth below m/3	107	105							1	107,00		
Mandible breadth below p/4-m/1		60			Ca 43,5				2	49,75	49,5	50
Mandible breadth below m/3	67	60,5	50				57	62	2	57,50	57	58
AP breadth ascending ramus	167							164				
Condyle breadth						125,5		95				
Condyle height								237				

Chilotheridium pattersoni					*P. mukirii*	*B. heinzelini*	IDA
	n	mean	min.	max.	F Teman	Langental	Karungu
Symphysis-talon distance	2	423,00	404	442			
Mandible depth below p/2-p/3	1	92,00			59,5		60
Mandible depth below p/3-p/4	3	84,50	71	98	64		59
Mandible depth below p/4-m/1	3	89,00	77	99	70		64
Mandible depth below m/1-m/2	3	91,67	77	104	82,5		66
Mandible depth below m/2-m/3	3	91,67	85	103	88,5	est. 82	70
Mandible depth below m/3	2	101,75	101,5	102	92		78
Mandible breadth below p/4-m/1					45		37
Mandible breadth below m/3					47	54	41,5
AP breadth ascending ramus							
Condyle breadth							98
Condyle height							

relief on the external wall, and there is only one internal fold, the crochet. There is a discontinuous crenulated lingual cingulum, apparent mainly below the spout of the internal valley. AD 730'00, in medium wear, has similar morphology but does not have a lingual cingulum, and has a closed medifossette, probably due to the coalescence of the crochet and a crista. The dimensions of these two teeth are close to those of *D. douariensis* (Tabl. 2).

Four complete specimens of M1/ or M2/ were discovered:

- AD 228'97 is probably an M1/ in which the wear is slight, with a hypsodonty index of about 85. On the ectoloph there is a large paracone fold and a weak vertical median fold. The crochet, which is weakly developed, is the only internal fold. The protocone has a weak constriction on its anterior surface. A deep post-fossette is limited posteriorly by horizontally well developed posterior cingulum with a point and forming a horizontal enamel surface on the postero-lingual side of the tooth; the presence of this surface is constant in M1/ and M2/, the P1 and the dM/. A weak crenulated lingual cingulum occurs below

Table 2: Comparisons of the measurements of the upper cheek teeth of *Diceros australis*. AP = antero-posterior; artic = articular; D diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

ARRISDRIFT		AD 292'94	AD 578'98	AD 649'97	AD 228'97	AD 285'95	PQ AD 339	PQ AD 2697	PQ AD 2661	PQ AD 1103	AD 720'00	AD 730'00	AD 259'99	AD 489'00	AD 490'00
D 4/	L	47										44,5			
	DT	47										46			
M 1/	L				59										
	DT				56,5										
M 2/	L					58								59	54
	DT					62,5								63	64
M 3/	L abs.						64,5	65,5	66,5	65,5					
	L anat.						55	53	52	54					
	DT						62	62	61	60					
P 2/	L												32,5		
	DT												41		
P 3/	L										39				
	DT										43				
P 4/	L		43,5	37,5											
	DT		60,5	54											

D. douariensis						*B. snowi*			
		n	mean	min.	max.	n	mean	min.	max.
D 4/	L	1	44,00						
	DT	1	49,00						
M 1/	L	2	60,25	59	61,5	2	61,50	55	68
	DT	3	61,33	59	64	1	71,00		
M 2/	L	3	62,83	60	67,5	2	67,00	63	71
	DT	2	68,75	66,5	71	2	76,50	74	79
M 3/	L abs.	1	63,00						
	L anat.	3	57,33	50	64	1	63,00		
	DT	3	61,17	59	64				
P 2/	L								
	DT								
P 3/	L								
	DT								
P 4/	L	2	40,50	37,5	43,5	1	49		
	DT	2	57,25	54	60,5	1	69		

Paradiceros mukirii F. Terran		*D. leakeyi* Rusinga	*A. campbelli*
D 4/	L		
	DT		
M 1/	L	40	58
	DT	50	68,5
M 2/	L	48	
	DT	56	
M 3/	L abs.	53	54
	L anat.	43	47,5
	DT	56,5	49,5
P 2/	L		
	DT		
P 3/	L		
	DT		
P 4/	L	31,5	48
	DT	45	63

the spout of the median valley.

- The other three specimens are probably M2/; their morphology is very similar, with a single fold on the ectoloph (the median swelling observed in the M1/ is not present), the paracone fold which projects strongly is separated from the parastyle which is perpendicular. AD 490'00 has a constriction on the anterior surface of the hypocone that is not present on any other cheek teeth from Arrisdrift.

The dimensions of these M1/ and M2/ (Tabl. 2) are slightly lower than those of *D. douariensis*, and much smaller than those of *A. campbelli* but greater than those of *D. leakeyi*.

The four M3/s all have the same morphology (Pl. 1, Fig. 4): a strong paracone fold, a crochet being the only internal fold, protocone with weak constriction, a discontinuous lingual cingulum, a crenulated postero-labial cingulum covering the posterior quarter of the ectometaloph. The dimensions are close to those of the three M3/s of *D. douariensis*.

The right P2/ AD 259'99 is deeply worn. The ectoloph, which is strongly oblique towards the apex (indicating the brachyodont nature of this tooth) has only one relief feature, the paracone fold; there is an uncrenulated continuous lingual cingulum, which passes uninterrupted into the anterior cingulum. The greatest width is at the rear of the tooth; the dimensions are provided in Tabl. 2.

AD 720'00 is a well worn right P3/, in which the medifossette is closed and shows only a remnant of the crochet; the morphology is close to that of the preceding tooth, with a stronger cingulum and larger size (Tabl. 2).

Two right P4/s were discovered, one in medium wear (AD 578'98) and the other deeply worn (AD 649'97). The ectoloph has a strong parastyle and a thick but not very projecting paracone fold; there is no mesostyle nor metacone fold. The only internal fold is the crochet, but specimen N° AD 649'97 has a closed medifossette. There is a strong continuous, crenulated lingual cingulum. The protocone has no sign of constriction. Such a morphology (Pl. 1, Fig. 3), and in particular the characters on the ectoloph - which constitute the best odontological criterion in the Rhinocerotidae, see Guérin (1980) - is very similar to that observed in *Diceros douariensis* and *D.* gr. *pachygnathus-neumayri*, and this similarity applies also to the dimensions (Tabl. 2).

Lower cheek teeth. There are two deciduous molars available, a dm/2 and a dm/3. The latter tooth, which is slightly worn, has two internal valleys whose transverse profile is sharply V-shaped, and whose spouts are at the same level; there are traces of labial cingulum on the posterior lobe (Pl. 1, Figs 5 and 8). The dimensions (Tabl. 3) are similar to those (43 x 24 mm) of isolated dm/3s of *D. pachygnathus* from Pikermi preserved at the Bologna Museum (Italy).

Two isolated m/2s of which one is complete and three isolated m/3s in good condition were collected (PI I, Figs 7 and 10). The latter are wider than the only known m/3 of *D. douariensis*, and almost the same size as those of *Brachypotherium heinzelini* and *B. snowi*; they are much larger than the m/3 of *Chilotheridium* and *Paradiceros*, as well as those of African medium-sized Aceratheriinae and Dicerorhininae (Tabl. 3). The anterior internal valley has a sharp V-shaped profile; the

Table 3: Dimensions comparées des jugales inférieures de *Diceros australis*. AP = antéro-posterieur; artic = articulaire; D = diamètre; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

ARRISDRIFT		AD 8'98	PQ AD 635	AD 44'98	AQ 200'98	AD 468'97	AD 163'97	AD 378'94	PQ AD 134	AD 86'98	AD 157'95	AD 432'95	PQ AD 827
D /2	L	30											
	DT	18											
D /3	L		45										
	DT		25,5										
D /4	L												
	DT												
M /1	L												
	DT												
M /2	L												
	DT			38,5									
M /3	L				59	52,5	60						
	DT				36,5	39	35						
P /2	L							31,5	33	30			
	DT							20,5		19,5			
P /3	L										38	39	38
	DT										28	29	27,5
P /4	L												
	DT												
L P/3-P/4													
L M/1-M/3													

ARRISDRIFT		PQ AD 330	AD 556'94	AD 300'97	AD 313'98	AD 437'97	AD 223'97	AD 260'98	AD 731'00	AD 355'00	AD 356'00	AD 505'99
D /2	L											
	DT											
D /3	L											
	DT											
D /4	L											
	DT											
M /1	L		45	46,5						50	ca 46	
	DT			37,5						36	39	
M /2	L		50,5	55	58						55	
	DT		37	39	33,5						36	
M /3	L		59	ca 60							60,5	
	DT		35,5								33,5	
P /2	L					32		29				
	DT					22		21				
P /3	L			39		45			43			35,5
	DT			29					29,5			27,5
P /4	L	40,5	40	44,5			46					43
	DT		32,5	35,5			37					33
L P/3-P/4				83								78
L M/1-M/3			156,5	157							166,5	

		Diceros douariensis				B. heinzelini	B. snowi	Chil. pattersoni				ADI	P. mukiri
		n	mean	min.	max.	Langental		n	mean	min.	max.	East Afr.	F. Ternan
D /2	L											28,50	
	DT											16,00	
D /3	L												
	DT												
D /4	L												
	DT												
M /1	L	2	48,00	47	49	48		2	42,00	40,5	43,5	39,00	35
	DT	1	30,50			34,5		2	30,00	27	33	30,00	27
M /2	L	2	56,75	55,5	58	50	51,50	3	54,50	50,5	57	47,00	42
	DT	2	33,75	32	35,5	36	35,00	3	31,00	29,5	37,5	32,00	26
M /3	L	1	54,00			60	58,00	2	59,50	56	63	54,00	43,5
	DT	1	31,50			ca 38	36,50	2	30,75	27,5	34	31,00	25
P /2	L	1	26,00				30,00	4	23,12	20	25	22,00	24
	DT	1	18,50				22,00	2	16,00	14	18		14
P /3	L	1	35,50				36,50	4	33,62	25,5	38,5	32,50	27,5
	DT	1	33,00				26,50	4	21,12	18,5	24	23,50	19,5
P /4	L	1	43,00				44,50	4	37,50	34	39	37,50	30,5
	DT	1	30,00				31,50	3	26,17	25,5	27	27,50	24,5
L P/3-P/4		1	80,00					3	67,00	53	74,5	66,00	59
L M/1-M/3		1	155,00			ca154	169,00	4	152,25	144	159	130,00	121

posterior one is V-shaped in one case and U-shaped .in two others; the difference in level of the spouts varies from medium to strong. There is no labial or lingual cingulum, but all the m/3s possess a posterior crenulated cingulum which varies considerably in shape.

Eight isolated lower premolars can be studied: three p/2s, four p/3s and one p/4. The p/3 n° AD 157'95, completely unworn, has a hypsodonty index of 108; the two internal valleys are V-shaped and show marked differences in the level of their spouts; there is no labial or lingual cingulum, but there are anterior and posterior ones, which extend a little onto the labial surface, a feature that also occurs in the p/2 (PI 1, Figs 6 and 9). The p/3 AD 731'00 has a trace of an external cingulum on its labial surface at the base of the median synclinal.

The lower cheek teeth present in tooth rows show the same features. In the hemi-mandible AD 356'00 the m/2 and m/3 possess an anterior cingulum that extends on the lingual side as far as the centre of the anterior valley; the m/1 is too worn to yield any information on this character, which does not occur in the dental row of AD 556'94. The most complete tooth row, (AD 300'97) has a segment comprising "two last premolars" and a segment "molars" whose respective lengths are very close to those of *D. douariensis* and *D.* gr. *pachygnathus-neumayri* (Tabl. 3).

Scapula. Three proximal fragments (= articular) of scapulae were found. The largest, AD 506'99, has a transverse articular diameter of 82.5 mm (it is greatest in the middle of the surface) for an antero-posterior diameter of 101 mm, and its tuberosity is massive. The other two specimens are smaller, with the greatest diameter located at the rear of the articulation, and they possibly represent immature individuals.

Humerus. A left humerus (AD 736'00) (Pl. 4) was recovered during the 2000 field season. It is incomplete proximally, the most proximal point being about mid-height of the greater trochanter; it measures 483 mm in length, and it was probably about 500 mm in total length. The transverse diameter of the diaphysis is 72.5 mm and the transverse and antero-posterior diameters of the distal epiphysis are 170 and 127 mm respectively.

The humerus of *D. schleiermacheri* is shorter (426 to 448 mm, the mean of four: 435. 7 mm), with a narrower diaphysis (60.5 to 63.5 mm) and a narrower distal epiphysis (130 to 146 mm) but almost as deep.

That of *D.* gr. *pachygnathus-neumayri* is also shorter (409 to 447 mm, mean of five: 429 mm), but its diaphysis is as wide (65 to 81 mm) and its distal epiphysis, for the same width (146 to 182 mm), is a bit less developed antero-posteriorly (102 to 120 mm).

Radius and ulna. Comparisons of the dimensions and proportions (Tabl. 4; Fig. 1) show that the radius is longer than the biggest specimens observed of *D.* gr. *pachygnathus-neumayri* and *D. schleiermacheri*, the latter being slimmer. The undifferentiated acerathere-dicerorhine from Rusinga, which has the same size and proportions as the medium-sized late Miocene aceratheres of Europe, is smaller and has different proportions. The radius of *Chilotheridium* and above all, of *Brachypotherium snowi* is more robust and much shorter. The proximal articulation, comprising a lateral facet and a medial facet, does not have the undulating anterior border nor the large re-entrant angle at the level of the coronoid process which characterises the genus *Ceratotherium*. It shows, however, a lateral facet which extends further transversally and the anterior margin of which is located only slightly behind the anterior border of the medial facet; the posterior margin of the lateral facet, which is regularly concave, makes an obtuse angle with the posterior border of the medial facet. These latter characters are typical of the genus *Diceros* (Guérin, 1980).

Three ulnae were discovered at Arrisdrift of which only one (AD 273'97) is complete; its maximum length reaches 533 mm; its proximal articular diameter is 95 mm and its antero-posterior diameter is 157 mm. The other two specimens consist of a distal epiphysis of an adult, and a proximal extremity of a young individual.

Carpals. The only complete semi-lunar has an anterior surface in which the width and height are identical: 42 mm; the most distal point of this surface, close to the median line, is rounded. The length is 69.5 mm. Only one dimension can be obtained

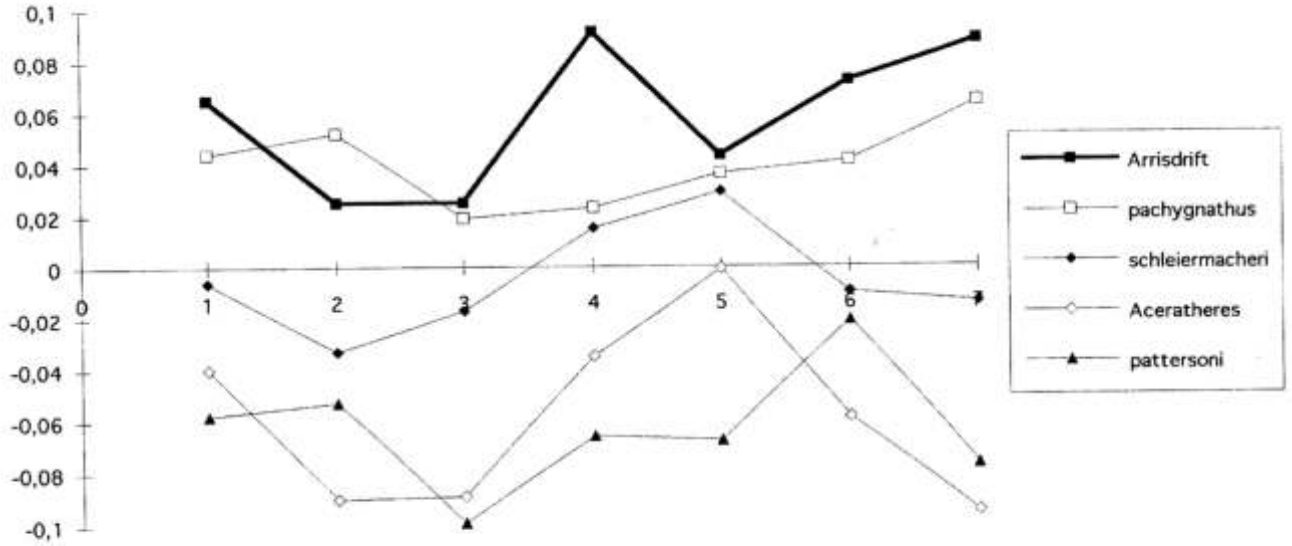

Figure 1: *Diceros australis*: Simpson diagram of the radius compared with that of other Miocene rhinoceroses. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3: DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT distal; 7: DAP distal.

Table 4: Comparisons of the measurements of the radius of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT				*B. snowi*	IDA
	PQ AD	AD	AD	AD		
	3099	731'99	506'00	99 n°	Djebel Zelten	Rusinga
Length	435				286,5	305
DT prox.	113		114		86,5	95
DAP prox.	70,5		68,5		51,5	57,5
DT dia.	64,5		68		48,5	51,5
DAP dia.	42		39,5		40	47,5
DT dist.	115			107	86	92
DAP dist.	83			73,5	53,5	69
DT artic. dist.	103	102		100,5	80,5	
DAP artic. dist.	54	51		52,5	41,5	

	D. gr. pachygnathus/neumayri						*Chilotheridium pattersoni*		
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.
Length	9	364,22	342	375	9,536	2,62	1	327,00	327	327
DT prox.	9	100,61	95	107	3,790	3,77	2	94,50	94	95
DAP prox.	9	65,00	55	72	5,315	8,18	1	53,00	53	53
DT dia.	9	59,11	55	63	2,667	4,51	2	45,00	44	46
DAP dia.	9	38,78	33	47	4,402	11,35	2	32,50	32	33
DT dist.	8	104,00	95	109,5	4,488	4,32	2	93,00	91	95
DAP dist.	9	65,78	60	71,5	3,833	5,83	2	56,75	54,5	59
DT artic. dist.							2	85,50	85	86
DAP artic. dist.										

	D. schleiermacheri						ACERATHERES					
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.	éc.-type	coeff. var.
Length	5	369,30	351,5	396	18,620	5,04	6	341,17	316	348	12,465	3,65
DT prox.	4	99,38	94,5	104,5	4,328	4,35	9	86,67	78,5	100	7,961	9,19
DAP prox.	3	64,00	63	66	1,732	2,71	10	54,25	50,5	59,5	2,781	5,13
DT dia.	5	54,20	48	57,5	3,785	6,98	6	48,33	44	52,5	3,656	7,56
DAP dia.	5	40,60	38	43	1,782	4,39	6	37,92	33	42,5	3,653	9,63
DT dist.	5	95,20	87	100	5,707	6,00	6	85,17	75	103,5	10,605	12,45
DAP dist.	5	65,60	61	69	3,991	6,08	7	54,50	50	61	3,926	7,20
DT artic. dist.	4	82,12	79	88,5	4,385	5,34	5	72,60	68,5	79,5	4,891	6,74
DAP artic. dist.	4	44,75	44	45	0,500	1,12	5	38,70	36,5	42,5	2,414	6,24

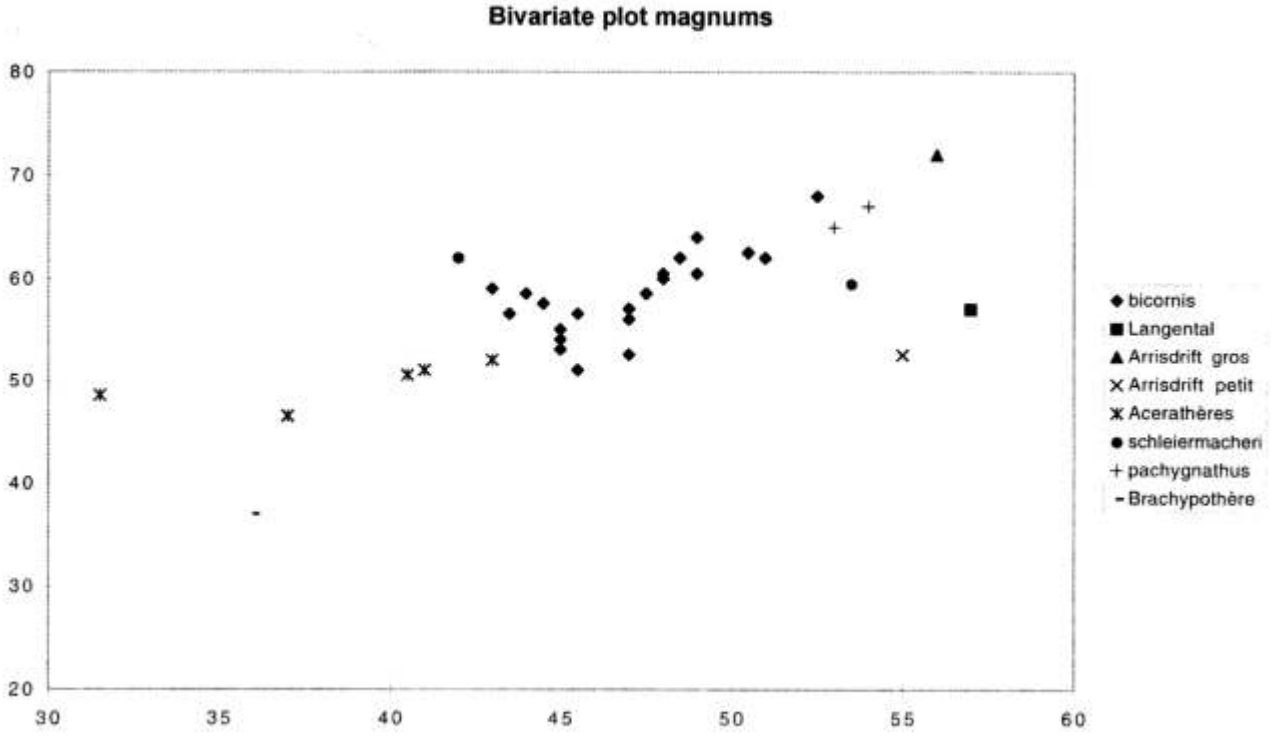

Figure 2: Dispersion diagram of anterior breadth as a function of sub-articular height (abcissa) of three magnums of rhinos from the Miocene of Namibia, other Miocene rhinos and extant *Diceros bicornis*.

from fragment AD 824'99, the height of the anterior surface, which is slightly greater than 40mm.

Only one of the two pyramidals collected is well preserved (PQ AD 3173); it is remarkably large, and clearly wider (71.5 mm) than high (63 mm).

The only pisiform preserved is 70 mm long and 29 mm wide with a height of 52 mm.

Two out of the three magnums found at Arrisdrift are complete, of which one (AD 538'97) is attributable to *D. australis* (Pl. 3, Fig. 4). In anterior view the bone has a rhomboidal outline which is rounded distally, and it is higher than wide. The distal articulation is about as wide in front as it is behind. The dimensions are as follows:

Total length:	104 mm
Anterior width:	56 mm
Anterior height:	45 mm
Maximum height:	74 mm
Sub-articular height:	72 mm

These dimensions and the proportions differ From those of *D. schleiermacheri* but are similar to three magnums of *Diceros* gr. *pachygnathus-neumayri*; they are completely different From those of the other complete magnum found at the site (Pl. 3, Figs 3-5 and text-fig. 2).

The only trapezoid known (AD 141'95) measures 44.5 mm in length and 26 mm width for a height of 35.5 mm.

Metacarpal II. The only specimen, a left one, is longer than the biggest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but is clearly slimmer. That of *Chilotheridium* is very short and thick, whereas that of true aceratheres is shorter and has very different proportions (Tabl. 5).

The proximal articulation is long and narrow, with a crescent shaped outline, with a clear notch on its posterior margin. On the lateral surface of the epiphysis there is a single articular facet, constricted in its median part but extending right across the bone in its median part. The transverse section of the diaphysis is a rounded triangle.

Metacarpal III. Two complete left and one right Mc III were found (Pl. 2, Figs 3 and 4) and the largest one is bigger than the maximal values known in *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but it is somewhat slimmer. The Mc III of *Brachypotherium snowi* and *B. heinzelini* are much shorter and thicker, and it is the same for *Chilotheridium*. Those of true aceratheres have more or less similar proportions but are much smaller (Tabl. 6).

A Simpson diagram (Fig. 3) shows that Mc IIIs From Arrisdrift do not belong to a brachypothere, nor to an acerathere, but that it has cleat analogies to those of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*.

The proximal articulation is very wide, triangular with a straight anterior margin. On the lateral surface of the proximal epiphysis there are two articular facets; the anterior one is pentagonal and subdivided into two parts of which the inferior one is more or less elongated; the posterior facet, which is lower than the anterior one, is a rounded triangle, of which the width varies From individual to individual. On the medial surface of the proximal epiphysis there is an articular facet in the shape of a sleeping S which is variable in height. The transverse section of the diaphysis is trapezoidal with a weakly convex anterior border and a slightly concave posterior one; the straight lateral margin is longer than the medial

Table 5: Comparisons of the measurements of the Mc II of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT AD 536'97
Length	188
DT prox.	41
DAP prox.	54
DT dia.	32,5
DAP dia.	25
DT max. dist.	43
DT artic. dist.	42
DAP dist.	45,5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*			
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.
Length	9	156,33	140,5	169	8,842	5,66	2	129,50	129,5	129,5
DT prox.	9	44,67	37	54	5,385	12,06	2	43,00	42	44
DAP prox.	6	46,50	40	51	4,231	9,10	2	37,25	37	37,5
DT dia.	9	40,78	33,5	44,5	4,374	10,73	2	31,75	31	32,5
DAP dia.	9	24,33	20	26	1,750	7,19	2	16,50	16	17
DT max. dist.	9	48,89	40	54	5,355	10,95	2	39,75	37	42,5
DT artic. dist.	9	43,17	34,5	48,5	4,644	10,76	2	34,00	31	37
DAP dist.	9	42,39	38,5	46	2,583	6,09	2	36,25	36	36,5

	D. schleiermacheri					ACERATHERES				
	n	Mean	min.	max.	éc.-type	coeff. var.	n	Mean	min.	max.	éc.-type	coeff. var.
Length	3	168,83	156,5	179	11,405	6,76	5	133,20	120,5	148	13,298	9,98
DT prox.	3	43,00	40	47	3,606	8,39	3	33,67	32	36	2,082	6,18
DAP prox.	3	42,50	40	44	2,179	5,13	3	33,17	29,5	40	5,923	17,86
DT dia.	4	36,88	34	40,5	2,720	7,37	4	32,38	28,5	36	3,092	9,55
DAP dia.	4	22,50	18,5	27	3,536	15,71	4	19,00	17	21,5	1,958	10,30
DT max. dist.	3	44,67	40	47	4,041	9,05	4	37,75	36	40	1,658	4,39
DT artic. dist.	3	40,17	39	41	1,041	2,59	4	34,38	32,5	36	1,493	4,34
DAP dist.	3	40,33	39,5	41,5	1,041	2,58	4	35,62	32	38,5	2,689	7,55

Table 6: Comparisons of the measurements of the Mc III of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT			*B. snowi*	*B. heinzelini*
	AD 52 '97	AD 243 '95	AD 369'99	Jebel Zelten	Rusinga
Length	200	212	219	159,5	149,5
DT prox.	68	63,5	64,5	74,5	66
DAP prox.	58	51,5	56,5	57	52
DT dia.	57,5	58,5	61,5	60,5	53
DAP dia.	27	26,5	26	22,5	24,5
DT max. dist.	65	63,5	67,5	73,5	72,5
DT artic. dist.	60	60	58	58	58,5
DAP dist.	48		44*	54,5	46,5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*			
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.
Length	9	187,17	181	198	5,668	3,03	3	157,67	150	169
DT prox.	6	65,50	62,5	74,5	4,461	6,81	3	54,33	50	61
DAP prox.	8	54,94	52	59	2,427	4,42	3	41,67	37	45
DT dia.	11	63,55	59	69	3,020	4,75	3	40,83	39	43
DAP dia.	9	24,56	22	26,5	1,333	5,43	3	19,17	17,5	21,5
DT max. dist.	9	71,22	66,5	76	2,705	3,80	3	54,83	51	61
DT artic. dist.	10	56,15	52	59	2,174	3,87	3	46,33	44,5	49,5
DAP dist.	10	48,05	45	53	2,619	5,45	3	38,17	37,5	39

	D. schleiermacheri						Acératheres					
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Length	6	195,42	181	204	8,546	4,37	10	163,75	139,5	181	13,382	8,17
DT prox.	9	62,67	58	69	3,700	5,90	10	53,35	50	59,5	3,092	5,80
DAP prox.	5	50,30	47,5	52	1,987	3,95	10	43,80	40	47,5	2,406	5,49
DT dia.	9	55,78	49,5	66	5,363	9,61	11	45,55	42	49	2,252	4,95
DAP dia.	8	23,38	22	25,5	1,188	5,08	10	20,20	17	24,5	2,163	10,71
DT max. dist.	7	63,50	60	69	3,149	4,96	10	55,25	49,5	60,5	3,676	6,65
DT artic. dist.	7	52,14	49	56	2,478	4,75	10	47,00	38,5	52	3,894	8,29
DAP dist.	7	46,71	45	49	1,410	3,02	7	41,71	38	44,5	2,563	6,15

one which is more or less straight.

Metacarpal IV. The bone is slimmer and much longer than the biggest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri* (Tabl. 7).

The proximal articulation is triangular, a little longer than wide; this length/width ratio is the opposite in rhinos with short feet such as *Brachypotherium* and *Chilotheridium*. The medial surface of the proximal epiphysis has two articular facets;' the anterior one, semi-elliptical in outline, is long and low, whereas the posterior one is a vertical ellipse which is much higher than wide.

Tibia. The only tibia recovered is very damaged; in particular at its proximal end which prohibits appreciating whether its morphology is typical of Dicerotinae or not, but it is nev-

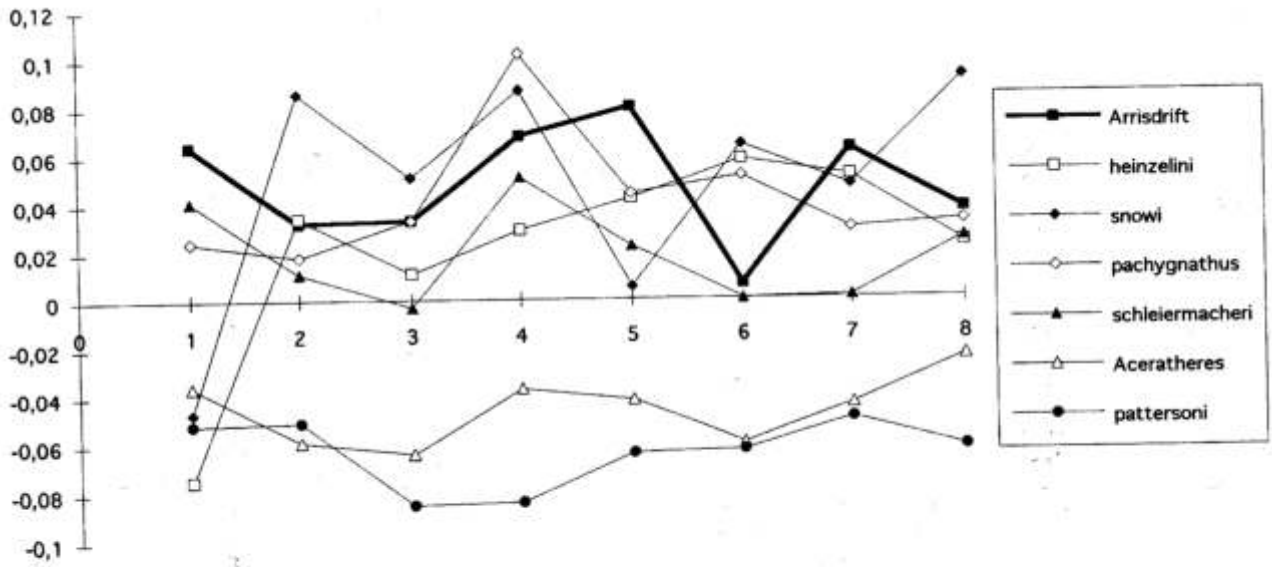

Figure 3: *Diceros australis*: Simpson diagram of Mc III compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3:DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT maximal distal; 7: DT articular distal; 8: DAP distal.

Table 7: Comparisons of the measurements of the Mc IV of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT	GRILLENTAL
	AD 404'97	GT 31'01
Length	ca 188	127
DT prox.	55	
DAP prox.	51,5	41*
DT dia.	37,5	29,5
DAP dia.	27	21
DT max. dist.	51	42
DT artic. dist.	45	38,5
DAP dist.	53	37*

IDA			
N	moyenne	min.	max.
2	158,75	152,5	165
1	52,00		
1	46,00		
2	34,00	34	34
2	21,25	20,5	22
2	46,25	42	50,5
2	43,00	40	46
2	38,75	37	40,5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*				
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Length	8	144,81	134	156	9,059	6,26	3	125,17	121,5	129,5	4,041	
DT prox.	8	47,81	43	53	3,535	7,39	2	35,50	34	37	2,121	
DAP prox.	8	42,12	37	47,5	3,410	8,09	2	38,00	32	44	8,485	
DT dia.	8	37,69	31,5	41	3,162	8,39	3	26,17	23	30,5	3,884	
DAP dia.	8	24,75	20	29	2,726	11,01	3	18,00	17,5	18,5	0,500	
DT max. dist.	8	46,69	39	52,5	4,166	8,92	3	42,17	37	47,5	5,252	
DT artic. dist.	8	43,06	37,5	47	3,590	8,34	3	35,50	33,5	37	1,803	
DAP dist.	8	41,00	37,5	46	2,712	6,62	3	34,33	33	37	2,309	

	D. schleiermacheri			
	n	mean	min.	max.
Length	1	145,00		
DT prox.	2	49,25	47,5	51
DAP prox.	1	43,00		
DT dia.	2	32,50	32,5	32,5
DAP dia.	2	21,50	21	22
DT max. dist.	2	45,25	43	47,5
DT artic. dist.	2	42,25	38,5	46
DAP dist.	2	40,50	40	41

	ACERATHERES				
n	mean	min.	max.	éc.-type	coeff. var.
5	144,50	141,5	147,5	2,475	1,71
7	42,86	38,5	48	3,579	8,35
7	39,21	32	42	3,315	8,45
5	30,10	27,5	32,5	2,382	7,91
5	22,40	19	25	2,329	10,40
5	39,00	37,5	40	0,935	2,40
5	38,90	36	43	2,903	7,46
5	37,60	34	40	2,382	6,34

Table 8: Comparisons of the measurements of the tibia of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT	*Chilotheridium pattersoni*	
	PQ AD 561	min.	max.
Length	440	319	355
DAP dia.	57	47	
DT dist.	100	88	
DAP dist.	80	66	
DT artic. dist.	87		
DAP artic. dist.	75		

	D. gr. pachygnathus/neumayri					*D. cf. douariensis*
	n	mean	min.	max.	éc.-type	coeff. var.	Baccinello V3
Length	5	390,40	368	420	19,970	5,12	
DAP dia.	7	58,36	49	73	8,797	15,07	58
DT dist.	6	107,92	99	115	7,088	6,57	101
DAP dist.	7	79,00	71	99	10,724	13,57	80
DT artic. dist.							
DAP artic. dist.							

	D. schleiermacheri			
	n	mean	min.	max.
Length	2	398,00	386	410
DAP dia.	2	58,25	57,5	59
DT dist.	2	103,50	101	106
DAP dist.	2	72,25	69	75,5
DT artic. dist.	1	82,50		
DAP artic. dist.	1	60,00		

	ACERATHERES				
n	mean	min.	max.	éc.-type	coeff. var.
9	361,22	328	383	20,663	5,72
9	47,39	38	53	5,819	12,28
9	86,17	72,5	91,5	6,260	7,26
11	62,55	53	68	5,007	8,01
3	71,00	60	79	9,849	
3	50,67	46	55	4,509	

Table 9: Comparisons of the measurements of the astragalus of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift AD 619'94	Arrisdrift PQ AD 1219	*D. gr. pachygnathus/neumayri* n	mean	min.	max.	éc.-type	coeff. var.
DT	101	100	7	98,57	94	104	3,645	3,70
Height	95	96	6	87,17	84	92	3,545	4,07
DAP medial	63,5	64,5	6	63,00	61	65	1,897	3,01
DT artic distal	75	78	7	81,07	76,5	86	3,101	3,83
DAP artic distal	55	53,5	7	50,86	45	53,5	3,326	6,54
DT trochlea	72	77	6	69,83	61	77,5	5,768	8,26
DT distal	80,5	85	5	84,90	82	90,5	3,471	4,09

	D. schleiermacheri n	mean	min.	max.	éc.-type	coeff. var.	*Brachypotherium snowi* n	mean	min.	max.
DT	11	91,45	86,5	99	3,595	3,93	2	108,75	105	112,5
Height	13	85,35	78,5	93	4,719	5,53	1	82,00		
DAP medial	12	61,79	55	70	4,126	6,68	2	59,00	58	60
DT artic distal	8	73,00	62	82	6,649	9,11	2	82,25	80	84,5
DAP artic distal	10	47,95	44,5	55	2,833	5,91				
DT trochlea	12	66,62	61	75	3,730	5,60	1	51,00		
DT distal	10	79,75	76	86	3,810	4,78	2	92,75	90,5	95

	ACERATHERES n	mean	min.	max.	éc.-type	coeff. var.	*Chilotheridium pattersoni* n	mean	min.	max.	éc.-type
DT	29	79,60	72	88,5	4,347	5,46	3	88,50	85,5	92	3,279
Height	30	70,07	62	81	4,584	6,54	3	70,17	68,5	71	1,443
DAP medial	26	52,44	45	59	3,593	6,85	3	53,67	52	55,5	1,756
DT artic distal	29	64,59	56,5	73	3,880	6,01	3	71,00	64	79	7,550
DAP artic distal	25	39,68	35	47	2,688	6,77	2	40,50	38	43	3,536
DT trochlea	31	52,39	46	65	5,228	9,98	3	55,33	52	58	3,055
DT distal	28	70,95	65	76,5	3,122	4,40	3	75,33	73	79	3,215

	IDA n	mean	min.	max.	éc.-type	coeff. var.
DT	8	80,62	75,5	84	3,410	4,23
Height	7	72,79	69	78,5	3,706	5,09
DAP medial	7	52,14	47,5	56	3,159	6,06
DT artic distal	8	68,00	65	74	3,024	4,45
DAP artic distal	6	38,83	33,5	43,5	3,804	9,79
DT trochlea	7	48,79	45	50	1,890	3,87
DT distal	8	73,81	70,5	78,5	3,093	4,19

ertheless possible to measure its total length. As for the Mc III the tibia is slightly longer than the biggest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, as well as being slimmer (Tabl. 8). The dimensions of a broken distal epiphysis of *Diceros* cf. *douariensis* from Baccinello V3 are identical to those of the tibia from Arrisdrift.

Astragalus. Three astragali were discovered, of which two are complete (P\. 3, Fig. 2). The dimensions (Tabl. 9) and the proportions (Fig. 4) are close to those of *Diceros* gr. *pachygnathus-neumayri*, and slightly different from *Dicerorhinus schleiermacheri*. The astragalus of *Brachypotherium snowi* is wider but clearly lower; its width/length ratio is lower, as for the much smaller *Chilotheridium*. In the true aceratheres the dimensions are lower and the proportions different, and the same applies to the undifferentiated sample of *D. leakeyi-A. acutirostratum*, which are remarkably similar to the former.

Among the qualitative characters is the median position, well above the distal margin of the bone, of the tubercle of the inferior part of the medial surface. The individual variation of the three astragali of *D. australis* is clear, especially in the height of the neck, in the obliquity of the medial margin of the distal articulation, and in the development towards the rear of the upper extremity of the medial lip of the pulley.

Calcaneum. There are four adult and one juvenile calcanea, of which three are complete (P\. 3, Fig. 1). As for the astragalus, the dimensions (Tabl. 10) and proportions of the calcanea are close to *Diceros* gr. *pachygnathusneumayri* and *D. schleiermacheri*, and have nothing to do with those of *Paradiceros*, *Chilotheridium* or the true aceratheres.

In posterior view the axis of the *sustentaculum tali* makes a right angle with the axis of the body of the bone; this is a Dicerotinae feature.

In lateral view, the summit of the tuberosity is located well behind the beak (which is the most anterior part of the bone); the anterior margin of the surface, which joins these two points, is oblique and slightly concave. The posterior margin of the lateral surface is globular in its superior two thirds and depressed in its lower third, particularly in specimen PQ AD 601 (in AD 353'00 the lower third is straight). The more or less globular outline of the lateral surface of the bone is another dicerotine character.

The individual variation occurs most obviously at the level of the proximal part of the bone, in rear view: the summit is an

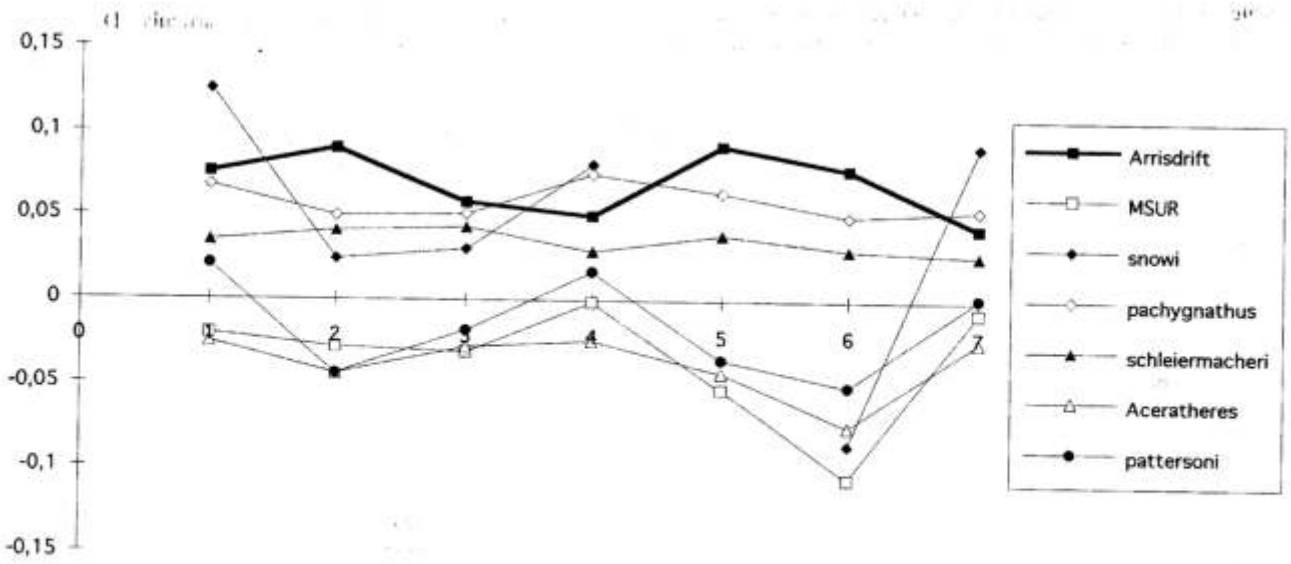

Figure 4: *Diceros australis*: Simpson diagram of the astragalus compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: DT; 2: Height; 3: DAP medial; 4: DT articular distal; 5: DAP articular distal; 6: proximal width of the trochlea; 7: DT maximal distal.

inverted V in calcaneum PQ AD 60 I and AD 353'00, whereas it is flat in AD 50'97.

Other tarsals. The cuboid is very large: its total length is 77 mm, its maximum height is 61 mm, and the greatest width is 52.5 mm. The anterior surface is higher than wide (respectively 53 and 41.5 mm), and its lateral border is longer than the medial one.

Two naviculars were collected (AD 920'97 and PQ AD 1841); the first is not completely free of matrix on its external edge and the second is rolled; they are wider than long: respectively 67 x 56.5 mm for a height of 40 mm and 78 x 56.5 mm for a height of 38 mm.

A small cuneiform (AD 16'00) is 38 mm long, for a width of 22 mm and a height of 20.5 mm.

The external cuneiform AD 399'00 is 66 mm high for a transverse diameter of 30 mm" and an anteroposterior diameter of 39 mm; it has a projecting transverse tuberosity in the middle of its medial surface.

Metatarsal II. Four Mt II were discovered of which two are complete or subcomplete (they were broken during fossilisa-

Table 10: Comparisons of the measurements of the calcaneum of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	ARRISDRIFT				*Paradiceros*	IDA
	AD 50'97	PQ AD 601	AD 530'95	AD 353'00	Kisegi	
Height	158,5	153	153	162,5	92,5	130,5
DP head	58	55	64	58	36	52,5
DAP head	77	67		76,5	50	54
DT middle	41,5	40			33	43
DT sustentaculum	77,5	79	77		50	81
DT max	81	81	80	76*	55,5	85,5
DAP max	84	75,5	ca 75	80		63
					50	60

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*				
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Height	7	143,36	132	151,5	6,296	4,39	3	120,83	113	132	9,929	8,22
DP head	6	58,42	54	63	3,639	6,23	3	44,33	42	48,5	3,617	8,16
DAP head	7	75,07	65	82	5,762	7,68	3	67,67	60	74	7,095	10,48
DT middle	2	46,50	45	48	2,121	4,56						
DT sustentaculum	7	82,07	74	87,5	4,641	5,65	2	70,00	70	70	0,000	0,00
DT max												
DAP max	5	77,90	72	83	5,030	6,46	3	59,17	57	62	2,566	4,34

	D. schleiermacheri					ACERATHERES				
	n	mean	min.	max.	éc.-type	coeff. var.	n	mean	min.	max.	éc.-type	coeff. var.
Height	5	142,10	134	149	6,712	4,72	20	108,82	98,5	123,5	6,660	6,12
DP head	6	53,17	50,5	55	1,780	3,35	20	42,97	35	49	3,925	9,13
DAP head	6	72,67	68,5	79,5	5,965	8,01	19	61,03	49,5	78	6,550	10,73
DT middle	4	40,12	37	43,5	2,780	6,93	6	33,75	26	41	6,031	17,87
DT sustentaculum	5	80,90	72,5	88	6,368	7,87	15	70,33	61	78,5	4,139	5,88
DT max												
DAP max	6	74,50	69	86	6,716	9,01	20	59,58	51	70	5,095	8,55

Table 11: Comparisons of the measurements of the Mt II of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift AD 744'97	Arrisdrift PQ AD 251	Arrisdrift AD 442'97	Arrisdrift AD 348'95	*Chilotheridium pattersoni* Loperot	Loperot	IDA Kiboko
Length	182,5	181			129	115	153
DT prox.	30	31	32	31	env. 36	30	27
DAP prox.	51	47	57	51		37,5	34,5
DT dia.	31	30	31,5			23	19,5
DAP dia.	30	25,5	29			21	18,5
DT max. dist.	40,5	39			42	35	29
DT artic. dist.	38,5	37,5			38,5	32,5	28
DAP dist.	46	40			43	36,5	30

D. schleiermacheri

	Mean	min.	max.	éc.-type	coeff. var.	coeff. var.
Length	3	153,33	150	156	3,055	1,99
DT prox.	3	33,83	27	40,5	6,752	19,96
DAP prox.	3	45,67	43	50,5	4,193	9,18
DT dia.	2	27,00	26	28	1,414	5,24
DAP dia.	2	27,75	27	28,5	1,061	3,82
DT max. dist.	3	37,17	35,5	39	1,756	4,72
DT artic. dist.	3	35,00	33	37	2,000	5,71
DAP dist.	3	39,17	37	40,5	1,893	4,83

D. gr. pachygnathus/neumayri

	Mean	min.	max.	éc.-type	coeff. var.	coeff. var.
Length	5	153,70	147,5	157,5	4,040	2,63
DT prox.	5	33,60	30,5	37	3,029	9,01
DAP prox.	5	45,70	42,5	49	2,729	5,97
DT dia.	5	34,80	32	37,5	2,080	5,98
DAP dia.	5	25,20	23,5	27	1,483	5,89
DT max. dist.	4	43,50	40	45	2,380	5,47
DT artic. dist.	5	39,30	36,5	41	1,754	4,46
DAP dist.	5	43,50	39	47	2,958	6,80

AERATHERES

	Mean	min.	max.	éc.-type	coeff. var.	coeff. var.
Length	8	137,06	117,5	165,5	14,374	10,49
DT prox.	9	28,00	25,5	31	1,696	6,06
DAP prox.	9	39,17	35	41,5	2,264	5,78
DT dia.	7	26,57	23,5	32	2,992	11,26
DAP dia.	7	21,93	19	25	2,130	9,71
DT max. dist.	7	36,07	31	40	3,181	8,82
DT artic. dist.	8	32,88	26	40	4,604	14,00
DAP dist.	7	36,50	33	40,5	2,799	7,67

tion, but recemented in place). They are much longer but slimmer than the largest specimens known of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*. The Mt II of *Chilotheridium* is very short and relatively more stocky, and that of true aceratheres is shorter with different overall proportions (Tabl. 11).

The lateral surface of the proximal epiphysis has two clearly separated articular facets, both with elliptical outlines that are higher than wide. In specimen n° AD 542'97 the posterior part of the proximal epiphysis is more strongly developed towards the rear than the others; the lateral articular facets are the widest and there are two well separated articular facets on the medial surface, that are also visible on AD 744'97.

The transverse section of the diaphysis is a rounded trapezoid, which is wider on its posterior margin and with a sharp anterior angle, especially in the superior third of the bone.

Metatarsal III. Arrisdrift has yielded four Mt III, of which two are well preserved (Pl. 2, Figs I and 2), one was broken in two but recemented in place and another has an incomplete

Table 12: Comparisons of the measurements of the Mt III of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift AD 618'94	Arrisdrift PQ AD 249	Arrisdrift PQ AD 1190	Arrisdrift PQ AD 183	*C. pattersoni* Lopercot
Length	197,5	197	ca 180	ca 178	128
DT prox.	57,5	61		54	43,5
DAP prox.	52			49	40
DT dia.	50	51,5	52,5	44	36
DAP dia.	26	25,5		25,5	18,5
DT max. dist.	61,5	60,5	57,5	55,5	48
DT artic. dist.	53	57	52,5	51	43
DAP dist.	46	47,5	42	42	35

D. schleiermacheri	n	Mean	min.	max.	éc.-type	coeff. var.
Length	2	173,25	171,5	175	2,475	1,43
DT prox.	1	48,00				
DAP prox.	1	40,00				
DT dia.	2	45,00	43,5	46,5	2,121	4,71
DAP dia.	2	23,25	23	23,5	0,354	1,52
DT max. dist.	2	55,50	53,5	57,5	2,828	5,10
DT artic. dist.	2	47,75	46	49,5	2,475	5,18
DAP dist.	2	39,00	33	45	8,485	21,76

D. gr. pachygnathus/neumayri	n	Mean	min.	max.	éc.-type	coeff. var.
Length	9	174,56	165	194,5	8,557	4,90
DT prox.	8	60,06	57	64,5	2,321	3,86
DAP prox.	8	50,88	45	57,5	4,955	9,74
DT dia.	9	53,22	51,5	55	1,228	2,31
DAP dia.	9	25,33	22,5	28,5	1,969	7,77
DT max. dist.	7	66,93	60,5	71,5	3,758	5,61
DT artic. dist.	8	54,50	49,5	60,5	3,645	6,69
DAP dist.	8	46,50	41,5	49	2,405	5,17

ACERATHERES	n	Mean	min.	max.	éc.-type	coeff. var.
Length	11	150,36	130	166	11,437	7,61
DT prox.	10	46,25	40	53,5	4,626	10,00
DAP prox.	10	41,90	38	46	2,757	6,58
DT dia.	11	41,32	37,5	46,5	2,704	6,55
DAP dia.	10	19,90	16,5	24,5	2,757	13,85
DT max. dist.	11	52,45	47	60,5	4,120	7,85
DT artic. dist.	11	45,45	40,5	51,5	3,228	7,10
DAP dist.	11	37,82	32	42,5	3,466	9,17

proximal epiphysis which has been attacked by gypsum.

The bone is about as long as the longest specimen known *Diceros* gr. *pachygnathus-neumayri* and has the same proportions, save for the sub-articular distal transverse diameter. It is significantly longer than that of *Dicerorhinus schleiermacheri*. The Mt III of *Chilotheridium* is much shorter and relatively more solidly built. In the true aceratheres the bone is smaller and its proportions are different (Tabl. 12, Fig. 5).

The proximal articulation is very wide, triangular with a convex anterior margin of which the point of inflexion is offset laterally; the antero-lateral angle is pointed; the medial border is convex in its anterior part, then weakly depressed towards the rear, and once more becomes convex in the posterior most part. The lateral surface of the proximal epiphysis has two articular facets; the anterior one is positioned higher than the posterior one, of which the outline is an elongated ellipse.

The median transverse section of the diaphysis is trapezoidal with a convex anterior border and a concave posterior one; the lateral margin is straight and the medial one slightly convex.

Individual variation concerns mainly the more or less triangular outline of the anterior articular facet on the lateral surface of the proximal epiphysis, as well as the convexity and concavity of the anterior and posterior edges respectively of the transverse section of the diaphysis.

Metatarsal IV. Only one specimen was found, and it is poorly preserved. As for the Mt II, it is much longer than the biggest known specimens of *Diceros* gr. *pachygnathusneumayri* and *Dicerorhinus schleiermacheri*, but without being much more gracile. The Mt IV of *Chilotheridium* is very short, and that of true aceratheres is relatively shorter with different proportions (Tabl. 13).

Phalanges. There are 6 incomplete or uncleaned phalanges and 5 in good condition:

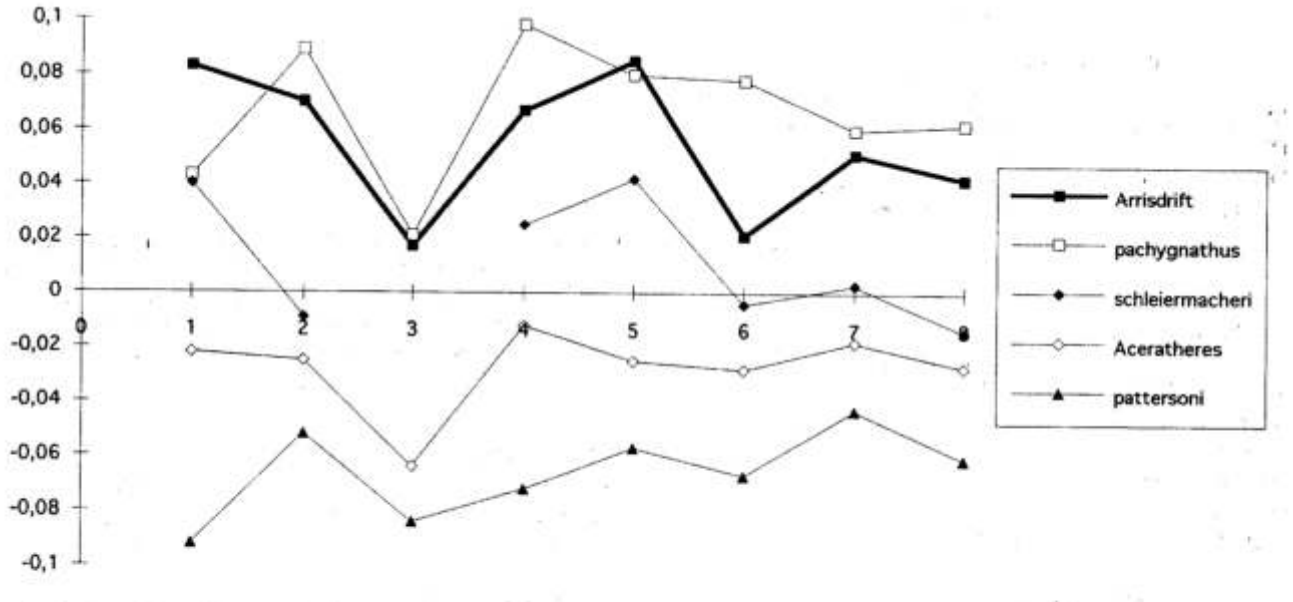

Figure 5: *Diceros australis*: Simpson diagram of the Mt III compared with other Miocene rhinos. The reference is *Diceros bicornis*. 1: Length; 2: DT proximal; 3:DAP proximal; 4: DT diaphysis; 5: DAP diaphysis; 6: DT maximal distal; 7: DT articular distal; 8: DAP distal.

Table 13: Comparisons of the measurements of the Mt. IV of *Diceros australis*. AP = antero-posterior; artic = articular; D = diameter; dist = distal; horiz = horizontal; prox = proximal; T= transversal.

	Arrisdrift PQ AD 253	Chilotheridium pattersoni Loperot	Chilotheridium pattersoni Loperot
Length	ca 182	111	113
DT prox.	44	41	40,5
DAP prox.	42	40	ca 38,5
DT dia.	35,5	22,5	22,5
DAP dia.	22,5	20,5	20
DT max. dist.	42	33	30,5
DT artic. dist.	41	34,5	32
DAP dist.	ca 36	35,5	34,5

D. schleiermacheri	n	mean	min.	max.
Length	2	153,50	152	155
DT prox.	2	42,25	37	47,5
DAP prox.	1	50,00	50	50
DT dia.	2	27,75	26,5	29
DAP dia.	2	29,25	28	30,5
DT max. dist.	2	36,00	35,5	36,5
DT artic. dist.	2	36,50	35	38
DAP dist.	2	42,50	42	43

D. gr. pachygnathus/neumayri	n	mean	min.	max.	éc.-type	coeff. var.
Length	8	148,31	138,5	166,5	9,047	6,10
DT prox.	8	48,62	43	53	3,148	6,47
DAP prox.	8	46,88	42,5	51	2,900	6,19
DT dia.	8	32,12	30	35	1,642	5,11
DAP dia.	8	29,00	24,5	32	2,790	9,62
DT max. dist.	8	41,12	37	45	2,615	6,36
DT artic. dist.	8	39,75	35,5	43	2,777	6,99
DAP dist.	8	42,75	40	45	1,927	4,51

ACERATHERES	n	mean	min.	max.	éc.-type	coeff. var.
Length	10	131,40	117,5	144	9,021	6,87
DT prox.	11	40,95	37	44,5	2,079	5,08
DAP prox.	11	38,09	32,5	42,5	3,590	9,43
DT dia.	10	26,85	23	30	2,082	7,76
DAP dia.	10	24,85	21	28	2,212	8,90
DT max. dist.	9	31,56	29	34,5	1,976	6,26
DT artic. dist.	8	30,25	27,5	35,5	2,866	9,47
DAP dist.	10	35,15	31	37,5	2,484	7,07

Two central phalanges I:

	AD 85'98	AD 225'99
Maximum height:	51.5	51.5
DT proximal:	61	61
DAP proximal:	37.5	39.5
DT diaphysis:	52	52.5
DT distal:	53	53.5
DAP distal	24.5	26

One lateral phalanx I:

	AD 774'00
Maximum height:	55
DT proximal:	44
DAP proximal:	39
DT diaphysis:	40
DT distal:	41
DAP distal	29

Two abaxial phalanges II:

	PQ AD 1836	AD579'98
Maximum height:	40	33.5
DT proximal:	61	58

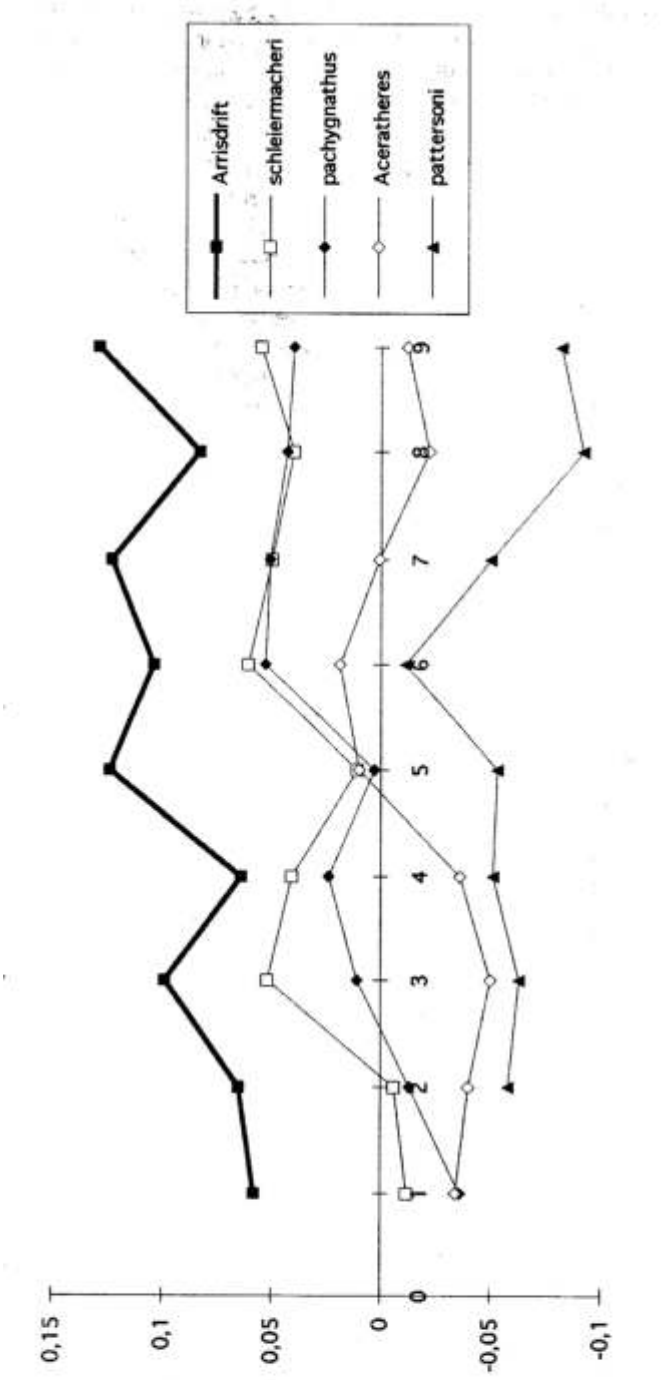

Figure 6: *Diceros australis*: Simpson diagram of the segments of the limbs compared with those of other Miocene rhinos. The reference is *Diceros bicornis*. 1: length of the ulna: 2: length of the radius; 3: length of Mc II; 4: length of Mc III; 5: length of Mc IV; 6: length of the tibia; 7: length of Mt II; 8: length of Mt III; 9: length of Mt IV.

DAP proximal:	27	26.5
DT diaphysis:	49.5	48
DT distal:	51.5	46.5
DAP distal	20.5	19

Other material. A patella (AD 580'98) is 115 mm high for a transverse diameter of 101.5 mm and an antero-posterior diameter of 54 mm.

Three sesamoids are preserved, as well as a dozen vertebrae

in poor condition or incompletely cleaned, which in their present state can only be identified to family.

Relations of the limb segments. A Simpson diagram of the limb segments (Fig. 6) shows once again many similarities with *Dicerorhinus schleiermacheri* and *Diceros* gr. *pachygnathus-neumayri*, with, in addition, a remarkable peculiarity: a much greater relative length of the abaxial metapodials with respect to the axial ones.

Affinities of *Diceros australis*

111 out of the 112 identifiable remains of rhinocerotids from Arrisdrift constitute a homogeneous sample which allowed the definition of *Diceros australis*. In comparison with the other rhinos from the Miocene of Africa, this species is characterised by the following:

- with the possible exception of *Kenyatherium*, of which the teeth are completely different, it is the largest of all;
- the size and proportions of the metapodials and long bones show clear similarities with *Diceros* gr. *pachygnathus-neumayri* of the Upper Miocene of the Near East, and to a lesser extent to *Dicerorhinus schleiermacheri* of the Upper Miocene of Western Europe;
- The morphology of the upper cheek teeth, notably P4/, is typical of Dicerotinae; these upper cheek teeth have great morphological and biometric resemblances to *Diceros douariensis* from the early Late Miocene of the Maghreb and Italy, the post-cranial skeleton of which is practically unknown.
- the morphology of the mandible has strong similarities to those of Dicerotinae, among others, the probable brevity of the symphyseal region. The same applies to other anatomical parts, such as, for example, the radius, calcaneum, etc...
- the i/2 which is very reduced could correspond to an evolutionary stage before the total loss of the anterior dentition.

It was the combination of these features that led me in 2000 to attribute the remains of the large rhinoceros from Arrisdrift to a new species of *Diceros*. In the present state of our knowledge it is the oldest known species of Dicerotinae; hitherto it was *Paradiceros mukirii*, of the latter part of the Middle Miocene of East Africa, which is a Dicerotinae but on a side branch. A hiatus of more than 7 Ma thus occurs between *Diceros australis*, of the basal Middle Miocene and *Diceros douariensis*, of the basal Late Miocene; it would be surprising if new discoveries don't fill this void.

Sub-family Chilotheriinae
Genus *Chilotheridium* Hooijer,1971
Species *C. pattersoni* Hooijer, 1971

Diagnosis (the same for the genus and the species, after Hooijer, 1971) : Single small nasal horn in both sexes; weak premaxillae, no upper incisors; frontals and parietals pneumatised; the orbit is further from the skull roof than in *Chilotherium*; skull and occiput narrow; parietal crests not far from each other; pseudo-auditive meatus opens ventrally; symphyseal part of the mandible narrow, widening slightly anteriorly. Very hypsodont cheek teeth, as in *Chilotherium*, and with the same kind of construction: uppers with the paracone fold disappearing towards the base, and the posterior part of the ectoloph flattened; protocone flattened on its internal side; anterior fold of the metaloph underlining the hypocone; anticrochet prominent at its base, recurving towards the interior at the entrance of the medisinus; crochet usually well developed, crista weak or absent; swelling of the metacone at the base of the M3/; strong anterior cingulum, weak lingual cingulum usually forming relief at the entrance of the medisinus. Lower tusk with subtriangular section, depressed dorsoventrally, with trenchant internal margin and with outer margin rounded below and keeled above. Scapula low and wide; limb bones very shortened; radius and ulna, as well as the tibia and fibula not fused; radius with a facet for the pyramidal; semilunar lacking radial facet; metacarpal V present and attaining 3/5 of the length of Mc IV; lateral metapodials slightly divergent towards the rear; small third trochanter in the femur; calcaneum lacking the tibial facet; navicular almost rectangular; cuboid wider than high; metatarsal III with a small cuboid facet.

Locus typicus and Stratum typicum: Loperot, volcano-sedimentary formation of Turkana Grit, Turkana District, Kenya; 17 Ma.

Other localities: Kirimum (15 Ma), Ngorora (12 to 11 Ma), Ombo (16 Ma) and Rusinga (18 Ma) in Kenya, and Bukwa (ca 17.5 Ma) in Uganda.

Holotype: Skull 2 (70-64K, B 12), Fig. *in* D.A. Hooijer (1971) Pl. 1.

Other specimens: The hypodigm corresponds to at least 8 individuals, the detailed list of which is given as an annex (p. 390-392) in D.A. Hooijer (1971).

Conservation: The material was collected by a team from the Harvard Museum of Comparative Zoology. It is currently in the National Museum, Nairobi, Kenya.

Material studied: A magnum AD 618'97 collected at Arrisdrift.

Description: By its morphology (Pl. 3, Fig 3), its size and proportions, this magnum is completely different from the one collected in the same locality and attributed to *Diceros australis*.

The dimensions are as follows:

Total length:	91 mm
Anterior breadth:	50mm
Anterior height:	27mm
Maximum height:	54.5 mm
Sub-articular height:	52.5 mm

Low and very wide, with an anterior surface that is flat and oblique, it has a width/height ratio (Fig. 2) opposite to that of *D. australis*, which reveals that we are in the presence of a small to medium sized species with short, strong feet, probably *Chilotheridium*, of which the type site is about the same age as Arrisdrift.

For 10 incomplete specimens of *C. pattersoni* from Loperot (Hooijer, 1971, Tabl. 14) the anterior height is slightly greater (30 to 33 mm) but the anterior breadth is slightly less (44 to 49 mm); these differences are not very significant, because

they could result from geographic variation, but more likely to a difference in measuring technique; whatever the case, they are the same order of magnitude.

Affinities: *Chilotheridium* is a monospecific genus and is the only Chilotheriinae known up to now in Africa. Its discovery at Arrisdrift increases its geographic range a great deal, hitherto being restricted to Kenya and Uganda. From the point of view of its stratigraphic distribution, it was limited to the Middle Miocene (it was known to occur between 18 and 11 Ma) but the recent discovery of a left Mc IV at Grillental (20 to 21 Ma) shows that the species also occurs in the lower Miocene.

Unidentifiable Rhinocerotidae from Auchas Mine

At Auchas Mine an atlas vertebra, still in its matrix, and a small fragment of mandible with several cheek teeth still covered in sediment were found during the excursion which followed the congress of the PSSA at Windhoek in 1998. As far as I can tell, the mandible appears to be close to the genus *Brachypotherium*.

Conclusions

Two of the Miocene vertebrate sites, Arrisdrift and Auchas Mine, excavated since 1991 by the Namibia Palaeontology Expedition are located in the Orange River Valley and have yielded remains of Rhinocerotidae.

The more important of the two is Arrisdrift, which is aged about 17 Ma and where 112 specimens of rhinos were collected, of which III constitute a homogeneous sample corresponding to a large cursorial Dicerotinae that I described in 2000 as *Diceros australis* nov. sp. This one, perhaps the largest species of rhino known up to now in Africa, is represented by teeth, mandibles, and all the elements of the postcranial skeleton, only the skull remaining unknown. The teeth, the mandible and the limb skeleton possess all the features of the sub-family; they show close morphological and biometric similarities with two species from the Late Miocene, *Diceros douariensis* from the Maghreb and Italy, and *Diceros* gr. *pachygnathus-neumayri* from the Near-East. *D. australis*, which is known only from the type locality, is at present the oldest known representative of the sub-family of Dicerotinae. Within this sub-family, it provides evidence of an evolutionary stage before that of species from the Late Miocene: lower tusks are still present but are vestigial and the limbs are not yet graviportal.

The only specimen from Arrisdrift which is not attributed to *D. australis* is a magnum corresponding in its morphology, size and proportions to a small to medium sized species with short legs. It is most likely to be a Chilotheriinae *Chilotheridium pattersoni*, first defined at Loperot in Kenya, which is similar in age to Arrisdrift, and known in five other East African sites and also recently discovered in the Sperrgebiet at Grillental, the latter specimen being the earliest known record of the species.

At Auchas Mine an atlas and a fragment of mandible were discovered; but being covered in sediment they cannot yet be identified.

From the point of view of the Rhinocerotidae, the works of the Namibia Palaeontology Expedition have thus led to the discovery of two localities in the Orange River Valley of which the richest, Arrisdrift, has yielded abundant well preserved remains of a new species, *Diceros australis*. This is the oldest known representative of the sub-family of Dicerotinae, which is of considerable interest for understanding the history and evolution of the entire family Rhinocerotidae.

Acknowledgements

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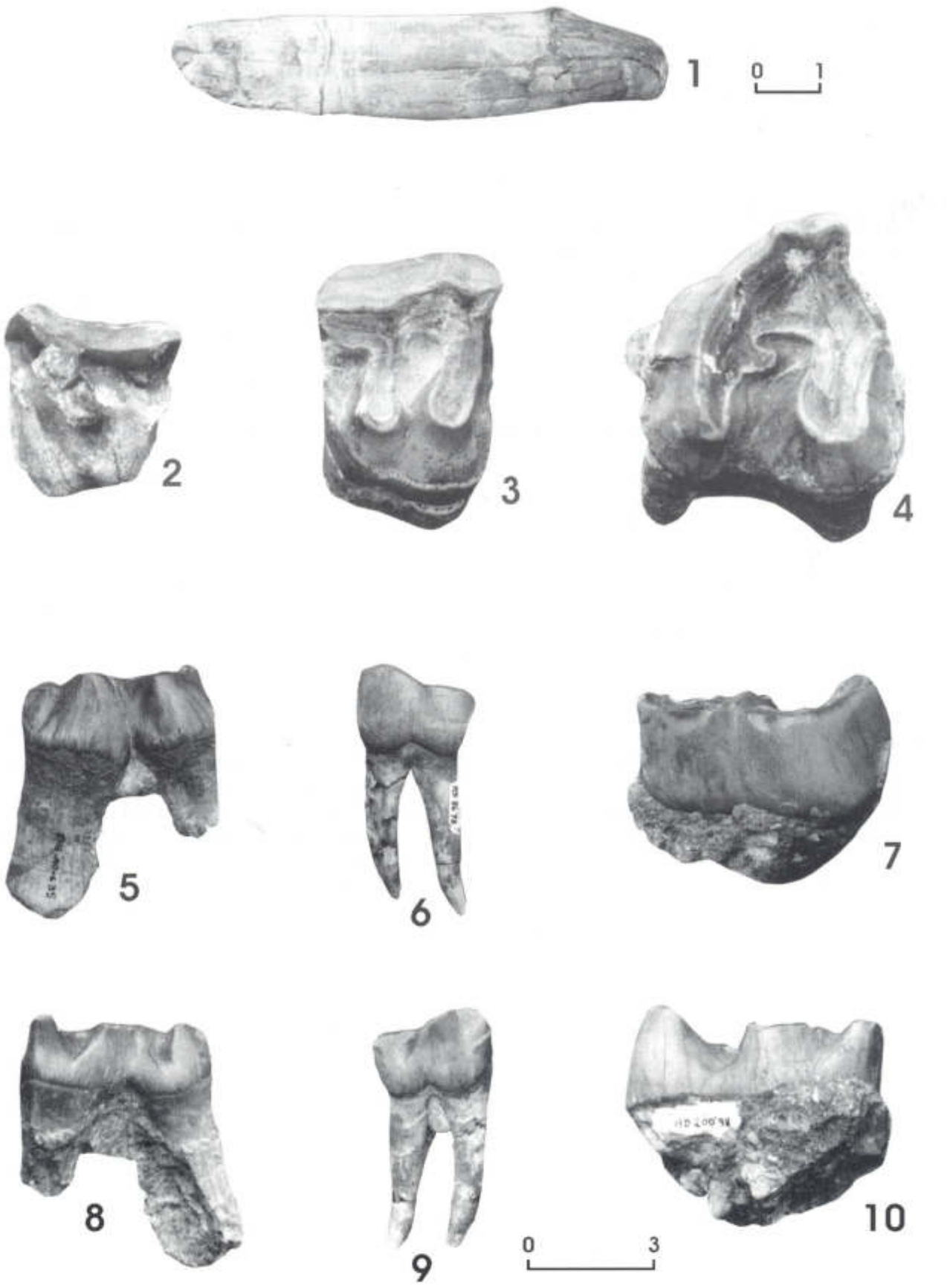

Plate I: Isolated teeth of *Diceros australis* : lower tusk (i/2) AD 87'98 (photo V. Eisenmann); 2: left dM4/ AD 292'94; 3: right P4/ AD 578'98; 4: right M3/ PQ AD 339; 5 and 8: left dm/3 PQ AD 635 (respectively in labial and lingual views); 6 and 9: left p/2 AD 86'98 (respectively in labial and lingual views); 7 and 10: left m/3 AD 200'98 (respectively in labial and lingual views). The scale is 1 cm for the tusk and 3 cm for the cheek teeth.

Plate 2: Axial metapodials of *Diceros australis* 1: Mt III AD 618'94, anterior view; 2: Mt III AD 618'94, posterior view; 3: Mc III AD 52'97, anterior view; 4: Mc III AD 52'97, posterior view. The scale is 3 cm.

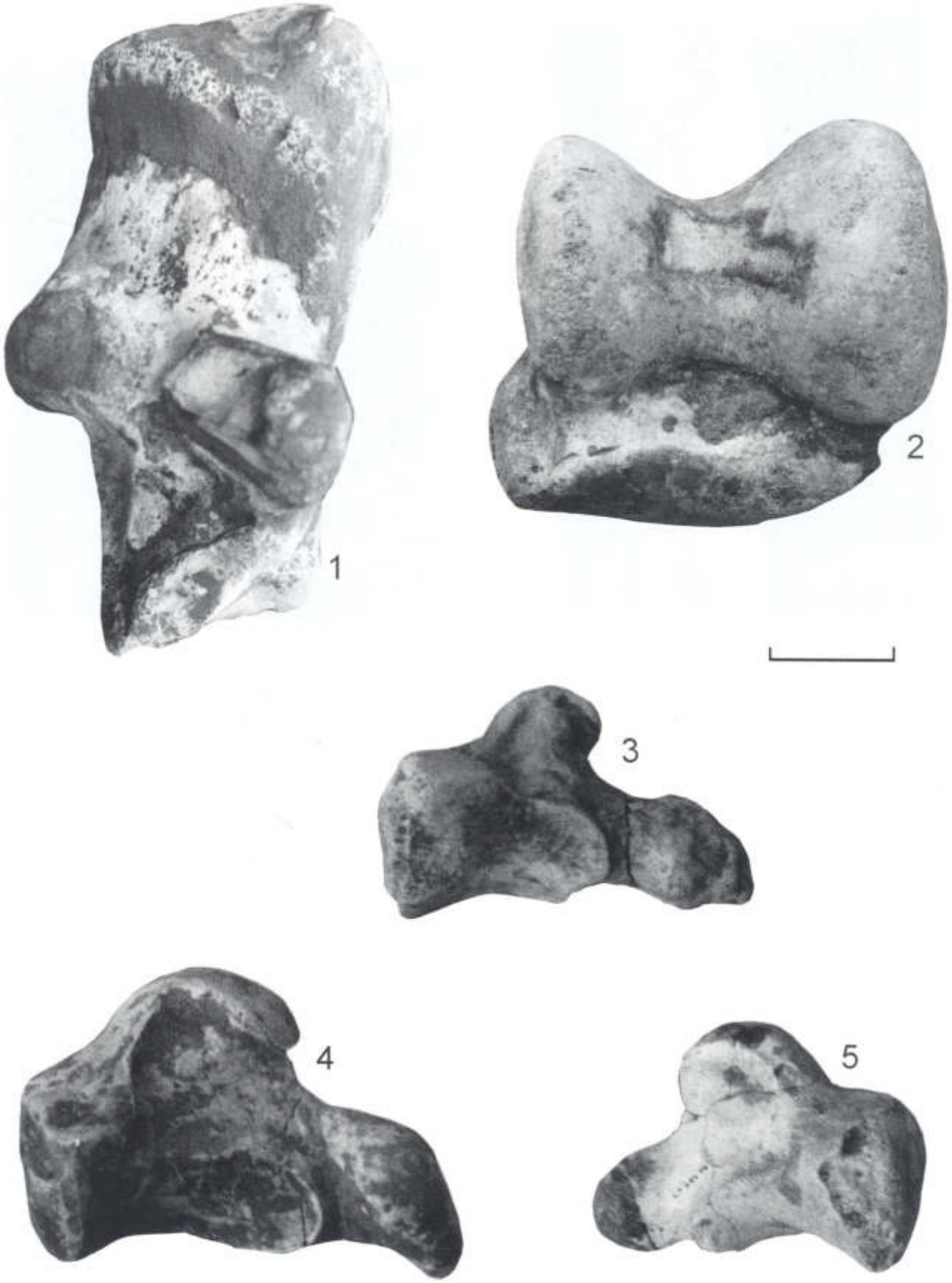

Plate 3: 1: right calcaneum (AD 50'97) of *Diceros australis*; 2: left astragalus (AD 619'94) of *Diceros australis*; 3-5: the three magnums of Miocene rhinos of Namibia: 3: cf. *Chilotheridium pattersoni* (AD 618'97), Arrisdrift, 4: *Diceros australis* (AD 638'97), Arrisdrift; 5: *Brachypotherium heinzelini* (LT 384'96), Langental. The scale is 3 cm.

Plate 4: 1: left humerus (AD 736'00) of *Diceros australis*; anterior and posterior views.