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in recognition of a lifetime of dedicated service to palaeontology

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CHARLES KIMBERLIN (BOB) BRAIN – A TRIBUTE

This volume of *Palaeontologia africana* comprising mainly papers presented at the tenth biennial conference of the Palaeontological Society of Southern Africa is dedicated to a remarkable person, a committed scientist, passionate naturalist, a leader in science, and dedicated family man and friend, who is an inspiration to all who know him.

Charles Kimberlin Brain was born on 7 May 1931 in what was then Salisbury, Rhodesia. From his earliest years he had close contact with natural history as his father was an entomologist, and his mother qualified as a botanist. At the time of his birth his father (also Charles Kimberlin) was Secretary for Agriculture in Southern Rhodesia, and his earliest memories were of accompanying his father on botanical outings as he was compiling a book on the flora of Southern Rhodesia. His independence of thought was manifested at an early age when he announced to his parents that his name was not Charles Kimberlin, but Bob, and this name has stuck ever since.

In the course of the Second World War his father retired from his position in the Department of Agriculture, and worked for two years at the National Museum in Bulawayo where the young Bob came into contact with Geoffrey Bond (later Professor of Geology and Vice-Principal of the University of Zimbabwe) and Neville Jones (retired missionary and pioneer in the study of Rhodesian prehistory). Both had inquisitive dispositions and had a strong influence in instilling a sense of questioning in young Bob's mind.

At the end of the war the Brain family relocated to South Africa and settled in Pretoria where Bob spent the last three years of his schooling, matriculating at Pretoria Boy's High School at the age of 16 in 1947. During these three years he began his association with the Transvaal Museum as he went there to learn to mount birds. On matriculating, Bob proceeded to the University of Cape Town to read for a BSc degree with geology and zoology as major subjects. This subject choice was made despite contrary advice by university staff, as they perceived it to be a senseless combination with poor prospects for job opportunities. However this particular combination of subjects was later to bring about great research possibilities for Bob. After completion of this degree, Bob wished to continue with an MSc in marine biology but a shortage of finance necessitated him taking a job in 1951 as a geologist with the National Building Research Institute at the CSIR in Pretoria. However, by 1954 he was keen to return to natural history research and this was the beginning of his professional association with the Transvaal Museum.

Although a great deal of international interest had been generated by the discovery of australopithecine ape-men fossils by Dart and Broom, the geological context of these discoveries was very poorly understood in the early 1950s. At the suggestion of John Robinson, then working at the Transvaal Museum, Bob began to apply sediment analysis techniques which he had learnt at the CSIR to the Transvaal cave deposits. He subsequently came up with the suggestion that ancient soils might be used as indicators of past climates and also undertook an investigation of the stratigraphy of the sites. This was the beginning of Bob's long and successful association with the Swartkrans fossil hominid site which has brought both him and the site international acclaim and fame. As a result of this initial geological work, and on the recommendation of Kenneth Oakley of the British Museum (Natural History), a substantial grant was made to the Palaeontology Department at the Transvaal Museum by the Wenner-Gren Foundation for Anthropological Research in New York. This made it possible for Bob to be employed as a Research Associate in the Palaeontology Department from 1954-1957. In this time he undertook the first systematic investigation into the stratigraphy of the fossil hominid-bearing cave deposits, and established that each cave deposit was of a different age and reflected a different climatic regime. An important consequence of this research was his discovery, for the first time, of stone artefacts associated with *Australopithecus* both



Figure 1. Early days – out in the field, where he loves to be.



Figure 2. Partners in all they do – Bob and his wife, Laura

at Makapansgat and Sterkfontein. In 1957 he obtained a PhD from the University of Cape Town for a thesis entitled "*The Transvaal ape-man-bearing cave deposits*" which was later published as a monograph by the Transvaal Museum.

In 1955 Bob married Laura (Kraan), who was then working as a geologist at the CSIR. This was a union made in heaven which has brought them great happiness and fulfilment. Together they have travelled southern Africa and the world, whether it be on research and collecting expeditions, to attend conferences, or to address different gatherings. Everything they have done they have done together and Bob's manifold achievements are Laura's too. Together they have established a warm, welcoming and peaceful atmosphere in their home in Irene, south of Pretoria

In the same year, at the second Pan-African Congress on Prehistory, Bob first heard Raymond Dart present his ideas on the bloodthirsty carnivorous origins of man. These ideas emanated from his research at the hominid-bearing site at Makapansgat where he analysed several thousand fossil bone fragments, and was particularly interested in how all these bones had accumulated in the ancient cave. Later, in a series of papers, Dart postulated that the fossilised bones of animals found in association with remains of *Australopithecus* had actually been used as tools by them. These ideas stimulated in Bob a desire to understand the behaviour of early hominids, a quest which was later to occupy a great deal of his research time.

At the end of his contract period in the Palaeontology Department in 1957, Bob was appointed curator of Lower Vertebrates, the only position then available at the Transvaal Museum. This position was previously occupied by Dr Vivian FitzSimons, the noted South African herpetologist, who was currently director of the Museum. Bob worked closely with FitzSimons in completing a major book, *The Snakes of South Africa*, and published several papers on frogs, snakes and lizards. One of the highlights of this period of his research career was in demonstrating that behaviour patterns of certain reptile species could be used as taxonomic criteria in the same way as morphological features are used.

In the early 1960s new exciting museum developments were taking place in Rhodesia as three new museums were about to be built. Keen to return to his country of birth, in 1961 Bob accepted appointment as Keeper of Zoology at the newly erected Queen

Victoria Museum in Harare and at the same time was Deputy Director of the National Museums of Rhodesia. These positions he held until1964. During this time he speculated on the nature and behaviour of early man and undertook pioneering comparative behavioural research on vervet and samango monkeys. He was also responsible for the planning and installation of the zoological display at this museum which remains virtually unchanged to this day.

At the invitation of Vivian FitzSimons, Bob returned to the Transvaal Museum in 1965 to take up the post of Curator in the Department of Palaeontology after John Robinson had left to take up a position at the University of Wisconsin. Three years later Bob was appointed Director of this museum, a position he held for twenty-three years. Being back in Pretoria, he now at last had the opportunity to research the fossils of the early man caves of the Transvaal, as he was convinced that these would provide new insights into the behaviour of early hominids. Because the existing fossil collections from Sterkfontein and Kromdraai seemed adequate for this purpose, his first objective was to accumulate a large and representative collection of fossil bones from Swartkrans. This was achieved by first sorting for seven years through the dumps of the lime miners, and later by extensive excavations and investigations. Wednesdays were set aside for fieldwork at Swartkrans, and for 21 years Bob assiduously kept this weekly appointment so that he could work with his technicians. In the process Bob discovered several hundred early hominid fossils, making him singly one of the greatest discoverers of early man in Africa. This broadly focussed model taphonomic study continued for twenty-eight years resulting in numerous publications and culminating in the publication of two milestone books, namely *The Hunters or the Hunted? An Introduction to African Cave Taphonomy* and *Swartkrans: a Cave's Chronicle of Early Man.*

With characteristic diligence and a multifaceted approach to solving scientific problems, Bob in addition collected and studied discarded bony food remains scattered around "Hottentot" (Nama) settlements along the banks of the Kuiseb River in Namibia in order to understand the effects of human behaviour on bone accumulations. This necessitated gathering every bone fragment lying around 15 villages. Because the skeletal representation from these accumulations was comparable to the fossil samples, Bob was able to deduce that only those skeletal parts which were robust enough to survive the feeding activities of humans and carnivores were the ones with the greatest chance of becoming fossilised. In addition, he studied the feeding behaviour of various carnivores, especially cheetahs which he kept in captivity, in order to establish the different ways in which fossil bone-accumulations occurred in cave deposits. Bob demonstrated that primate skeletons were more vulnerable to damage from chewing than those of antelope of equivalent body weight in that the postcranial skeletons of baboons tended to disappear while the heads survived, whereas most components of the antelope skeletons survived. This work showed that the disproportional representation of skeletal parts in bone assemblages that had originally been recognised by Dart at Makapansgat, and had been attributed by him to human activity, possibly had other explanations. This research led directly to the new discipline of cave taphonomy, a study which allows reconstruction of early hominid and other animal behaviour, and in which Bob established himself as an international leader.

Meticulous analysis by Bob of thousands of fossil remains as well as stone and bone artifacts from Sterkfontein, often with numerous international collaborators, produced the most detailed information available on the fauna of this part of Africa. Of particular significance were his findings relating to the cultural status of hominids at this time, 1.8 to 1 million years ago, as well as information on the importance of predation in early hominid life. He came to the conclusion that the australopithecine remains in the caves of the Sterkfontein valley had been taken to the caves by carnivores and eaten there, the fossils representing discarded food remains. One of the most dramatic findings during the later years of the Swartkrans excavation was the discovery of burnt bone through a vertical profile of six metres. After a great amount of careful histological and experimental work by Bob, with chemical confirmation by Andrew Sillen, these burnt bones were shown to provide the earliest evidence for the controlled use of fire by hominids, dating to about one million years ago, and suggested that fires were repeatedly made on the floor of the cave over a period of some thousands of years. An additional highlight was the discovery of bones with characteristic scratch marks and smooth tapering points that Bob considered had been used as digging tools, a conclusion confirmed by his son Conrad, who conducted digging experiments using modern bone flakes.

From this thorough work at the Swartkrans site Bob was also able to identify cycles of deposition within the Quaternary period. He linked habitat changes to global variability in temperature and correlated these, for the first time, with hominid evolutionary events in Africa. For the results of this multi-faceted research Bob was awarded a DSc by the University of the Witwatersrand in 1981.

Bob Brain, together with Bernard Carp, Vivian FitzSimons and Charles Koch was one of the founders and initiators of the Namib Desert Research Station in 1959 when they organised an expedition to the Gobabeb area to select a site for the station. As director of the Transvaal Museum, Bob was later responsible for guiding Gobabeb to becoming a research station of international repute for the work on desert ecology undertaken by its staff and collaborators. Several times a year he visited Gobabeb where he camped in the same spot under the acacia trees and always made a wood fire to give a homely atmosphere to his camp. Bob himself undertook research and wrote papers on various aspects of natural history of the Namib. These ranged from



Figure 3. The consummate communicator – Bob explains what happened at Swartkrans

taxonomic work on micro-organisms, the use of protozoans as palaeoecological indicators, through observations on the temperature balance of lizards, the description of new gecko species, speculations on the origin of sidewinding locomotion in adders, to taphonomic studies on "Hottentot" food remains.

During his term as Director, Bob established the Transvaal Museum as a happy and highly productive institution with an international reputation for its research endeavours. This he achieved by allowing his staff considerable personal freedom, provided that productivity was maintained. He strove to maintain the Transvaal Museum as a place of quiet scholarship staffed by committed people who derived real pleasure from working at the museum.

Apart from leading from the front with his own busy research schedule, Bob was in addition a dedicated museum educationalist. During his directorship the education department of the Museum was greatly expanded under the stimulating guidance of O.P.M. ("Proz") Prozesky. Bob also planned and co-ordinated the completion of three new display halls: The Austin Roberts Bird Hall, Life's Genesis I and Life's Genesis II. For the latter two exhibits he successfully experimented with a 'narrative concept' where visitors were treated to a series of displays depicting the development of life from its simplest beginnings to its present complexity. The advantage of this display technique is to provide the visitor with a unified experience rather than a set of disjointed displays.

In addition to all his other activities Bob has given long, loyal and distinguished service to the museum profession, has served on the Council of the Southern African Museums Association for many years and has been its President for two terms. In addition he has served on the councils of many professional societies and been president of the Southern African Archaeological Society, Zoological Society of Southern Africa, South African Biological Society, South African Society for Quaternary Research, Southern African Association for the Advancement of Science (President of section D - Zoology), and was the first President of the Palaeontological Society of Southern Africa. He has also inspired others to undertake research and has acted as supervisor to at least 18 masters and doctoral students.

When he retired as Director of the Transvaal Museum in 1991, Bob became Curator of Lower Invertebrates at the Museum and his research interest shifted to micro-invertebrates, where he gave particular attention to the fauna of saline and temporary water bodies in the arid western regions of South Africa. His attention was attracted to rotifers in particular, on which he undertook mainly taxonomic research. These simple multi-celled organisms led him to think about the origins of multicellularity and resulted in his pioneering search for ancestral multicellular micro-invertebrate fossils in limestones of the Neoproterozoic Nama Group. This has proved to be a very labour intensive project in which his wife Laura has played an important part, as she is responsible for cutting and grinding numerous rock samples and preparing hundreds of thin sections in the hopes that some prehistoric ancestral multicellular creature would be revealed. This research is now producing internationally significant results. Recognising the importance of predation to the evolution of animal sense organs and intelligence, Bob is currently investigating the roots of predation in these very early animal communities.

As is evidenced by the more than 150 scientific papers and several books he has published, Bob Brain has had and still pursues an extraordinarily diverse and productive research career. He is heralded as one of the foremost naturalists Africa has produced. Being a naturalist in the truest and best Darwinian tradition, all research projects undertaken by him have been well formulated, imaginative, innovative and have produced significant results with universal applicability. For his scientific pursuits he has received many awards including: One of the Four Outstanding Young South Africans (1966), Gold Medal of the Zoological Society (1978), Senior Captain Scott Memorial Medal of the South African Biological Society (1987), Achievement Award of the Claude Harris Leon Foundation (1992), John F W Herschel Medal of the Royal Society of South Africa (1991), and the South African Medal of the South African Association for the Advancement of Science for exceptional contributions to science (1997). He was categorised as an A-rated scientist of the Foundation for

Research Development (from its inception in 1984 till his formal retirement in 1997), and he holds honorary DSc degrees from the Universities of Cape Town, Natal, Pretoria, and Witwatersrand.

In all his research endeavours Bob always had the assistance of Laura and their delightful daughters, Rosemary (Mel) and Virginia (Ginny), and sons Tim and Conrad (Nad). While growing up each of them derived great enjoyment, personal involvement, fulfilment and commitment in the Brain family research endeavour. They have all played a role in the development of Bob's research visions and Bob once described his house as "children inter-stratified with rocks and fossils". The Brain home has always been one of love, laughter and enjoyment, and much banter amongst individuals of the family. The children lovingly tell the story that Bob had once collected a snake, and in order to preserve it before taking it to the museum, he had coiled it up in an opaque plastic bag and placed it in the freezer. You can imagine Laura's surprise, and the children's delight, when she removed the package from the freezer to prepare sausage for breakfast!

Bob has always stressed the importance of fun in research, and maintained that if this was in place then self-motivation, creativity and productivity would follow naturally. He warned against the dangers of obsession with performance and productivity to the detriment of creativity as he felt that scientists could become project driven to the point that they function badly as whole and integrated personalities.

This volume of palaeontological papers is dedicated by colleagues and friends in admiration of a truly great palaeontologist who has pursued science for the sake of enjoyment and fulfilment. This broad-minded and good-natured naturalist has many friends and the admiration of all his colleagues.

ACKNOWLEDGEMENTS

I am indebted to numerous people who have had a close association with Bob through the years for discussions and anecdotes, and also for reading various drafts of this document. In particular I am grateful to Lucinda Backwell, Lee Berger, Tim Brain, Chris Gow, James Kitching, Mike Raath, Francis Thackeray, John Ward and Ginny Watson.

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A CAPTORHINID WITH MULTIPLE TOOTH ROWS FROM THE UPPER PERMIAN OF ZAMBIA.

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ABSTRACT

Captorhinids are some of the best known early amniotes. They range throughout the Permian and occur in North America, Europe, India and Africa. There are several small forms with single rows of marginal teeth, medium sized multiple-rowed forms typified by *Captorhinus*, and large forms most of which possess numerous rows of marginal teeth. As a group, captorhinids are extremely conservative in cranial morphology in most other respects. A small Late Permian, single rowed form has been recorded from the Madumabisa Mudstone of Zambia, equivalent in age to the *Cistecephalus* Assemblage Zone of the Karoo Basin of South Africa. This paper records a multiple-rowed form from these rocks similar in size to *Captorhinus*, but with distinctive dentition.

KEYWORDS: Upper Permian, Captorhinidae, Zambia.

INTRODUCTION

In 1960 and 1961 J W Kitching made a large collection of tetrapod skulls from the upper Luangwa valley, Zambia (then Northern Rhodesia). Two horizons within the Madumabisa Mudstone yielded fossil amniotes, the lower horizon being equivalent to the *Tropidostoma* Assemblage Zone of the South African Karoo, while the upper horizon yielded a typical *Cistecephalus* Assemblage Zone fauna (Kitching1963). This latter assemblage, of Upper Permian age, included the captorhinid described here, which was originally catalogued as a procolophonid.

Gaffney and McKenna(1979) described two small single-toothrowed skulls from the Upper Permian Madumabisa Mudstone of Zimbabwe (then Southern Rhodesia), and referred them to the Lower Permian *Protocaptorhinus* of North America. More recently Modesto (pers. com. and in press) has collected and described a small single rowed captorhinid from the *Cistecephalus* Assemblage Zone of the main Karoo Basin.

MATERIAL AND METHODS

The skull, BP/1/3899, including lower jaw and teeth, is encased in a very hard and brittle haematitic matrix, as is most of the Luangwa Valley material. Most of the superficial bones have been lost to weathering, leaving most of the skull roof represented by steinkern, itself partially weathered. Several features on the steinkern are clearly the result of cracks in the overlying bone, and such internal traces of sutures as exist are not comparable with true surface sutures. Typical captorhinid dermal bone sculpturing is visible in only two places, on a small area of jugal, and on the mid-dorsal surface of the exposed supra-occipital. The occiput and palate having been still encased in matrix responded quite well to airscribe preparation, though as the lower jaw and teeth are present in occlusion and in poor condition, the anteriormost part of the palate has not been prepared. A vexing feature of this specimen is that several sutures have opened up very slightly post mortem, none the less, the overall *Captorhinus*-like shape of the skull is not compromised. Very few tooth tips are exposed, but as several teeth are represented by high fidelity impressions these could be usefully studied with a soft, fast setting dental impression material. A single articulated digit was found lying against the skull and is now stored separately.

SYSTEMATIC PALAEONTOLOGY

Reptilia Laurenti, 1768
Eureptilia Olson, 1947
Family Captorhinidae Case, 1911
Genus *Captorhinus* Cope, 1897

Species. *Captorhinus* sp. indet.

This specimen is some 20 million years younger than the two species of *Captorhinus* (*C. aguti* and *C. laticeps*). In nearly every observable feature apart from detailed morphology of the dentition, it is typical of the genus. Pristine post caniniform multi-rowed cheek teeth are robust, conical, and sharp pointed, as opposed to those of *C. aguti* which have mesio-distally aligned blade-like tips (Modesto 1998 and pers. obs.), and those of *C. laticeps* which are described as triangular with cutting edges (Modesto 1998). The latter is, in any case, a single-rowed form. Several teeth have the tips worn to flat, lingually sloping micro-pitted facets. The absence of scratches on worn crowns indicates that occlusion was purely orthal. These details of wear and occlusion may all prove to be individual characters. Another potentially diagnostic character is the attitude of the paroccipital processes: these angle ventrad distally, whereas in *C. aguti* they angle dorsad.

DESCRIPTION

The skull (Figure 1) is the typical size and shape of *Captorhinus aguti*. As can be seen from the Figure the skull is badly eroded: a small patch of jugal and the dorso-medial projection of supraoccipital are the only parts which show the typical dermal bone pitting. Apart from the midline, naso-frontal, and fronto-parietal (and the impression of the pineal opening), sutures on the steinkern are uninformative with the exception of the posterior edge of jugal, which is typically captorhinid (Figure 1 C).

The elements of the palatal surface are all standard captorhinid, the stapes (Figure 1 B) and the median projection of the jugal being the most diagnostic elements. The basal articulations, the contact of the median projection of the jugal with the palatine and pterygoid, and the pterygo-palatine sutures, have all opened up slightly postmortem. An important consequence of this is that the depressions visible on the palatines (Figure 1 B) are actually where the pterygoids would normally lie (Fox and Bowman 1966, describe this sutural relationship in detail). Palatal teeth are sparse. None can be seen on what is exposed of the palatines. Teeth are present on the pterygoids, including their flanges, absent from the basiparasphenoid. However, but palatal teeth are known to be variable in number and distribution in *C. aguti*, so this has no taxonomic significance. The parasphenoid rostrum is directed steeply upwards, as is typical in captorhinids. A single hyoid element lies on the right side on the palatal surface (Figure 1 B). Of possible significance is the shape of the quadrate ramus of pterygoid: this is visible only on the left side where it is seen to terminate in a narrow ventral projection. No details of the corresponding surface of

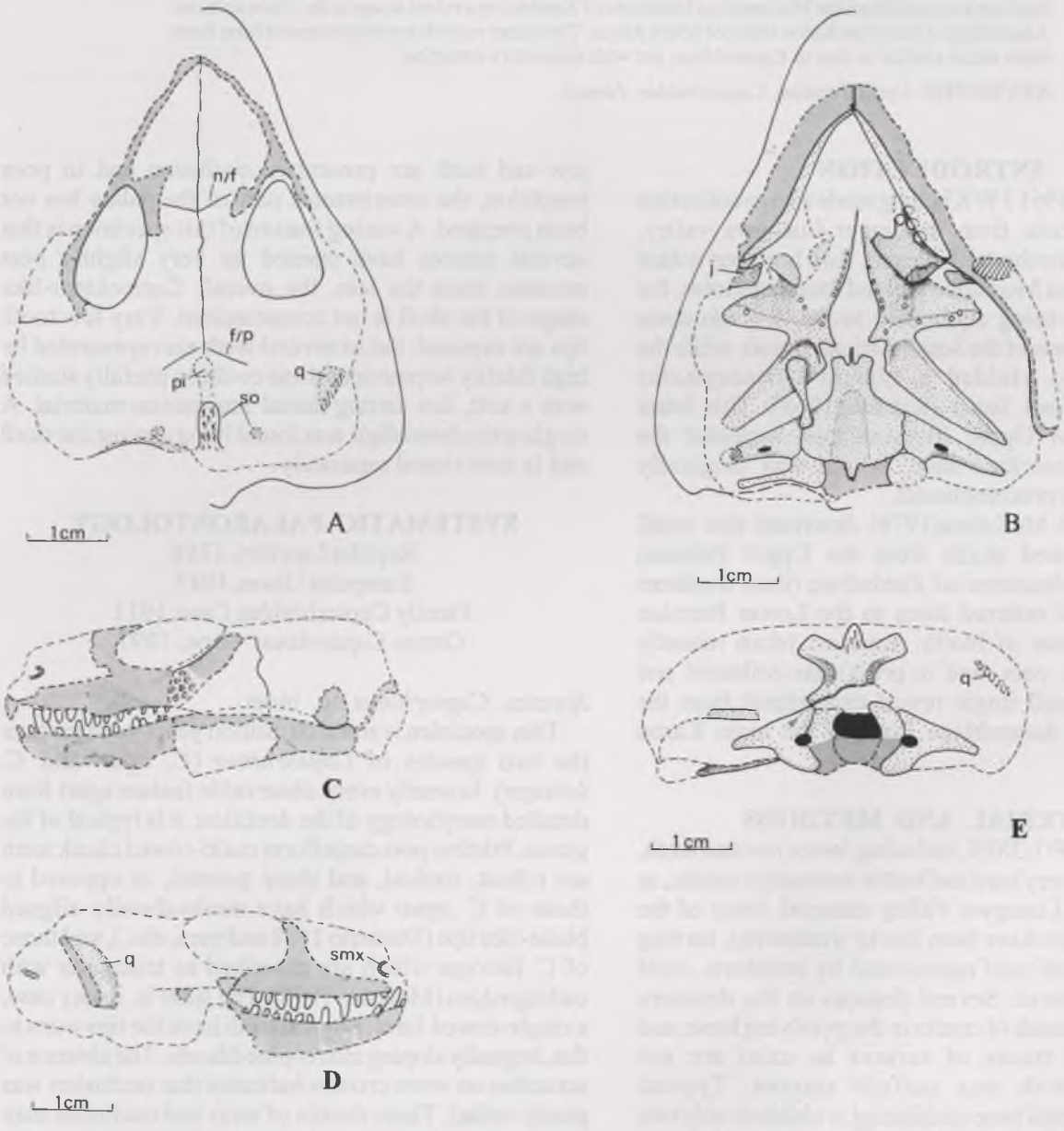


Figure 1. Skull of *Captorhinus sp.* from Zambia. In A dorsal, B ventral, C left lateral, D right lateral, and E occipital views. Dense shading indicates broken bone. Estimated original outline of skull is indicated.

the quadrate are exposed. The pterygoid ramus of quadrate is typically tall: it has been partially prepared on the right side where the rest of the bone is missing; further preparation would compromise other details (Figure 1 D & E).

On the occiput the supratemporal is well dispayed and just as described for *C. aguti* (Modesto 1998). Though the occipital condyles have been eroded off, the opisthotics and exoccipitals are quite well preserved. The paroccipital processes project slightly ventrad: this may be a real difference between this taxon and *C. aguti*, in which the paroccipital processes project somewhat dorsad (Modesto 1998, Figure 6 D), and cannot be due to any distorting postmortem effects.

The left lower jaw ramus is sufficiently complete to show the typical sigmoidal flexure of this structure in ventral aspect, but erosion makes it impossible to determine the morphology of the articular region. The splenials can be seen to participate in the symphysis.

The dentition (Figure 2) is uncannily similar to that of *C. aguti*. All the premaxillary teeth have been lost to erosion. The maxillary and dentary marginal rows contain a minimum of 13 and 17 teeth respectively, in a manner very similar to *C. aguti*. The surfaces of both maxillae and both dentaries have been completely eroded off and most of the exposed teeth are damaged. Thus it is likely that those visible are not marginal rows. However, the right maxilla contains a perfectly preserved caniniform tooth in the fourth tooth position which even displays typical theco-acrodont attachment. This tooth is symmetrically pointed in labial view. In mesial or distal view it is convex labially and concave distally on the lingual surface, with blunt mesial and distal edges, just as in *C. aguti*. Subsequent teeth are symmetrically conical and robust, becoming very small at the posterior end of the row. With the exception of the right caniniform, all exposed upper teeth are damaged.

Each dentary has a small procumbent tooth anteriorly, followed by the two largest teeth in the row; these are followed by a series of stout conical teeth, again becoming very small at the posterior end of the row. Two adjacent intact teeth have been prepared out on the ligual side of the left dentary (shown schematically in Figure 1 B): these are sharply pointed, robust cones. High fidelity impressions of two worn teeth are preserved in the right dentary: these exhibit wear facets dipping linguad at aproximately 30 degrees. The facets are finely pitted, not scratched, and the extremely thin enamel, being harder than the dentine, forms an uninterrupted, slightly raised rim. This wear indicates that jaw movements were purely orthal: it could have resulted from tooth-to-food contact as easily as tooth-to-tooth contact. The simple captorhinid jaw mechanism would generate maximun speed with the adductor muscles near full stretch and maximum force when the jaws were nearly closed. Multiple tooth rows seem "designed" to exploit the force component, either for crushing and cutting plant food in the case of *C. aguti* (Dodick and Modesto 1995; Modesto 1998), or in the case of *C. zambiensis*, for crushing invertebrate prey.

DISCUSSION

Dodick and Modesto (1995) present a useful cladogram of captorhinid relationships. Of the characters they use to diagnose Captorhinidae the Zambian specimen has the following three: 1) caniniform region present anteriorly on dentary, 2) pineal foramen anterior to midpoint of interparietal suture, and 3) maxillary dentition reduced to 25 or fewer teeth. Only one character places it in *Captorhinus*, namely, anterior teeth procumbent - true of the lowers but inferred for the premaxillary teeth which have all been lost.

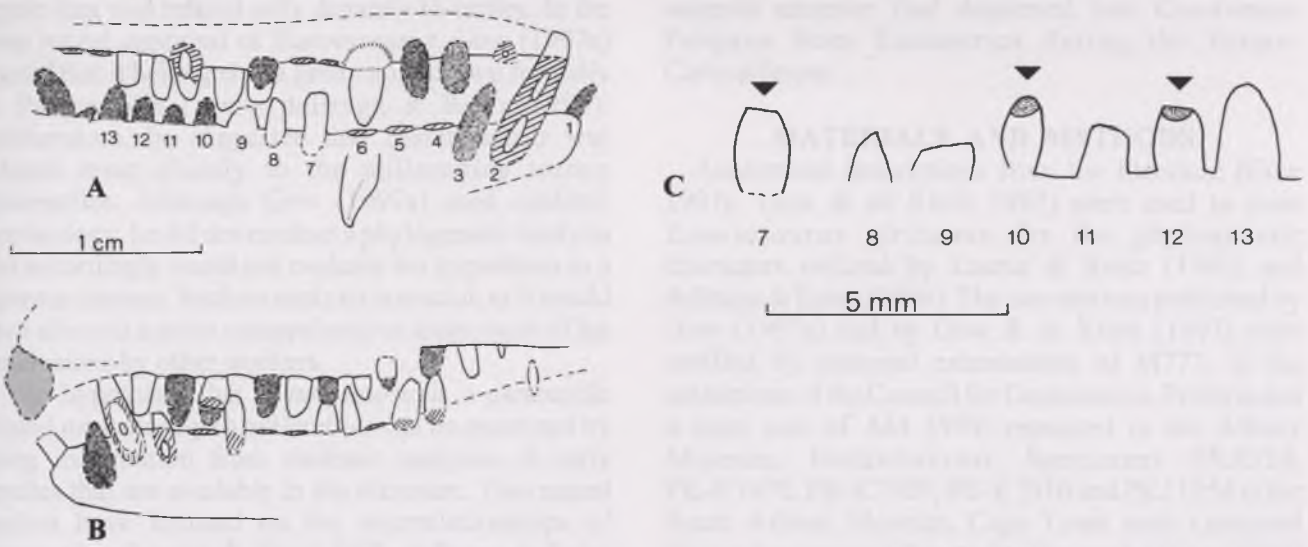


Figure 2. Dentition of *Captorhinus sp.* from Zambia drawn with the dentition horizontal. Shading indicates impressions, oblique lines indicate damaged teeth.A right side; maxillary caniniform sketched in mesial view beneath the number 6; B left side, disruption of maxillary row due to bone being broken at different depths; C three dentary teeth exhibiting crown tip wear (10 and 12 are impressions).

In the new Zambian specimen the only tooth which may be described as having anterior and posterior cutting edges is the maxillary caniniform, the rest of the teeth are conical and pointed. Modesto (1996) suggests that "teeth with cutting edges" is probably a synapomorphy of captorhinids. If this is so, then *C. zambiensis* with its connical pointed teeth is more derived than its sister taxon of *C.aguti* plus *C.laticeps* both of which have cutting cheek teeth.

ABBREVIATIONS

bo	basioccipital
f/p	fronto-parietal suture
hy	hyoid
j	jugal
n/f	naso-frontal suture
pi	pineal
ptgd	pterygoid
q	quadrate
smx	septomaxilla
so	supraoccipital
st	stapes

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EUNOTOSAURUS AFRICANUS AND THE GONDWANAN ANCESTRY OF ANAPSID REPTILES

by

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ABSTRACT

Phylogenetic analyses confirm that the turtle-like Late Permian reptile *Eunotosaurus africanus* is a parareptile (*sensu* deBraga & Reisz 1996) and identify it as the sister taxon of Procolophonomorpha. The tree topology for anapsid reptiles suggests that a distribution in Gondwanan Pangaea is ancestral for anapsids (*sensu* Gauthier, Kluge & Rowe 1988). Minimum divergence times (MDTs) determined from stratigraphic calibration of anapsid phylogeny suggest that anapsids were diversifying in Early Permian Gondwana as early as the Sakmarian. MDTs also support the idea that a preservational bias was operating on terrestrial vertebrates in Gondwana prior to the onset of continental sedimentation in the Late Permian.

KEYWORDS: Anapsida, *Eunotosaurus*, Gondwana, palaeobiogeography, parareptiles

INTRODUCTION

The Permian reptile *Eunotosaurus africanus* was described over a century ago by Seeley (1892) on the basis of a partial skeleton from a locality near Beaufort West, South Africa. Although he recognised the turtle-like nature of the vertebrae and ribs of his specimen, Seeley (1892) concluded tentatively that *Eunotosaurus* was a close relative of the mesosaurs. Watson (1914), having at his disposal an additional four specimens, suggested that *Eunotosaurus* was a suitable turtle ancestor. Since those early studies, further skeletons of this enigmatic reptile have been collected, although one with a complete skull was recovered only twenty years ago. That specimen allowed Keyser & Gow (1981) to concur with Cox's (1969) assessment that *Eunotosaurus* was a very basal reptile that was related only distantly to turtles. In the most recent appraisal of *Eunotosaurus*, Gow (1997a) argued that it belonged to a group now known formally as Parareptilia (*sensu* deBraga & Reisz 1996). Furthermore, he suggested that *Eunotosaurus* was related most closely to the millerettids among parareptiles. Although Gow (1997a) used cladistic terminology, he did not conduct a phylogenetic analysis and accordingly could not evaluate his hypothesis in a rigorous manner. Such an analysis is crucial, as it would have allowed a more comprehensive assessment of his conclusions by other workers.

The hypothesis that *Eunotosaurus* is a parareptile related most closely to millerettids can be examined by using information from cladistic analyses of early reptiles that are available in the literature. Two recent studies have focused on the interrelationships of parareptiles (Laurin & Reisz 1995; deBraga & Reisz 1996). Data from Gow (1997a) and Gow & de Klerk (1997), the two most recent descriptions of *Eunotosaurus*, can be incorporated into the data matrices of those phylogenetic studies and analyzed using the same phylogenetic programs employed by Laurin & Reisz (1995) and deBraga & Reisz (1996). This procedure was used by Modesto (1999b) for mesosaurs, who identified those early aquatic amniotes as the closest relatives of parareptiles within the clade Anapsida (*sensu* Gauthier *et al.* 1988; see Modesto 1999b for a discussion of the phylogenetic taxonomy of 'Anapsida' and 'Parareptilia'). Bearing in mind that mesosaurs, *Eunotosaurus*, and the latter's possibly closest relatives, millerettids, are all restricted to Gondwana, the resultant phylogenetic tree(s) can be used to examine the hypothesis that these reptiles originated in that region of Pangaea. It seems likely, given the basal phylogenetic positions of these taxa within Anapsida, that they are descended from an anapsid ancestor that dispersed into Gondwanan Pangaea from Euramerica during the Permo-Carboniferous.

MATERIALS AND METHODS

Anatomical descriptions from the literature (Gow 1997a; Gow & de Klerk 1997) were used to code *Eunotosaurus africanus* for the phylogenetic characters utilized by Laurin & Reisz (1995) and deBraga & Reisz (1996). The descriptions published by Gow (1997a) and by Gow & de Klerk (1997) were verified by personal examination of M777, in the collections of the Council for Geosciences, Pretoria and a latex cast of AM 5999, reposited in the Albany Museum, Grahamstown. Specimens PK4328, PK-K7670, PK-K7909, PK-K7910 and PK11954 in the South African Museum, Cape Town were examined during the course of this study. The work of Cox (1969) was used to code for several characters of the appendicular skeleton. Modified data matrices from Laurin & Reisz (1995) and deBraga & Reisz (1996)

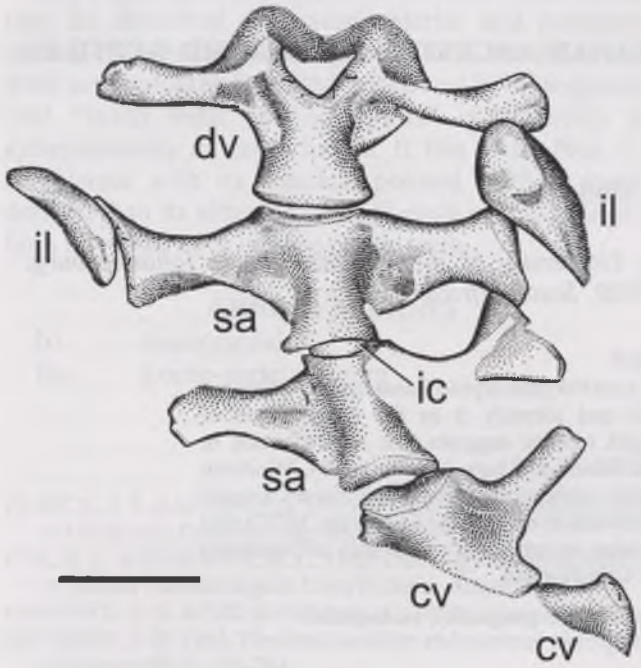


Figure 1. Ventral view of the pelvic region of *Eunotosaurus africanus*, showing the two sacral vertebrae, their ribs, and neighbouring elements. Drawn from a latex cast of AM 5999. Abbreviations: **cv**, caudal vertebra; **dv**, dorsal vertebra; **ic**, intercentrum; **il**, ilium; **sa**, sacral vertebra. Scale bar equals 5 mm.

were constructed in MacClade 3.07 (Maddison & Maddison 1997) and then evaluated (separately) using PAUP 3.1 (Swofford 1993) following the parameters used by those authors. The exact modifications made to both data matrices, including the character codings for *Eunotosaurus*, are outlined in the appendix.

RESULTS

The most recent anatomical descriptions of *Eunotosaurus africanus* (Gow 1997a; Gow & de Klerk 1997) were found to be accurate in all details save two. Gow & de Klerk (1997) concurred with Cox (1969) that only a single sacral vertebra was present, but examination of a latex cast of AM 5999 indicates that two sacral vertebrae are present (Figure 1): what was regarded by Gow & de Klerk (1997) as the first caudal vertebra bears ribs that are expanded distally and differ from the slender rib of the succeeding caudal vertebra and the tapering first caudal ribs of other early reptiles. The left rib of what is interpreted here as being the second sacral vertebra of AM 5999 is even marginally broader distally than either rib of the preceeding one (*i.e.*, the first sacral), although, because of foreshortening in the angle of view, this is not apparent in Figure 1. Gow & de Klerk (1997) deduced that the ribs in question were caudal ribs because their distal ends did not meet those of the (first) sacral. That line of reasoning is difficult to believe because the ribs of the first and second sacral vertebrae of an adult skeleton of the basal parareptile *Milleretta* clearly do not meet laterally in the specimen illustration of Gow (1997b). Furthermore, the outline of the right second sacral rib of AM 5999 is not complete owing to loss of the matrix that preserves the anterior margin of the rib (Figure 1), and what can be determined from the left rib suggests that distally there could have been a narrow contact between the first and second sacral ribs. Such an organization for the sacral ribs is regarded to be a parareptilian apomorphy (Laurin & Reisz 1995). The other emendation is the observation that at least one intercentrum is preserved in AM 5999 (Figure 1), which confirms Cox's (1969) report that intercentra are present in this reptile (*contra* Gow 1997a).

In the most parsimonious trees of both analyses, *Eunotosaurus africanus* forms a clade with parareptiles that excludes millerettids. In the analysis that uses a modified version of the data matrix of Laurin & Reisz (1995), *Eunotosaurus* forms a sister group with Procolophonia within Parareptilia (Figure 2). This sister-group relationship is relatively robust, requiring 3 extra steps to collapse (*i.e.*, to make *Eunotosaurus* form a sister-group relationship with Parareptilia *sensu* deBraga & Reisz 1996). Three extra steps are also required for *Eunotosaurus* to become the sister taxon of Millerettidae. In the analysis that uses a modified version of the data matrix of deBraga & Reisz (1996), *Eunotosaurus* falls within Parareptilia and forms a clade with Procolophonomorpha (Figure 3); 2 additional steps are required to place *Eunotosaurus* into a sister-group relationship with millerettids, and 3 extra steps to exclude it from Parareptilia. It can be noted here that Procolophonomorpha Romer 1964, as defined phylogenetically by Lee (1995), is the senior synonym of Ankyramorpha deBraga & Reisz 1996.

The two resultant trees are mutually compatible. Although the data matrix of deBraga & Reisz (1996) incorporates three more parareptilian taxa (*Acleistorhinus pteroticus*, Lanthanosuchidae, and *Macroleter poezicus*) than that of Laurin & Reisz (1995), the topology of the tree shown in Figure 3 would be equivalent to that seen in Figure 2 if these taxa are removed. A composite tree of the anapsid phylogenies shown in Figures 2 and 3 is reproduced as a stratocladogram in Figure 4. Ghost lineages and taxa (Norell 1992) have been drafted to establish minimum divergence times (MDTs) for anapsid taxa. The implications of the MDTs are discussed in the following section.

DISCUSSION

The phylogenetic analyses confirm Gow's statement that *Eunotosaurus africanus* is 'a good parareptile' (Gow 1997a: 33). Much more interestingly, it identifies procolophonomorphs rather than millerettids as the closest relatives of *Eunotosaurus* within Parareptilia. The new topology has interesting implications for anapsid evolution. Two issues that will be addressed here include the early biogeography and biostratigraphy of anapsid reptiles. The former issue has received some minor attention in the literature (Milner 1993; Modesto & Rybczynski 2000), whereas the latter has come under scrutiny for Anapsida (*sensu lato*) in concert with

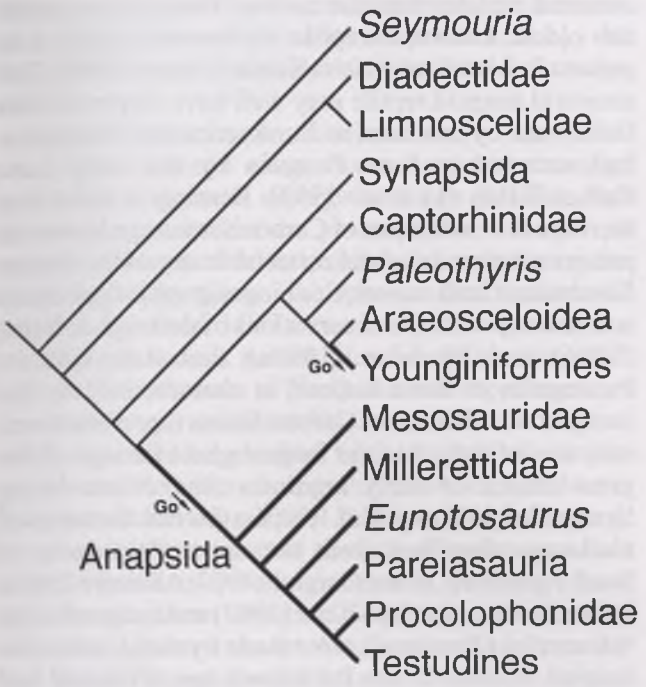


Figure 2. Most parsimonious resolution resulting from a PAUP analysis of a data matrix modified from Laurin & Reisz (1995). Thin branches indicate the taxon is present in Euramerican Pangaea, whereas thick branches signify a distribution in Gondwanan Pangaea. The arrows indicate dispersal events into Gondwana (**Go**) from Euramerica. A Gondwanan distribution is inferred to be ancestral for both Procolophonidae and Pareisauria based on phylogenies for these groups provided by Lee (1995, 1997). The palaeobiogeographical analysis here suggests that a Gondwanan distribution is ancestral for anapsids, but this tree does not include some Euramerican taxa seen in the succeeding figure.

recent phylogenetic work (Laurin & Reisz 1995; deBraga & Reisz 1996).

In a recent consideration of Palaeozoic tetrapod biogeography, Milner (1993) recognized a 'Mesosaurid Province' comprising the mesosaurs of Lower Permian South America and southern Africa. Milner's (1993) 'Mesosaurid Province' marks the earliest manifestation of endemism among anapsid reptiles ('parareptiles' of Gauthier *et al.* 1988). Following the systematic work of Ivakhnenko (1987), Milner (1993) regarded pareiasaurs and nyctiphruretids as having a cosmopolitan distribution in the Late Permian, and considered the contemporaneous lanthanosuchids and nycteroleterids as endemic groups of Euramerican Pangaea (although he viewed the latter two as anamniote taxa). Interestingly, Milner (1993) did not consider millerettids and *Eunotosaurus*, nor did he discuss the implications of their Gondwanan distributions for the idea of homogeneity among Late Permian amniote faunas.

Milner's (1993) biogeographic conclusions require some reconsideration in the wake of recent systematic work on anapsids. In contrast to Ivakhnenko's (1987) views, Lee (1995) regarded the Russian taxon *Nyctiphruretus ineptus* as the sole valid nyctiphruretid and identified the Gondwanan 'nyctiphruretids' (*Owenetta*, *Barasaurus*) of Ivakhnenko (1987) as basal procolophonoids. Nycteroleterids, comprising *Nycteroleter* and *Macroleter*, form a Russian clade, and thus represent, like the lanthanosuchids, a parareptilian group that was restricted to Euramerica (Lee 1995). More recently, Lee (1997) published a phylogeny for pareiasaurs in which the most basal members (*Bradysaurus*, *Embrithosaurus*) are Gondwanan taxa. Optimization of Gondwanan and Euramerican distributions of pareiasaurs onto Lee's phylogeny suggests strongly that pareiasaurs diversified initially in Gondwana and that northern Pangaea was colonised by more recently derived taxa on at least two separate occasions (Modesto & Rybczynski 2000). Other recent studies reveal the existence of a clade of early parareptiles, Acleistorhinidae, that was restricted to Early Permian North America (deBraga & Reisz 1996; Modesto 1999a). Collectively these revisions of

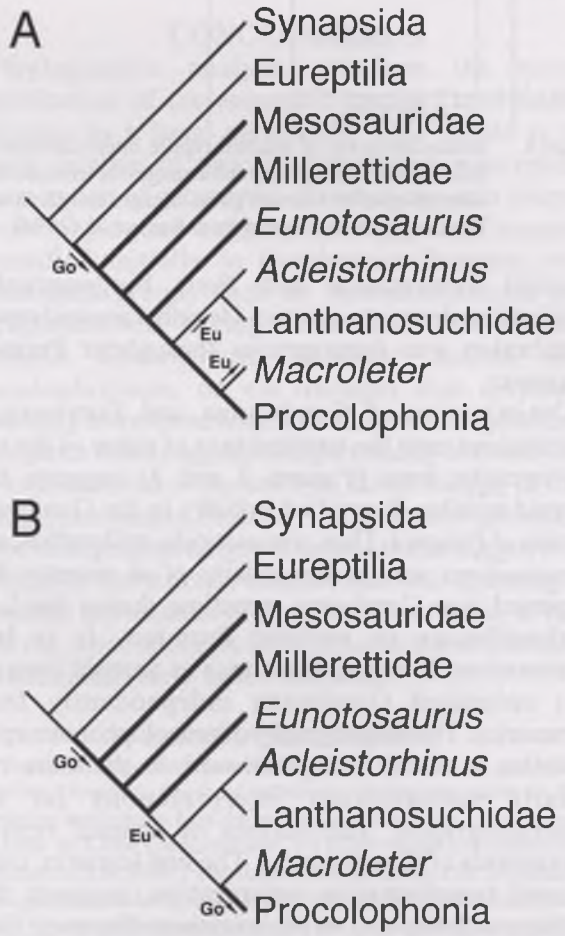


Figure 3. Most parsimonious resolution (MPR) resulting from a PAUP analysis of a data matrix modified from deBraga & Reisz (1996). Acleistorhinidae, Lanthanosuchidae and *Macroleter* are anapsid taxa in addition to those seen in the preceding figure. Procolophonia includes the terminal taxa Pareiasauria, Procolophonidae, and Testudines of the preceding figure. A, The MPR with distributions optimized using delayed transformation. B, The MPR optimized using accelerated transformation. As in the previous figure, thin and thick branches signify distributions in Euramerica and Gondwana, respectively. The arrows indicate dispersal events into Gondwana (**Go**) from Euramerica or into Euramerica (**Eu**) from Gondwana. The ancestral Gondwanan distribution inferred for Procolophonia is discussed in the text.

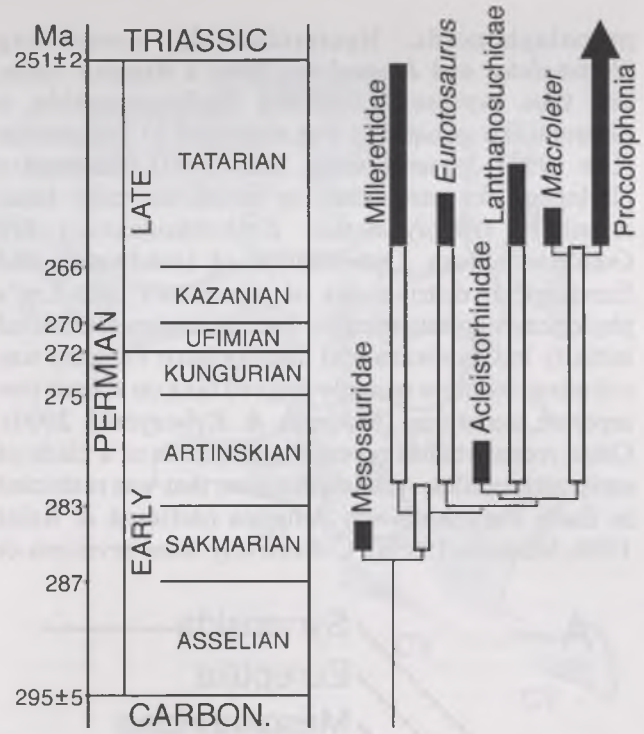


Figure 4. Stratocladogram of anapsid reptile interrelationships. Solid bars indicate stratigraphic ranges for terminal taxa, whereas open bars denote ghost lineages and ghost taxa. The time scale is adapted from Ross *et al.* (1994).

anapsid systematics and their biogeographic implications draw into question ideas that anapsid reptile distribution was homogenous throughout Permian Pangaea.

Optimization of Gondwanan and Euramerican distributions onto the terminal taxa of either of the two phylogenetic trees (Figures 2 and 3) suggests that anapsid reptiles diversified initially in the Gondwana portion of Pangaea. Thus, mesosaurids, millerettids, and *Eunotosaurus* are the descendants of an ancestor that dispersed into Gondwana sometime during the Late Carboniferous or earliest Permian. It is less parsimonious to regard these taxa as anapsid lineages that colonised Gondwana independently from Euramerica. The biogeography of procolophonomorphs, however, is not as straightforward, as there are two equally parsimonious interpretations for the palaeogeographic distributions of anapsid reptiles crownwards of *Eunotosaurus*. The first scenario, using delayed transformation optimization, suggests that lanthanosuchoids and nyctiphruretians dispersed from Gondwana to colonise Euramerica separately (Figure 3A); pareiasaurs and procolophonoids evolved in Gondwana because their recent common ancestor had arisen there. The second scenario, using accelerated transformation, suggests that the ancestral procolophonomorph dispersed from Gondwana into Euramerica, whereupon lanthanosuchoids, nyctiphruretians, and the ancestral procolophonian appeared, with the last then emigrating back into the former area from the latter, subsequently giving rise to procolophonoids and pareiasaurs (Figure 3B).

The primary dichotomy in reptilian evolution, the division into anapsid and eureptilian lineages, must have occurred no later than the earliest Westphalian, when the oldest known eureptile *Hylonomus lyelli* was present in what it now Nova Scotia (Carroll 1963). The ancestral anapsid reptile may well have dispersed into Gondwana by this time, as Euramerica and Gondwana had accreted to form Pangaea by the early Late Carboniferous (Li *et al.* 1993). Bearing in mind that there are few sediments of Carboniferous age known to preserve tetrapod skeletal material in any of the former Gondwanan land masses, this biogeographic hypothesis is consonant with the observations of deBraga & Reisz (1996) and Modesto (1999a) that Anapsida (= Parareptilia of those authors) is characterized by the conspicuous absence of Carboniferous representatives, and, accordingly, has the longest ghost lineage of the great clades of early amniotes (the others being Synapsida and Eureptilia). It is possible that the tetrapod trackways described from the upper Palaeozoic of South America (Cei and Gargiulo 1977; Aramayo 1993), reconsidered in part by Milner (1993) and assigned to his 'Mesosaurid Province', were made by early, unknown anapsid reptiles. Given the knowledge of manual and pedal morphology of mesosaurs that has been drawn from several excellent specimens (Modesto 1996, 1999b), it is unlikely that any of the known South American trackways represent terrestrial excursions of those aquatic reptiles.

Within Anapsida itself, the stratigraphic ranges of the constituent members are suggestive of an extensive, unrecorded tenancy in Gondwana for anapsid reptiles (Figure 4). Mesosaurs, restricted to the Sakmarian of southern Africa and eastern South America (Oelofsen & Araújo 1987), are the oldest known anapsid reptiles. The next oldest anapsids in Gondwana are *Eunotosaurus*, millerettids, pareiasaurs, and procolophonoids (Gow & Rubidge 1997), which appear in the *Tapinocephalus* Assemblage Zone of the Beaufort Group in South Africa (Smith & Keyser 1995). This terrestrial vertebrate biozone is either latest Kazanian or earliest Tatarian in age, so that there is a substantial temporal gap between the time that mesosaurs disappear and when parareptiles make their first appearance in Gondwana. It is in this interval during the Early Permian that the acleistorhinids are present in western Euramerica. Using Acleistorhinidae as the first appearance datum for Parareptilia, minimum divergence times suggest that at least four lineages of Late Permian parareptiles can trace their origins as far back as the Artinskian (Figure 4). Accordingly, the presence of two endemic Gondwanan lineages, Millerettidae and *Eunotosaurus*, can be extended well into the Early Permian. The extensive ghost lineages of these two taxa, together with information from the biogeographical analysis, suggest that millerettids and *Eunotosaurus* must have been present in Gondwana prior to Beaufort times, yet we have no record of these reptiles until well into the *Tapinocephalus* Assemblage Zone. Thus, the phylogeny and the biostratigraphy of anapsid reptiles provide support for the hypothesis that a preservational bias acted on terrestrial vertebrates in Early Permian and earliest Late Permian Gondwana.

This preservational bias was not alleviated until the onset of continental sedimentation represented by the Beaufort Group in South Africa (Modesto & Rubidge 2000).

Identification of *Eunotosaurus* as the procolophonomorph sister taxon suggests strongly, again using minimum divergence times (MDTs), that there were at least four parareptilian lineages in existence from the late Artinskian onwards during the Early Permian. Given the known distributions of parareptilian taxa, MDTs can be used to predict the presence of various parareptiles for given strata and regions. The absence of Early Permian specimens of *Eunotosaurus*, millerettids and other terrestrial vertebrates can be ascribed to the dearth of suitable continental deposits during this time in Gondwana (Modesto & Rubidge 2000). It is less straightforward, however, to account for the absence of lanthanosuchids in uppermost Lower Permian deposits. In Europe there appears to have been a hiatus in continental sedimentation between the Asselian (earliest Permian) and the Ufimian (earliest Late Permian), which accounts for the absence of lanthanosuchids in the Lower Permian of western Russia. Their absence in Lower Permian North American deposits might be taphonomic, or it may reflect a true restriction of lanthanosuchids to Eastern Euramerica. *Lanthanosuchus watsoni*, the first described species, has long been regarded as an aquatic form (*e.g.*, Watson 1954), although this assessment was based solely on its remarkably temnospondyl-like skull. If lanthanosuchids did indeed inhabit the freshwater systems of Permian Eastern Euramerica, this habitat preference could explain why there is no evidence of them in Lower Permian rocks of North America, especially in light of Milner's (1993) observation that aquatic Permian tetrapods appear to have been strongly characterized by endemism. Following his description of two additional taxa, Ivakhnenko (1980) disputed the idea that lanthanosuchids were aquatic and proposed instead that they were Permian analogues of species of the extant genus *Phrynosoma*, the horned lizards of North America. If that idea is correct, then it is possible that future collecting efforts in uppermost Lower Permian deposits of North America will yield lanthanosuchids.

Accounting for the absence of nyctiphruretians and procolophonians in North American deposits of Early Permian age is complicated by the ambiguous nature of the biogeographic scenarios that can be drawn from the available phylogeny (Figure 4). If representatives of either procolophonomorph group were present in Euramerica during the late Early Permian, either their remains have gone unrecognised or they remain uncollected. On the other hand, Early Permian nyctiphruretians and procolophonians may have been upland forms, and because Lower Permian localities preserving such tetrapods appear to be rare (Olson & Vaughn 1970; deBraga & Reisz 1996; Modesto 1999a), it is possible that these two taxa have not been preserved amongst known late Early Permian faunas of Euramerica. Further work on vertebrates from the Chickasha, San Angelo and Flower Pot formations of south-central North America, strata regarded as lowermost Upper Permian by previous workers but better regarded as uppermost Lower Permian (Modesto *et al.*, unpublished), may provide important clues for establishing the geographic origins of nyctiphruretian and procolophonian parareptiles.

CONCLUSIONS

Phylogenetic analyses confirm the recent identification of the enigmatic reptile *Eunotosaurus africanus* as a basal parareptile. This reptile is the closest relative of procolophonomorph parareptiles. Optimization of geographic distributions onto anapsid reptile phylogeny suggests strongly that anapsids diversified initially in Gondwanan Pangaea, with descendant groups such as lanthanosuchoids and nyctiphruretians having descended from either a common Euramerican ancestor shared with procolophonians, or via lineages that dispersed separately from Gondwana into Euramerica. Minimum divergence times suggest a longer tenancy in Gondwana for anapsids than is implied by a direct reading of their stratigraphic ranges. Similarly, phylogenetic calibration of the stratigraphic ranges of anapsids also supports the hypothesis that a preservational bias was operating on terrestrial vertebrates in Permian Gondwana, at least until the onset of terrestrial sedimentation at the end of the Kazanian (early Late Permian).

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APPENDIX

Eunotosaurus africanus was coded for the data matrix of Laurin & Reisz (1995) as follows, with uncertain character states separated by a virgule ('/'), from 1 to 124: ?1001 ????? 01111 1101/2? ?1110 12100 20210 2012? ???? 0 1???1 000?1/2 1???? ????? 011?? ?0??? 0??0? 1???? 1011? ?00?? 11000 1100? 0010? 00002 00100 0000. Furthermore, two characters in the data matrix of Laurin & Reisz (1995) were modified, following the reasons outlined by Modesto (1999b): captorhinids were recoded as '0' for character 51, and character 54 was 'deleted' (by recoding all taxa for that character as '?' in MacClade). New information permitted the rescoring of two characters for Mesosauridae (Modesto 1999b): mesosaurs were recoded as '1' and '2' for characters 17 and 55, respectively. The two additional characters of Modesto (1999b, app. 1) were added to the data matrix of Laurin & Reisz (1995), with *Eunotosaurus* coded as '1' for character 125 and '?' for character 126.

Eunotosaurus africanus was coded for the data matrix of deBraga & Reisz (1995) as follows, using the organisation of the above paragraph: ???0? ?00?? 00000 ?010? 01101 ????0 ????? 00010 011?? 1???? 00000 1?101. Furthermore, character 6 of deBraga & Reisz (1996), concerning the angle of the frontal-nasal suture, was 'deleted' (again, by recoding all states as '?' in MacClade) because it cannot be subdivided into discrete character states (Modesto 1999a).

The two additional characters used in Modesto (1999a) were added to the data matrix of deBraga & Reisz (1996). The first character, which concerns the posterior margin of the skull roof (embayed bilaterally, 0; with a single, median embayment, 1; straight, 2), is recoded from Modesto (1999b), and should appear as follows when added as character 61 to the data matrix of deBraga & Reisz (1996): 0-1-1-1-1-1-1/2-0-1. The second, concerning the nature of the epipophysis (present, 0; absent, 1), is recoded from Lee (1995), and should appear as follows when added as character 62 to the data matrix of deBraga & Reisz (1996): 0-1-1-?-?-?-1-0-?. *Eunotosaurus* is represented by the last character state in these two sets of codings.

Palaeont. afr., **36**, 21-23 (2000)

A NEW PROCOLOPHONID (PARAREPTILIA) FROM THE *LYSTROSAURUS* ASSEMBLAGE ZONE, BEAUFORT GROUP, SOUTH AFRICA.

by

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ABSTRACT

This paper describes the skull of a new genus and species of procolophonid from the *Lystrosaurus* Assemblage Zone. It is strikingly different from its contemporaries, *Procolophon trigoniceps* and *Owenetta rubidgei*, but has a mosaic of characters of each.

KEYWORDS: procolophonid, Triassic, parareptile

INTRODUCTION

The fauna of the Beaufort Group is well documented, yet new, and increasingly, rare forms continue to crop up to stimulate further field work. The present specimen is a new procolophonid that displays a mosaic of the characters seen in other procolophonids and whose autapomorphies are restricted to the dentition and palate. It is possible that a specimen previously referred to *Procolophon trigoniceps* (Gow 1977) may belong to the same or a similar taxon as it is also small and has a large number of marginal teeth, though it is poorly preserved.

MATERIAL

The specimen, number GHG 228 in the collections of the Council for Geosciences, Pretoria, was collected by Dr Gideon Groenewald on the farm Brakfontein 333, in the Katberg Formation, *Lystrosaurus* Assemblage Zone. It is a small skull, 30mm long, lacking the braincase but little distorted, consisting of well preserved white bone in a hard matrix which consists of large rounded quartzitic grains in a fine green cement, this when it breaks sometimes follows the outlines of the grainy inclusions and as these are large relative to the bony structures 3-dimensional preparation is hazardous.

SYSTEMATIC PALAEONTOLOGY

Reptilia Laurenti, 1768

Parareptilia Olson, 1947

Family Procolophonidae Lydekker, 1890

Genus and species. *Coletta seca*, gen. et sp. nov.

Etymology: The genus name is a combination derived from *Procolophon* and *Owenetta* and coinsidently also the name of a friend, Colette. The species name is Latin for various short stabbing weapons, and refers to the relatively enormous vomerine fangs which are the only teeth on the palate.

Diagnosis: Small procolophonid (skull length 30 mm), snout more pointed than in *Owenetta*, nasals and frontals meet between the prefrontals, jugal slender and without lateral flange, postfrontals small, palatines and pterygoids lack teeth, vomers large and each bears four relatively enormous pointed cylindrical fangs. Marginal dentition relatively larger than in *Owenetta* and smaller than in *Procolophon*, teeth little differentiated decreasing in length very slightly from front to back. Teeth conical, pointed, and not hooked as is the case in *Owenetta.* Tooth count 16 over 15 - more than in *Procolophon trigoniceps* and fewer than in *Owenetta rubidgei*.

Laurin and Reisz (1995) list seven cranial autapomorphies of Procolophonidae; these are, using their numbers, 1. Narial shelf present; this is a curious description of the prominent depression behind the external naris involving both nasal and maxilla: it is present in this specimen. 8. Prefrontal medial process present; this character lies so deep within the orbit that to expose it would only be justified if the diagnosis was in doubt. 11. Anterior process of jugal extending to anterior orbital rim: present in this specimen. 33. Ventral margin of postorbital region of skull emarginated: present in this specimen. 37. Orbit enlarged posteriorly: present. 57. Paroccipital process sutured to supratemporal: cannot be determined. 61. Unossified region between basioccipital and basisphenoid: present, and in fact the basioccipital has been lost, as often happens in *Procolophon* as well.

Holotype: GHG 228, Skull and lower jaw. In the collections of the Council for Geosciences, Preotoria.

Geological Horison: *Lystrosaurus* Assemblage Zone, Katberg Formation, Beaufort Group.

DESCRIPTION (Figure 1)

The premaxillae are held between the nasals dorsally and have a small area of contact with the maxillae laterally. The region where they meet the vomers is still encased in matrix. Each premaxilla bears four teeth. A septomaxilla is present. The maxillae rise steeply behind the nares (but not to the same marked extent as in *Owenetta)*, where they are dished or depressed as is

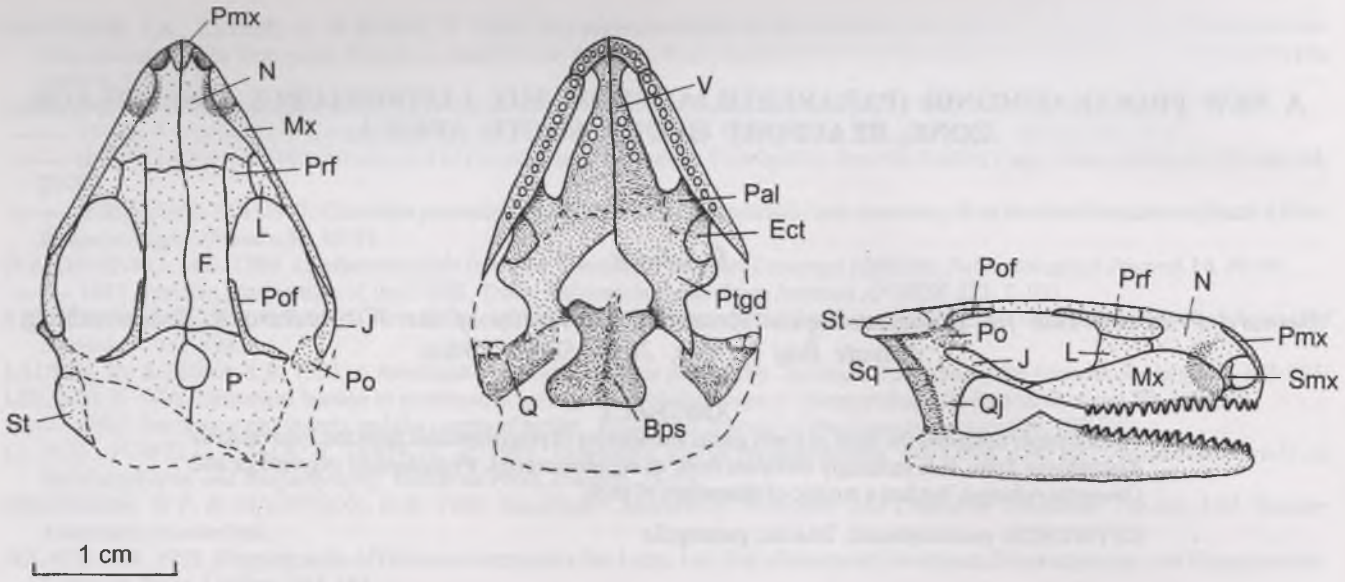


Figure 1. *Colletta seca* gen. et sp. nov. Skull in dorsal, ventral and left lateral views.

typical of procolophonids. They extend back half way along the ventral margin of the orbits. They contact the nasals and lacrimals dorsally and are braced internally by the palatines, ectopterygoids, and jugal. Each maxilla bears 12 pointed, conical acrodont teeth, which decrease very slightly in crown height from front to back. The nasals have a broad contact with the frontals. Lacrimal prefrontal and frontal are typically procolophonid. The postfrontal is very narrow in dorsal aspect as it is in *Procolophon*. In *Owenetta* the postfrontal makes an extensive contribution to the skull table. The parietals are damaged, but enclose a large, anteriorly situated pineal opening. The very slender jugal extensively overlaps the maxilla, extending to the front of the orbit (only seen in dorsal view). Posteriorly the jugal sutures with postorbital, quadratojugal and squamosal (this region is distorted on the left side and damaged on the right). The supratemporals are mostly lost, but were clearly large. Squamosal and quadratojugal are exposed laterally as in *Owenetta*. On the palatal surface the vomers are broad as in *Owenetta* and each bear a longitudinal row of four robust conical fangs, which are the only palatal teeth. The pterygoids surround a large vacuity and have weakly developed flanges. The basiparasphenoid is almost as broad as long, and the basal articulations were freely movable. Most of the occiput is badly damaged or missing as is the braincase. One nearly complete lower jaw is present but its sutures are indistinct.

DISCUSSION

This new procolophonid skull has a suite of characters that are plesiomorphic for procolophonids, but has a uniquely derived palate. The configuration of the bones of the skull roof is primitive as in *Procolophon* (Carroll and Lindsay 1985). *Owenetta* is peculiar in that the prefrontals of some specimens meet in the midline (Reisz and Laurin 1991). The jugal is even more slender than in *Owenetta* whereas in *Procolophon* it is uniquely derived.

In 1977 I described and figured a small partial skull as a juvenile *Procolophon trigoniceps* (Gow 1977 Text Figure 6). That specimen, BP/1/1187, is about the same size, and also has an unmodified jugal and the same number of teeth, but the teeth have labiolingually broadened crowns with raised points at each side. The possibility thus exists that yet another taxon of small procolophonid is present in the *Lystrosaurus* Assemblage Zone.

ABBREVIATIONS

BPS	basiparasphenoid
Ect	ectopterygoid
F	frontal
J	jugal
Mx	maxilla
N	nasal
P	parietal
Pal	palatine
Pmx	premaxilla
Po	postorbital
Pof	postfrontal
Prf	prefrontal
Ptgd	pterygoid
Q	quadrate
Qj	quadratojugal
Smx	septomaxilla
Sq	squamosal
St	supratemporal

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Palaeont. afr., **36**, 25-41 (2000)

SEDIMENTOLOGY AND TAPHONOMY OF LATE PERMIAN VERTEBRATE FOSSIL LOCALITIES IN SOUTHWESTERN MADAGASCAR.

by

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ABSTRACT

This is the first report of a project that tests the accuracy of the currently accepted palaeoposition of southern Madagascar during the late Permian in juxtaposition to the coast of Tanzania. This is done by comparing the sediments and fossils that accumulated in a series of rift valleys, each around 25 km wide, that formed in this part of Gondwana at the beginning of pull-apart some 250 million years ago. The study reported here on the Madagascan side of the rift system will be followed by a similar study of the Tanzanian portion.

Field data on the sedimentology and vertebrate taphonomy of three separate fossil localities in the Late Permian, Lower Sakamena Formation of southwestern Madagascar are used to reconstruct the subenvironments of the Sakamena axial rift valley lake.

1. *Ranohira*: dominated by microlaminated mudrocks with three horizons of fossil bearing micrite nodules. The fossils are mostly complete articulated skeletons of an ?aquatic procolophonid reptile, *Barasaurus*, which inhabited the offshore epilimnion of a deep, thermally-stratified closed lake.
2. *Zavoloa River*: alternating cross-bedded conglomeratic sandstone and laminated siltstone are interpreted as braided delta deposits entering the linear margin of the lake from the passive side of the half graben. These deposits contain some fully articulated skeletons and numerous winnowed bonebeds of a supposedly semi-aquatic reptile, *Claudiosaurus*, that may be related to sauropterygians.
3. *Mount Eliva*: is dominated by the younginiform reptile, *Hovasaurus*, which occurs as articulated skeletons inside micritic siltstone nodules in the mudrocks of a sub-lacustrine deltaic sequence. Pebble masses in the abdomen of *Hovasaurus* are interpreted as ballast to facilitate swimming. The taphonomic style and sedimentary environment of the host strata confirm this interpretation.

Thermal shock from periodic overturn and poisoning from algal blooms are the most likely causes of mass mortality among the aquatic fauna. Hydrogen sulphide released from anaerobic bacterial decay of soft tissue and girdle cartilage formed reduction halos around the newly buried reptile carcasses. At least 3 "micritization episodes" led to the precipitation of calcium cabonate in the reduction halos forming nodules around the vertebrate fossils. They are interpreted as periods of extended lowstand when thermal stratification could not be maintained and oxygenated waters came into contact with previously anoxic sediments. If such lowstand events were climatically controlled, they may be useful timelines to accurately correlate strata within and between these ancient rift valley lakes in both Madagascar and Tanzania.

KEYWORDS: Madagascar, *Barasaurus, Claudiosaurus, Hovasaurus*.

INTRODUCTION

The concept of continental drift was first proposed by the American F.B.Taylor in 1910 and widely publicised by the German Alfred Wegener in 1915 (Holmes 1965). Until that time the theory was based mainly on the on the congruence of opposing shorelines of the Atlantic. Wegener also demonstrated contiguous mountain ranges, ancient glaciated pavements and palaeobiogeographic similarities and in his opinion the eastern coast of the Americas and the western coast of Africa and Europe matched "as closely as the lines of a torn drawing would correspond if the pieces were placed in juxtaposition". Later, Du Toit (1937) documented the similarity of sediments, fossils, climates and earth movements on each side of the Atlantic. His corroborative evidence was enough to convince the scientific community that the super-continent of Pangaea had formed some 250 million years ago and had slowly fragmented into the present day continental configuration. There followed much research, mainly by geophysicists, into tracking the movements of continental plates through geological time and by the 1960's, plate tectonics was widely accepted as the driving mechanism of continental drift.

The palaeoposition of Madagascar in relation to the African continent has always been controversial. The major conflict was between palaeomagnetic data, which fitted the north coast of Madagascar alongside the coast of Somalia (Smith 1976), and the geological data which placed the northern margin of Madagascar against Mozambique (Tarling and Kent 1971). Subsequent magnetometer surveys of the seabed have identified a spreading ridge which mirrors the outline of the north coast of Madagascar halfway between

Madagascar and the coast of Somalia (Rabinowitz. *et al* 1983; Coffin 1987; De Wit *et al.*1998). Thus the weight of evidence is firmly in favour of the northerly palaeoposition and the purpose of this study is to report palaeontological and sedimentological details that corroborate this fit. Rayner (1992) began this process by comparing plant fossil assemblages in the Sakoa Formation with those of the Ecca Group of the South African Karoo Basin. This study aims at more precise resolution based on fossil skeletons of aquatic reptiles within the uppermost siltstones of the Lower Sakamena Formation (Late Permian, Tatarian) of southwestern Madagascar. Similar reptile fossils have been recovered in equivalent-aged beds in southern Tanzania and it is the ultimate aim of this project to confirm that these strata were once in continuity.

The Sakamena vertebrate fossils were first discovered in 1906, by Captain Colcanap, a scientist employed by the French army. He first encountered vertebrate-bearing nodules in the lower reaches of the Sakamena River, a northerly flowing tributary of the Onilahy River in southwestern Madagascar. Later he amassed a large collection from a conical hill called Mount Eliva (Figure 1) at the head of the Sakamena valley, some 50 km further south. The discovery and preliminary identification of these fossils was published by Boule in 1908 but it was not until 1925, when Piveteau found more localities in the vicinity of Benenitra and Ranohira, that these occurrences were properly documented (Piveteau 1926). A collection of some 300 specimens is still housed in the Museum National d'Histoire Naturelle in Paris. Since then sporadic but important prospecting, mainly by French survey and exploration geologists, added a few more localities in the area between Ranohira and Benenitra (Tortochaux 1949; Piveteau 1955; Cliquet 1957; and Besairie 1972).

The most common tetrapod fossils in the Paris museum's Sakamena collection are of *Hovasaurus*. These are medium-sized (up to 900mm long, estimated 10kg mass (Currie 1981)) younginiform eosuchian reptiles with long slender digits of variable length, pachyostotic ribs (De Buffrénil and Mazin 1989), strong caudal epiphyses and abdominal quartz pebble masses which are together interpreted as adaptations for an aquatic lifestyle (Currie 1981; Carroll 1981). Another less common younginiform eosuchian, *Thadeosaurus*, is very similar in overall body plan but its limb proportions are considered to be terrestrial (Carroll 1981; Currie and Carroll 1984). It generally, but not always, lacks abdominal stone masses (Carroll 1981). Other minor, but significant elements of the fossil fauna are the supposedly semi-aquatic sauropterygian reptile *Claudiosaurus* (Carroll 1981), the rare gliding diapsid *Coelurosauravus elivensis* (Piveteau 1926), small procolophonid reptiles of the genus *Barasaurus* (Piveteau 1955), fragments of rhinesuchid temnospondyls and one or two palaeoniscoid actinopterygians (*Atherstonia*). Some therapsid fossils of terrestrial origin have been recovered from the Lower Sakamena, including a single dentary of an unknown theriodont (Piveteau 1955), a few dicynodont vertebrae and tusks, and a single skull of *Oudenodon* (Mazin and King 1991).

Piveteau (1955) initially established biostratigraphic correlation with the main Karoo Basin by linking

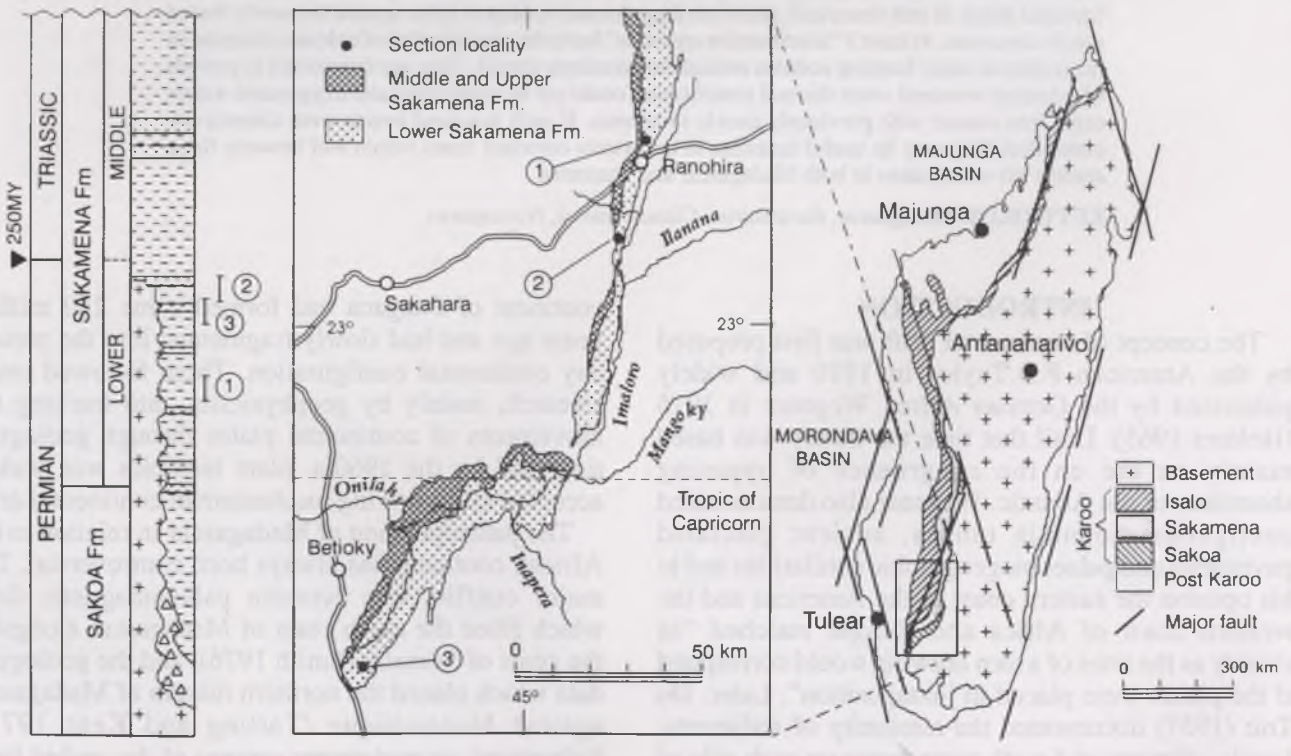


Figure 1 Stratigraphic and geographic location of the 3 Sakamena Formation fossil localities visited in this study. 1=Zavoloa River, 2=Ranohira Cemetery, 3=Mount Eliva.

Barasaurus with *Owenetta* from the former *Cistecephalus* Zone (now *Cistecephalus* Assemblage Zone (Smith and Keyser 1995)). More recently, the Malagasy dicynodont *Oudenodon sakamenensis* has been correlated with the same genus in both *Cistecephalus* and overlying *Dicynodon* Assemblage Zones which are the uppermost Permian (LateTatarian) strata of the Karoo Supergroup (Mazin and King 1991). Currie (1981) compared the Malagasy fauna with the Russian Dzulfian standard stage of the Upper Permian, and recently the similarity of the Sakamena procolophonids with the Russian *Nyctiphruretus* (Arduini 1993) from Russian Zone 111 has reinforced this correlation, giving an absolute age estimate for these strata of 255+/-2Ma.

Having reviewed the Paris Museum collections, Tortochaux's field notes and Germain's private collection, Currie (1981) recognised 4 distinct fossil associations in the Lower Sakamena Formation: 1. Marine invertebrates with no identifiable reptiles; 2. Terrestrial reptiles (*Thadeosaurus, Daedalosaurus, Coelurosauravus*) dominant with the actinopterygian *Atherstonia* well represented; 3. Aquatic reptile *Hovasaurus* abundant, with terrestrial *Acerosodontosaurus* and *Atherstonia* present; 4. Partly aquatic *Claudiosaurus* strongly dominant with terrestrial *Acerodontosaurus*, the glider *Daedelosaurus* and therapsids present. These associations were, however, based on Piveteau's locality data and Currie was unable to accurately confirm their distribution or stratigraphic relationships. Nevertheless, he regarded them as contemporaneous and possibly representing different depositional environments of the fluvio-lacustrine plains.

A fifth fossil association dominated by the procolophonid reptile *Barasaurus* was identified during the course of this investigation in the Ranohira district.

This is a report on the first phase of a field-based study which is modelled on that of Alex Du Toit (1937), that looks at how closely the sediments and fossils corroborate the structurally and geophysically defined palaeoposition of Madagascar, relative to the African continent, during the latest Permian. It also adds to the pioneer work of Piveteau (1955) and Currie (1981) in providing more details of the palaeo-environmental conditions that existed in this part of central Gondwana at that time. The present study focuses on fossiliferous strata of the Sakamena Group in the southern Morondava Basin of southwestern Madagascar. Future research will concentrate on the contemporaneous and probably laterally continuous strata in the Tanga Basin of southeastern Tanzania.

GEOLOGICAL SETTING

The stratigraphic successions of Karoo-aged basins of western Madagascar are directly related to the tectonics of progressive rifting and subsequent detachment of eastern Gondwana (Figure1). During the Late Carboniferous to Late Permian, extensional block faulting brought about by the closure of the Cape Fold Belt to the south resulted in horst and graben formation along a NS trending belt on the eastern side of southern Gondwana (Jeans and Meerbeke 1995). Two linear grabens formed the Sakamena Basin (Cliquet 1957) which rapidly filled with thick glacial (150m), fluvio-deltaic (700m) and lacustrine (100m) sequences of the synrift Sakoa and lower Sakamena formations. The fluvio-lacustrine sediments of the Lower Sakamena Formation accumulated in the incipient rift as extensional block faulting tilted the basement down to the west (Fabian 1996; Wescott and Diggens 1998). It is these latest Permian reptile-bearing fluvio-lacustrine facies of the Lower Sakamena Formation that are under investigation here. Tectonic activity migrated from east to west and deposition began in the south somewhat earlier than in the north. In the Early Triassic, a period of tectonic quiescence allowed a significant flooding of the Sakamena Basin and deposition of the first basinwide marine sediments, the Middle Sakamena Formation. Renewed block faulting in the basin ensured that terrestrial conditions continued through to the Early Jurassic with the accumulation of the arenaceous Upper Sakamena and Isalo Formations. During the Early Jurassic the previous NE-SW and N-S Karoo structural lineaments were re-activated by the onset of rifting to the north in the Somali Basin. Initially forming restricted lacustrine basins, the rift widened and deepened as eastern Gondwana began to separate from western Gondwana, resulting in a second basinwide marine incursion represented by the Middle Jurassic Dogger limestones. Post-rift subsidence on the passive margin promoted the formation of the Cretaceous Majunga and Morondova Basins.

Thus the overall palaeotopography during deposition of the Lower Sakamena strata in southern Gondwana was of two narrow (+/- 25km wide) fault-bounded grabens trending roughly N-S and separated by an upland interfluve (Fabian 1996). The interfluve continued to separate the basins until the Early Triassic when it was overtopped by the alluvial fan deposits of the basal Isalo Group. To the south the rift valleys were closed by alluvial fans giving way to axial river deltas sourced in the northwardly migrating and rising Cape Fold Mountains (Wescott and Diggens 1998). To the north they opened to a shallow epicontinental sea, as is evidenced by the regional distribution of several marine incursions and two major flooding episodes. Landscapes on the graben floor between these two end 'members' were mainly lowland fluvio-lacustrine, becoming more estuarine northwards and more fluvial southwards (Figure 2). By the Late Permian, the Sakamena Basin was situated at approximately 50° S (Smith, Hurley and Briden 1981) so that climatic conditions in these intra continental rift valleys would have been relatively warm and humid with highly seasonal rainfall, possibly monsoonal (Parrish, Parrish and Ziegler 1986).

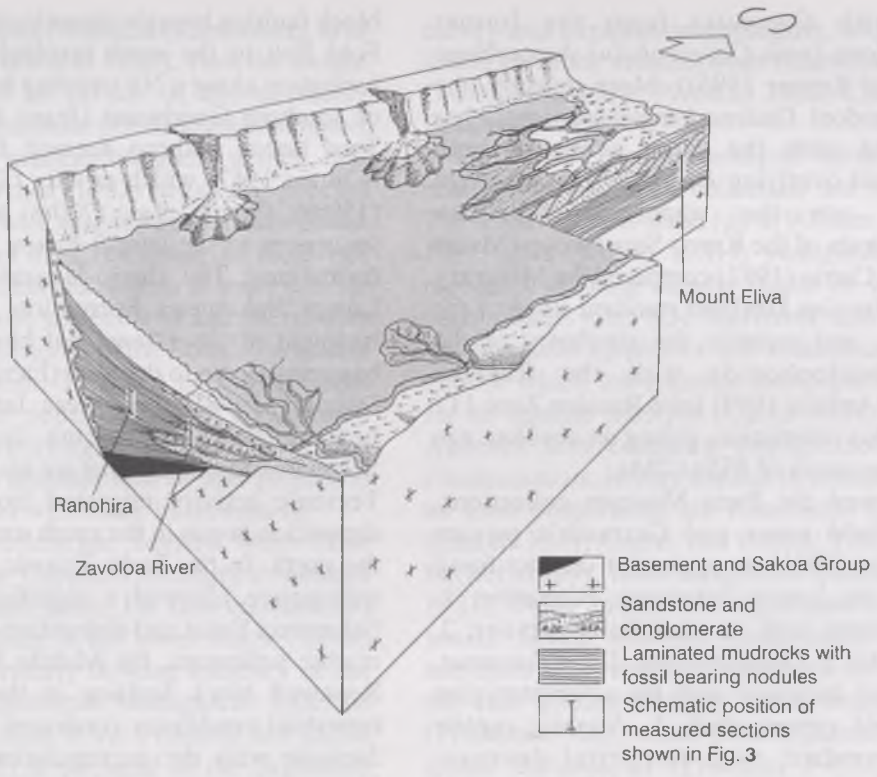


Figure 2. Sedimentary environments of the Sakamena rift valley lake during the Latest Permian, showing interpreted sub-environments of the 3 fossil localities studied.

SEDIMENTOLOGY AND TAPHONOMY OF SAKAMENA FOSSIL LOCALITIES

Two field visits of 3 weeks each were made to the Ranohira, Leoposa and Mt Eliva localities (see Figure 1) in 1994 and 1996. These trips were made possible within a collaborative research project, the 'Gondwana Project', involving research geologists and students from Rand Afrikaans University, University of Cape Town and University of Antananarivo.

At each locality care was taken to locate *in situ* nodules and accurately plot their occurrence on a sedimentological log of the outcrop, which was measured with a graduated staff to an accuracy of 5cm. Each fossil-bearing nodule was split and taphonomically assessed on site, recording the taxon, degree of disarticulation, orientation and attitude of the skeleton, type of bone mineralization and associated plant material. A total of 48 specimens have been accessioned by the South African Museum (SAMPK8263-8297 & 8569-8581) and an equivalent number reside in the palaeontology store of the University of Antananarivo.

Findings indicate that the fossil-rich strata of the Lower Sakamena accumulated in both nearshore and offshore facies of linear rift-valley lakes (Figure 2). Both facies were episodically affected by floodwater discharge, creating turbulent bottom currents which transported coarse-grained sand and gravel into an otherwise mud-dominated environment. Each facies contains a distinctive faunal and taphonomic signature that has significance for palaeoecological interpretations.

Ranohira Cemetery [S22°32'51.4" E45°25'25.2"]

Sedimentology

This *Barasaurus*-rich locality lies some 500m north of the edge of the village of Ranohira in southwestern Madagascar (Figure 1). The outcrops are formed by the incision of the Menamety River and its tributaries into the virtually flat-lying uppermost Lower Sakamena strata, exposing a maximum stratigraphic thickness of approximately 25m. (Figure 3). The succession is composed of drab greenish-grey (Munsell colour code 5Y4/2) siltstone with minor interbedded lenses of horizontally laminated fine-grained sandstone. Towards the top of the outcrop the sandstone beds become coarser textured, thicker and more laterally extensive with conglomeratic lags at the base and structured throughout with trough cross-bedding. It is onto this sandstone cliff that the villagers have constructed numerous white painted tombs from baked clay.

The siltstones at the base of the outcrop are microlaminated with 3-5mm thick lighter coloured bands separated by much thinner, <1mm-thick dark grey (5Y3/1) intermittent laminae. The lighter laminae are clean siltstone, the dark, paper-thin laminae are highly compacted claystone. Higher up in the section the siltstone is more evenly laminated and contains minor flaggy-weathering tabular sandstone bodies, most of which have sharp basal contacts (Figure 3). The upper contact of the sandstone is invariably gradational with fissile weathering horizontally laminated siltstone. No evidence of bioturbation could be found in or on the mudrock laminae or within the tabular

sandstones which might suggest hostile benthic conditions. The question of whether this lack of bioturbation is due to anoxia or a low carbon content of the bottom sediments is discussed later.

The mudrock interval between these thin tabular sandstone sheets contains three "horizons" of light-grey coloured calcareous nodules. The nodules occur as discrete, sharply contacted, smooth-surfaced, biconvex and commonly elongate bodies which roughly delimit the shape of the skeleton around which they have formed (Figure 4). The outer surface of the nodules displays concentric colour banding reflecting the original light/dark laminae of the host siltstone, demonstrating that the nodules are formed by cementing the original sediment rather than displacing it (Figure 4). Not all the *Barasaurus* skeletons are permineralized with nodules, and in many cases the skulls and tail are preserved as highly compressed weathered bones on the bedding plane outside the nodule (Arduini 1993). The sedimentological interpretation of the formation of the *Barasaurus*-bearing nodule horizons must account for a death event followed by a period of intermittant suspension/ traction current sedimentation sufficient to bury the carcass before it could be destroyed. Finally, a change in porewater chemistry around the decaying carcasses

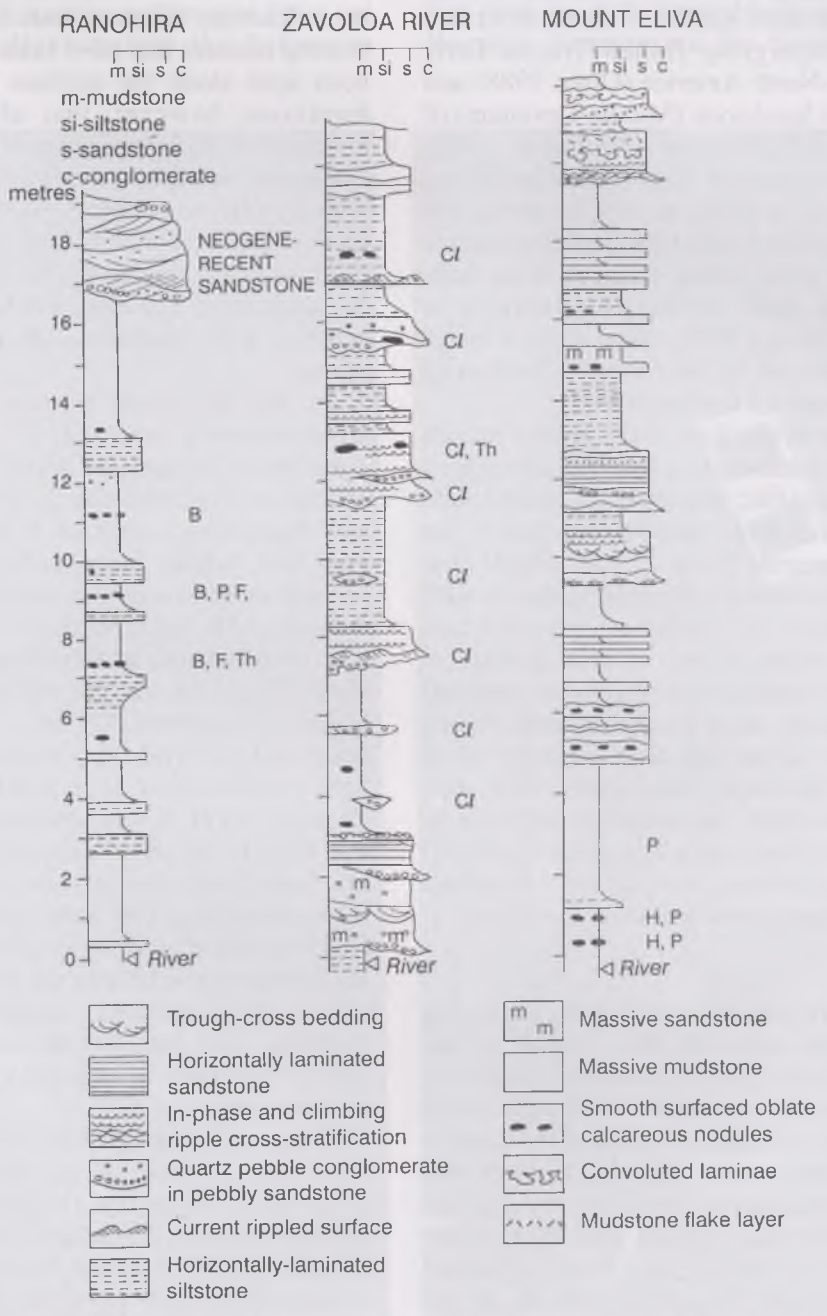


Figure 3. Lithology, sedimentology and fossils of 3 vertebrate fossil localities in the upper Lower Sakamena Formation of southwestern Madagascar. Legend to fossils B=*Barasaurus*, Cl=*Claudiosaurus*, Th=Therapsid, F=Actinopterygian , P=Glossopterid flora, H=*Hovasaurus*.

caused the localised precipitation of micrite. These nodule-forming processes and their controls are discussed later.

Above the three nodular intervals, the mudrocks become dominated by light greenish-grey and fissile-weathering claystone with no nodules or fossils. The upper 5m of the exposure at Ranohira comprises a Neogene crust of a single 2m-thick conglomeratic channel sandstone body overlain by smaller sand-filled scour channels (Figure 3). The base of the main channel is eroded into the fissile Sakamena mudrocks with wide, shallow scours filled with planar cross-bedded poorly sorted matrix-supported conglomerate.

The lithologies and sedimentary sequences of the Sakamena Formation at Ranohira are interpreted as distal lacustrine turbidites similar to those described from the Newark Supergroup (MiddleTriassic-Early Jurassic) of eastern North America (Olsen 1988) and the Middle Old Red Sandstone (Middle Devonian) of northern England and Scotland (Donovan 1980; Trewin 1986). In such narrow fault-controlled basins, subsidence and uplift episodes as well as rising and falling lake water levels all affect the fluvial/lacustrine transition, creating rapid facies changes from fully terrestrial floodplain facies to marginal lacustine to offshore lacustrine (Cojan 1993). Similar rapid facies changes are evidenced in the Lower Sakamena between the three sections studied here.

Lake Turkana lies in the floor of the eastern branch of the African Rift System and is of similar dimensions and in comparable tectonic and climatic settings such that it may serve as suitable modern analogue to the Late Permian Sakamena basin. It has similar low organic content of profundal laminated mudrocks with minimal bioturbation and carbonate precipitation (Cohen 1989). The water column of Lake Turkana is unstratified, but it is subject to storm influxes, seasonal water level fluctuations, algal blooms in summer and seismic disturbance during volcanic eruptions. It is possible that the Sakamena lake waters were also unstratified and therefore permanently oxygenated. However the microlamination and preferential micritization of articulated vertebrates (described below) strongly indicate anoxic benthic conditions.

Taphonomy

In situ fossil-bearing nodules tend to be somewhat more convex on the underside than topside of the skeleton. This suggests that the chemical conditions that induced carbonate cementation of the enclosing mudrocks were either stronger or operated for a longer time below the buried carcass. The 56 *in situ* fossil-bearing nodules recorded at this locality had no preferred orientation, their attitude and shape being clearly determined by the organic material around which they had formed. Many but not all of the elongate smooth-surfaced nodules contain articulated remains of the procolophonid reptile *Barasaurus* (Figure 4). The larger flatter nodules contain articulated skeletons of the palaeoniscid *Atherstonia* (Figure 5). Some of the latter contain an assortment of plant debris including *Glossopteris* leaves, *Schizoneura* and *Lepidopteris* stems, and some woody fragments along with articulated *Barasaurus* limbs and other isolated post-cranial elements. The middle horizon contains more regular muffin-shaped ellipsoidal nodules that are similar in colour and composition but are difficult to break apart and contain no macrofossils.

Skeleton-bearing nodules part easily along the midline, causing most of the bones to break along their length. In the formation of the present-day landscape there has been a period during which groundwaters have flushed through the partings of these nodules and weathered the fossilized bone much more rapidly than the calcareous siltstone nodule. All the *Barasaurus*-bearing nodules that have been collected to date have been split along the midline of the skeleton. It is fortuitous, however, that after cleaning out the remnants of decomposed fossil bone, the fine-grained calcareous siltstone moulds are ideal for casting with latex or silicone rubber. Casting part and counterpart gives a perfect replica of both dorsal and ventral sides of the skeleton (Figure 6). This 3-dimensional view of the articulated skeleton would be very difficult to achieve with mechanical preparation of the fossil bones.

Of the 65 fossil bearing nodules that were taphonomically assessed, 57 contained articulated *Barasaurus* remains, of which only 5 had preserved skulls (see Figures 6 and 7). The orientation of loose and fragmentary nodules is difficult to determine. However, whole loose nodules are slightly more bulbous on the lower side and this makes it possible to determine the upper surface of these fossils. Twelve fossil-bearing nodules were found still embedded in the shale. Thus, the attitude of the skeletons could be reliably documented. Of these, 10 were lying on their belly, and two were lying on their backs, all with their legs spreadeagled in typical aquatic death pose (Weigelt 1989). Several nodules were found to contain two or three skeletons that were invariably curled-up and whose limbs were disassociated. This suggests that some scavenging may have taken place before burial. However, these multiple specimens most often contain the fully preserved skulls and distal sections of the tail, which are commonly missing from the single skeletons. The complete skeletons measured between 230-250mm from snout to tail tip and are considered to be adult size.

Clumps of rounded quartz pebbles occur within the abdominal region of all the *Barasaurus* fossils collected at Ranohira (Figure 7). The number of pebbles in each clump ranges from 2-15, although most contain 8-10. They tend to lie between vertebrae 16-19, on and slightly to the left of the midline of the abdomen. The pebbles are composed of opaque, grey, brown and white quartz ranging in maximum diameter from 8-13 mm. Some have dark coloured inclusions of tourmaline that suggests a granitic source. The clasts are in contact

with each other and there is a tendency for the larger pebbles to be confined to the anterior half of the clump. Pebbles range in shape from rod to ovoid to spherical, and surface textures may be rough, pitted, smooth with pits or completely smooth (Figure 7). A few of the pebbles are polished. Unlike the abdominal stones of *Hovasaurus*, the *Barasaurus* clumps have no associated grit- or sand-sized particles.

Zavoloa River, Ambohitra [GR. S 22° 46' 45.7" E 45° 20' 29.3"]

Sedimentology

This locality lies some 25km south of Ranohira on the eastern banks of the Zavoloa River just south of the river crossing to the village of Ambohitra (Figure 1). It consists of a series of erosion gullies that have cut through sub-recent alluvium into the Sakamena sediments below. The outcrop comprises at least 20 stratigraphic metres of laminated mudrocks with subordinate pebbly sandstone and conglomerate lenses in a ratio of 3:1(Figure 3). The section dips gently (20°) towards the west away from two N-S trending normal faults. The mudrocks are generally olive grey (5Y4/2), thinly bedded and finely- to micro- laminated. They contain light grey (5Y7/2) isolated smooth-surfaced oblate calcareous nodules up to 120mm in diameter, some of which contain articulated vertebrate fossils, although most are non-fossiliferous. Mudstone laminae are, in places, clearly visible as extremely thin (<0.2mm thick) dark-coloured organic claystone laminae separated by thicker (0.5-1mm) lighter-coloured silty layers with vague intermittent laminae. An obvious difference between this locality and Ranohira Cemetry are the bone-rich quartz pebble



Figure 4. Ranohira locality. Two *in situ* micrite nodules containing articulated *Barasaurus* skeletons. Note the similarity in the shape of the nodules, which is determined by the attitude of the skeleton inside. The preservation of the original siltstone laminae in the nodules indicates that the micrite precipitation was post-burial and non-displacive.

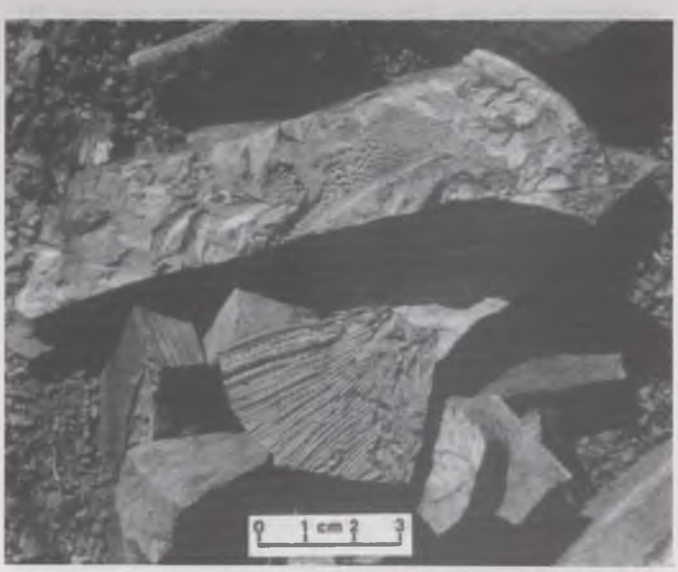


Figure 5. Ranohira locality: Fragments of a calcareous siltstone nodule containing an articulated palaeoniscid fish, probably *Atherstonia*.

conglomerate lenses within most of the sandstone beds in the lower part of the section (Figure 8). At the bases of the sandstones, longitudinal runnels that have been scoured up to 60cm into the underlying argillaceous sediments are floored with stringers of clast-supported pebble conglomerate and filled with medium grained pebbly sandstone displaying undulating "swaley" laminae. Thin sheets (<20cm) of well-sorted matrix-supported pebble conglomerates occur within the 2-3 metre-thick tabular sandstone bodies that overlie the basal scour. These sheet conglomerates (Figure 8) are sharply bounded. Larger intraclasts of well-rounded chert and quartz pebbles and post-cranial bones of *Claudiosaurus* commonly protrude from their upper surfaces. The matrix of fine- to medium-grained sandstone appears to have been dense enough to support these larger clasts during and after sedimentation, a feature that is indicative of cohesive debris flows. In places the gravel stringers are structured into planar-convex barforms displaying high angle epsilon cross-stratification. *Claudiosaurus* long bones and ribs are aligned with their long axes parallel to the dip of the foresets, indicating that these



Figure 6. Ranohira locality: Silicone cast of the moulds of part and counterpart of a *Barasaurus*-bearing nodule. Note the intricate details of the maxillary teeth and skull roof bones in the close-ups (scale bars=1cm).

bars were, at least in part, accreted laterally. Each conglomerate sheet is sharply overlain by horizontally-laminated pebbly sandstone which grades upward into ripple cross-laminated sandstone. This sandstone is rarely capped by a mega-rippled surface that resembles hummocky cross-stratification (which is commonly attributed to submarine reworking during storm surges) (Figure 9).

The larger conglomerate-based, trough cross-bedded sandstone bodies are interpreted as subaerial braided river channel deposits, and the thinner matrix-supported conglomerate and horizontally laminated sandstone units are interpreted as overbank splays lateral to the braid channels on the distal surface of an alluvial fan. Rarely, thin sheets of granule conglomerate occur as discrete beds within the mudrock sequences. They have been deposited as low amplitude starved megaripples. These are interpreted as subaqueous debris flow lobes that have been locally reworked, either at the time of emplacement or sometime later, by storm-generated wave action. The rapid interdigitation of coarse-grained, fluvially-generated sands and gravels with laminated fines suggests that this succession lies in the distal parts of a sublacustrine fan that prograded from the tectonically inactive margin of the lake onto a relatively shallow shelf (Wescott and Diggens 1998). Similar facies sequences have been reported from cores drilled into the margins of Lake Turkana in northern Kenya, a modern rift valley lake (Cohen 1989). It is notable that the coarse clastics enter the lake from rivers entering along its narrow shoreline but they rarely get transported more than 1km offshore. These sands and gravels accumulate in narrow bodies parallel to the shoreline. The gravels are typically matrix-supported with angular to sub-angular quartz and volcanic rock pebbles. A similar setting is interpreted for the Sakamena facies sequences at Zavoloa River.

Taphonomy

The common vertebrate fossils at Zavoloa River locality are of the medium-sized (total adult body length approximately 640mm) sauropterygian reptile *Claudiosaurus germaini*. They occur rarely as fully articulated skeletons and far more commonly as disarticulated, transported and sorted bones within quartz pebble conglomerates. The articulated skeletons are found inside calcareous siltstone pods that occur within the olive grey mudrocks and within the lower parts of the thin tabular splay sandstones (Figure 10). The biscuit-shaped calcareous pods are approximately 10 cm thick with flattened upper and lower surfaces, and are up to 45cm in longest diameter. Unlike the *Barasaurus*- bearing nodules at Ranohira Cemetery, these nodules show no parting on the outer surface as a telltale sign that there is a skeleton inside. The pachyostotic postcranial bones are characteristically very dark grey (2.5Y3/0) sometimes with a greyish brown (2.5Y3/2) colour and preserved uncrushed and unweathered (Figure 10). As with the Ranohira locality, there are many calcareous nodules that do not contain macrofossils, although there is no record of any

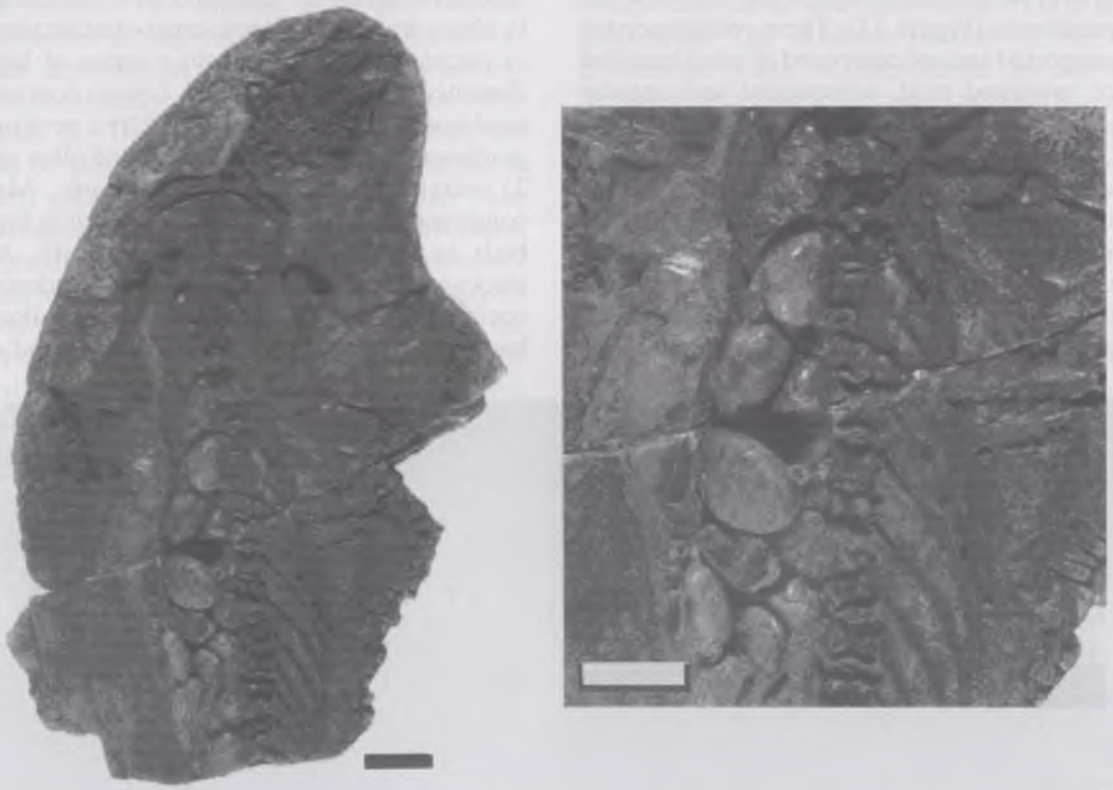


Figure 7. Ranohira locality: Anterior half of a *Barasaurus* skeleton preserved in dorsal-up attitude. Note the clump of roughly equal-sized quartz pebbles lying lateral to the mid-line (right side in life) in the abdomen. The close-up shows that unlike *Hovasaurus*, *Barasaurus* pebble masses do not have any grit or sand-sized clasts.

articulated *Claudiosaurus* skeleton that was not contained inside a nodule. The skeletons are mostly preserved in dorsal-up attitude with limbs trailing backwards along the sides of the body, in a pose similar to the inferred swimming position (Carroll 1981). Rarely are the skulls or distal portions of the tail preserved within the nodules, suggesting that decomposing tissue and muscle, rather than skin, determined the distribution and degree of micrite precipitation. The few skulls that are preserved are lying lateral-up and are inevitably crushed with slight displacement of the lower jaw elements (Carroll 1981, Figure 11).

Isolated post-cranial elements such as ribs, vertebrae, interclavicles, and long bones occur scattered within the olive-grey mudrocks. These are generally well preserved, showing little signs of abrasion or weathering. Adult *Claudiosaurus* long bones and ribs are comparatively heavy and brittle because they were originally composed of more compact bone tissue. This was possibly a buoyancy adaptation that evolved after the animal re-entered an aquatic niche (de Ricqlès 1974; de Buffrénil & Mazin 1989). A scattered skeleton of a dicynodont therapsid was found in the mudrocks at this locality. Unfortunately, no skull material could be located, but the post-cranial elements are of the size of *Oudenodon*, which is the only therapsid to have been identified in this basin (Mazin & King 1991).

In the lower half of the section exposed at Zavoloa River, bonebed type accumulations of disarticulated *Claudiosaurus* post crania and plant debris are associated with conglomerate lags at the base of some channel sandstones (Figure 12). These conglomerates are clast-supported and are composed of small rounded pebbles of reworked mud, subrounded and angular quartz, feldspar and mica set in a coarse dirty arkose matrix. On the upper surface of the conglomerate lenses, patches of disarticulated bones lie along the axes of troughs and on the downstream-fining "tails" of side-accreted gravel bars. They comprise mainly ribs, vertebrae, long bones and girdles in a chaotic melange with a relatively weak current alignment (Figure12). The ribs appear to be the most strongly orientated with their proximal ends upstream. Most of the long bones are unbroken but show slight abrasion of the articular surfaces; a few are broken and well worn to the extent that they resemble rounded pebbles. The associated plant trash consists of impressions of *Schizoneura*-like leaf and woody stem fragments. Rounded clasts of silicified wood are a rare intraclast in the conglomerates, although a few metre-long silicified logs were recovered from the intervening mudrocks. Dr Marion Bamford (University of Witwatersrand) has made a preliminary identification of the wood as *Araucarioxylon africanum*, which is a relatively common conifer that occurs in Late Permian to Mid-Triassic sediments throughout southern Africa.

Mount Eliva, Andamilamy District [G.R. S 23°59'41.4" E44°25'55.0"]

Sedimentology

The strata exposed at Mt Eliva are the most southerly outcrops of the Lower Sakamena Formation, and they lie stratigraphically nearer to the top of the formation than in either of the previously described localities (Figure 1). They comprise roughly 1:1 ratio of sandstone to mudrock, and are interpreted as having accumulated on a submerged lacustrine delta at the southern end of the Sakamena lake (Figures 2 and 13). Predominantly fine to medium-grained light yellowish-brown (2.5Y 6/4) sandstones form tabular sheets between 0.5-1.25m thick, which are traceable up to 1km. They have flat basal surfaces with shallow scour troughs filled with clast-supported clay- and quartz-pebble conglomerate. The main body of the sandstone sheets is structured with lenticular beds of in-phase and in-drift ripple cross-stratification, which, in places, has deformed into a series of large (1-2m diameter) pillow structures. Upper contacts of the sandstone bodies in the Mt Eliva section are all gradational into rhythmically bedded olive grey (5Y5/2) siltstone/mudstone alternations. Mud flake conglomerate lenses 2-5 cm thick occur in the siltstone beds in the lower part of these units. Arthropod trackways of the *Umfolozia*-type (Anderson 1975) occur on some of the flaggy weathering siltstone beds but the majority of surfaces are smooth and devoid of



Figure 8. Zavaloa River locality: Vertical section of matrix-supported quartz pebble and bone conglomerate that fills isolated scour troughs at the base of tabular low sinuosity channel sandstone units.



Figure 9. Zavoloa River: Wave-rippled surface of a fine grained splay sandstone interpreted as part of the submerged distal facies of an alluvial fan entering the side of the Sakamena lake.

trace fossils. The rhythmites commonly grade upwards into a 2-4m thick interval of olive (5Y4/3), very finely laminated siltstone with scattered small oblate calcareous nodules, some of which contain vertebrate and plant fossils. The tabular lenticular bedded sandstone bodies at this locality are interpreted as having been deposited in wide shallow low-sinuosity channels on the distal portion of a large sub-lacustrine delta (Figure 2). The lack of significant scour, the dominance of unidirectional ripple cross-laminated, fine-grained sand, and the gradational rather than interdigitating upper contact with essentially overbank facies are good indications that this was a low sinuosity system with high suspended sediment load. The layers of slumped laminae that occur near the top of the uppermost sandstones in the Mt Eliva section show the characteristics of post-depositional soft sediment deformation caused by gravity sliding of waterlogged fine sand soon after it was deposited. The lack of any emergence or desiccation features in the section suggests a sub-aqueous setting for the entire section. Rapidly alternating siltstone/mudstone rhythmites and mud flake conglomerate lenses are the commomly associated "overbank" facies deposited on the flanks of the channels in the middle and distal parts of the delta slope. The rhythmites are interpreted as having been deposited by episodic density underflows and are similar to the interdistributary bay facies of large deltas. The very finely laminated mudstone facies is indicative of the "background" sedimentation of suspension fines that characterises a closed lake system with restricted circulation and probably for most of the time, a thermally-stratified water column. In the geological record of rift valley lakes, the Devonian Escuminac Formation of southern Quebec (Dineley and Williams 1968) has similar lithologies, sedimentary facies and taphonomic style to the Lower Sakamena. The offshore portion of the elongate Escuminac Lake is interpreted as having been stratified, with anoxic bottom conditions that gradually become more fluvially influenced towards the axial ends of the lake where distal turbidites grade into deltaic and sub-aerial floodplain facies. This scenario could well describe the geomorphology at the southern end of the Sakamena lake.

Taphonomy

The fossil assemblage in the Lower Sakamena at Mount Eliva is dominated by the aquatic younginiform *Hovasaurus* along with rare palaeoniscid fishes, glossopterid fructifications and *Schizoneura* leaf fragments. They are preserved within oblate, smooth-surfaced, calcareous nodules similar to those at Zavoloa River and generally larger than those at Ranohira (Figure 14). The nodules are scattered within the fine-grained laminated siltstone facies only. None were found within the sandstone facies. The *Hovasaurus* skeletons are fully articulated, although rarely entirely enveloped by the nodule. The skull and tail are usually missing, suggesting that nodule formation in the surrounding matrix is controlled by the amount of decomposing soft tissue in the carcass. Currie (1981) estimated the length of an adult *Hovasaurus*, based on the largest incomplete specimen

in Piveteau's collection, to be approximately 900mm. The calcareous cement that forms the nodule is most thickly developed around the quartz pebble mass within the abdomen of *Hovasaurus* specimens. Piveteau (1926) considered the abdominal pebble masses to have provided the nucleus of the nodule formation. It is interesting to note that all the articulated *Barasaurus* skeletons at the Ranohira locality also have abdominal pebbles, but they are fewer in number and do not have any grit-sized clasts. Currie (1981) concluded that the pebbles were deliberately ingested and may have been used in a gastric mill as an aid to digestion, but he considers them more likely to have been used as ballast to assist swimming. No plant fragments have been observed in any of the pebble masses of either *Barasaurus* or *Hovasaurus*, although several nodules have lycopod stems and *Schizoneura* leaf fragments preserved next to the skeletons. Although it is negative evidence, the presence of a gastric mill would imply that the animal was eating fibrous plant tissue. Therefore, plant trash remains should be preserved within the pebble mass. The lack of such remains favours the ballast stone interpretation.

The attitude of the smooth-surfaced siltstone nodules and the fossils contained within can only be determined whilst they are still embedded. Unfortunately, Piveteau did not record attitude for his collection that resides in Paris. Therefore, the original orientation can only be determined on the few specimens that were excavated during fieldwork for this study. Only three *Hovasaurus*-bearing siltstone nodules were collected in situ and all three contained skeletons that were buried dorsal-up. This was determined in the field after splitting the nodule and noting that the ribs and vertebrae overlie the gastralia and are slightly displaced. In these orientated

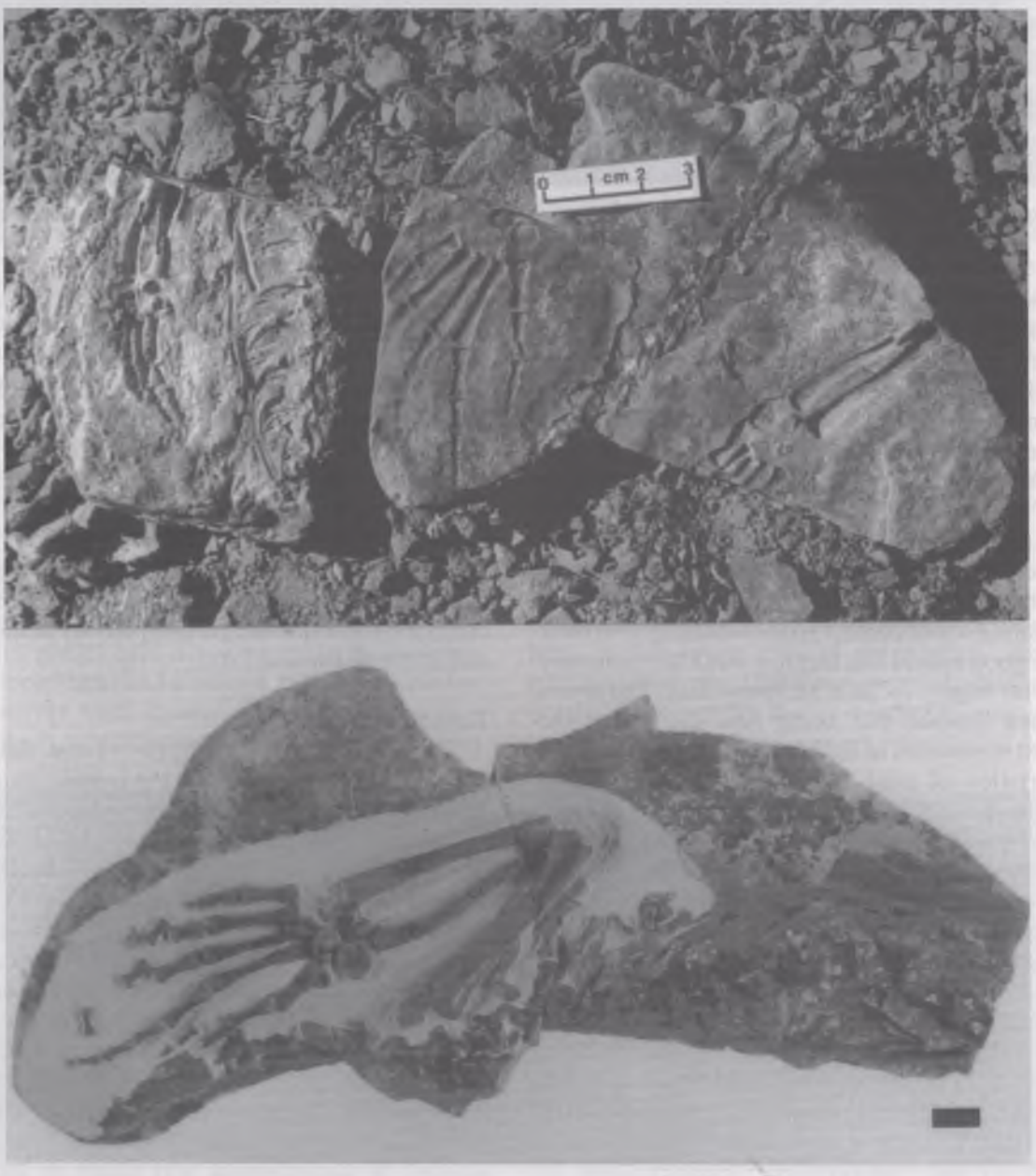


Figure 10. Zavaloa River: *Claudiosaurus*-bearing calcareous nodules in the field and after preparation a right arm and manus of the semi aquatic reptile *Claudiosaurus* (scale bar=1 cm)

specimens, the pebble mass is parted by the ribs and the gastralia are not visible. One specimen of a juvenile *Hovasaurus* collected by Piveteau from Mt Eliva (numbered 1925-5-20) is preserved lateral-up and clearly shows a mass of small quartz pebbles lying ventral to the spine just anterior to the pelvic girdle and dorsal to the gastralia. Incidentally this specimen also shows a possible tail "fin" impression above the neural spines of the caudal vertebrae. From taphonomic evidence it is concluded that *Hovasaurus* was aquatic and ingested quartz pebbles and grit to weigh down and stabilise the abdomen in an effort to counteract the upward thrust generated by the lungs (Laurin pers. comm.) and/or tail (Currie 1981) when swimming.

DISCUSSION OF MODE OF DEATH, BURIAL AND PRESERVATION OF SAKAMENA AQUATIC VERTEBRATES

Mode of death

In modern large, deep lakes, perhaps the most common cause of mass mortality among teleosts is oxygen deficiency and thermal shock when large volumes of cool anoxic bottom water mix with warm oxygenated surface water. This breakdown of thermal stratification, or overturn, is most commonly caused by sudden influx of cold sediment-laden floodwaters during and immediately following thunderstorms in the catchment area. Within hours large numbers of fish suffocate, especially when plumes of suspended silt and clay effectively clog the gills (Eric Anderson, pers.comm.). The thermocline in small, deep lakes may also be destabilised during extended periods of drought, as the lake becomes shallower (Behrensmeyer and Hooke 1992). Other common causes of mass fish kills in lakes are poisoning by algal blooms (McGrew 1975), and sudden cold winds and rainstorms (Perkins 1970). Rarely, seismically induced degassing of the anoxic bottom sediments can cause mass mortality in and around the lake. The presence of thick sequences of microlaminated and non-bioturbated mudrock containing horizons of fully-articulated, non-scavenged and undisturbed aquatic vertebrate fossils is compelling evidence that the bottom conditions in the centre of the Sakamena lake were anoxic for much of the year.

Despite the bias caused by preferential collecting of nodules, it is evident that the most common taphonomic mode of aquatic reptiles and fishes in the Lower Sakamena is as complete articulated skeletons lying dorsal-up. It is also evident that many individuals of all ages died within a short-term event and that they were buried soon after death, before complete decomposition and before significant skeletal disarticulation took place. There is no evidence of macro-predation or scavenging on these carcasses. Scale impressions on some specimens and abdominal stone clumps confirm that most individuals were intact when they arrived at their final burial site. The most plausible cause of death in this setting is overturn of the thermocline caused by storm-generated flooding. Sedimentological evidence suggests several sources of sediment-laden braided channels issued into a linear standing water body. Fresh plant material and newly drowned carcasses of terrestrial animals such as *Oudenodon* would have floated further offshore before sinking beyond the influence of bottom traction currents.

Unlike the actinopterygians, *Barasaurus*, being an air-breathing, potentially amphibious or fully-aquatic reptile, would not have been suffocated by an overturn event but may have been debilitated by the sudden drop in temperature of the surface waters. Immediately after death, the ballast-weighted cadavers sank, belly-down, to the lake floor, where they lay with limbs spread-eagled in a dorsal-up attitude. The newt-like "tail fin" came to rest on its side and it would have tended to rotate the abdomen until the pelvic girdle fell apart. Methane generated by bacterial decomposition of the stomach contents would have bloated the abdomen but this was clearly not enough to re-float the cadaver. Studies of modern fish cadavers in similar settings show that in water temperatures of less than 16°C, anaerobic decay of the gut contents does not generate enough buoyancy to re-float the cadaver (Elder and Smith 1988). Further anaerobic decay of the flesh and muscle tissue continued for an estimated 2-5 years, during which time the carcass was undisturbed by scavengers or turbulent bottom currents until it simply collapsed on itself. Before complete decomposition of the soft tissue, the carcasses had become completely covered with a layer of microlaminated silt. The silt drape settled from clouds of suspended fines that were rafted offshore on the thermocline during subsequent flood events. Anaerobic bacterial decay generated a sulphate-rich halo in the surrounding sediment that in some cases became the locus for early diagenetic precipitation of micrite from groundwater. Details of the controls and timing of this nodule formation are discussed later.



Figure 11. Zavoloa River: Severely crushed skull and lower jaw of *Claudiosaurus* preserved in a tabular sandstone but without having been peri-mineralized with a calcareous nodule (Scale bar=0.5cm)

Towards the margins of the Sakamena lake, the bottom waters were permanently oxygenated and, following thunderstorms in the catchment, were subjected to high-energy mass transport episodes. Sheet wash and flood discharge resulted in the injection of sand and poorly sorted gravels into the lake, where they accumulated in sheets parallel to shore. These short-lived debris flows transported pebble-sized basement rock fragments and numerous disarticulated skeletal elements of another aquatic reptile, *Claudiosaurus*. The repeated occurrence of conglomerates rich in *Claudiosaurus* bones suggests that this taxon was also a victim of mass mortality but in an environment that was not conducive to preservation. It is likely that *Claudiosaurus* preferred to forage in shallower waters and was possibly semi-terrestrial (Carroll 1981), spending time on the shore alongside *Oudenodon* and other therapsids (Mazin & King 1991). However, it too probably suffered from thermal shock during overturn events that resulted in numerous cadavers in the nearshore parts of the lake, which were then reworked by low-density turbidity currents. Those fully articulated skeletons preserved in the thicker sheet sands were entombed soon after death, possibly in the same depositional episode, and have escaped subsequent reworking.

Nodule Formation

It is evident that in the chemical environment that existed in the Sakamena lake sediments soon after deposition, decomposing organic matter was preferentially enveloped in calcareous nodular material. This preferential perimineralization occurred after burial and before compaction, and possibly before replacement of the carbonate component of the bone. This implies an early diagenetic origin for the nodules, which is almost certainly linked in some way to the bacterial decomposition of the organisms. A tendency



Figure 12. Zavoloa River: *Claudiosaurus* bone conglomerate lining the axis of a trough in a braided channel sandstone. Note the weak orientation of long bones and the stronger alignment of ribs with their proximal ends upstream.



Figure 13. Mount Eliva locality: View of the *Hovasaurus* collecting grounds, closely guarded by the local residents, with Mount Eliva in the background.

for nodules to thicken on the underside suggests that the reducing conditions necessary for precipitation of calcium carbonate out of the interstitial water in the sediment occurred whilst the topside was still exposed. Only later, after burial of the organic remains, was calcification of the overlying sediment able to take place. It is clear that the calcium carbonate precipitation was not displacive because the original fine sedimentary structures remain undisrupted within the nodules. The sharp outer boundary of the nodules indicates that the calcium carbonate precipitation was probably incremental and the nodule grew outwards from the decaying organic matter over an extended period. The lack of compaction of the enveloped fossils indicates early lithification of the calcareous sheath that increased mechanical strength and prevented vertical compaction resulting from continued accumulation of sediment.

Arduini (1993) noted that several articulated *Barasaurus* skeletons were preserved on bedding planes within the nodular horizons but without any associated nodule formation. He also noted that in some cases only the girdle sections of the skeletons are perimineralized, with the rest of the skeleton preserved outside the nodules, on the siltstone bedding planes. Arduini (1993) interprets this as evidence that the nodule formation was centred on the products of bacterial decay of cartilage within the pelvic and pectoral girdles. It is clear from the field results that collecting bias has distorted the importance of nodule

formation in the preservation of the Late Sakamena flora and fauna. Many articulated skeletons and plant fossils have no associated nodule formation and were overlooked by previous workers (with the exception of Arduini (1993)). Even within the three nodular "horizons," the perimineralization is rarely complete, so that many partial skeletons of *Barasaurus* have been collected because only the nodular portion was recovered. It is also apparent that the particular chemical conditions that led to early diagenetic precipitation of calcium carbonate in interstitial spaces surrounding decomposing organic remains occurred at least three times in the Sakamena lake sediments.

After death, the carcasses settled into an anaerobic environment on the lake bottom. Bacterial decomposition of the soft tissues released hydrogen sulphide into the overlying water column and underlying sediments. Silt and clay-sized fines, originating from rivers feeding into the lake and rafted on the thermocline into the offshore regions, slowly draped the decomposing carcasses. Most were buried fully articulated, but in some cases, after the skin had rotted, the limbs became detached at their proximal ends to lie next to the carcass. After burial to a depth of 2-3 cm below the sediment/water interface, the ligaments and cartilages rotted and the rib cages collapsed. At the same time, hydrogen sulphide continued to accumulate in the interstitial fluids of the surrounding sediment. With further sediment accumulation, the skeletons passed slowly through the zone of bacterial decarboxylation around 10cm below surface, further concentrating the halo of diffused hydrogen sulphide-rich fluids around the carcass. Under normal circumstances bacterial activity would result in complete decomposition of the organic tissues including the collagen networks of the skeletons, leaving the bones brittle and vulnerable to compression. Plant material was for the most part completely denatured, leaving only impressions; only the lignin-rich stems remained intact.

However, on at least three occasions, this process was interrupted by the interstitial precipitation of calcium carbonate within the sulphide-rich halos around the decomposing organic matter. The micrite crystallised in response to the lowered pH in the diffusion gradient around each decomposed carcass. The threshold for precipitation was determined by the sulphide concentration in the halo. Thus, those carcasses that were buried quickly had thicker and more continuous micrite nodules, whereas those buried more slowly had not enough organic matter left to form a continuous micrite envelope. This resulted in selective micritization around the cartilage-rich parts of the skeleton such as the girdles.

What caused the "micritization events" that resulted in the three calcareous nodule horizons in the upper Lower Sakamena? Evidence suggests that these were periods when the generally anoxic sediments situated in the offshore areas of a linear rift valley lake became oxygenated. It appears that each micritization event resulted from oxygenated water penetrating at least 0.1m below the sediment water interface over a large area, suggesting that they could have been the result of prolonged lowstand. During periods of low lake level, the thermal stratification could not be sustained, and oxygenated bottom waters with carbonate in solution percolated through the upper layers of sediment, precipitating Mg-rich micrite around all partially decomposed organic remains. Similar calcareous precipitates have been detected on decomposing fishes in thermally stratified lakes (Elder and Smith 1988), which are the result of algal blooms depleting the water of carbon dioxide. This mechanism is most effective during lowstand when the water volume is insufficient to dissipate the algal toxins (Prescott 1948). If such lowstand events were climatically controlled, they should prove to be useful timelines to accurately correlate strata within and between these ancient rift valley lakes both in Madagascar and Tanzania.

SUMMARY

The upper Lower Sakamena Formation in southwestern Madagascar was deposited in open-ended rift valley lakes that formed in the axial regions of two half grabens some 255 million years ago. Three discrete sediment/fossil associations reflect contemporaneous subenvironments of the Sakamena lakes. Restricted circulation and thermal stratification of the relatively deep offshore waters resulted in thick



Figure 14. Mount Eliva locality: Local residents demonstrating how they excavate nodules in the search for *Hovasaurus* fossils that are sold to a foreign dealer on his yearly visit.

deposits of microlaminated muds which contain at least three mass mortality horizons of an aquatic procolophonid reptile, *Barasaurus*. Nearer to the lateral margins of the lake, especially on the inactive side of the half-graben, numerous transported remains of *Claudiosaurus* are commonly preserved in braided stream channel conglomerates. This diapsid, possibly sauropterygian reptile is believed to have been semi-aquatic, a conclusion corroborated by the nearshore environment of preservation and the taphonomy of its fossils. Another younginiform reptile, *Hovasarus*, is believed to have been fully aquatic. It is found in abundance in sediments deposited on a sub-aqueous delta that prograded into the southern end of the Sakamena lake (see Figure 2).

In large, deep, thermally stratified lakes, thermal shock from periodic overturn and poisoning from algal blooms are the most likely causes of mass mortality among the aquatic fauna. Sulphides released from anaerobic bacterial decay of soft tissue and girdle cartilage formed reduction halos around the newly buried reptile carcasses. At least three times during the infilling of the lake, oxygenated waters flushed through the bottom sediments to precipitate carbonate nodules in the reduction halos. These 3 "micritization episodes" are interpreted as extended periods of lowstand when thermal stratification could not be maintained and oxygenated waters came into contact with previously anoxic sediments. If such lowstand events were climatically controlled, they may be useful timelines to accurately correlate strata within and among these ancient rift valley lakes both in Madagascar and Tanzania.

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AFRICAN CHELONIANS FROM THE JURASSIC TO THE PRESENT: PHASES OF DEVELOPMENT AND PRELIMINARY CATALOGUE OF THE FOSSIL RECORD.

by

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ABSTRACT

The five major phases in the palaeontological history of African chelonians are presented: 1) autochthonous development of the north Gondwanan pleurodires from a Pangean source group; 2) littoral expansion of a member of this group (Bothremydidae), accompanied by the arrival of Laurasian marine turtles; 3) *in situ* development of pleurodires and the immigration of Eurasian cryptodires (Oligo-Miocene) traversing the Tethys in several waves; 4) great diversification and endemism (Pliocene to Holocene); 5) important faunal reduction due to climatic changes at the end of Holocene times (cooling, aridification); elsewhere, great speciation and arrival during the Present of the last European immigrant in the north. Throughout the period under consideration there were several reductions in taxonomic diversity and emigrations from Africa.

A preliminary catalogue of the fossil record of African chelonians is given, presented country by country followed by a taxonomic listing.

KEYWORDS: Fossil chelonians, Africa, stratigraphy, taxonomy

INTRODUCTION

This work is based on data collected for a presentation on the settlement of chelonians in Africa which I gave at the PSSA'98 conference in Windhoek, Namibia (Lapparent de Broin 1998). It is not the result of a systematic study of African chelonians and the catalogue presented here does not pretend to be complete but it attempts to include all named taxa. Some data on Pliocene to more recent archaeological sites are not included, in particular those published recently (from 1998), nor are references to chelonians in more general works where descriptions of the forms dealt with are not included. However, the data presented here can reasonably claim to document the spread of chelonians in Africa.

The classification adopted here is based on phylogeny (Gaffney & Meylan 1988, emend. Bour & Dubois 1986; Broin 1988a,b, Lapparent de Broin & Murelaga 1999; Lapparent de Broin & Werner 1998) ; it reflects the diversification of taxa as well as their palaeobiogeographic history (continental drift, geographic barriers, changes in climate) from the Triassic to the Present. Phenetic systematics is rejected in this study; such classifications are still employed by a number of neontologists who establish compilations only for the practical purposes of determination and distribution of extant forms, without the necessity of a historical analysis (e.g. David 1994; Iverson 1992). They include artificial polyphyletic taxa. However, it should be noted that, in the classifications adopted in this study, parts are not fully phylogenetic because several proposed cladograms do not integrate the fossil forms (except for a few genera) (Bour 1985; Gaffney & Meylan 1988; Hirayama 1985), as for example with two important African taxa: Trionychidae and Testudinidae. Step by step, the suppression of artificial genera is in progress, as has happened with the partition of *Clemmys*, *Trionyx* (based on extant forms only), *Testudo* s.s. and *Agrionemys* (a part of *Testudo* s.l.) and *Podocnemis*, but not yet with *Geochelone*, probably the last artificial taxon (with the remaining part of *Testudo* s.l.). At family level, the partition of the Pelomedusidae in the several families constituting the hyperfamily Pelomedusoides, is also widely admitted by the scientific community.

Environment

An important point about the analysis of the African chelonians is recognition of the role of the environment in the geographic spread of taxa.

In the catalogue that follows, the environment is specified in the catalogue only when it is littoral or marine: the term 'littoral' is assigned to some pleurodire turtles, e.g. the Bothremydidae which lack paddled limbs, and followed coastlines, not crossing wide seaways. The term 'marine' is attributed to the cryptodires Chelonioidea and Dermochelyoidea (here separated for better comprehension), which have paddled limbs, are able to cross oceans and to live in deep seas. They are also found, as fossils, in littoral palaeoenvironments. Originally they were continental and then become littoral (as did the Bothremydidae), before they conquered deep seas. The other chelonian taxa are continental, i.e. either freshwater (the majority), sometimes possibly semi aquatic-semi terrestrial, or fully terrestrial, similar to the primitive Triassic chelonians and their pareiasaurid ancestors

(see Lee 1997). Thus, in Africa, the oldest known form, the very primitive Hettangian South African taxon *Australochelys* from the Stormberg group of the Karoo, was unquestionably a continental form. In the Testudininei the relatively large forms are also able to cross short seaways, floating in suitable currents (Bour 1985, 1987, 1994, conquest of Indian Ocean islands). Some small freshwater forms, such as *Pelomedusa* or *Pelusios* were probably carried on floating debris, by currents during typhoons, or tsunamis, or freshwater floods and brackish water currents and were able to colonize Indian Ocean islands separated by considerable distances from the African mainland. The small freshwater forms have never been known to cross oceans unaided and in order to spread they utilised a network of freshwater rivers, lakes and ponds. The Trionychoidea are freshwater turtles with paddled limbs and they are able to cross a short seaway or to follow a coastline, from the mouth of the home river, being carried by inshore currents to enter other rivers farther down the coast, as observed for example in *Trionyx* in western Africa (Hughes pers. comm.) and various observations in the Mediterranean and colonization of New Guinea and Australia by Trionychidae and Carettochelyidae.

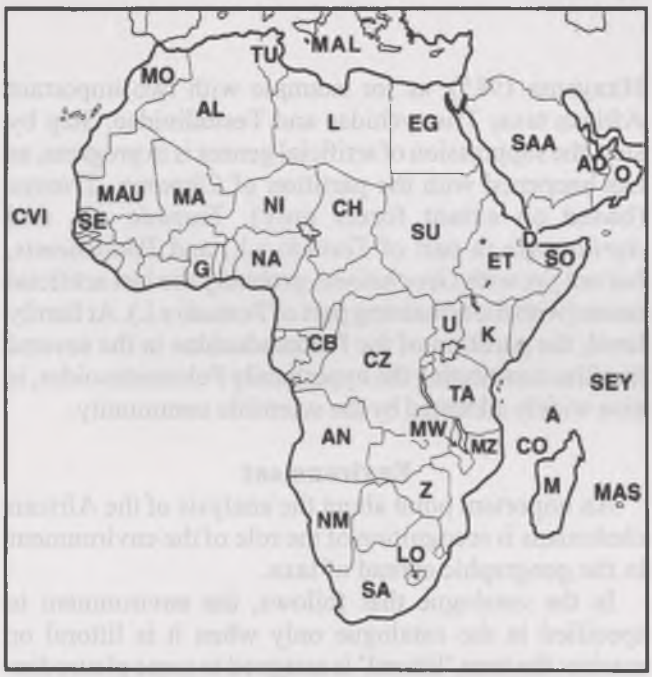


Figure 1. Countries of Africa, the Arabian Peninsula and the vicinity of Madagascar, with a record of fossil chelonians. **Africa**: AL, Algeria; AN, Angola; CVI, Cape Verde Islands; CB, Congo: People's Republic of (ex Congo-Brazzaville); CH, Chad; CZ, Congo: Democratic Republic of (ex Zaïre, Congo-Kinshasa); D, Djibouti: Republic of; EG, Egypt; ET, Ethiopia; G, Ghana; K, Kenya; L, Libya; LO, Lesotho; MA, Mali; MAL, Malta; MAU, Mauritania; MO, Morocco; MW, Malawi; MZ, Mozambique; NA, Nigeria; NI, Niger; NM, Namibia; SA, South Africa; SE, Senegal; SO, Somalia; SU, Sudan; TA, Tanzania; TU, Tunisia; U, Uganda; Z, Zimbabwe. **Arabian Peninsula**: SAA, Saudi Arabia; AD, Abu Dhabi: Emirate of, United Arab Emirates; O, Oman: Sultanate of. **Madagascar area**: M, Madagascar and Gloriosa; A, Aldabra and SEY, Seychelles islands; CO, Comoros islands (Mayotte), MAS, Mascarene islands: La Réunion, Mauritius, Rodrigues.

PHASES OF DEVELOPMENT

Fossil chelonians are known from 32 African-Arabian countries and seven groups of islands (Figure 1). Arabia (the Arabian Peninsula), Madagascar, the surrounding Indian Ocean islands, Malta and Cape Verde Islands are an integral part of the African domain (Figures 7 and 8). The Canary Islands and Mediterranean islands other than Malta have not been integrated into this study, although they share faunas which are similar in part to those from the northern part of Africa. Fossil African chelonians are known from the earliest Jurassic until the Present. The extensive geographic and stratigraphic data now available allow a very close idea of the truth concerning the progressive colonization of the continent by chelonians. Study of the taxa already defined shows that Africa was initially populated by primitive forms, already present during the Pangean period, very soon after the appearance of the first known chelonians (Norian-Keuper). Continental drift then separated the land masses. Until the relatively recent arrival of Eurasian forms during the Oligocene, Africa was isolated during the Cretaceous and Palaeogene as far as continental forms of chelonians are concerned. Africa was still linked to India during Cretaceous times at least and had filtered relations with southwestern Europe during Late Cretaceous-Early Palaeogene times. The Pleurodira (chelonians with a pelvis linked by sutures to the shell and which progressively acquired a neck retracting in an horizontal plane) principally developed in the territories of the fragmented Gondwana (although some forms, e.g. the Dortokidae, evolved in Europe, Lapparent de Broin & Murelaga1996, 1999; Gheerbrant *et al.* 2000), while the Cryptodira (which progressively acquired a neck retracting in a vertical plane) were spreading in Laurasia. But Cryptodira progressively immigrated into Africa, in waves, to the point where they now comprise the majority of the African chelonian fauna.

First phase: autochthonous development from a Pangean group

First chelonians known in the world

The earliest known chelonians are Late Triassic (Keuper-Norian) but it is not possible to say which is the oldest taxon (Figure 2). The form that seems the most primitive (taken as a whole, because, apart from its primitive traits, it also has derived characters), is *Proganochelys quenstedti* Baur 1887, Germany (Fraas 1899; Gaffney 1990; Jaekel 1918), but this form, which is placed in its own infraorder, is not the oldest in the German Triassic. The supposedly related forms, aff. *Proganochelys* sp., from the Norian of Greenland (Jenkins *et al.* 1994) and aff. *P. ruchae* Broin 1985 (Broin *et al.* 1982), from the Norian of Thailand, are poorly known but they appear a little more derived. They share the character of epiplastral points, only four rather than five in *Proganochelys,* that are flattened and

laterally diverging, rather than rounded at the base and directed forwards. *Proterochersis robusta* Fraas 1913, is from the same German beds as *P. quenstedti* and, although it is much more derived, it appears earlier in the stratigraphy. It is already in the Pleurodira lineage according to some shell elements, particularly its posterior bifid lobe, its pelvis already derived in the pleurodiran manner, linked to the shell by sutures, much reduced in width with respect to plastral width and with joined thyroid fossae (Broin1985; 1988a; Lapparent de Broin et Fuente 1996; Lapparent de Broin & Murelaga 1999). *P. robusta* is the oldest known taxon which can be considered at the remote origin of the pleurodiran fauna, including that of Africa. *Palaeochersis talampayensis* Rougier *et al.* 1995, from the Norian of Argentina, is more primitive than *Proterochersis,* judging from some characters such as those of the pelvis and plastron but it is difficult to compare them directly because the *Proterochersis* skull is unknown. However, its affinities with Pleurodira although possible (e.g., beginning of sutural link of the very primitive pelvis to the shell), are difficult to prove.

Australochelys africanus Gaffney & Kitching 1994, from the Early Jurassic of Bormansdrift, Orange Free State, Karoo, South Africa (Table 1) is next in chronological sequence. It is the oldest chelonian taxon known from Africa, but is known only from a fragment from the bridge area of the carapace, not described, and a relatively poorly preserved skull in which the sutures are largely obliterated (Gaffney & Kitching 1995). Its relationships with other taxa are still uncertain, even for its authors (see Gaffney 1996). Rougier *et al.* 1995, consider it to be related to *Palaeochersis* and do not accept any possible relationship with *Proterochersis*. However the shared characters of *Australochelys* and *Palaeochersis* are weak and these skulls seem too primitive to offer good synapomorphies. As the skull of *Proterochersis* is not preserved, no comparison is possible with *Australochelys*. The oldest known African taxon therefore remains mysterious as to its origins and it is impossible to determine wether or not it is related to the infraorder Pleurodira, which developed in Africa before the arrival of Cryptodira.

Kayentachelys aprix Gaffney *et al.* 1987, from the Early Jurassic of Arizona, USA, is approximately as old as *Australochelys* but it is a confirmed cryptodire. The skull characters are more derived and it has no obvious relationships with *Australochelys.*

The next oldest chelonians from Africa are from the Middle Jurassic of El Mers, Morocco (Termier *et al.* 1940). No determination is possible on the poorly preserved material which consists of fragments of some plates. Approximately as old are the cryptodiran chelonians from the Middle Jurassic of China, such as *Chengyuchelys baenoides* Young & Chow 1953, *C. zingongensis* Yeh 1982 and *Xinjiangchelys junggarensis* Yeh 1986a (Yeh 1986b); they cannot be compared with the very poorly preserved African Middle Jurassic material. Besides, the large variety of Pleurodira found in Africa from Early Cretaceous times,

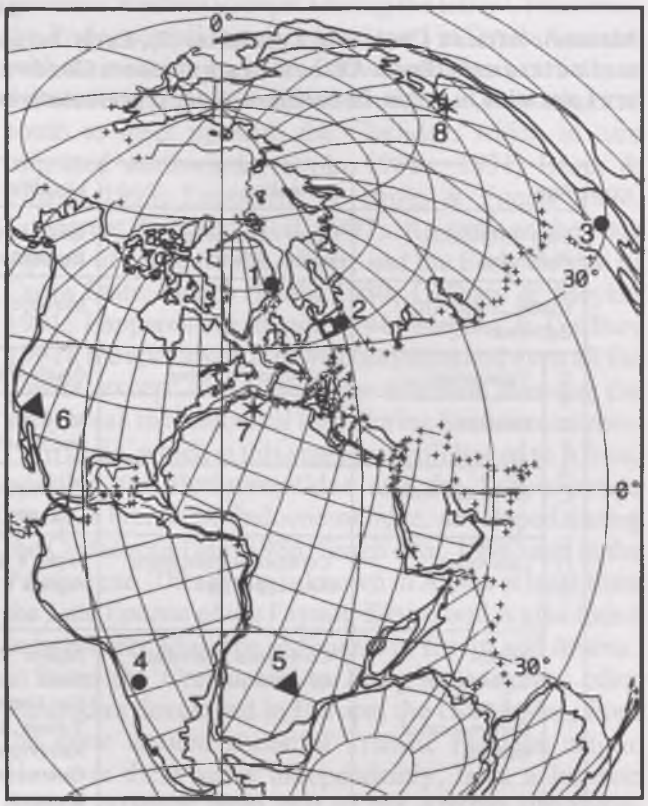


Figure 2. Localities of oldest chelonians in Pangea: Triassic: 1, aff. *Proganochelys* sp., Greenland, Norian; 2, *Proterochersis robusta*, *Proganochelys quenstedti*, Germany, upper Keuper; 3, aff. *Proganochelys ruchae*, Thailand, Norian; 4, *Palaeochersis talampayensis*, Argentina, Norian. Early Jurassic, Hettangian: 5, *Australochelys africanus*, South Africa (see Table 1: (5)). Early Jurassic 6, *Kayentachelys aprix*. Middle Jurassic: 7, Chelonii indet., Morocco (see on Tab. 1:1); 8, *Chengyuchelys baenoides*, *C. zingongensis* and *Xinjiangchelys junggarensis*, China. From Smith & Briden 1977, Rhaetian period.

and typical of Africa, indicates that this group was present on the continent much earlier than the Cryptodira.

The Pleurodira

From the Cretaceous onwards (Figure 3, Table 1), some chelonians are comparable with extant forms. The fossil material recovered from the Early Cretaceous of Cameroon and from the Algoa Basin, South Africa, have not yet been described. Material from the Early Cretaceous of the Anoual Basin, Morocco, although insufficient, shows signs of the presence of northern Gondwanan pleurodires (cf. *Taquetochelys* Broin 1980). The fossils from the upper part of the 'Continental Intercalaire' of the Sahara (Kilian 1931 in Furon 1955), in the Early Cretaceous of the northern part of Africa, are well preserved. They are all Pleurodira and belong to the same group as remains found from the Early Cretaceous of Brazil, South America (Pelomedusoides, see Broin 1988a, b) and its plesion the Araripemydidae. This continent was still linked to Africa during very early Cretaceous times. Pelomedusoides + Araripemydidae are vicariant to the Chelidae,

TABLE 1.

Mesozoic African Chelonian Localities: (5), Early Jurassic on Figure 2; 1 to 32, Cretaceous, on Figure 3. Littoral and marine taxa underlined. All the taxa are northern Gondwanan elements except the Dermochelyoidea-Chelonioidea, which are Laurasian in origin. In bold face, older representatives of the groups.

Age		Formation	Locality	Taxa
Early JURASSIC, Hettangian		Upper Stormberg, Karroo, Elliott F.	South Africa, Orange Free State **Bormansdrift (5)**	***Australochelys africanus***
Middle JURASSIC, Bathonian			Morocco: **1** El Mers	Chelonii indet.
C R E T A C E O U S	Valanginian	Kirkwood Formation	South Africa: **2** Algoa Basin	?Chelonii indet
	Barremian		Morocco: **3 Anoual Basin** at Oussikis and Ksar Metlili	**Plesion Pelomedusoides** + Chelonii indet
	Barremian-Aptian		Cameroons: **4** Mayo-Rey River, Mayo Djarendi (E Koum Basin)	Chelonii indet
	Late Aptian	"Continental Intercalaire", lower upper part	Niger: **5 Gadoufaoua, Ebrechko**, Algeria: **6 Aoulef, 7 Timimoun**?	**Araripemydidae, Pelomedusoides including Pelomedusidae**
	Albian-Cenomanian, prior to Early Cenomanian of Baharija	"Continental Intercalaire", late upper part	Algeria : **7** Timimoun, **8** Gara Samani, **9** Garet Touidjine, **10** Djoua at 120 km E Fort Flatters, In Akhamil, 17 km S Alrar; Tunisia: **11** Touil Dehibat, Remada, Bir Kamboute, Dehibat, Gara Er Rehi, Guermessa, Er Ronda, Chenini trail; Morocco: **12** Kem-Kem, Hamada of Guir; Niger: **13** In Abagarit; Mali: **14 Tikarkas**	Araripemydidae, Pelomedusoides, Pelomedusidae, **Bothremydidae, Podocnemididae**
	Early Cretaceous		Ethiopia: **15** Abay River Basin	Araripemydidae, Pelomedusoides as in In Abangarit and Kem Kem (see above)
	Early Cretaceous	Lupata Group	Malawi: **16** Mwakasyunguti area, "Nyassaland", NW Lake Malawi	Pelomedusoides
	Albian-Cenomanian		South Africa: **19 Umtata mouth**, Coast close to Umtafuna & Umzambawi Rivers	**Chelonioidea or Dermochelyoidea indet.**
	Cenomanian		Egypt: **17** Baharija	Bothremydidae
	Cenomanian		Madagascar: **18** Betioky	Bothremydidae
	Cenomanian	Wadi Milk and Shendi F	Sudan: **20** Wadi Abou Hashim and NW Shendi loc., loc. F1/89 and F 2/89	Pelomedusoides, Podocnemididae, Pelomedusidae; - Pelomedusoides
	Senonian		Niger: **21 Ibeceten 1**	Pelomedusoides incl. Podocnemididae, ***Erymnochelys*** group
	Senonian		Madagascar: **22** Berivotro	Bothremydidae
	?Late Cretaceous	Gokwe F., middle of Calcareous Member	Zimbabwe: **23** Gokwe area	Pelomedusoides (aff. *Platycheloides*?)
	Campanian-Maastrichtian	Kababish Formation	Sudan: **24** Abyad Basin	Chelonii indet. (?Bothremydidae)
	Maastrichtian		Niger: **25** Ibeceten 2	Bothremydidae
		Senonian probable Maastrichtian	Angola: **26** Ambrizette	Bothremydidae
			Nigeria: **27** Sokoto: Wurno, Gada, Kworre, Gilbedi	Bothremydidae + indet.
		Dakhla Formation	Egypt: **28** Ammonite Hills	Bothremydidae, Chelonioidea
		Phosphates	Morocco: **29** Benguerir, **30** Oued Zem, **31** Oued Erguita	Bothremydidae, Chelonioidea
			Mali: **32** Tagnout Chaggeret	Bothremydidae

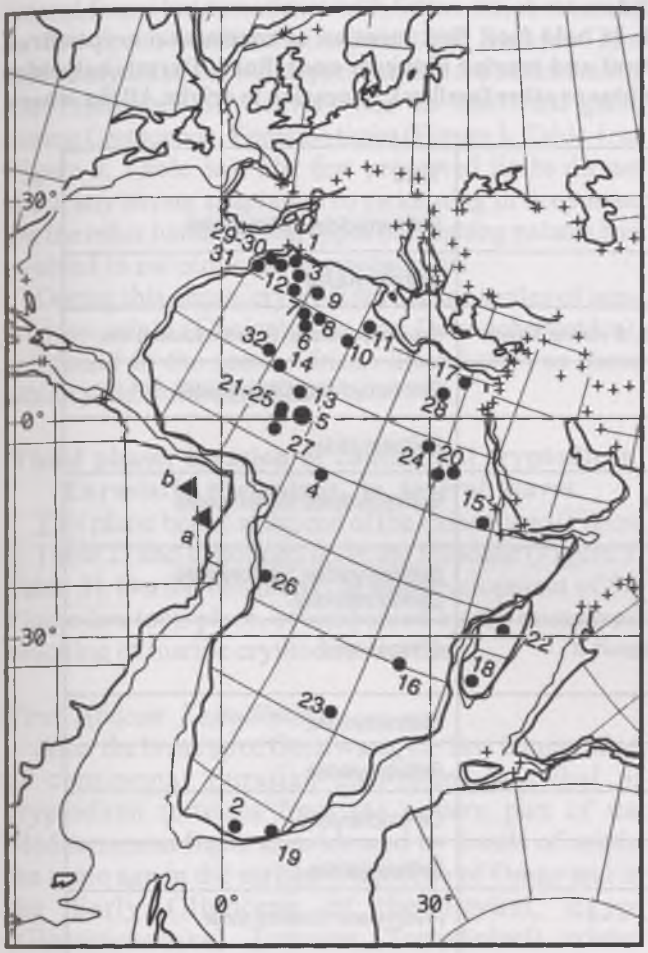


Figure 3. Cretaceous African localities with chelonians, localities 1 to 32, see Table 1 and early Cretaceous close Brasilian localities: a, Bahia and Reconcavo-Tucano Basins, Barremian-Aptian, primitive Pelomedusoides; b, Chapada do Araripe, Ceará, Early Albian, Araripemydidae, various Pelomedusoides including primitive Pelomedusidae and pre-Podocnemidoidea. All the defined taxa are northern Gondwanan elements except the Chelonioidea, which are Laurasian in origin. From Smith & Briden 1977, Hauterivian period.

Pleurodira which developed in southern Gondwana – South America (restricted to Patagonia in Cretaceous times, and probably Antarctica) and Australia. The two extant groups are principally differentiated by the formula of their cervical vertebral joints, which they acquired independently from the formula of primitive amphicoelous vertebrae.

From the Cretaceous to the present, the northern Gondwana Pleurodira evolved various continental forms typical of Africa (Figure 3, Table 1, to Figure 6, Table 4) and others typical of South America. These are, firstly, the plesions of the extant Pelomedusidae, a family which developed only in Africa; then the Podocnemididae and Bothremydidae diverged from the Pelomedusidae and they are known in South America and Africa. The Bothremydidae first developed in Africa; they are not known in the very early Cretaceous of South America. Within the Podocnemididae, the Erymnochelyinae evolved in Africa and later a branch emigrated to southern Western Europe. During the Early Cretaceous, the Podocnemididae also developed in South America with their own branch, the Podocnemidinae, initially in the northern part of South America. Later, they migrated south to meet up with the Chelidae, which in turn migrated northwards (Broin 1988a, 1991, Broin & Fuente 1993; Lapparent de Broin & Fuente 1998; Lapparent de Broin *et al.* 1997). As early as the Late Aptian of Gadoufaoua, Niger, and the Early Albian of Ceará State, Brazil (Broin 1980; Gaffney & Meylan 1991; Lapparent de Broin 1994; Meylan & Gaffney 1991), the species on the two continents and even all the genera, except *Araripemys*, are different, showing the early break in continental links during Cretaceous times.

In India, which at this stage was still linked to Africa, possibly the Bothremydidae and the *Schweboemys* group, a branch of Podocnemididae, developed during the Cretaceous (Jain 1986; Singh *et al.* 1998) and in the Palaeocene. This group is known in Africa at least from the Late Eocene of the Fayum, Egypt, and is also found in late-Early Miocene sediments of Egypt and Arabia.

From the Cretaceous to Early Palaeogene, other Pleurodira developed in Europe, the Dortokidae, from the same ancient ancestral Triassic Pangean origin. However these arose independently, from a Jurassic branch different from that of the African Pleurodira (Lapparent de Broin & Murelag 1996, 1999; Gheerbrant *et al.* 2000).

Undefined marine Cryptodira (Chelonioidea?)

During the Mesozoic period, no Laurasian continental migrations are known into Africa. There is only one record of a possibly marine turtle of uncertain Laurasian origin, on the southeastern coast of South Africa (Albian-Cenomanian). It is possibly an Australian

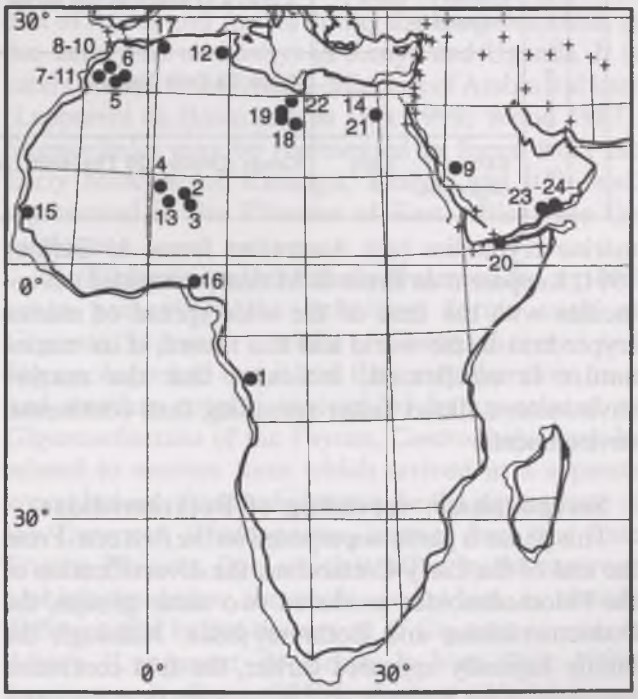


Figure 4. Palaeogene African localities with chelonians, 1 to 24, see Table 2. From Smith & Briden 1977, Early Miocene period.

TABLE 2.

Palaeogene African Chelonian Localities: 1 to 24, Figure 4. In bold face, first mention of continental cryptodires, Testudininei, terrestrial tortoises, Laurasian in origin. Littoral and marine elements underlined, Dermochelyoidea (Dermochelyidae or other families) and Chelonioidea (Cheloniidae or other families), Laurasian in origin. All the others, northern Gondwanan in origin.

Age		Formation	Locality	Taxa
PALAEOGENE	Paleocene	Landana Cliffs	Angola: **1** Cabinda	Bothremydidae, Cheloniidae
			Mali: **2** Cheit Keni, **3** In Farghas	Bothremydidae
		Jbel Guersif F.	Morocco, E Ouarzazate Basin: **5** Ilimzi, **6** Hadrar Mgorn	Pelomedusoides, Pelomedusidae incl.
		Phosphates	Morocco: **7** Benguerir, **8** Oued Zem	Bothremydidae, Chelonioidea
			Saudi Arabia: **9** Jabal Umm Himar	Bothremydidae
	Eocene	Phosphates, Ypresian	Morocco: **10** Oued Zem, **11** Benguerir	Bothremydidae, Chelonioidea
		Phosphates, Ypresian	Tunisia: **12** Gafsa-Metlaoui	Bothremydidae, Chelonioidea, Dermochelyidae
		Ypresian, Ait Ouarhitane F	Morocco, E Ouarzazate Basin: **6** N'Tagourt 2	Chelonii indet.
		Ypresian, Lutetian	Mali: **13** Samit, **4** Tamaguilelt	Bothremydidae
		Early Eocene	Senegal: **15** Popenguine	Bothremydidae
		Middle Eocene	Nigeria: **16** Ameki, Ombialla district	Dermochelyidae
			Somalia: **20** Las Daban (Berbera)	Bothremydidae
		Eocene, Middle-Late	Algeria: **17** El Kohol	Fresh-water Chelonii indet.
		Qasr es Sagha F., Late Eocene	Egypt: **14** Fayum at Birket el Kurun, Abusir, Dineh, NW Qasr es Sagha	Podocnemididae, Dermochelyidae Cheloniidae
		Late Eocene + Early Oligocene?	Libya: **18** Djebel Coquin, **19** Dor et Talha	Pelomedusoides: ?Podocnemididae
	Oligocene	Qatrani F., Early Oligocene	Egypt: **21 Fayum at NW Birket el Kurun**	Podocnemididae, **Testudininei**
			Libya: **22** Zella Oasis	Fresh-water Chelonii indet.
		Ashawq F., Early Oligocene	Oman (Dhofar): **23 Thaytiniti, 24 Taqah**	Podocnemididae, **Testudininei**

marine cryptodire (see Australian forms in Gaffney 1991; Lapparent de Broin & Molnar, submitted). It coincides with the time of the wide spread of marine cryptodires in the world and this record, if its marine nature is confirmed, indicates that the marine environment allows faster spreading than continental environments.

Second phase: spreading of Bothremydidae.

This phase is partly superposed on the first one. From the end of the Early Cretaceous, the diversification of the Pelomedusoides produced two sister groups, the Podocnemididae and Bothremydidae. Although the family logically appeared earlier, the first confirmed members of the Bothremydidae is a form from the Early Cretaceous of the Tafilalt, Morocco (Lapparent de Broin & Werner 1998), equivalent to the late upper part of the 'Continental Intercalaire' of the Sahara. The Bothremydidae rapidly developed new larger forms, including giants, first in the Early Cenomanian of Baharija, Egypt, then in the Cenomanian of Madagascar and Israel. The family diversified into a variety of genera belonging to several groups during Late Cretaceous times (Senonian-Maastrichtian). As early as the Cenomanian, the fossils come not only from sediments deposited in freshwater environments, but also from littoral-marine environments. Taking advantage of the opening of the Atlantic Ocean and progressing along the coast-lines, the family rapidly reached North and South America, along the northern as well as the southern route (Broin 1988b; Lapparent de Broin & Werner 1998). The family is found in the Africa-Mediterranean Basin, Western Europe and the two Americas, from the Cretaceous to the Early-Middle Miocene, mostly with

littoral forms but sometimes with forms which returned to the fresh-water environment in Europe. The Bothremydidae are well represented in the sediments of the Trans-Saharan Seaway and its restricted gulfs during Cretaceous-Ypresian times (Figure 3, Table 1, to Figure 5, Table 3a). The few preserved limbs do not show any strong adaptation to swimming in deep seas. On the other hand, several types of crushing palates had evolved to eat molluscs or crustaceans.

During this phase, cryptodiran marine turtles of non-African origin (Chelonioidea and Dermochelyoidea), are found in the same African littoral sites as those which yield Bothremydidae.

Third phase: invasion of continental cryptodiran Eurasiatic chelonians, in several waves.

This phase began at the end of the Palaeogene (Figure 3, Table 2) and continued up to the Pliocene (Figure 5, Table 3). During this phase, *in situ* development of the Pleurodira took place, accompanied by the occasional beaching of marine cryptodiran turtles.

First African Testudininei

After the breakup of Gondwana, the first immigration of continental Eurasian chelonians was that of cryptodiran tortoises from the eastern part of the Mediterranean Basin as evidenced by fossils of nearly the same age in the earliest Oligocene of Oman and in the Early Oligocene of the Fayum, Egypt (*Gigantochersina*). Tortoises (Testudininei) existed from the Early Eocene of Laurasia: Early Eocene of USA (*Hadrianus majusculus* Hay 1904) and Europe (Broin 1977) and Middle Eocene of Asia (Gilmore 1931; Yeh 1963 and others). The lineages were already differentiated in North America, Europe and Asia by the Middle Eocene at the latest (Broin 1977; Hay 1908; Williams 1950, 1952). From the North American branch leading to the *Gopherus* group diverged the Central and South American group (*Chelonoidis* group). The African forms clearly issued from one of the differentiated genera of Eurasia between the Eocene and Miocene (Eurasiatic *Hadrianus*, *Ergilemys*, *Cheirogaster*, others indeterminate in Asia including ancestors of the living Indian general). Testudininei begin with relatively large forms (at least 40 cm in carapace length) and those arriving in Africa belong to a relatively primitive generalized type '*Hadrianus*' which still retained a cervical scute. Upon their arrival, these Testudininei developed forms typical of Africa but, after the Early Oligocene, there are no records of continental chelonians in Africa until the Early Miocene. Therefore, African Testudininei had nearly all of the Oligocene in which to diversify before the fossil record resumes in the Early Miocene, by which time they had differentiated relative to the primitive Eurasian forms. It is therefore difficult to determine the precise area of their origin. Besides, there is evidence of a second wave of immigrant chelonians in the Early Miocene (see below) which may also have brought tortoises.

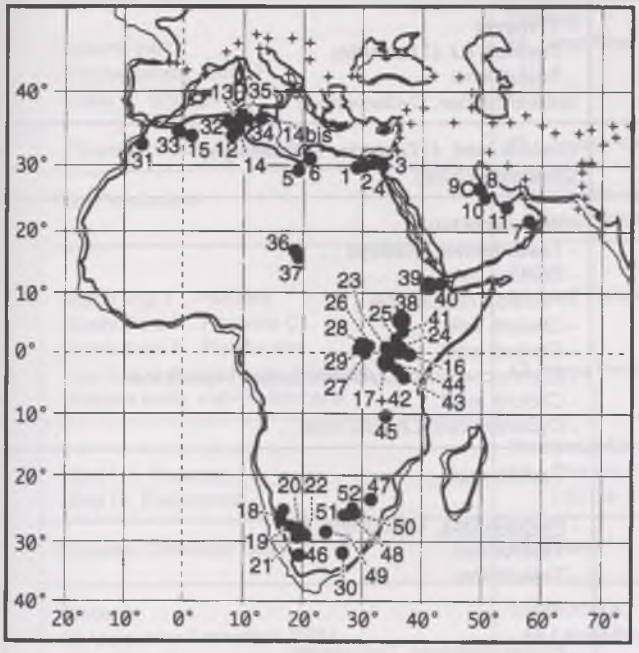


Figure 5. Neogene, Mio-Pliocene African localities with chelonians, 1 to 52, see Table 3a,b,c. From Smith & Briden 1977, Present period.

During the Early Miocene, fossil remains indicate that the diversification of the extant Ethiopian endemic *Kinixys* (a tortoise with a hinged dorsal carapace) from Uganda, and Kenya, (ca. 19-20 myr), and another form related to the Ethiopian endemics, *Impregnochelys* from Kenya (ca. 18 myr) had already occurred. This indicates the minimum age of separation, among African tortoises, of the derived group of Ethiopian endemics from *Centrochelys* Gray 1872, and *Stigmochelys* Gray 1873. In this paper these two taxa are separated from the polyphyletic '*Geochelone*' s.l. (see below). *Centrochelys* may also be represented in the northern part of Africa and Arabia during the Early Miocene, at the same time as *Kinixys* in Kenya and Uganda. It is surely present in the Middle-Miocene of Arabia and later (Lapparent de Broin & Van Dijk 1999; Wood 1987). *Stigmochelys* may be represented in forms from the Early Miocene of Karungu, Kenya, and it is well represented in the Pliocene of East Africa (see the catalogue).

The Ethiopian endemics have preserved the cervical scute present in the primitive forms such as *Gigantochersina*, while *Centrochelys* and *Stigmochelys* had lost it and they may therefore have had another origin: instead of being related to *Gigantochersina* of the Fayum, *Centrochelys* may be related to another form which arrived in a separate wave. Indeed, *Centrochelys* may be the sister group of the European *Cheirogaster*, known from the Late Eocene-Pliocene, from which it differs by the narrower xiphiplastra below the anals, and which is already differentiated before the arrival of *Gigantochersina* in Africa (Lapparent de Broin & Van Dijk 1999; Lapparent de Broin 2000). Among primitive and generalized characters of Testudininei, which give to forms attributed to '*Geochelone*' an erroneous

appearance of close relationship, *Cheirogaster*, *Centrochelys* and *Stigmochelys* share the loss of the cervical (a highly homoplastic character among Testudininei throughout the world) and the associated nuchal notch, as do the two Indian species *Geochelone elegans* (Schoepff 1795), type species of the genus *Geochelone* Firtzinger 1835, and *G. platynota* (Blyth 1863). Relative to *Centrochelys* and *Cheirogaster*, the shell of *Stigmochelys* is different: always higher and often more vaulted, narrower and with a wider dorsal epiplastral lip, rounded instead of flat-concave.

Bour (1985) has already demonstrated, on skull characters, the paraphyly of *Geochelone* including *Cylindraspis*, which is the sister group of *Stigmochelys*. Actually, the two latter forms might just as possibly be related to *Centrochelys* or to the Indian forms as proposed by Bour (1985), or to endemic African forms, an hypothesis which has not been tested because of an arbitrary separation of large forms of '*Geochelone*' from small forms, true *Geochelone* s.s. species excepted. These two extant species are relatively small, respectively ca. 25 cm and 26 cm carapace length, and they do not fit a concept of a '*Geochelone*' being constituted of large forms (carapace length more than 35 cm up to 200 cm).The attribution to the genus *Geochelone* was done by

TABLE 3, a, b, c.

Neogene (Mio-Pliocene) African Chelonian Localities: 1 to 52, Figure 5. In bold face *and* underlined, oldest record of modern pelomedusid genera, 23, *Pelusios* and 19, *Pelomedusa* (not the oldest possible record, *Pelusios* being derived from a *Pelomedusa* stage), northern Gondwanan in origin. To the Gondwanan fauna, addition of Eurasian elements, oldest records in bold. Marine Laurasian elements (Dermochelyidae and Chelonioidea including Cheloniidae) underlined.

Age. Formation		Locality (oldest representatives, age in MY)	Taxa
M I O C E N E	Early	Egypt: - **1 Moghara, 2 Wadi Faregh** (ca18)	- **Carettochelyidae,** Podocnemididae, **Cyclanorbinae**
	Late	- **3** Suez Canal - **4 Wadi Natrun** (ca 6.3)	- Cheloniidae - *Pelusios*. ***Trionyx, triunguis* lineage**, *Mauremys*, Cheloniidae
	Early Late	Libya: - **5 Djebel Zelten** (ca16,5) - **6 Sahabi** (ca 6,5)	- Podocnemididae, **Testudininei: cf. *Centrochelys*** - ***Trionyx, triunguis* lineage**,Testudininei
	Early: Dam F.	Oman: **7 Ghaba** (ca18)	Bothremydidae, Podocnemididae, **Carettochelyidae, Cyclanorbinae,**Testudininei
	Early to Middle: - Dam F - ?Dam F. - Hofuf F.	Saudi Arabia: - **8** As-Sarrar - **9** Chalon - **10** Al-Jadidah	- ?Bothremydidae, Podocnemididae, Carettochelyidae, Cyclanorbinae, Testudininei - Cyclanorbinae - Testudininei
	Middle. Bayunah F.	**11 Abu Dhabi**, Western Region (ca 8)	**Trionychinae, *Mauremys*,Testudininei: *Centrochelys***
	Lower part of Late Mlocene	Tunisia: - **12 Bled Douarah** (ca 11) - **13 Djebel Semene** (ca 10+) - **14** Djebel Krechem Malta: **14bis**	- ***?Trionyx*** - ***Testudo s.l.* (*?Testudo*)** - Testudininei Bothremydidae, Cyclanorbinae
		Algeria: **15 Bou Hanifia** (ca 10,5), Saint-Eugène	Chelonii indet. **(*?Testudo*, *?Mauremys*)** Cheloniidae indet
	Early	Kenya: **16**: - **Koru,** (ca19-20) - **Songhor** (ca 19-20) - Mteitei area **17**: - Rusinga Island, - Mfwangano Island - Uyoma Peninsula. - **Karungu,** (ca 18) - Gwasi Peninsula, - Ombo	- **?Cyclanorbinae** - **Testudininei: *Kinixys*** - Chelonii indet. - *Pelusios*,Testudininei - Chelonii indet. - Chelonii indet. - Erymnochelyinae, **Cyclanorbinae**, Testudininei - Chelonii indet. - Cyclanorbinae, Chelonii indet.
	Early Middlle Early	Namibia: **18** - Fiskus, Grillental, Elisabethfeld **19**: - **Langental** (ca 19), - Glastal **20**: - Rooilepel (wardi, laini), Karingarab, North of Gypsum Plate Pan, **21** - Arrisdrift **22** - Auchas	- Testudininei - ***Pelomedusa***, Testudininei - Testudininei - Testudininei - Erymnochelyinae, Testudininei - Erymnochelyinae, Testudininei
	Early	Uganda: **23**: - **Napak,** (ca 19-20) - Moroto	***Pelusios***. Testudininei: ***Kinixys*** Chelonii indet.

Age, Division, Formation		Locality	Taxa
Mio-Pliocene	Ngorora F., Mpesida beds, Lukeino F., Miocene; Kaperyon F., Chemeron F., Aterir beds, Pliocene; Chemoigut beds, Pleistocene	Kenya: **24**: Baringo Basin	- *Pelusios*, Cyclanorbinae, Testudininei, Chelonii indet.
	(1) Late Miocene (2) Pliocene	**25**: Kerio River Basin: (1) Lothagam (2) Kanapoi, Ekora	Erymnochelyinae, Cyclanorbinae, Testudininei
	Mio-Pliocene: (1) Late Miocene, Oluka F. Early to Late Pliocene: (2) - Nkondo F. and (3) - Warwire F. (4) - Nyakabingo F. (5) - Kaiso beds	Uganda, SW and E Lake Albert (1) - **27** Kisegi-Nyabusosi area (2) - **26** Nkondo-Kaiso (3) - **26** Nkondo-Kaiso (4) - **27** Kisegi-Nyabusosi area (5) - **26** Kaiso Village	- Cyclanorbinae - *Pelusios*, Cyclanorbinae - *Pelusios* - *Pelusios* - Cyclanorbinae - Pelomedusoides indet., Cyclanorbinae, Testudininei
	- Kaiso beds, Pliocene - Late Miocene-Pliocene, Ongoliba and Sinda beds, - Lusso beds, Pliocene	Congo-Zaïre, West Lake Albert: - **28** Lower Semliki River, - **28** Sinda-Mahori Rivers Region, Lower Semliki River - **29** Upper Semliki-Senga Rivers	-Testudininei - Pelomedusoides, Erymnochelyinae, Carettochelyidae, Cyclanorbinae - Pelomedusoides, *Pelusios*, Cyclanorbinae, Testudininei
	Tertiary, probable Late Neogene	South Africa: **30 Carlisle Bridge**	Testudininei: **first *Homopus***

Age, Division, Formation		Locality	Taxa
Pliocene/Plio-Pleistocene	Pliocene	Tunisia: - **34** Hamada Damous - **35 Ichkeul** (ca 3,5)	- ?*Mauremys*, ?*Testudo* - *Trionyx*, ?*Mauremys*, ***Testudo s.s.***, Testudininei
	Pliocene	Chad, Koro Toro: **36** Ouadi Derdemi, **37** Bahr el Ghazal	*Pelusios*, *Trionyx*, Testudininei, Chelonii indet.
	Pliocene	Morocco: **31** Ahl Al Oughlam (ca 2-2,5)	*Testudo*
	Pliocene	Algeria: - **32 Aïn Boucherit** (ca 2) - **33** Puits Karoubi	- ***Mauremys leprosa***, *Testudo*, ?*Trionyx* - Chelonii indet.
	Pliocene part: - Yellow Sands, Mursi F. - Usno F., Shungura F., - Pliocene, Hadar F. included	Ethiopia: **38** Omo River Basin: - (1), - (2) **39** - Awash Valley, Afar	- *Pelusios*, Cyclanorbinae - *Pelusios*, cf. *Trionyx*, Cyclanorbinae, Testudininei - *Pelusios*, Cyclanorbinae, Testudininei
	Plio-Pleistocene	Djibouti: **40** - Annabokôma Chekheyti, - Gobaad plaine	- Testudininei - *Pelusios*
	- Koobi Algi F., Pliocene - Koobi Fora F., Pliocene C - Koobi Fora F., Pleistocene - Homa and Kanam beds, Pliocene - Kanjera beds, Plio-Pleistocene	Kenya: **41** East Turkana - (1), - (2), - (3) **42** Homa Peninsula, Kanam (1), Kanam (2)	- *Pelusios* - *Pelusios*, Cyclanorbinae, Testudininei - *Trionyx*, Cyclanorbinae, Testudininei Chelonii indet. Chelonii indet.
	- Bed I, II, Pliocene, - Bed IV, Pleistocene	Tanzania: **43 - Laetoli area** (ca 3,6-3,8) **44** - Olduvai (1) - Olduvai (2)	- **Testudininei, incl. *Stigmochelys*** - *Pelusios*, Pelomedusoides, Testudininei - Testudininei
	Pliocene, Chiwondo beds	**45** Malawi	*Pelusios*, Cyclanorbinae
	Pliocene 46: Varswater Formation, PPM	South Africa: - **46 Langebaanweg** (ca 4-4,5) - **47** Makapansgat, **48** Sterkfontein Member 5 - **49** Taungs - **50** Kromdraai A, B, **51** Swartkrans, Member 2 - **52 Drimolen** (ca 2 - 1,8-1,6)	- Testudininei **?incl. first *Chersina*** ?*Pelomedusa* - Testudininei - *Pelomedusa* - Testudininei
	Plio-Pleistocene		**Testudininei: *Psammobates***

TABLE 4, a, b, c.

Quaternary (Pleistocene-Holocene) African Chelonian Localities: 1 to 70, Figure 6. Underlined, marine Laurasian elements. In bold face, oldest records of tortoises from Madagascar area. Table 4a, locality 'Haaskraal', South Africa, Late Holocene: unlocalized on Figure 6, see Sampson, 1998.

Age	Locality	Taxa
Pleistocene-Holocene	Morocco: Occidental Morocco **1** - Kenitra **2** - Coast from Rabat to Temara (a), Rabat 8, 9, 10, - Coast from Rabat to Temara (b), Rabat 6, - Carrière Thomas I, Aïn Bahya, - Dar Es Soltane, - Bouknadel, - Doukkala II, - Mehdia, Toulkine-Bou Ben Adam **3** - Jebel Irhoud, Oualidia, - Aïn Rohr, El Khenzira Oriental Morocco: **4** - Taforalt **5** - Rhafas Cave, El Heriga, Abri Rhirane, Keneg Kenadsa - Abri Bou Guennouna - Oued el Haij Terrace, Jorf el Anngra	 - *Testudo* - *Testudo* - *Trionyx* - *Testudo* - *Mauremys*, *Testudo*, - Testudinidae - *Mauremys*, *Testudo*, - *Testudo* - *Testudo* - Testudinidae - *Mauremys*, *Testudo* - Testudinidae - *Testudo*, Testudinidae - Testudinidae
Pleistocene-Holocene	Algeria: **6** -Tighenif - Archaelogical sites Oran province, North of Aurès **7** - Mansourah - Archaelogical sites, Constantine province Tunisia: **7bis**, Archaelogical sites Malta: **7ter**	- *Mauremys*, *Testudo* -*Testudo*, *Mauremys*? - *Mauremys* -*Testudo*, *Mauremys*? *Testudo*, *Mauremys*? Testudininei, *Mauremys*
Pleistocene	**8** Cape Verde islands: Pedra de Lume	Testudininei
Pleistocene-Holocene	Chad: **9** - Djourab, El Djour, Goz Kerki Recent, Bochianga, Neo-Bochianga, - **10** Low Lands of Chad, **9** Borkou and **11**Tibesti, - **11** Puits Tirenno (Tibesti)	- *Pelusios*, *Trionyx*, Cyclanorbinae, Testudininei - *Trionyx* - *Pelusios*, Cyclanorbinae
Pleistocene	Sudan: **12** Wadi Halfa	Chelonii indet.
Pleistocene	Saudi Arabia: **13** An Nafud	Testudininei
Pleistocene	Kenya: **14** Rawi	Testudininei
Pleistocene	Tanzania: **15** Lake Eyasi - Mumba Cave	*Pelusios* - Testudininei
Pleistocene-Holocene	Mozambique: **16** Zambezi tributary Lesotho: **17** Holocene sites	Cyclanorbinae Testudininei, Chelonii indet.
Pleistocene-Holocene Historic	South Africa: **18** (N to S), Leliehoek Shelter; Oakleigh; Edgehill-Welgeluk; **19** Hantam Mountains; **20** (N to S) Elands Bay Cave, Klipfonteinrand Cave,Hopefield, Die Kelders 1, Byneskranskop Cave 1 - (Haaskraal) **21** Brandberg	Chelonii indet.; Testudininei; *Pelomedusa*, *Stigmochelys*, *Chersina*, *Homopus*; *Homopus*, *Chersina*; - (*Pelomedusa*, *Stigmochelys*, *Psammobates*, *Homopus*) *Stigmochelys*

reference to the large African species *Testudo sulcata* (up to 90 cm) which was attributed by Fitzinger (1836) to *Geochelone* before the erection of the genus *Centrochelys* Gray 1872, for that species. The mistake of many zoologists was then to consider as monophyletic a special group of large forms, when it was nothing more than a regrouping of large forms with the practical aim of determination (Auffenberg 1974; Wermuth & Mertens 1961; Iverson 1992). Cladograms have therefore been proposed for the large forms : - for '*Geochelone*' by Crumly (1982); - for the 'phylum' (sic) Chelonoidina Gray, approximately corresponding to the extant '*Geochelone*' s.l. by Bour (1985). Another cladogram has been proposed for all the group of tortoises, called the 'Testudinidae', by Gaffney & Meylan (1988), also separating the large '*Geochelone*' forms from the others. All these studies are principally based on skull characters without any accurate study of the shells and they do not include the fossil elements of the various radiations from their appearance in Eocene times, in each continent.

Even though all the fossil African forms have not yet been determined, it is possible that there were two or three waves of immigration, besides which there are three lineages of Testudininei in Africa, which deserve separate names, namely: *Centrochelys*; the Ethiopian

Age	Locality	Taxa
Holocene - Historic †	Madagascar: **57 Gloriosa, 58** Mahajanga area, **59** Ampasambazimba, **60** Antsirabe, western-southern area between **61** Ambato (Morondava) and **64** Andrahomana (Taolanaro) including **62** Etsere and **63** Ambolisatra,	***Dipsochelys***
Holocene - Historic † Present	- **61 Ambato, 61 Ankevo, 60 Antsirabe**, **63** Ambolisatra, **64** Andrahomana, Antinosi	***- Astrochelys***
Holocene - Historic Present, in part †	Aldabra area: **65** Granitic Seychelles islands, **66** Seychelles atolls including Aldabra	*Dipsochelys*
Historic	Comoros islands, Mayotte island: **67** Dembeni 1 (introduced from Madagascar)	*Erymnochelys*, *Pyxis*, *Astrochelys*, *Chelonia*
Holocene - Historic †, Present	Mascarene islands : **68 La Réunion**, **69** Mauritius, **70** Rodrigues **69** Mauritius (introduced with other taxa)	***- Cylindraspis*** - *Dipsochelys*

Age	Locality	Taxa
Holocene	Algeria: **22** Ti-n Hanakaten	*Pelomedusa*, Testudininei
Holocene	Mauritania: **23** Chami	Testudininei
Protohistoric	Senegal: **24** Sintiou Bara, **25** Tulel-Fobo - Faboura	Cyclanorbinae - Cheloniidae, *Trionyx*
Holocene	Mali: Taoudenni Basin: **26** - Araouan, Guir, Djouf **27** - Hassi el Abiod **28** - Erg Ine Sakane **29** - Kobadi	 - *Trionyx*, Cyclanorbinae - *Pelusios*, *Trionyx*, Cyclanorbinae - *Pelusios*, Cyclanorbinae - *Trionyx*
Holocene	Niger : Tenere: **30** - Adrar Bous - **31** Tin Ouaffadene, **32** - Bilma, Kaouar **33** - Azaouak Valley : - In Aruinat - Ikawaten - Takane Barva - Pr Baumhauer site	- *Pelusios* - Testudininei - *Pelusios* - *Pelusios*, Cyclanorbinae - Cyclanorbinae - *Trionyx* - *Pelusios*, *Trionyx*
Protohistoric	Chad: **34** - Sao de Mdaga **35** - Koyom	- *Pelusios* - *Pelusios*, Cyclanorbinae
Protohistoric	Ghana: **36** Mole National park	Cyclanorbinae
Holocene	Nigeria: **37** N Maiduguri, Chad basin	*Pelusios*
Protohistoric	Cameroons: **38** - Sou, - Lake Chad	- *Pelusios*, Cyclanorbinae - *Pelusios*
Holocene	Libya: **39** - Djebel Zelten, - ?S Cyrenaïca, Libyan desert	- Cyclanorbinae - *Pelusios*
Holocene	Egypt: **40** - Toukh, **41** Fayum at Birket el Kurun, **42** Adaïma **43** - Berenike **44** - Abu Ballas	- *Trionyx* - *Chelonia*, Testudininei - Testudininei
Holocene-Protohistoric	Sudan: Nile Valley at **45** - Saggai and Geili, - Umm Marihi **46** - El Kadada **47** - Debbat Bangdit **48** - Debt El Eheima. Atbara River Valley at: **49** - Khashm el Girba **50** - Jebel Shaqadud West to Nile Sudan at: **51** - Burg et Tuyur **52** - Wadi Howar 80/73	- *Pelusios*, *Trionyx*, Cyclanorbinae - *Pelusios*, Testudininei - *Pelomedusa*, *Trionyx*, Cyclanorbinae - *Pelusios*, *Trionyx*, Cyclanorbinae - *Pelusios*, Cyclanorbinae - *?Pelusios*, *Trionyx*, Cyclanorbinae, Testudininei *Pelusios*, Testudininei - Testudininei - *Pelusios*
Holocene Delta	Ethiopia: **53** Awash Valley, Afar	Testudininei
Holocene	Congo-Brazza: **54** Ntadi Yomba	Testudininei
Holocene	Congo-Zaïre: **55** - Matupi Cave **56** - Malemba-Nkulu, Sanga	- Testudininei - *Pelusios*

endemics; and *Stigmochelys*. The lineages separated at ca. 20 myr, each one having developed several species since then. Furthermore, it is no longer possible to attribute to '*Geochelone* s.l.' large forms which have not been accurately studied and compared, and which are actually included in constituted lineages of different continents, themselves separated from Early Eocene times and in Africa at least from the Early Miocene. There is no diagnosis of *Geochelone* which corresponds to all the taxa that are attributed to this artificial genus and its definition is confused in the literature (Auffenberg 1974; Loveridge & Williams 1957; and others). Meylan & Auffenberg (1986), acknowledge that the 'genus' is not monophyletic and employ it simply for convenience. Because there is no consensus on the definition of *Geochelone*, the name must therefore be restricted to the extant Indo-Asiatic type species, *G. elegans*, and possibly to *G. platynota*, which is regarded as close by some workers, and their possible fossil relatives which are not yet recognized in the fossil forms from Asia.

Arrival of first Trionychoidea:

The oldest Trionychoidea, including Carettochelyidae and Trionychidae, are known from the Late Jurassic–Wealden of China. The Carettochelyidae are represented in Arabia-northern part of Africa at the base of the Miocene. This family is known from the base of the Early Eocene in North America and in Europe (MP 7-8) (Broin 1977). However, the African-Arabian form has shell characters of the Eurasiatic subfamily Carettochelyinae, with an anterior carapace border more similar to that of *Allaeochelys* (the European form) and more primitive than that of the extant *Carettochelys* of New Guinea-northern Australia. The Carettochelyinae of the Indian subcontinent could also be an ancestor (Broin 1987), but they are too poorly preserved for meaningful comparison.

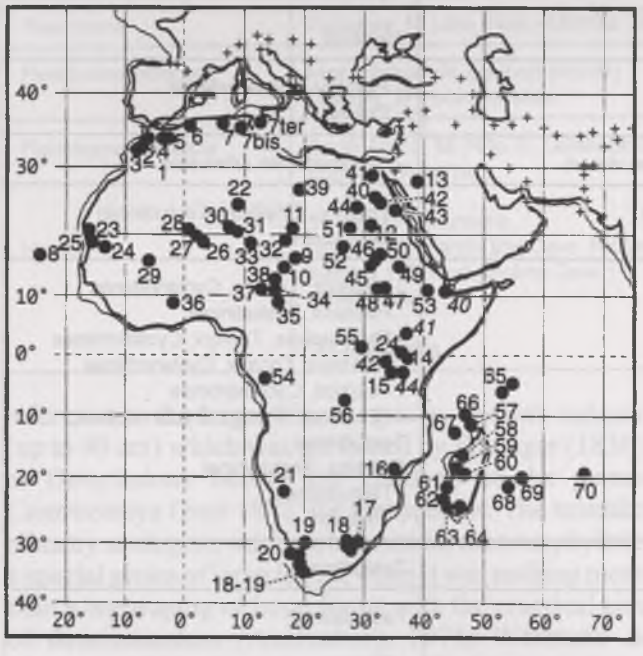


Figure 6. Quaternary, Pleistocene-Holocene and Historic African localities with chelonians, 1 to 70, see Table 4a,b,c. Missing locality: 'Haaskraal', South Africa, late Holocene (unlocalized; see Sampson 1998). From Smith & Briden 1977, Present period.

Trionychidae Cyclanorbinae must have originated from an undifferentiated Asiatic trionychid. Cyclanorbinae are unknown before their arrival in Africa, first appearing in the fossil record at the same time as the Carettochelyidae in Arabia and the northern part of Africa. The two taxa might have arrived together, crossing eastern Tethys by following the coastline. Cyclanorbinae are also recorded farther south at Karungu, Kenya (ca. 18 myr), and an undefined trionychid was already present at Koru (ca. 20 myr), which might indicate that Cyclanorbinae were present a little earlier than Carettochelyidae. The Cyclanorbinae developed forms typical of Africa, *Cycloderma* and *Cyclanorbis*, while *Lissemys* developed only in India. As well as the primitive African Testudininei, the primitive African Cyclanorbinae are not yet well defined because of insufficient material. The origin of the Cyclanorbinae is completely unknown but probably should be sought in the Indian subcontinent: once India contacted Asia, as early as the Eocene in Pakistan, trionychid remains are found which might be related to the Cyclanorbinae (Broin 1987), but the sub-family itself is known in this subcontinent only from the Late Miocene (Siwaliks of the Potwar Plateau, Pakistan, and of Ramnagar, India, in the Chinji Formation, ca. 10,5 and 13-14 myr respectively), long after their record in Africa. While Cyclanorbinae still survive today, the Carettochelyidae disappeared during the Early Pliocene, the last known remains coming from the Lower Semliki in the Democratic Republic of Congo.

Arrival of the extant Palaearctic fauna

A new wave of Eurasiatic immigrants occurred during the Middle-Miocene which brought in *Trionyx*, *Mauremys* and *Testudo* s.s. (Figure 5, Table 3a, 3c). The first references to these taxa are of dubious value (lower part of the Late Miocene, Algeria, Tunisia). However, a true Trionychinae, although not *Trionyx* s.s., and a *Mauremys,* primitive or related to the extant *M. caspica* from the eastern Mediterranean Basin (including the Arabian Peninsula on the Arabian Gulf border) are confirmed in the Baynunah Formation of the Emirate of Abu Dhabi (ca. 8 myr), probably coming to northern Africa from the east of the Mediterranean Basin. During the Pliocene, the presence of *Trionyx* s.s. (lineage of *Trionyx triunguis)*, *Mauremys* and *Testudo* s.s. is confirmed in the northern part of Africa (Sahabi, Wadi Natrun and later the Maghreb, with extant lineages). The first *Trionyx triunguis* is attested in Kenya (Koobi Fora Formation, upper members) only during the beginning of the Pleistocene. On the other hand, *Mauremys* and *Testudo* did not reach the southern Nile valley and become permanently established in northern Africa. *Trionyx* disappeared from this area during the Late Pleistocene, after the conquest of all the

northern mid-part of Africa and a part of the south-western margin.

The origin of the Palaearctic chelonian fauna of Africa is probably from the Mediterranean Basin because *Trionyx* s.s. belongs to a group represented in Europe from the Palaeocene, although the lineage of the extant *T. triunguis* truly diversified only during the Late Miocene in northern Africa. The same is true for *Mauremys*, represented in Europe from the Oligocene, with possible earlier plesions (*Palaeochelys* s.s.): however the lineage of the extant *Mauremys* is confirmed only from the Pliocene. The earliest confirmed occurrence of the extant Maghrebian and Franco-Spanish form, *M. leprosa*, is from the Pliocene of Aïn Boucherit, Algeria (ca. 2 myr) although it had most probably already differentiated before that (*fide* some of the material from the Maghreb, most of which regrettably is lost).

As far as *Testudo* s.s. is concerned, a genus characterized by the presence of a hypo-xiphiplastral hinge in both males and females, poorly preserved Maghrebian forms attributed to the genus *Testudo* s.l. are known from the lower part of the Late Miocene, but the definitive presence of *Testudo* s.s. in Africa is only from the Pliocene of Ahl Al Oughlam, Morocco (ca. 2 to 2,5 myr), and possibly from Ichkeul, Tunisia (ca. 3,5 myr). The first mention of a true *Testudo* s.s. in Europe is only from the Late Miocene of Pikermi and Saloniki, MN 12-13, Turolian (Gmira 1995), but ancestral forms of *Testudo* s.l. existed from the Oligocene. Its precise point of differentiation remains unknown.

During all of the Late Miocene and Pliocene in the northern part of Africa, large and giant forms of tortoises attributed to '*Geochelone*' s.l. or to '*Testudo*', coexisted with *Testudo* s.s.: their phyletic relationships and their origin are unknown, although a relationship with *Centrochelys* is possible or even probable in some localities.

Continuation of in situ development of Pelomedusoides during theTertiary

The *Erymnochelys* group, characterized by its gulars linked behind the intergular, is first recorded from Early Cretaceous sediments of Niger (Ibeceten 1), and it continued its development in the northern part of Africa (Egypt, Arabia) during the Late Eocene and Early Miocene (no data available from the Palaeogene up to Fayum times), with its principal collaterals, *Stereogenys* and *Schweboemys*, known from the Late Eocene of Fayum. The oldest known occurrence of the latter is from the Cretaceous of the Indian subcontinent. Later, the group migrated to Pakistan (Early Miocene) and to Burma (Plio-Pleistocene) but there are no post-Early Miocene records from Africa-Arabia. The *Erymnochelys* group first reached East Africa and Namibia during the Early Miocene, and continued its development during the Late Miocene-Pliocene only in East Africa. This *Erymnochelys* group is no longer known from Africa from the Early-Mid Pliocene; *Erymnochelys* survives today as a refugee in Madagascar. Its disappearance is comparable to that of Carettochelyidae.

After their record from the Early-Mid Cretaceous of Sahara and Thanetian of Morocco, the Pelomedusidae disappear from the record throughout the Palaeogene. They reappear in the Early Miocene of Langental, Namibia (ca. 19 myr), with a new species of *Pelomedusa* discovered recently (1998). This genus is a fragile form which is rarely fossilized (Wood 1973b). There is no further record until the Pliocene of Langebaanweg, South Africa, and then it is known from only a few citations up to the Present. On the other hand, *Pelusios*, a box-turtle and a form robust and more derived than *Pelomedusa*, is currently found from the Miocene of Uganda (ca. 19-20 myr) and Kenya (ca. 18 myr) and it still survives today.

Marine cryptodiran forms

There are very few records of marine Cryptodira in Africa during the Late Palaeogene-Neogene; some localities in Egypt (Fayum, Suez, Wadi Natrun) record their passage between the Mediterranean Basin and the northern Atlantic up to the North American coast.

Emigration from Africa

Other than the littoral Bothremydidae, only the Erymnochelyinae seem to have emigrated from Africa during the Tertiary. *Neochelys,* a genus also possibly represented in the Late Eocene of the Fayum, is known in western Europe from the earliest part of the Early Eocene (MP 7; Broin 1988a). It may have arrived earlier, but it is not yet recorded in the rare European Palaeocene localities. *Erymnochelys eremberti* Broin 1977 (with the intergulars linked behind the gular, the curved premaxillary and mandibular hook, the prolongated temporal roof and the absence of lateral cheek emargination, characters typical of the genus) is known from the Mid-Eocene of France. The members of the *Schweboemys* group present in the Late Tertiary-Pleistocene of Pakistan and Burma may also be immigrants from the north of Africa-Arabia.

Phase of diversification and endemism

From the Pliocene to the Holocene (Figures 5 and 6, Tables. 3b-ç and 4), localities with continental chelonians are more abundant, first in the Maghreb, the East African Rift Valley and in South-Africa, then in the northern part of Africa. The communicating basins of the Nile, Chad, Niger and Senegal constituted a favourable area for the spread of turtles. All the extant genera of turtles then diversified and no new taxon entered Africa during that time. However, the diversity of species increased locally. Several independent waves of chelonians, tortoises and turtles, entered Madagascar and the surrounding Indian Ocean islands from Africa at an uncertain date (data from 125 000 years at Gloriosa) (Figure 8) and they diversified widely. The oldest known tortoise, *Dipsochelys*, is probably related to

Astrochelys (itself possibly linked to the Ethiopian endemics); *Cylindraspis* is probably related to *Stigmochelys* (Bour 1984a,b, 1985, 1987); *Pyxis* (no known fossil record, but sub-fossil historical data) is linked to the African Ethiopian endemics. *Dipsochelys* and *Cylindraspis* were exterminated by humans, the last citations being from ca. 150 years ago, except for *D. e. elephantina*, which is still present in Aldabra and recently introduced to other islands. Gerlach & Canning (1998) consider that some individuals living in captivity on granitic Seychelles belong to the extinct *D. hololissa* and to *D. arnoldi*. However, such a sensationally novel suggestion has not yet gained acceptance among the scientific community, partly because the morphological data are unclear and not fully in accord with the original descriptions of the species, and partly because the published genetic data are inconclusive. Without deliberately rejecting these results, it seems premature to give them full confidence, and we prefer to wait for further, more decisive data (Bour pers. comm.).

The freshwater Pelomedusidae also entered Madagascar and Seychelles, at an uncertain date (Figure 7) but sufficiently long ago to allow for their known diversification.

Regressive phase (end of Holocene-Present)

The figures showing extant turtle distribution (Iverson 1992; Figures 7 & 8) compared with figures of fossil data (Figures 5 & 6) during the Miocene-Holocene time, show the important faunal reduction due to climatic change at the end of the Holocene. Climatic alternations of cooling and/or drying periods with intercalations of humid periods, eliminated *Trionyx* and the large tortoises from the Maghreb, leaving only the extant palaearctic elements, *Testudo* and *Mauremys*. The aridification of the Sahara pushed back the other elements of the African endemic chelonian fauna to the limits of the Sahel (Broin 1983, fig. 50; Roset *et al.* 1990, fig. 5) and in the reduced area of the Sahel, extant records are few and isolated. Even the desert tortoise, *Centrochelys sulcata*, no longer occupies all of its potential distribution area after so many Holocene climatic fluctuations. *Emys orbicularis* (unknown as a fossil in Africa) arrived in the Maghreb from the Mediterranean Basin and it is the last known immigrant of the Palaearctic fauna into Africa. It is a recent genus, known from the Late Miocene of Ukraine, Pliocene of Poland and Slovakia and the Pleistocene-Holocene of southern Europe. It has the most northerly distribution of the extant European fauna (Iverson 1992; Figure 8) and its adaptation to Africa is most probably linked to climatic changes.

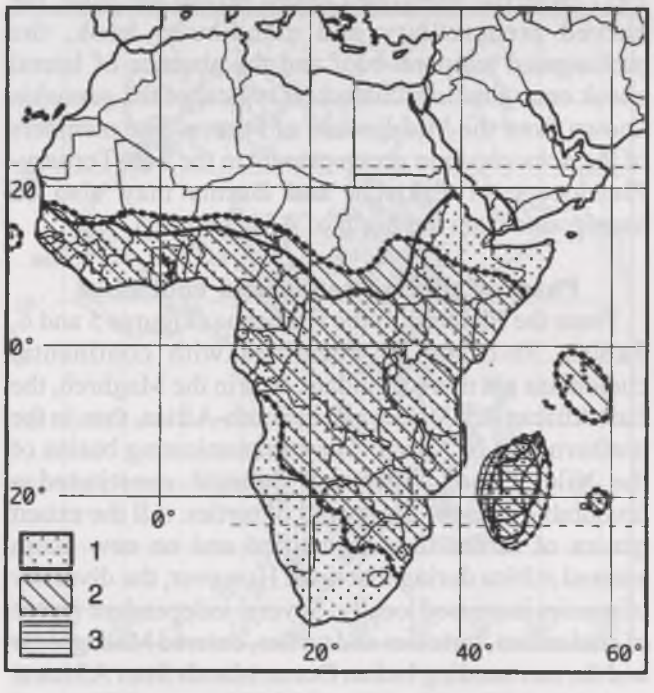


Figure 7. Present approximate limit of distribution in Africa, Arabian Peninsula and Madagascar area, of extant Pleurodira: Pelomedusidae, 1, *Pelomedusa*, 2, *Pelusios*; Podocnemididae, 3, *Erymnochelys* (Madagascar only). From Smith & Briden 1977, Present period.

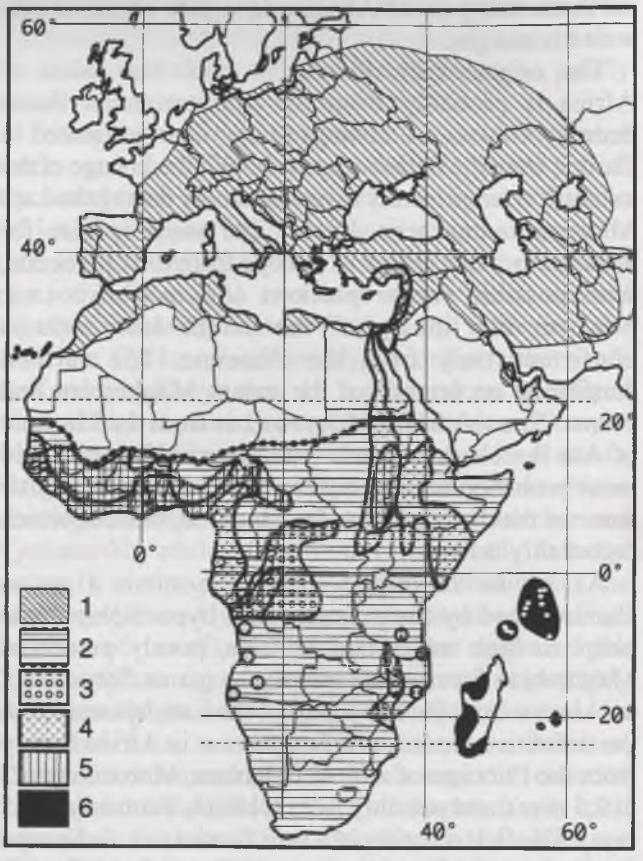


Figure 8. Present approximate limit of distribution, in Europe, Africa, Arabian Peninsula and Madagascar area of extant continental Cryptodira: 1, Palaearctic fauna, freshwater *Emys* and *Mauremys*, tortoise *Testudo* s.l.; 2, African tortoises, Testudininei, endemics and *'Geochelone' i.e. Stigmochelys* and *Centrochelys*; freshwater turtles, outside of North Africa: 3, *Cycloderma* (left, *C. aubryi*, right, *C. frenatum)*, 4, *Trionyx*, 5, *Cyclanorbis* (both left and right, *C. elegans* and *C. senegalensis*); 6, Indian Ocean and Madagascar islands, Testudininei. From Smith & Briden 1977,

PRELIMINARY CATALOGUE OF THE FOSSIL CHELONIANS OF AFRICA

Stratigraphic and geographic distribution of the taxa

The countries are presented in alphabetical order and for each country, the order of information supplied is: stratigraphic division: locality, area, geological formation (when known), age, taxa (new and first determination and references).

When possible, an appropriate determination is proposed for the reviewed material, following recent taxonomies which divide the families s.l. or genera s.l. (for example 'pelomedusid', 'trionychid' or *Geochelone*, *Testudo*, *Podocnemis*) into monophyletically more precise elements. The original definition is given (quotation marks, brackets). The determinations may differ from those proposed in earlier works of mine.

The present geographic distribution of the taxa is given in Iverson's (1992) figures. Some general stratigraphic and geographic data on fossil localities are given in Cooke (1978) (all Africa), Pickford *et al.* (1993) and in references given by the authors of taxa. The position of the land masses from the Jurassic to Present are from Smith & Briden (1977) (see also Smith *et al.* 1994).

The museum repository of the undescribed or reviewed material is given. The references to localities are not exhaustive, including only those with the first mention of chelonian taxa and their further taxonomic modification and at least one for the stratigraphic and geographic position of the localities.

Lists of fossil and living chelonians are principally given by Kuhn (1964), Wermuth & Mertens (1961, 1977) and determinations of the extant African chelonians are principally from Loveridge (1941) and Loveridge & Williams (1957); general ecological information is presented in Pritchard (1979). It is impossible in this catalogue to cite all the references relating to extant African chelonians but additional references may be found in the following older works: Baur (1888a, b); Boulenger (1889); Cope (1868); Duméril (1855-1856); Duméril & Bibron (1835); Fitzinger (1826, 1835, 1836, 1843); Gray (1825, 1855-1870, 1872, 1873); Hewitt (1914, 1927); Schweigger (1812); Siebenrock (1902); Smith (1838-1849); Wagler (1830); or in more recent such as: Bour (1981, 1983, 1986); Broadley (1981a,b, 1983, 1993, 1997a,b); Gerlach (1998, 1999); Laurent (1956, 1964, 1965) etc. The given MN ('Mammal Neogene') ages are from Mein (1990), the given MP ('Mammal Palaeogene') ages are from Escarguel *et al.* (1997).

AFRICA

ALGERIA

Cretaceous: 'Continental Intercalaire' of Sahara, of Kilian (1931) (see Furon 1955; Lapparent 1960), upper part, Early Cretaceous MNHN (Broin det.):

Late Aptian, A.F. de Lapparent coll.,

Aoulef, Tidikelt, Late Aptian, Araripemys sp.: Fuente & Lapparent de Broin (1997).

Timimoun, Gourara (Foggara Amerhaïer), Late Aptian?, Araripemys sp.,

Albian-Cenomanian prior to Cenomanian age of Baharija and to marine Cenomanian transgression,

Timimoun, Gourara (Foggara Amerhaïer), ?*Araripemys* sp.: Fuente & Lapparent de Broin (1997), first given as 'Primitive trionychoids': Broin (1977); Pelomedusoides indet.; A.F. de Lapparent coll.

Gara Samani, between El Golea and Timimoun (Broin *et al.* 1971), *Araripemys* sp.: Fuente & Lapparent de Broin (1997), first given as 'Primitive trionychoids': Broin (1977); Fuente & Lapparent de Broin (1997); Pelomedusoides indet. including Podocnemidoidea (?Podocnemididae, Bothremydidae).

Oued Boudjihane area, close to Atlas (Ksour), E of Aïn Sefra, (Bassoulet & Iliou 1967), Iliou coll. and MNHN (coll. Bassoulet):

a - Garet Touidjine, *Araripemys* sp.: Fuente & Lapparent de Broin (1997);

b - Gouret Tin (high level, East), Pelomedusoides indet.

Djoua (El Djoua), type locality of the 'Continental Intercalaire' of Kilian (1931, see Furon 1955),

120 km E Fort Flatters, In Akhamil and 17 km S Alrar, E Algeria close to Libyan border; several taxa of Pelomedusoides indet., including Bothremydidae (Djoua) and at least one Podocnemididae (cervical vertebra at In Akhamil); coll. Nougarède and A.F. de Lapparent.

Eocene:

El Kohol (El Kohel), S Oran Province, near Brezina, between Early Eocene and Late Eocene, ?Pelomedusoides: 'Paludine turtle': Bergounioux (1954-1955) = fresh-water indet., unknown localization; Mahboubi *et al.* (1986).

Late Miocene:

Saint-Eugène, 'Carrière des chaux et ciments', Oran Province, Sahelian, Late Miocene (Tortonian, see Pomel references *in* Bleicher 1875), Cheloniidae indet., Dr L. Geslin coll., MNHN (Broin det.).

Bou Hanifia (Oued El Hammam), Oran Province, Late Miocene, Vallesian, MN 9+, ca. 10,5 myr, Chelonii indet.: '*Testudo*': Arambourg (1952b, and 1954) '*Emys*': Arambourg (1958) (possibly a *Testudo* s.l.? sp. and *Mauremys* sp., unverified presence, unknown localization).

Pliocene:

Puits Karoubi, ca. 2 km SW Eckmühl, Oran, Chelonii indet.,'Argiles du niveau b à Tortue' (Clays, level b with chelonians): Arambourg (1950) (unknown localization) (Pomel 1878).

Aïn Boucherit (area of Aïn Hanech and El Eulma, ex Saint-Arnaud), Constantine Province, towards Setif, Pliocene, Ruscinian, MN 14-15, ca. 2 myr. ?*Trionyx* sp. ('*Trionyx*': Arambourg 1953, unverified presence, unknown localization); *Testudo* s.l. indet. (possible s.s.) sp., *Mauremys leprosa* (Schweigger 1812), MNHN (Broin det.).

Pleistocene:

Tighenif (Ternifine, Palikao), 20 km E Mascara, Oran Province, Early Middle or Middle Pleistocene, ca. 400 000 to 700 000 yr BP (Geraads *et al.*1986: Hublin 1985), *Testudo* s. l. (probable s.s.) sp., *Mauremys leprosa*, MNHN.

Mansourah, Constantine Province, Pleistocene, *Mauremys* sp., probable *M. leprosa* ('*Emys*, close to the extant *Emys sigriz*', Thomas 1878, 1880, *i.e. Mauremys leprosa)*; MNHN (Broin det.).

Holocene:

Epipalaeolithic, Capsian (see references *in* Roubet 1966, localizations fig. 2, 1979),

Cubitus, near Tiaret,

Aïn Keda, near Tiaret,

Abri Alain, Oran, Eckmühl quarries, *Testudo g. graeca* : Roubet (1966), 'Tortue de Maurétanie', *'T. ibera'*.

Various localities, *Mauremys leprosa*? Vaufrey (1955).

Neolithic (see references *in* Roubet 1966, localizations fig. 2, 1979) from East to West,

Abri du Relilaï, **Col des Kifène**, **Damous el Amar** (3770-3450 years BC),

Capeletti cave, Khanguet Si Mohamed Tahar (between 3950±150 and 2390±200 years BC),

Djebel Fartas, **Djebel Marhsel**, **Hyènes Cave**, **Bou Zabaouine Cave**, **Ours Cave**, **Hadrar Gueldaman**, **Columnata**, **Rhar Oum el Fernan**, **Cascades Cave**, **Oued Saida**, **Troglodytes Cave**, **Polygone Cave**, **Cuartel Cave**, **Ciel Ouvert Cave**, **Forêt Cave**, **Chabet Sardi Cave**, **El Bachir Cave**, **Coralès fireplaces -Escargots cemetery**, **Aïn Guedara** upper cave, Dahar Mendjel, *Testudo g. graeca* : Roubet (1966), 'Tortue de Maurétanie', *'T. ibera'*. South:

Hassi Mouilah (Ouargia), *Testudo g. graeca*: Roubet (1966), 'Tortue de Maurétanie', '*T.ibera*'.

Ti-n Hanakaten, NE Hoggar Djanet Province, around 7000 yr BP (Chaïd-Saoudi 1987): *Pelomedusa* cf. *subrufa* (Lacépède 1788); *Centrochelys sulcata* (Miller 1779): coll. G. Aumassip (Broin det.).

ANGOLA

Senonian (littoral):

Ambrizette, 1 km S Ambrizette, N'Zeto, lat. around 7°15', N Ambriz, Late Senonian (ca. Campanian), Bothremydidae indet., MNHN (Broin det.).

Palaeocene (littoral and marine):

Landana cliffs, Cabinda, Montian, *Taphrosphys congolensis* (Dollo 1913), *(Bantuchelys* Dollo 1924 *ex parte)*; ?Toxochelyidae indet. (*Bantuchelys* Dollo 1924, *ex parte*) (see: Antunes & Broin 1988; Dollo 1924; Lapparent de Broin & Werner 1998; Wood 1973a, 1975).

CAPE VERDE ISLANDS

Pleistocene:

Pedra de Lume crater, Sal Island, ar 16° N, 24° W, Middle Quaternary, *Centrochelys sulcata*: Chevalier *et al.* (1935) (unknown localization).

CAMEROONS

Early Cretaceous:

Koum Basin, 150 km SE Garoua, Mayo Djarendi, loc. KB6, Mayo-Rey River, North Cameroons, Barremian-Aptian, Chelonii indet.: 'Chelonia': Brunet *et al.* (1990) (not seen).

Protohistoric:

Sou, Lake Chad, 75 km S Middle South shore, (Lebeuf; W. Van Neer pers. comm., Broin det.), 7th-19th Century; *Pelusios adansonii* (Schweigger 1812), *Cyclanorbis senegalensis* (Duméril & Bibron 1835).

Lake Chad, S shore, probably close to Sou, Middle Age (S. Bécouch & H. Thomas, pers. comm. from Lebeuf?, Broin det.), *Pelusios adansonii*.

CHAD

Pliocene to Recent:

Koro-Toro: **Ouadi Derdemi (Ouadi Derdemy)**, close to Goz Kerki fossil bank, ca. 46 km E Koro-Toro, NE Fort-Lamy, ca. 3-3,2 myr, Pliocene (Coppens 1962a, 1965, 1967), *Pelusios sinuatus* (A. Smith 1838), cf. *Trionyx* sp., *Centrochelys* cf. *sulcata* (Miller 1779): Broin (1969; Chad coll., deposited MNHN. **Bahr el Ghazal**, E Koro-Toro, KT 12 site, 'Abel' site, 16°00'21" N, 18°52'34" E, Chelonii indet.: '*Trionyx* sp., *Geochelone* sp.', (provisional determinations, unverified); other sites, Pliocene, ca. 3-3,5 myr, Chelonii indet.: Brunet *et al.* (1996).

Other Chad localities, Plio-Pleistocene-Holocene (Broin det.):

El Djour, *Centrochelys* sp., *Pelusios* cf. *sinuatus*, likely prior to Holocene, Pliocene as Ouadi Derdemi; **Yayo**, *Trionyx* sp., *Pelusios* cf. *sinuatus*;

Goz Kerki, Koula, *Trionyx triunguis* (Forskål 1775), *Centrochelys* sp.;

Bochianga (diatomite, fauna 2), Pleistocene-Holocene, *Cyclanorbis senegalensis* (Duméril & Bibron 1835) (small form);

Neo-Bochianga (Stone Age with harpoons), *Trionyx triunguis*; (Coppens 1962a,b, 1965a,b, 1967a,b, 1968; see references not given here in Broin 1969);

Puits Tirenno, 21°36' N, 17°25' E, Tibesti, Pleistocene-Holocene, *Pelusios* cf. *castaneus* (Schweigger 1812), *Cyclanorbis senegalensis*, (small form), cf. *Centrochelys* sp.; Y. Coppens coll.;

Low Lands of Chad, Egueï, Kanem,

Djourab, **Borkou** and **Tibesti**, Pliocene?, Pleistocene-Holocene, old mentions (unknown localization of fossil chelonians), *Trionyx* sp.: Priem (1914) (and Arambourg 1934; Joleaud 1934, 1936; Roman 1935).

Protohistoric:

Koyom, 9°48' N, 15°52' E, Middle Logone, S. Chad, ca. 19th Century, *Pelusios adansonii* (Schweigger 1812); *Cyclanorbis senegalensis*; *Cycloderma aubryi*; Trionychidae indet. (*Trionyx* sp.?); *Kinixys belliana* Gray 1831: Broin and Van Neer in Rivallain & Van Neer (1983, 1984). **Sao de Mdaga**, 12°12'45" N, 15°03'30" E, ca. 12 km N to N'Djaména on Massakori road, Lake Chad basin, from 425 BC to 1780 years AD: *Pelusios* sp.: Thomas (1980) (Broin det.).

CONGO, PEOPLES REPUBLIC OF (EX CONGO-BRAZZAVILLE):

Holocene, around 7090-6890 yr BP:

Ntadi Yomba, W Brazzaville, 13°46' E, 4°15' S, Tshitolian Abri, Testudininei indet. including ?*Kinixys* sp.: Van Neer & Lafranchi (1985) (Broin det.).

CONGO, DEMOCRATIC REPUBLIC OF (EX ZAÏRE, CONGO-KINSHASA)

Late Miocene - Pliocene of West Lake Albert (Makinouchi *et al.* 1992):

Sinda-Mohari Rivers Region, Lower Semliki River; Late Miocene, Sinda beds; Ongoliba Horizon, lower member, Late Miocene, site 5, Pelomedusidae indet., site 11, aff. *Erymnochelys* sp.; Mio-Pliocene or Pliocene?: sites 3, 7, middle member, 15, upper member, aff. *Erymnochelys* sp.; site 3, middle member, Carettochelyidae indet.; sites 1, 3, middle member, 15, upper member, Trionychidae, probable Cyclanorbinae, apparently including *Cyclanorbis senegalensis* (Duméril & Bibron 1835) group ('Trionychidae': Hirayama 1992, pl. 5). The remaining presence of Carettochelyidae and aff. *Erymnochelys* should be more favourable to an oldest possible age during the Pliocene.

Lower Semliki River, Kaiso beds (old coll.), Pliocene, Testudininei indet. (giant terrestrial form: Leriche 1939).

Upper Semliki-Senga Rivers, Lusso beds, Senga 5 and other localities, Pliocene, ca. 2,4-2,5 myr (Boaz 1990; Verniers & Heinzelin 1990), Pelomedusoides indet., either Erymnochelyinae or Pelomedusidae ('Pelomedusidae indet.'), cf. *Pelusios sinuatus*, cf. *Cycloderma* sp., Testudininei indet., Ethiopian endemics group? ('Testudinidae indet.'): Meylan (1990).

Holocene-Protohistoric:

Matupi Cave, northeastern Zaïre, just east of Lake Albert shore: 1) Late Stone Age, between 22 000 and 2000 yr BP, *Kinixys erosa*, Testudininei indet. ('*Testudo*' sp., 'Testudinidae'), 2) Iron Age, before 2000 yr BP, *Kinixys erosa*, Testudininei indet. ('Testudinidae') (Van Neer 1984, 1989).

Malemba-Nkulu, Sanga, Upemba depression, ca. 26° to 27° E, ± 8° S, Iron Age, *Pelusios* sp.: Van Neer (1978) (including *Pelusios nanus* Laurent 1965, at Malemba-Nkulu, Broin det.).

DJIBOUTI, REPUBLIC OF

Plio-Pleistocene (Broin det.):

Annabokôma-Chekheyti site, loc. NW 100, Gobaad plaine, 1,2-1,8 myr, ? cf. *Centrochelys* sp.: *'Geochelone'* sp.: Thomas *et al.* 1984).

Undefined site of Gobaad plaine: *Pelusios* cf. *sinuatus* (A. Smith 1838) (Gasse & Rognon 1973: 'chelonians').

EGYPT

Cretaceous:

Baharija, SW Cairo, Western Desert, ca. 28° N, 29° E, Early Cenomanian, *Apertotemporalis baharijensis* Stromer 1934; (Antunes & Broin 1988; Broin 1988a; Dacqué 1912; Lapparent de Broin & Werner 1998; Stromer 1934); material destroyed.

Idfu, just N of Idfu, Nile Valley, a 25° N, 33° E, Turonian-Early Senonian, Chelonii indet.: Dacqué (1912) (unverified).
Ammonite Hills, NW Dakhla Oasis, ca. 26° N, 26° E, SSW Cairo, Western desert, Dakhla Formation, Maastrichtian (littoral and marine): *Arenila krebsi* Lapparent de Broin & Werner 1998; *Zolhafah bella* Lapparent de Broin & Werner 1998 and Bothremydidae indet. of *Bothremys* group, *Taphrosphys* cf. *sulcatus*, cf. *Taphrosphys* sp., aff. *Tasbacka* sp. (see Barthel 1980; Barthel & Herrmann-Degen 1981; Quaas 1902 in Lapparent de Broin & Werner 1998; Dacqué 1912; Wanner 1902); TUB.

Eocene (mixed, continental and marine forms):
Fayum, S Cairo area, Qasr El Sagha Formation, at:
Birket el Kurun (Andrews 1901, 1903),
Abusir, Dineh (Dimêh), N of West border of Birket el Kurun,
Qasr es Saga (Reinach 1903, Dacqué 1912); upper Mokattam, Late Eocene, *Stereogenys cromeri* Andrews 1901; *Schweboemys antiqua* (Andrews 1903) (see Andrews 1906, pl. 25, fig. 1; Wood 1970) (= *'Podocnemis stromeri* Reinach, 1903' and *'Podocnemis stromeri* var. *major*, Reinach 1903'); genus indet., '*Stereogenys*' *podocnemoides* Reinach 1903 (a *Neochelys* group member, n.g.?); Pelomedusoides indet. (NHM); *Egyptemys* Wood *et al.* 1996: *Psephophorus eocaenus* Andrews 1901; genus indet., '*Thalassochelys*' *libyca* Andrews 1901 [a cheloniid: '*Thalassochelys* (*Chelone*?) *libyca* Andrews'; *'Thalassochelys* Boul. (*Caretta* Raf.)' in Dacqué 1912]; Cheloniidae indet.: ?*Trachyaspis*: Dacqué (1912) (= *'Trachyaspis* cf. *aegyptiaca* Lydekker 1889' in Reinach 1903); material MNHB, NHM and SMNS only observed (other material in CM or destroyed).

Oligocene:
Fayum, NW Birket el Kurun, Dimêh, Tamieh, 'Schweinfurthplateau' (Dacqué 1912), S Cairo area, Qatrani Formation, Early Oligocene: *Stereogenys libyca* Andrews 1903; aff. *Erymnochelys fajumensis* (Andrews 1903) = *Dacquemys palaeomorpha* Williams, 1954b: ? ['Podocnemis *fajumensis* Andrews 1903', *'Podocnemis blanckenhorni* Reinach 1903', '*Podocnemis blanckenhorni* var. *ovatum* Reinach, 1903', *'Pelomedusa progaleata* Reinach 1903', *'Dacquemys palaeomorpha* Williams 1954b = *Erymnochelys fajumensis'* (Andrews 1903): ? in Williams 1954c] (Dacqué 1912; Broin 1988a); *Gigantochersina ammon* (Andrews and Beadnell 1903) ('*Testudo ammon* Andrews & Beadnell 1903' = *'T. isis*, Andrews 1906'? = *'T. beadnelli* Andrews 1906'?) (Andrews 1904; Chkhhikvadze 1989; Lapparent de Broin & Van Dijk 1999); NHM and SMNS material only observed, other in CM.

Mio-Pliocene (marine):
Suez Canal, Tertiary indet., probable Miocene, *Trachyaspis aegyptiaca* Lydekker 1889 (see Weems 1980, erroneous attribution to *Syllomus* Cope 1896, instead of *Trachyaspis* Meyer 1843); NHM.

Early Miocene:
Moghara, ca. 30° N 29° E, Early Miocene, Burdigalian, Orleanian, MN 3+, ca. 18 myr, aff. *Erymnochelys aegyptiaca* (Andrews 1900), '*Erymnochelys aegyptiaca* (Andrews 1900)': Williams (1954c); genus indet., '*Podocnemis*' *bramlyi* Fourtau 1920 (= ?*Schweboemys*, rather than a Bothremydidae?); genus indet., '*Sternothaerus' blanckenhorni* Dacqué, 1912 (= a member of the *Schweboemys* group?) ('a precursor of *Peltocephalus*: Williams 1954c'); Erymnochelyidae indet. ('Podocnemide': Williams, 1954c); aff. *Allaeochelys* sp.? and Cyclanorbinae (*'Trionyx senckenbergianus* Reinach 1903', pl. 17, figs. 2, 5 and 6) (Broin 1983; Lapparent de Broin & Gmira 1994; Wood 1970).
Wadi Faregh, ca. 30° N, 30° E, Early Miocene, Burdigalian,Orleanian, MN 3+, ca. 18 myr, aff. *Allaeochelys* sp., ('?*Cyclanorbis* n. sp.': Dacqué 1912; *'Trionyx senckenbergianus* Reinach 1903' *ex parte*); ?Cyclanorbinae (*'Trionyx senckenbergianus* Reinach 1903' *ex parte; Trionyx* sp.: Dacqué 1912) (Broin 1983; Lapparent de Broin & Gmira 1994; Wood1970).
El Arag area, ca. 28°40' N, 26°30' E, N of El Bahrein, Th. Monod coll., Egypt, Neogene, Burdigalian? Cf. or aff. *Erymnochelys*, Chelonii indet. (large Testudininei indet.?); MNHN.

Late Miocene:
Wadi Natrun (Natrontal) **(Djebel El Muluk, Garet El Muluk, Dêr Baramûs)**, Late Miocene, Late Turolian, MN 13+ (ca 6,5 myr), *Pelusios sinuatus* (A. Smith 1838) (*'Sternothaerus dewitzianus* Reinach 1903': Dacqué 1912'; = *'Pelomedusa pliocaenica* Reinach 1903': Dacqué (1912) (Broin 1969, 1983). *Trionyx* sp.: '*Trionyx pliocaenicus* Reinach 1903', *'Trionyx* sp. = *Trionyx pliocaenicus* Reinach 1903', *'protriunguis* serie, Reinach 1903': Dacqué (1912) (Broin 1983; Lapparent de Broin & Gmira 1994). *Mauremys* sp. ('*Ocadia* n. sp. ind.': Dacqué 1912) (Lapparent de Broin & Van Dijk1999). *Trachyaspis* cf. *aegyptiaca* Lydekker 1889 ('indet': Dacqué 1912); material partly destroyed.

Holocene:
Abu Ballas, 200 km SW Dakhla Oasis, Mudpans, site 83/89, ca. 8300 yr BP, site 85/50-1, ca. 6800 yr BP, site 85/51-3, ca. 6800, Testudininei; Van Neer & Uerpmann (1989).
Toukh, close to Negadah, 30 km N Louxor, Neolithic (Amratian and Gerzean), *Trionyx triunguis* (Forskål 1775): Joleaud (1936).
Anteopolis (Siout, Asyut), Nile Valley ca. 400 km S Cairo, Pleistocene-Holocene tomb, ?*Cyclanorbis senegalensis*: *'Emyda sivalensis'* Lyd. : Parona (1918) = *'Emyda sivalensis'* Lydekker 1885, a junior synonym of *Lissemys punctata* (Lacépède 1788), the Indian form which has a similar decoration to that of this African form *C. senegalensis*; ?*Trionyx* sp.: Parona (1918); (unknown localization) (Gautier 1984; Joleaud 1936).
Fayum, Birket el Kurun, Pleistocene-Holocene; *Trionyx triunguis* (Forskål 1775), TUB; 'Chelonians': Andrews (1906).
Adaïma, between Luxor and Esna, pre-dynastic site, Neolithic, *Trionyx triunguis*: Midant-Reynes *et al.* (1993).
Berenike, Egyptian Red Sea Coast, Roman period, 2000-1500 yr BP, *Chelonia mydas*; ?'*Centrochelys sulcata* (?'*Geochelone sulcata*'): Van Neer & Ervynck (1998) (Van Neer & Lentacker 1996).

ETHIOPIA

Cretaceous:
Abay River Basin (Blue Nile Basin), North of Addis-Ababa, Mugher Mudstone, Early Cretaceous, aff. *Araripemys*, Podocnemidoidea indet.: fauna comparable to that of the upper part of the 'Continental Intercalaire' of Sahara, late upper part (Kem Kem of Morocco, In Abangarit of Niger, Albian-Early Cenomanian prior to marine transgression) (Schmidt & Werner 1998; Werner 1995, 1996); TUB (Broin det.).
Plio-Pleistocene of Omo River Basin (Arambourg 1947; Arambourg *et al.* 1967, 1969; Bonnefille *et al.* 1973a,b; Brown *et al.* 1985), NME, MNHN (Broin det.):
Yellow Sands, Mursi Formation, older than 4 myr, Pliocene, *Pelusios* cf. *sinuatus* (A. Smith 1838), *Cyclanorbis* cf. *elegans* (Gray 1869).
Shungura Formation, Plio-Pleistocene, chelonians seen from bed A1, ca. 3,79 to beds H sup., K 11, ca. 1,6 myr: *Pelusios sinuatus* (including *'Sternothaerus rudolphi'* Arambourg 1947) and *P.* cf. *sinuatus* (beds A1 to G13), *P. adansoni* (Schweigger 1812) (beds G4-13, Omo 75, H Upper Kalam 11); cf. *Trionyx* sp. (bed A3), *Cyclanorbis elegans* (bed B9-10); *Cycloderma frenatum* Peters 1854 (beds A1, B2, E, G27); Testudininei indet., large sp., *Stigmochelys pardalis* (Bell 1828) group (beds B9-12, C5 to C9, D3): Arambourg (1947) (Broin 1979).

Pliocene-Holocene of Awash Valley (NME) (Broin det.):
Pliocene of Central Afar (Johanson 1996; Taieb *et al.* 1976),

Hadar Formation, Pliocene; Sidi Hakoma Member, ca. 3,40 to 3,28 myr, *Pelusios gabonensis* (Duméril 1856), *Pelusios* sp., *Centrochelys sulcata* (Miller 1779) (SH-SH3), large *Stigmochelys* sp. (SH-SH3; SH1-SH2); Denen-Dora Member, < 3,18 myr, *Pelusios gabonensis*, large (DD1-DD3), gigantic aff. *Stigmochelys* sp. (DD1-DD3), indet. round eggs (Chelonii? Testudininei or Trionychidae; not revised) (DD3=KH1-KH2).

Central Ledi Basin, *Pelusios* cf. *gabonensis*, *P.* sp., *Cycloderma frenatum*.

West of Central Ledi Basin, *Pelusios* cf. *gabonensis*, *C. frenatum*.

Amado Basin?, **Geraru Basin**, cf. *Cycloderma* sp.

Holocene,

Delta, Loc. AL 42-1, ?cf. *Centrochelys* sp., large form.

GHANA

Protohistoric:

Mole National park, Nyanga camp, Mole River, 9°32' N, 1°57' W, *Cyclanorbis elegans* (Gray 1869), *C. senegalensis* (Duméril & Bibron 1835): Hughes (1979).

KENYA

Early Miocene of Koru-Songhor-Muhoroni area:

Koru, ca. 19-20 myr (Pickford *et al.* 1986b), ?Cyclanorbinae: Lapparent de Broin & Gmira (1994); NHM.

Songhor, ca. 19-20 myr (Pickford *et al.* 1986b), *Kinixys erosa* (Schweigger 1812): Meylan & Auffenberg (1986); NHM.

Mteitei area, Chelonii indet.: Pickford (1986).

Mio-Pleistocene of Lake Victoria area:

Rusinga Island, NE Lake Victoria, Upper Katwanga series, Early Miocene, ca. 18 myr (Pickford *et al.* 1986b), *Pelusios rusingae* Williams 1954a; *Impregnochelys pachytectis* Meylan & Auffenberg 1986; other testudinineine (BM, NH, R 6422)?; NHM.

Formations Wayondo, Hiwegi and Kulu, Chelonii indet.: mentions in Pickford (1986) ('Testudinidae', 'Pelomedusidae', *i. e.* undecorated chelonians such as Testudinidae, Pelomedusidae, Podocnemididae etc.; and 'Trionychidae', *i.e.* decorated forms, possible Cyclanorbinae, not probable Carettochelyidae and Trionychinae at that time).

Mfwangano Island, Walangani and Higeni Formations, Early Miocene, ca. 18 myr (Pickford 1986), Chelonii indet. ('Testudinidae': Pickford 1986, *i.e.* undecorated chelonians; possible Testudinidae but also Pelomedusidae, Podocnemididae or other indet.).

Uyoma Peninsula, Early Miocene, as Rusinga, Chelonii indet., possible Cyclanorbinae ('*Trionyx*', '*Cycloderma*', Pikford 1986).

Karungu, NE Lake Victoria, Kachuku beds, Early Miocene, ca. 18 myr (Pickford *et al.* 1986b), aff. *Erymnochelys* sp., young ('*Podocnemis aegyptiaca*': Andrews 1914), bed 22; aff. *Cycloderma victoriae* (Andrews 1914) ('*Cycloderma victoriae* Andrews 1914'), bed 31; Testudininei indet., ? *Stigmochelys* group?: '*Geochelone crassa* (Andrews 1914)': Meylan & Auffenberg (1986), bed 31; NHM. Gwasi Peninsula, Simenya, Early Miocene, Chelonii indet.: Pickford (1986).

Ombo, Maboko Formation, Early Middle Miocene, ca. 15-16 myr (Pickford *et al.* 1986b), Cyclanorbinae indet.; Lapparent de Broin & Gmira (1994); NHM; Chelonii indet. ('Pelomedusidae', 'Trionychidae': Pickford 1986, i.e. undecorated Chelonii, Testudininei and/or Pelomedusoides, and probable Cyclanorbinae).

Homa Peninsula: Kanam (1), Homa and Kanam beds, Pliocene, ca. 4 myr, Chelonii indet. ('Pelomedusidae', 'Trionychidae', Pickford 1986, i.e. undecorated Chelonii, Testudininei and/or Pelomedusoides, and Trionychoidea).

Kanam (2), Kanjera beds, Plio-Pleistocene, ca. 1-2 myr, Chelonii indet. ('Pelomedusidae', Pickford 1986, i.e. undecorated Chelonii, Testudininei and/or Pelomedusoides).

Rawi (3), upper Kanjera beds, Pleistocene, ca. 1 myr, *?aff. Stigmochelys* sp. (*'G.* aff. *pardalis'*: Broin 1979: possible *Stigmochelys* group), NHM.

Mio-Pliocene of Lake Baringo Basin, Baringo district (Bishop & Chapman 1970; Bishop & Pickford 1975; Bishop *et al.* 1971; Pickford *et al.* 1986b, 1993; Wood 1973b):

Ngorora Formation, Middle Miocene, ca. 11-12 myr, Pelomedusoides including *Pelusios sinuatus* ('Pelomedusidae', *'Pelusios* cf. *sinuatus* Smith'), Cyclanorbinae indet. ('Trionychidae', '*Trionyx*' sp.'), Testudininei indet. ('Testudinidae, *Testudo* sp.') (Bishop & Pickford 1975; Bishop & Chapman 1970; Bishop *et al.* 1971). Giant Testudininei indet., **loc. 2/106**, Member D, ca. 11,7 myr and Chelonii indet., a giant freshwater chelonian ca. 2 m long, at **Ngeringuerwa**, ca. 10 myr, Baringo Basin, Miocene (pers. comm. M. Pickford).

Mpesida beds, Late Miocene, ca. 6,2 myr, Trionychoidea indet. (?Carettochelyidae, ?Cyclanorbinae: 'Trionychidae indet'), Testudininei indet. ('Testudinidae': Bishop *et al.* 1971).

Lukeino Formation, Late Miocene, ca. 5,8-6 myr, Pelomedusoides indet. ('Pelomedusidae indet.' i.e. ?Pelomedusidae ± Podocnemididae), Trionychoidea indet. (?Carettochelyidae, ?Cyclanorbinae: 'Trionychidae indet.'), Testudininei indet. ('Testudinidae') (Pickford 1975; Bishop *et al.*1971).

Kaperyon Formation, Pliocene, ca. 5 myr, Trionychoidea indet. (?Carettochelyidae, ?Cyclanorbinae: 'Trionychidae', Bishop *et al.* 1971). **Chemeron Formation**, Pliocene, <2,2 myr, *Cyclanorbis* sp. (*'Cycloderma* sp'. in Meylan 1990) (Bishop *et al*; 1971; Lapparent de Broin & Gmira 1994). Aterir beds, Pliocene (> 4 to ca. 2,2 myr), Pelomedusoides indet. (possible Pelomedusidae and still possible Podocnemididae at that time: 'Pelomedusidae'; Bishop *et al.* 1971).

Chemoigut beds, Pleistocene, 1,2 myr, Pelomedusoides indet. ('Pelomedusidae', *i.e.* probable *Pelusios*), Cyclanorbinae indet. ('Trionychidae') (Bishop *et al.* 1971, 1975).

Lake Turkana, (Brown *et al.* 1985):

Mio-Pliocene of Kerio River Basin, SW Lake Turkana, (Patterson *et al.* 1970; Behrensmeyer 1976) NMK (Broin partly observed), **Lothagam Hill**, Late Miocene, above 8,5 myr, around 6 myr at Lothagam 1, to Pliocene, older than ca. 3,8 myr at Lothagam 3: Lothagam 1, aff. *Erymnochelys* sp. A (*'Podocnemis* sp. A' of Patterson *et al.* 1970; Witmer 1990?), *Kenyemys williamsi* Wood 1983 (*'Podocnemis* sp. B' of Patterson *et al.* 1970); aff. *Cycloderma debroinae* (Meylan *et al.* 1990), lowest horizon; Testudininei, indet. group ('*Geochelone*' sp.); Lothagam Unit 2, Chelonii indet. ('turtles'), Lothagam 3, aff. *Erymnochelys* sp. A ('*Podocnemis* sp. A: Witmer 1990?), ?Cyclanorbinae ('Trionychidae indet.'), Testudininei indet. group ('*Geochelone*' sp.); undefined horizon ('Pliocene'), *Cycloderma frenatum* Peters, 1854: Meylan *et al.* (1990). Pelomedusoides indet. (abnormal *Pelusios*?) ('Chelonii indet.': Wood 1976). **Kanapoi**, 50 km S Lothagam, Pliocene, from < 4 myr? to < 2,6 myr. Aff. *Erymnochelys* sp. A (*'Podocnemis* sp. A'), Cyclanorbinae ('Trionychidae indet.', Patterson *et al.* 1970), including 'Cyclanorbini indet.' in Meylan *et al.* (1990) and *Cyclanorbis turkanensis*, Meylan *et al.* 1990, bed E; Testudininei indet. (*Stigmochelys* group?) (*Geochelone crassa* Andrews, 1914 in Meylan & Auffenberg 1986).

Ekora, ca. 23 km NE Kanapoi, Pliocene (just above 4 myr), Aff. *Erymnochely* sp. A (*'Podocnemis* sp. A' of , Patterson *et al.* 1970), Testudininei indet. group ('*Geochelone*' sp.).

Plio-Pleistocene of East Lake Turkana, Koobi Fora beds, NMK (Broin 1979, 1983; Harris 1978; Harris *et al.* 1988; Lapparent de Broin & Van Dijk 1999; Meylan & Auffenberg 1986; Meylan *et al.* 1990; Wood 1979), **Koobi Algi Formation**, areas 201, 202, 204, Early Pliocene, ca. 3,9-4,5 myr, *Pelusios sinuatus* (A. Smith 1838). **Koobi Fora Formation** (Brown *et al.* 1985): Lower member, Pliocene: area 116, above Tulu Bor

tuff, (ca 3,35 myr), below KBS tuff (ca 1,88 myr), *Pelusios sinuatus*. Lower-upper member limit, Late Pliocene: - 25m below tuff KBS (ca 1,88 myr) area 102, 130-1, *P. sinuatus*, area 102, *Cyclanorbis elegans*: Meylan *et al.* (1990); 20 m below KBS, area 105, *Cycloderma frenatum* and *Cyclanorbis senegalensis* (Duméril & Bibron 1835), Trionychidae indet.: Meylan *et al.* (1990); - 20 m below KBS, unknown area, *C. elegans* (Gray 1869) or *C. turkanensis* : Meylan *et al.* (1990); - below to above KBS, KF II, *Pelusios* sp.; - just above KBS, area 130-1, *P. sinuatus*; - upper member, above KBS, ca. 1,88 myr (Pliocene), around 'Okote tuff' (ca 1,57 myr, age of J7 in Shungura F. of Omo, Pleistocene) and below Chari tuff (ca 1,39 myr), area 104-5, 104-A, *Trionyx triunguis* (Forskål 1775): Broin (1983), Harris (1978), Meylan *et al.* (1990); (*Trionyx* cf. *T. triunguis*: Wood 1979); area 103, 104-A, *Cycloderma* cf. *frenatum*; area 104, Testudininei indet. (large sp.); - undefined horizon and area: Trionychinae indet, *Cyclanorbis elegans*: Meylan *et al.* (1990); gigantic Testudininei indet. (Harris pers. comm.).

LESOTHO

Holocene:

Ntloana Tsoana, north-western Lesotho, 8780 ±80, 12110 ±120 yr BP, Chelonii indet.: Mitchel (1993, in Branch *et al.* 1995),

Tloutle, north-western Lesotho, 6140 ±100 yr BP, Testudininei indet.; see Carter Mitchell & Winnicombe (1988, in Branch *et al.* 1995),

Sehonghong Rockshelter, Qacha's Nek District, western Lesotho, 1400±50 yr BP, Testudininei indet.; see Carter, Mitchell & Winnicombe (1988, in Branch *et al.* 1995),

Hololo Crossing, 28°44'S; 28°, 27'E, 330-260 yr BP, Testudininei indet.; see Mitchell, Parkington & Yates (1994, in Branch *et al.* 1995).

LIBYA

Eocene-Early Oligocene:

Dor et Talha, E Fezzan, S Syrta Major, 25°45' N, between 17°50' and 19°15' E: - **Dor et Talha**, 15 and 80 km E of Oriental border of Djebel Harouj el Assoued, Podocnemidoidea indet., probable Podocnemididae: 'Chelonian plates': Bellair *et al.* (1954), the same layer as Djebel Coquin: Arambourg (1963); Late Eocene; MNHN, coll. Lefranc; - = **Djebel Coquin**, 25°45' N, between 17°50' and 19°15' E, Pelomedusoides indet., probable Podocnemididae: 'palustral tortoises': Arambourg (1963); 'palustral turtles': Arambourg & Magnier (1961), Late Eocene, Priabonian (collected? unknown localization); - = **Dor et Talha**, 25°45' N, between 17°45' E and 19°05' E, Evaporite Unit, Late Eocene, Chelonii indet.; Idam Unit, ?Early Oligocene, Pelomedusoides indet., probable Podocnemididae: 'Pelomedusidae': Savage (1969) (Wight 1980).

Oligocene:

Zella Oasis, S Syrta Major (Sirte Desert), 28°30' N, 17°37' E, Chelonii indet.: 'paludal turtles': Arambourg (1963); 'palustral turtles': Arambourg & Magnier (1961) (collected? unknown localization).

Miocene:

Djebel Zelten, SE Syrta Major, 28°45' N, 19°30' E, Early Miocene, Burdigalian, Early Orleanian, MN 4+, ca. 16,5 myr; Podocnemididae indet. (including *Stereogenys?*: an epiplastron): 'palustral turtles': Arambourg (1963), Arambourg & Magnier (1961), cf. *Centrochelys* sp., large (a femur conform to *C. sulcata*; see Lapparent de Broin & Van Dijk 1999) and very large (a plate); MNHN (Broin det.).

Sahabi: Bir Guetin, Gara el Beda, Cyrenaïca, SSE to Benghazi, Late Miocene, Late Turolian, MN 13+, ca. 6,5 myr (Geraads 1989), *Trionyx triunguis* (Forskål 1775): '*Trionyx* sp.': D'Erasmo (1934); '*Trionyx* cf. *triunguis*': Wood (1987); *Centrochelys* aff. *sulcata* (Miller 1779): 'cf. *Geochelone*': Wood (1987) (Lapparent de Broin & Van Dijk 1999).

Holocene:

Djebel Zelten, surface coll. Magnier, *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form; MNHN (Broin det.).

?Cyrenaïca, Libyan desert, unprecised, surface coll. Magnier? (Coll. Arambourg) (or from more western part of Africa), *Pelusios* sp., sub-group *P. castaneus* (Schweigger 1812); MNHN (Broin det.).

MALAWI

Cretaceous:

'Nyasaland', NW Lake Malawi, Dinosaur beds of the Mwakasyunguti area, Siwe Valley, Karonga district, Early Cretaceous, Lupata group, upper member (new finds, Jacobs *et al.* 1996); *Platycheloides nyasae* Haughton 1928; SAM.

Pliocene:

Chiwondo beds, Pliocene, 2,5-4,8 myr, *Pelusios sinuatus* (A. Smith 1838): pers. comm. Wood (1971) (*Pelusios*: Wood 1973b), *Cycloderma frenatum*: Meylan *et al.* (1990), Wood (1979).

MALI

'Continental Intercalaire' of Sahara, late upper part, Early Cretaceous, Albian-Cenomanian - prior to Cenomanian transgression (see Lapparent 1960):

Tikarkas, 4 km S, 115 km NW Tessalit (Bellion *et al.* 1992); Bothremydidae indet.: '*Eusarkia*' sp.: Bergounioux & Crouzel 1968; not a *Taphrosphys*, contra Lapparent de Broin & Werner (1998); MHNT.

Maastrichtian (littoral):

Tagnout Chaggeret, Erg Ine Sakane, MK 42 loc. (Broin 1983), Bothremydidae indet., aff. *Arenila* sp., *Nigeremys* group: Lapparent de Broin & Werner (1998); MNHN.

In Afarag, E balise 560, S Tanesrouft, Bothremydidae indet., coll. A.F. de Lapparent.

Palaeocene-Eocene of the Tilemsi valley (Lavocat & Radier1953; Buffetaut1980) (littoral, marine) MNHN:

In Farghas, Cheit Keni, Palaeocene, Bothremydidae indet., *Taphrosphys* sp. (Mali C, Lapparent de Broin & Werner 1998).

Samit, Ypresian, Bothremydidae indet. (Mali B, Lapparent de Broin & Werner 1998).

Tamaguilelt, Lutetian, Bothremydidae indet. (Broin det.).

Holocene:

Taoudenni Basin, North Mali (MMB; MNHN), **Araouan** (Arawan, Araouan(e) and Guir (Gir) area, **Djouf**, unspecified Holocene, old coll. (see data in Broin 1983: Gallay 1966; Joleaud 1934, 1936 - Capitaine Poggi coll., 50 km NNW Araouan-; Monod 1958; Roman,1935); *Trionyx triunguis* (Forskål 1775), figured in Monod (1958), 45 km NW Arawan, and in Gallay (1966), from Outeidat, as *Trionyx triunguis*, pro parte, figs. 9, 15, and as indetermined vertebrate, figs. 10, 44; *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form ('*Clarias*' pro parte, fig. 2, and '*Trionyx, T. triunguis* size', fig. 6, in Roman, 1935, pl. 4, 10 km S Guir; figured as *Trionyx triunguis* pro parte, 16-18, in Gallay, 1966, Outeidat, fig. 9).

Hassi el Abiod, 19°10' N, 3°50' W, 70 km NW Araouane, 6970±130 yr BP, *Pelusios adansoni* (Schweigger 1812), *P. castaneus* (Schweigger 1812), *Trionyx triunguis*, *Cyclanorbis senegalensis*, small form: Broin (1983), and new coll. Petit-Maire *et al.* 1983.

Erg Ine Sakane, 21°10' N, 0°40' W, 9500-6400 yr BP, *Pelusios castaneus*, *Cyclanorbis senegalensis*, small form: Broin (1983).

South Mali,

Kobadi, KBD 84, E Nampala, 15°21'30" N, 5°29'30" W, Peul country-Mauritania frontier (pers. comm. M. Raimbault), *Trionyx* cf. *triunguis* (Broin det.).

MALTA

Miocene:

Bothremydidae genus indet., '*Podocnemis' lata* Ristori, 1894: Lapparent de Broin & Werner (1998), Aff. *Cycloderma melitensis* (Lydekker 1891) (*'Trionyx' melitensis* Lydekker 1891): Lapparent de Broin &Van Dijk (1999).

Pleistocene:

Mauremys leprosa (Schweigger 1812) ('*Lutremys Europœa*?' in Leith-Adams 1877), from Zebbug cavern; Testudininei genus indet., '*Testudo' robusta* Leith-Adams 1877; = '*Testudo Spratti* Leith-Adams, 1877', a giant tortoise from Benghisa Gap, Mnaidra Gap and Zebbug, ossiferous caverns.

MAURITANIA

Holocene:

Chami, (well of) or **Nouaferd**, 25 km E Cape Tafarit, Neolithic, ca. 2100 to 3500 yr BP, *Centrochelys* cf. *sulcata* (Miller 1779): Broin (1983) (Petit-Maire 1979); MNHN deposit.

MOROCCO

Middle Jurassic:

El Mers, Middle Atlas, 100 km S Fes, Bathonian, Chelonii indet.; (Termier *et al.* 1940) one fragment in MNHN.

Early Cretaceous of High Oriental Atlas:

Anoual area, Oussikis ans Ksar Metlili, Barremian, Chelonii indet., ?Pelomedusoides indet., cf. *Taquetochelys* sp.: Gmira (1995) (Sigogneau-Russell *et al.* 1988, 1990); MNHN deposit.

'Continental Intercalaire' of Sahara, late upper part, Early Cretaceous, Albian-Cenomanian prior to Early Cenomanian of Baharija and to Cenomanian transgression (see Lapparent 1960; Lavocat, 1954), MNHN; part in CMN:

Hamada of Guir, Kem-Kem, E and S to Tafilalt, S Maroc, *Araripemys* sp., Pelomedusoides indet., Bothremydidae indet., Podocnemididae indet, *Hammadachelys escuillei* Tong & Buffetaut 1996; (Fuente & Lapparent de Broin 1997; Gmira 1995; Lapparent de Broin & Werner 1998; Russell 1996).

Phosphates (marine, littoral) (Arambourg 1952a):

Maastrichtian,

Oued Erguita, N Taroudant, Oued Sous tributary, Chelonii indet. ('chelonians indet'.: Ambroggi & Arambourg,1951) (unknown localization).

Benguerir, Ganntour Basin, aff. *Euclastes* sp. ('Aff. *Rhetechelys* sp.': Gmira 1995), G. Termier coll.; Chelonioidea indet: Moody (1976).

Oued Zem, Bed III, E Ouled Abdoun Basin, Chelonioidea indet., new undescribed large form (private coll.).

Between Kouribga and Oued Zem, Ouled Abdoun Basin, Chelonioidea indet., giant pre-cheloniid, SMNS.

Palaeocene,

Benguerir, Ganntour Basin, aff. *Taphrophys* sp. ('close to *Podocnemis*', Pelomedusidae indet.: Moody 1976) (Antunes & Broin 1988; Lapparent de Broin & Werner 1998); Musée du Ministère de l'Energie et des Mines, Rabat.

Palaeocene-Ypresian,

Oued Zem, E Ouled Abdoun Basin, Bothremydidae indet., Osteopygidae indet. (sold osteopygid skulls artificially linked to pleural discs of *Taphrosphys*), new undescribed possible Dermochelyidae (private coll.).

Paleogene of Ouarzazate Basin, N of Oriental border, Anti Atlas (Gheerbrant 1987; Gheerbrant *et al.*, 1993):

Palaeocene,

Several localities with chelonians, Jbel Guersif Formation, Thanetian, including: Ilimzi, aff. *Pelomedusa* sp., Broin det. *(in* Nicolas 1984, see Gmira 1995); Pelomedusoides indet., MNHN deposit.

Adrar Mgorn, Pelomedusoides indet., MNHN deposit.

Ypresian,

N'Tagourt 2, Ait Ouarhitane Formation, Chelonii indet.

Pliocene:

Ahl Al Oughlam, carrière Déprez, Casablanca, Occidental Morocco, Pliocene, ca. 2 to 2,5 myr, ?cf. *Centrochelys:* (*'Geochelone* s.l. sp'.: Raynal *et al.* 1990); *Testudo* aff. *kenitrensis* (Gmira *et al.* in prep.); INSAP.

Pleistocene-Holocene (*in* Gmira 1995: see Ennouchi 1949, 1954, 1969, 1976, Michel 1988, 1990):

Occidental Morocco,

Kenitra, Middle Pleistocene, Inter Amirian-Tensiftian, *Testudo kenitrensis* Gmira 1993a (Gmira 1993b, 1995); MNHN et FSR.

Carrière Thomas I, (Thomas Quarry I), Late Pleistocene, Tensiftian, ca. 400 000 yr BP, Hublin, 1985, *Testudo graeca* Linnaeus, 1758, FSR. Gmira (1995). Rabat 8, 9, 10, coast from **Rabat to Temara a**, small dune (Choubert & Marçais 1947), Tensiftian, lower part of Late Pleistocene, *Testudo g. graeca*, *Testudo* sp., FSR.

Rabat 6, coast from Rabat to Temara b, pink sandstones, Temara Formation, Late Pleistocene, Tyrrhenian, *Trionyx* sp., FSR.

Aïn Rohr, Late Pleistocene, Early Soltanian, Testudinidae indet. (*'Testudo*': Ennouchi 1949). **Jebel Irhoud**, Late Pleistocene, Early Soltanian, *Testudo graeca*: Gmira (*in* Amani & Geraads 1993; Gmira 1995); FSR. **Aïn Bahya**, Late Pleistocene, Soltanian, Testudininei indet.: Gmira (1995) (*'Testudo g. graeca*': Michel, 1988, 1990); INSAP. **Oualidia**, Late Pleistocene, Soltanian, *Testudo g. graeca*; FSR. **El Khenzira**, near El-Jadida,Cap Blanc, Cave 1, bed C, Late Pleistocene-Holocene, Epipalaeolithic, Testudinidae indet. (*'Testudo* sp. ': Ruhlmann 1936). **Dar Es Soltane**, Late Pleistocene-Holocene, Soltanian-Rharbian, *Mauremys* sp, *Testudo* cf. *graeca*; FSR.

Bouknadel, Middle-Late Pleistocene, Testudinidae indet. (Michel 1990); INSAP.

Doukkala II, Late Pleistocene-Holocene, Soltanian-Rharbian, *Mauremys leprosa* (Schweigger 1812), *Testudo g. graeca*, INSAP. **Mehdia**, Holocene, Neolithic probable, *Testudo* cf. *graeca*; FSR. **Toulkine-Bou Ben Adam**, Neolithic, *Testudo* cf. *graeca*; FSR. Gmira (1995).

Oriental Morocco,

Taforalt, 55 km NW Oujda (Roche 1953, 1963), Late Pleistocene, Aterian, *Mauremys leprosa*, *Testudo g. graeca*; MNHN (Broin det. and Roubet 1966).

Rhafas Cave, Late Pleistocene, Soltanian and Middle Holocene, Testudinidae indet., **El Heriga**, Late Pleistocene, Soltanian, and Holocene, Testudinidae indet., **Abri Rhirane**, Late Pleistocene, Soltanian, and Holocene, Testudinidae indet., **Oued el Haij Terrace, Jorf el Anngra**, Holocene, Testudinidae indet.: '*Testudo graeca, T. g. graeca'*: Michel (1990), INSAP.

Abri Bou Guennouna, Holocene, Neolithic, *Testudo* cf. *graeca*, Testudinidae indet.; INSAP. **Kheneg Kenadsa**, Tendrara, Neolithic, Testudinidae indet.: *'Testudo g. graeca*': Jodin (1956).

MOZAMBIQUE

Pleistocene-Holocene of Zambezi (NHM):

Tributary stream of the Zambezi about 8 miles below Mazzaro, right bank, 40 miles from the present coast-line. Collected during the first Livingstone Expedition, 1858, by Sir John Kirk. Pleistocene-Holocene. Due to the association of various extant mammals, including a Cape buffalo, etc., and the presence of human activity (pottery) in the alluvions collected by the stream, possibly Holocene, Neolithic; but this activity is not clearly established as contemporaneous with the fossils (Kirk 1864; Murchison 1864a,b): cf. *Cycloderma frenatum.*

NAMIBIA

Miocene, South-West to Namib Desert, Sperrgebiet = Diamond area, SW Namibia (MSGN) (Broin det.):

Western part, from North to South, Early Miocene,

Fiskus, ca. 19-20 myr, Testudininei n.g. a (large form), sp. **Grillental**, ca. 19-20 myr, Testudininei n.g. a (large form), sp.

Elisabethfeld, ca. 19-20 myr, Testudininei n.g. a (large form), sp. *namaquensis* (Stromer 1926) = *'Testudo namaquensis* Stromer 1926' (material destroyed in Münich); ['*Geochelone namaquensis* (Stromer 1926)' and *'G. stromeri* ': Meylan & Auffenberg 1986]. **Langental**, ca. 19 myr, *Pelomedusa* n. sp., Testudininei indet., n.g. a (large form), n. sp. (also AMNH) and n.g. b, n. sp. (small form, *Stigmochelys* group,?). **Glastal**, ca. 19 myr, Testudininei indet. n.g. a (large form) sp.

Southern part, N Orange River, (from North to South and West to East), Early-Middle Miocene,

Rooilepel: - wardi level, Middle Miocene, ca. 10-12 myr, Testudininei n.g. a sp. ; - laini level, Middle Mocene, ca. 8 myr, Testudininei n.g. a sp. **Karingarab**, wardi level, Middle Miocene, ca. 10-12 myr, Testudininei n.g. a (large form) sp. **North of Gypsum Plate Pan**, ca. wardi level, Middle Miocene, 10-14 myr, Testudininei n.g. a (large form) sp. **Arrisdrift**, Early Miocene, ca. 17 myr, Eymnochelyinae indet., Testudininei n.g. a (large form), n. sp. ['*Geochelone namaquensis* (Stromer 1926'): Meylan & Auffenberg 1986]; Testudininei n.g., n. sp. ('*Chersina* sp.': Meylan & Auffenberg 1986); (Hendey 1978).

Auchas, Early Miocene, ca. 18 myr, Erymnochelyinae indet., Testudininei n.g. a (large form), n. sp. (also OMS).

Historic site:

Brandberg, north of Namibia, 1600-1750 AD, *Stigmochelys pardalis*: Cooper & Branch (1999).

NIGER

'Continental Intercalaire' of Sahara, late part, Early Cretaceous (see Lapparent 1960), MNHN:

Aptian,

Gadoufaoua, Tegama Formation, upper part of lower member, Gad 5, Late Aptian, (Taquet 1976), *Araripemys* sp., *Taquetochelys decorata*, Broin 1980; *Teneremys lapparenti*, Broin 1980, *Platycheloides* cf. *nyasae* (Lapparent de Broin & Cooper in prep,; (Broin 1980, 1988a). **Ebrechko**, Barremian-Aptian, Pelomedusoides indet.; coll. A.F. de Lapparent.

Albian-Cenomanian - prior to Cenomanian age of Baharija and to Cenomanian transgression. (Lapparent 1960),

In Abangarit, Tamesna, Aff. *Araripemys* sp., coll A.F. de Lapparent and Brennand (Fuente & Lapparent de Broin 1997); Pelomedusoides indet., including Bothremydidae, coll. A.F. de Lapparent; Chelonii indet., Tiguedi Sandstones, Brennand coll.

Senonian:

Ibeceten 1, Pelomedusoides indet, several taxa including Podocnemididae (cervical vertebrae) including Erymnochelyinae of the *Erymnochelys* group (gulars meeting behind the intergular): Broin *et al.* (1974).

Maastrichtian (Trans-Saharan Seaway, littoral-marine):

Ibeceten 2, *Nigeremys gigantea* (Bergounioux & Crouzel 1968) ('*Potamochelys' gigantea* Bergounioux & Crouzel, 1968); Bothremydidae indet.; (Broin 1977 Antunes & Broin 1988, Lapparent de Broin & Werner 1998). **Tamaske**: surroudings of Tamaske including Garadoume, ca. 40 km SE Taouha, Maastrichtian to Lutetian, Chelonii indet. (Lapparent 1904) (Buffetaut 1979).

Holocene (Broin det.):

Tenere (Roset *et al.* 1990),

Adrar Bous, loc. 10, 20°19'50" N, 9°02'00" E, N Niger, ca. 9130 yr BP, *Pelusios castaneus* (Schweigger, 1812). **Tin Ouaffadene**, 25 km SE Adrar Bous, 20°10'40" N, 9°11'30" E, N Niger, ca. 9220-9260 yr BP, *Centrochelys sulcata* (Miller 1779).

Tenere-Bilma,

Kaouar, E13, NE Bilma, E Tenere, 19°00' N, 12°17' E, N Niger, Interdunary site, 5500 yr BP (Pr Baumhauer, Würzburg pers. comm. W. Van Neer), *Pelusios* sp.

Azawagh Valley,

In Aruinat, 3500 yr BP, *Pelusios* cf. *castaneus*, *Cyclanorbis senegalensis* (Duméril & Bibron 1835) (small form); **Ikawaten**, 8000-4000 yr BP, *C. senegalensis*; **Takane Bawat**, 6500 yr BP, *Trionyx* cf. *triunguis* (Forskål 1775); between 4500 and 9000 yr BP, pers. comm. Columeau, sites 1985-1. **Pr Baumhauer site**, E2, FR1, 18°16' N, 10°40' E, E Niger, ca. 7000 yr BP (Pr Baumhauer, Würzburg pers. comm. W. Van Neer), *Pelusios adansonii* (Schweigger 1812), *P. castaneus*, *Trionyx* cf. *triunguis*.

NIGERIA

Maastrichtian (littoral):

Wurno, Gada, Kworre, Gilbedi, Sokoto State, Bothremydidae indet., *Nigeremys* group, probable *Sokotochelys*: 'Chelonia' indet., compared to *Podocnemis*: Swinton (1930). **SE Gilbedi village**, northern face Benbow Hill, Sokoto State, Dukamaje Formation, *Sokotochelys lawanbungudui* and *S. umarumohammedi* Halstead 1979 (Walker 1979) (lost material).

Eocene (marine):

Ameki, Ombialla District, Ameki Formation, type locality mile 73 mile to mile 87, Eastern Railway near Ameki Station, N of Port-Harcourt, South Nigeria, Lutetian, *Cosmochelys dolloi* Andrews 1919 (Reyment 1965; Savage & Russell 1983).

Holocene:

N Maiduguri, Chad basin, SW lake Chad, 3000 yr BP, *Pelusios* sp.: Breunig *et al.* (1996).

SENEGAL

Eocene:

Popenguine (Poponguine), Ypresian (littoral): cf. *Taphrosphys* sp.: '*Chelone*': Bergounioux (1936), *in litt.* to Monod (1950) (Antunes & Broin 1988; Lapparent de Broin & Werner 1998; Villiers 1958); DMD.

Protohistoric:

Sintiou Bara, Senegambia, 20 kn of Matam, toggere site, 400 to 1050 af J.C. (Descamps 1979), *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form: Broin (1983); University of Dakar.

Tulel-Fobo, 16°38' N, 15°39' W, 65km NNW Matam, Middle Valley of Senegal River, IV-Vth Ctry, *Cyclanorbis senegalensis*: Van Neer & Bocoum (1991).

Faboura, kjœkken-mœdding, just north to Saloum River, west of Kaolack, 1940-1360±80 yr BP, Cheloniidae indet., 95-594 cm depth, *Trionyx triunguis*, 596 cm depth: Descamps *et al.* (1977) (Broin det.); University of Dakar.

SOMALIA

Eocene (littoral):

Las Daban, Bijo Gora River, 10°22' N, 45°14' E, ca. 23 km ESE Berbera, Lower Daban Series, Lutetian, aff. *Bothremys somaliensis* (Walker 1966): '*Podocnemis' somaliensis* Walker, 1966 = a Bothremydidae of the *Bothremys* group (Lapparent de Broin & Werner 1998).

SOUTH AFRICA

Early Jurassic:

Bormansdrift, Orange Free State, 28°57'33" S, 27°26'05" E, Karroo, Middle *Tritylodon* Acme Zone, Elliott Fm., 'Rhaetian' (Kitching & Raath 1984; but now considered Hettangian), *Australochelys africanus* Gaffney & Kitching 1994 (Gaffney & Kitching 1995).

Cretaceous:

Early Cretaceous,

Algoa Basin, Kirkwood Formation, Valanginian (De Klerk *et al.* 1998), Chelonii indet. (W. J. De Klerk pers. comm.).

Albian-Cenomanian (marine),

Umtata River mouth: Cliffs of South African coast, near the Umtafuna and Umzambawi Rivers, Chelonioidea or Dermochelyioidea indet.: 'Chelonians indet.': Baily (1855) (marine environment of ammonites, molluscs, echinids and a squale); '... reasonably be ascribed to marine turtles': Wood (1973a).

Plio-Pleistocene:

Langebaanweg, E Quarry, 104 km NNW Cape Town, Varswater Formation, Pellatal Phosphate Member. (Hendey 1970a, b, 1973,1981), Pliocene, ca. 4-4,5 myr (Cooke & Hendey 1992), Testudininei genus indet., *'Geochelone stromeri* Meylan & Auffenberg 1986' (Testudininei n.g., see Namibia; 'two gen. and sp. not det.': Hendey, 1981), *Chersina* sp.: Meylan & Auffenberg (1986); ?*Pelomedusa*: Wood (1973b). **Makapansgat**, Transvaal, Pliocene, 2,5 to 3 myr, *Stigmochelys pardalis* (Bell 1828) (*'Testudo pardalis'*: Broadley 1962; *'Geochelone'*: Broadley 1997c). **Sterkfontein**, Sterkfontein area, ca. 6 miles (10 km) N Krugersdorp, Member 5, Pliocene, ca. 2,5 (2,6 to 2,8) myr, Testudininei indet.: 'Testudinidae, gen et sp. indet.': Brain (1981); 'most of these would probably be *Geochelone*': Broadley 1997c (i.e. *Stigmochelys*, probably).

Taungs (=Taung), ca. 2 or 2,5 myr, *Pelomedusa* sp.: Wood (1973b).

Kromdraai, Sterkfontein area, ca. 10 km N Krugersdorp, south side Bloubank River, 1750 m ENE Sterkfontein, Pliocene, ca. 2 myr, **Kromdraai A**, 'Testudinidae, cf. *Testudo*' and **Kromdraai B**, 'cf. *Testudo* sp': Brain (1981); 'most of these would probably be *Geochelone*': Broadley (1997c) (i.e. *Stigmochelys*, probably).

Swartkrans, Sterkfontein area, ca. 10 km N Krugersdorp, 1300m WSW Sterkfontein, Member 2, Pliocene, 2 to 1,8 myr, 'Testudinidae and Chelonian indet.' and channel fill, 'Testudinidae, gen et sp. indet. Tortoise': Brain (1981).

Drimolen, farm Sterkfontein 519JQ, Krugersdorp district, Gauteng Province, Plio-Pleistocene, ca. 2 to 1,8-1,6 myr, *Psammobates antiquorum* Broadley 1997c.

Pleistocene-Holocene:

Hopefield, N. Cape Town, Late Pleistocene, ca. 100 000 yr BP, *Chersina* sp.: Meylan & Auffenberg (1986).

Die Kelders 1, Middle Stone Age, ca. 75 000 to 50 000 yr BP, **Byneskranskop Cave 1**, later Stone Age, 13 000 to 250 yr BP, 160 km E-SE of Cape Town, southern Cape Province, **Klipfonteinrand Cave**, Clanwilliam District, later Stone Age, *Chersina angulata* (Schweigger 1812): Klein & Cruz-Uribe (1983). Elands Bay Cave and nearby sites, Pleistocene-Holocene, from 18 000 to 300 yr BP, about 190 km N of Cape Town, Western Cape Province, *Chersina angulata*: Klein & Cruz-Uribe (1987).

Holocene:

Haaskraal, Late Holocene, *Pelomedusa subrufa*, *Stigmochelys pardalis*, *Homopus femoralis*, *H. boulengeri*, *Psammobates tentorius*: Sampson (1998) (not consulted).

Edgehill and **Welgeluk**, Koonap River near Adelaide, Eastern Cape, from 6000 yr BP to the present, *Pelomedusa subrufa*, *S. pardalis*, *Chersina angulata*, *H. areolatus*: Hall (1990, in Branch *et al.*, 1995); **Hantam Mountains**, north-west of Calvinia, 3119 BC, *H. boulengeri*: in Branch *et al.* (1995); **Oakleigh** near Queenstown, levels 3-4, 500-400 yr BP, Testudininei indet: Welbourne in Derricourt (1977, in Branch *et al.*, 1995); **Leliehoek Shelter**, eastern Orance Free State, Chelonii indet.: Esterhuysen, Behrens & Harper (1994, in Branch *et al.* 1995).

Tertiary, probably Late Neogene:

Carlisle Bridge, Albany district, Cape Province, *Homopus fenestratus* Cooper & Broadley 1990.

SUDAN

Cretaceous:

Wadi Abou Hashim, NW Khartoum, Wadi Milk Formation and **Shendi Formation, new loc.**, NW Shendi, Cenomanian (Bussert 1998; Werner 1994), Pelomedusoides indet.: at least 5 taxa including Pelomedusidae indet., Erymnochelyinae indet.: Werner (1993); TUB (Broin det.). **Localities F 1/89 and F 2/89**, ca. 16°15' N, 31°7' E, NW Khartoum, same area of Wadi Milk Formation, Pelomedusoides indet. :'Chelonia': Bufettaut *et al.*(1990).

Abyad Basin, northern desert, NW Sudan, Kababish Formation, Campanian-Maastrichtian (Barazi 1985), Chelonii indet., possible Bothremydidae; C. Werner (TUB) (Broin det.).

Pleistocene:

Wadi Halfa, Nile, ca. 80 km S Abou Sinbel, close Egypt frontier. Chelonii indet., possible Cyclanorbinae *Cyclanorbis senegalensis:* '*Emys* cf. *sivalensis*': Joleaud (1936), = *'Emyda sivalensis* Lydekker 1885, a junior synonym of *Lissemys punctata* (Lacépède 1788), the Indian form which has a similar decoration to that of this African form (unknown localization); see references in Gautier (1984).

Holocene-Present of Nile Valley area (A. Gautier, GU) (Broin det.):

Nile Valley (Khartoum area), Holocene, Gautier 1984,

Saggai 1, ca. 45 km N Khartoum, right Nile bank, ca. 6500 yr BP, *Pelusios adansonii* (Schweigger 1812), *Trionyx triunguis* (Forskål 1775), *Cyclanorbis senegalensis* (Duméril & Bibron 1835), small form, *Cycloderma elegans* (Gray 1869): Broin in Gautier (1983).

Geili, ca. 45 km N Khartoum, right Nile bank, ca. 5500 yr BP: *Pelusios adansonii*, *P.* cf. *castaneus* (Schweigger 1812), *Trionyx triunguis*, *Cyclanorbis cf elegans* (*in errore Cycloderma* cf. *aubryi*): Broin in Gautier 1983.

Umm Marihi, between Khartoum and Esh Shaheinab, left bank Nile, ca. 6700 yr BP (pers. comm. A. Gautier GU; Khartoum U), *Pelusios adansonni* (Schweigger 1812), cf. *Kinixys* sp. **El Kadada**, close to Shendi, N Khartoum, ca. 4800 yr BP, *Pelomedusa subrufa olivacea* (Schweigger 1812), *Trionyx triunguis*, *Cyclanorbis senegalensis*.

Er Renk area, S Khartoum, 600 km N Malakal, Holocene-Recent (Gautier & Van Neer 1997),

Debbat Bangdit, UN 25, ca. 400-500 to1000 AD, *Pelusios adansonii*, *Trionyx* cf. *triunguis*, *Cyclanorbis senegalensis*, *Cyclanorbis elegans*.

Debbat El Eheima, UN 24, ca. 1600-1000 BC, *Pelusios adansonii*, *Cyclanorbis senegalensis*, *Cyclanorbis elegans*.

Atbara River Valley (Peters, GU),

Khashm el Girba, ca. 80 km S Kassala, E Khartoum: sites: KG 0, ca. 2800 yr BP, *Kinixys* sp. (large form); KG 23, ca. 4400 yr BP, ?*Kinixys* sp.; KG 29N, 4500 yr BP, Trionychidae indet.; KG 14, ar; 6500 yr BP, *Trionyx* cf. *triunguis*; KG 55, ca. 7500 yr BP, *Trionyx* cf. *triunguis*, *Kinixys* sp.; KG 68, ca. 7700 yr BP, ?*Pelusios* sp., *Kinixys belliana* Gray 1831, *K.* sp., *Cyclanorbis elegans*; Broin *in* Marks *et al.* (1987) and undescribed data. **Jebel Shaqadud**, 16°15' N, 33°26' E, S Atbara, towards Kiteiyab, N Khartoum, ca. 4200-7500 yr BP; site A, cave deposits, ca. 4200 to 4900 yr BP, *Pelusios* sp., *Centrochelys sulcata* (Miller 1779)., *Kinixys* sp.; site B, in front of cave, ca. 6500 to 7500 yr BP, cf. *Pelusios* sp. (possibly *P. adansonii*), *Kinixys* sp. (possibly *K. belliana*) (Peters 1991; Broin det.).

West to Nile Sudan,

Burg et Tuyur, Selima sandsheet, ca. 120 km N of Laqiya Arbain, 6000 yr BP, *Centrochelys* sp. (likely *C. sulcata*): '*Geochelone* sp.': Van Neer & Uerpmann (1989).

Wadi Howar, NE extremity of Wadi Howar oued, site 80/73, 5200 yr BP, *Pelusios adansonii*, *P. castaneus*. Van Neer & Uerpmann (1989).

TANZANIA

Pliocene of Laetoli beds, ca. 3,59 to 3, 77 myr, NMK (partly observed by Broin):

Endulen, 8 km W, ioc 2, top tuff 6, *Stigmochelys brachygularis* (Meylan & Auffenberg 1987) [*'Geochelone (Geochelone)' brachygularis* Meylan & Auffenberg 1987]. **Endulen, 5 km W, loc. 5,** between tufs 2 and 5 and 0,50 m below tuff 6, loc. 6, tuff 7 and loc. 10W, below tuff 3, ?Aff. *Stigmochelys* sp. [*'G. (Aldabrachelys) laetoliensis'* Meylan & Auffenberg 1987: surely not a *'Aldabrachelys' sensu auct., i.e.* a *Dipsochelys*; possibly a *Stigmochelys* group member]. **Ndolanya beds**, *Stigmochelys pardalis* (Bell 1828): *'Geochelone' pardalis*: Meylan & Auffenberg (1987). **Marumbu, Garussi area,** *Stigmochelys brachygularis*, MNHB (Broin det.).

Pleistocene:

Olduvai Gorge (Auffenberg 1981; Leakey 1951, 1965), NMK (partly observed):

Bed II (or Bed I upper member?) ca. 1,70 myr, *Latisternon microsulcae* Auffenberg 1981.

Bed I upper member, bed II, ca. 1,70 to 1,75 myr, *Pelusios sinuatus* (A. Smith 1838) (Broin 1969; Williams, 1954a). Bed I, Middle part of upper member, ca. 1,75 myr, large Testudininei indet. sp. B (='*Geochelone* sp. B': Auffenberg 1981). Bed I, lower part of upper member, bed II, upper part, *Stigmochelys pardalis* (*'Geochelone' pardalis*: Auffenberg 1981), ca. 1,70 to 1,75 myr. Bed IV, Pleistocene, large *Stigmochelys* sp., 0,4 to 0,7 myr. Leakey (1965) mentions *Trionyx* in Olduvai beds: unverified presence.

Korongo, Njarasa Gorge = Lake Eyasi, north-eastern shore, Late Pleistocene, *Pelusios sinuatus*: 'Chelonians': Reck & Kohl-Larsen (1936) (Leakey 1951), MNHB. **Mumba Cave**, north-east of lake Eyasi, ?*Stigmochelys pardalis* (*'Testudo pardalis' in* Lehmann 1957, not verified).

TUNISIA

'Continental Intercalaire' of Sahara, upper part, Early Cretaceous (Lapparent 1960), MNHN (Broin det.):

Late Aptian, coll. A.F. de Lapparent,

Touil Dehibat, Late Aptian, cf. *Taquetochelys* sp.; . **Remada, Bir Kamboute, Guermessa,** Pelomedusoides indet. (small).

Albian-Cenomanian - prior to Cenomanian of Baharija and to Cenomanian transgression,

Dehibat-Gara Er Rehi, Guermessa, Er Ronda-Chenini trail, Pelomedusoides indet. (large; probably including Bothremydidae), coll. A.F. de Lapparent, coll. Captain Laumond.

Ypresian Phosphates (partly in MNHN, others in Tunisia):

Gafsa-Metlaoui basin, Moularès, Redeyef (marine, littoral), *Taphrosphys phosphaticus* (De Stefano 1903) - *T. rotundiformis* (Bergounioux 1952) group: Antunes & Broin (1988) (Broin 1977; Lapparent de Broin & Werner 1998; Moody 1972); Chelonioidea, genus indet., *'Euclastes' douvillei* De Stefano 1902 *(= 'Lytoloma elegans'* Bergounioux, 1952 = n. g., pre-cheloniid; = *'Lytoloma crassa'* Bergounioux 1952?); Chelonioidea genus indet., *'Thalassochelys' phosphatica* De Stefano 1903 (n.g., Osteopyginae?); Dermochelyidae genus indet., *'Thalassochelys' testei* Bergounioux 1956 (unpublished n.g., Moody 1997); (Bergounioux 1952, 1956; Moody & Buffetaut 1981).

Miocene:

Bled Douarah, Central Tunisia, Late Miocene, Vallesian (Geraads 1989), MN 9-, ca. 11 myr, ?*Trionyx* sp.: *'Trionyx* sp.': Robinson & Black (1974) (unverified) (Lapparent de Broin & Gmira 1994, Lapparent de Broin & Van Dijk 1999). **Djebel Semene** mine, or **Djebel Semama**, SW Tunis, 6 km Sidi N'Sir station, railway-Mateur to Béja, Late Miocene, Early Vallesian, MN9+, ca. 10 myr, *Testudo semenensis* Bergounioux 1954-1955 (a small form of *Testudo* s.l. with a gular pocket, but posterior plastron not preserved); MHNT. **Djebel Krechem El Artsouma**, Central Tunisia, Late Miocene, Late Vallesian, MN 10 (Geraads 1989), giant ?cf. *Centrochelys* (*Geochelone* sp.': Geraads 1989) (Lapparent de Broin & Van Dijk 1999), MNHN deposit.

Pliocene:

Hamada Damous, near Bou Arkoub, 50 km S Tunis, Pliocene, Ruscinian, MN 14, ca. 4,5 myr, Testudinidae indet.: ?*Mauremys* sp., ?Testudininei, ?possible *Testudo* (*'Testudo'*: Coppens 1971; material lost). **Ichkeul**, Garet or Lake Ichkeul, SW Bizerte, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr, *Trionyx* sp., *Testudo* s.l. (probable s.s.) sp., ?*Centrochelys punica* (Arambourg 1979): *'Testudo' punica* Arambourg, 1979; MNHN (Broin det.); *?Mauremys* sp. (*'Emys'*: Arambourg & Arnould 1949) (Arambourg1949, 1962, 1970, 1979).

Holocene:

Epipalaeolithic, Capsian,

Abri Clariond, near Aïn Moularès, Capsian, *Testudo g. graeca* : *'T. mauritanica'* (= *T. ibera*) *in* E. & L. Passmemard (1941, see Roubet 1966). **Oued Bou Haya**, near Feriana, Capsian, *Testudo g. graeca*: 'Tortue mauresque', *'T. ibera'*: Roubet 1966 (Vaufrey 1955); **Various localities**, *Mauremys leprosa*? Vaufrey (1955).

Neolithic,

Abri de Redeyef, W Gafsa, (Vaufrey 1955), **Djebel Hamra**, S Haïdra, (Gobert *in* Camps Fabrer 1966), **Kef el Agab**, Souk el Arba, (Bardin 1953): *Testudo g. graeca* ('Tortue mauresque', *'T. ibera'*: Roubet 1966) (ref. in Roubet 1966).

UGANDA

Early Miocene of Karamoja District, NE Uganda (Bishop 1958, 1964; Bishop & Whyte 1962; Pickford *et al.* 1986a,b), UM:

Napak, Early Miocene, ca. 19-20 myr, revised coll. Bishop, *Pelusios* sp. indet. group (loc. I?, IV, V, IX), Testudininei, a medium sized and a small form, including *Kinixys* sp. (loc. I, V, IX). Chelonii indet.: 'chelonians', Napak (19-20 myr) and Iriri (18 myr) members, Pickford *et al.* (1986a). **Moroto**, Sites I, II, Early Miocene, ca. 13-15 myr, Chelonii indet.; 'Chelonians': Bishop (1958); 'Chelonia': Pickford *et al.* (1986b).

Late Miocene-Pliocene of Occidental Rift, Lake Albert (Pickford *et al.* 1993):

Kisegi-Nyabusosi area, SW Lake Albert, Oluka Formation, lower member, Late Miocene, ca. 7-7,5 myr, *Cyclanorbis*, sp. A; Nyakabingo Formation, Late Pliocene, ca. 2,5-3 myr, *Pelusios sinuatus* (A. Smith 1838), *P.* sub-group *castaneus* (Schweigger 1812) sp. B, *Cyclanorbis*, sp. C: Lappparent de Broin & Gmira (1994), UM. **Nkondo-Kaiso**, East Lake Albert: Nkondo F., Nyaweiga Member, Early Pliocene, ca. 5-5,5 myr, *Pelusios sinuatus*, *P.* sub-group *castaneus* sp. A, cf. *Cyclanorbis*, sp. B. ; Warwire F., Middle Pliocene, ca. 3,5 myr, *Pelusios sinuatus*: Lappparent de Broin & Gmira (1994), UM. **Kaiso Village**, East Lake Albert (old coll.), Pliocene, Kaiso Beds, 2 to 2,3 myr (Cooke 1997), Pelomedusoides indet.: possible aff. *Erymnochely* sp. ('Pelomedusidae, ... closely resembling *Podocnemis*': Swinton1926); Cyclanorbinae indet. ('Trionychidae, ... large form closely allied to *Cycloderma* sp.': Swinton 1926; Arambourg 1947), NHM; Testudininei indet., large form ('fairly large *Testudo'*: Swinton 1926)(Lapparent de Broin & Gmira 1994).

ZIMBABWE

?Late Cretaceous:

Gokwe area, 18°21' S; 28°42' E, Gokwe F., Middle of Calcareous Member, Pleurodira indet., i.e. probable Pelomedusoides indet. (Chelonians indet: Nesbitt & Bond 1972; indet: Gaffney & Kitching 1995).

ARABIAN PENINSULA
SAUDI ARABIA

Palaeocene:

Jabal Umm Himar, near Turabah, Taif region, Bothremydidae, undetermined form, possible *Nigeremys* group : Lapparent de Broin & Werner (1998) ('Pelomedusidae': Wood 1995).

Miocene:

Chalon, Arabian Desert, Miocene, possibly Dam Formation, Cyclanorbinae indet.: '*Trionyx* sp.': Lydekker 1889 (Hummel 1932; Lapparent de Broin & Van Dijk 1999); NHM (Broin det.). **As-Sarrar**, Eastern Province, Dam Formation, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr, *Schweboemys* sp., aff. *Stereogenys* sp. or /± a Bothremydidae, aff. *Cycloderma* (new form), aff. *Allaeochelys* sp., ? cf. *Centrochelys* sp. ('*Geochelone* s.l. sp.') : Broin (in Thomas *et al.* 1982). **Al-Jadidah**, Hasa Province, Hofuf Formation (Thomas *et al.* 1978), Middle Miocene, Early Astaracian, MN 6, ca. 13 myr, ? cf. *Centrochelys* sp.: '*Geochelone* s.l. sp.': Lapparent de Broin & Van Dijk (1999).

Pleistocene:

An Nafud desert, SW sand sea, northern Saudi Arabia, ca. 28°N, 39-40°E, Pleistocene, *Centrochelys* cf. *sulcata* (Miller 1779): Thomas *et al.* (1998).

ABU DHABI, EMIRATE OF, UNITED ARAB EMIRATES

Miocene:

Baynunah Formation, Western Region, Middle-Miocene (Whybrow 1989), ca. 8 myr, *Trionyx* s.l. sp. (not *Trionyx* s.s.), *Mauremys* sp., *Centrochelys* aff. *sulcata* (Miller 1779): Lapparent de Broin & Van Dijk (1999); NHM, AUH.

OMAN, SULTANATE OF

Oligocene of Dhofar, base of Ashawq Formation, Shizar Member, base of Early Oligocene (Thomas *et al.* 1989, 1991):

Thaytiniti, slightly older than Taqah, Podocnemididae indet., *Stereogenys* group?, Testudininei indet. (aff. *Gigantochersina*?). **Taqah**, aff. *Erymnochelys* sp. a and sp. b, aff. or cf. *Schweboemys*, Testudininei indet. (possible aff. *Gigantochersina*?): '*Geochelone* group': (Thomas *et al.* 1991).

Miocene of Huqf area:

Ghaba, 50 km E of Ghaba, Dam Formation, Early Miocene-earlier Middle Miocene, Orleanian, ca. 18 myr, Bothremydidae n.g., n. sp., aff. or cf. *Schweboemys* sp., aff. *Cycloderma* sp. (new form), aff. *Allaeochelys* sp. (formerly given as 'aff. *Carettochelys*'), ?*Centrochelys* sp. ('cf. *Geochelone* s.l. sp'): Roger *et al.* (1994).

MADAGASCAR AREA
MADAGASCAR

Cretaceous, MNHN:

Betioky, Menarandroy valley, SW Madagascar, Cenomanian (marine, littoral), Bohremydidae indet., form A (?*Bothremys)*: Antunes & Broin (1988) (Lapparent de Broin & Werner 1998). **Berivotro**, Majunga area, Senonian, Bothremydidae indet., form B: Antunes & Broin (1988) (Lapparent de Broin & Werner 1998; Russell *et al.* 1976).

Holocene-Present (extinct, fossil and subfossils) (Bour 1982, 1984a,b, 1985, 1987, 1994), MNHN, NHM,

Gloriosa, < 125 000 yr BP, *Dipsochelys* sp.: Bour (1994).

Mahajanga area, Ampasambazimba, Antsirabe, western-southern area between Ambato (Morondava) and Andrahomana (Taolanaro), including **Etsere**, type locality of '*Testudo grandidieri* Vaillant, 1885', and **Ambolisatra**, type locality of '*Testudo abrupta* Grandidier 1868'; detailed 38 localities in Bour (1994), <3000 to ca. 750 yr BP, *Dipsochelys grandidieri* (Vaillant 1885), *D. abrupta* (Grandidier 1868): Bour (1994). **Ambato, Ankevo, Antsirabe,** < 10 000 yr BP, **Ambolisatra, Andrahomana**, <1000 yr BP, *Astrochelys radiata* (Shaw 1802)? *A.* cf. *radiata*; **Antinosi**, *Astrochelys* sp.: Bour (1994); still present in Madagascar.

ALDABRA AND SEYCHELLES ISLANDS (Bour 1982, 1984a,b, 1985, 1987), MNHN, NHM.

Holocene-present:

Granitic Seychelles, < ?10 000 to 150 yr BP, *D. daudini* (Duméril & Bibron 1835), *D. arnoldi* Bour, 1982, *D. hololissa*, Günther 1877. 'Gerlach & Canning (1998) considered that some individuals [of *D. hololissa* and *D. arnoldi*] were still living. However partly because the morphological data are unclear and not fully in accordance with the original descriptions of the species, partly because the published genetic data are not conclusive and without deliberately rejecting these results, it seems to us premature to give them full confidence, and we prefer to wait for further and decisive data' (Bour pers. comm.).

Aldabra atoll, 100 000 yr BP, *Dipsochelys* sp.

Seychelles atolls, including Aldabra, *Dipsochelys e. elephantina* (Duméril & Bibron 1835), fossil < 10 000 yr BP and still present, *D. e. sumerei* (Sauzier 1892), < ?10 000 to ?150 yr BP. Gerlach & Canning (1998) have revived the earlier name *Testudo dussumieri* Gray 1831, for the Aldabra tortoise *D. elephantina*. Bour (1985: 54) was the first to show the priority of the name *dussumieri* on *elephantina*. 1) The type is a juvenile and the study of the Galapagos forms has shown that the species are not well defined on juveniles: the International Commission of Zoological Nomenclature recommends not to use juveniles as type specimens. 2) Besides, Bour explained that the name '*dussumieri*' was no more utilized (*nomen oblitum*): in order to respect the stability of the nomenclature, its reviving is not recommended by the International Commission of Zoological Nomenclature (Bour pers. comm.).

COMOROS ISLANDS

Historic:

Dembeni 1, Mayotte Island, 850-880 AD, introduced from Madagascar: *Erymnochelys madagascariensis* (Grandidier 1867), *Pyxis* sp., *Astrochelys yniphora* (Vaillant 1885), cf. *Chelonia* sp. (Linné 1758): Broin (1990) (*in* Allibert *et al.* 1989-1990).

MASCARENE ISLANDS (Bour 1980b, 1984, 1985, 1987), MNHN, NHM.

Holocene-Present:

La Réunion, *Cylindraspis borbonica* Bour 1978, 2000 to 200 yr BP.

Mauritius, *Cylindraspis inepta* (Günther 1873), *C. triserrata* (Gunther 1873) = ?*C. graii* (Duméril & Bibron 1835), ca. 1700 to 300 yr BP.

Rodrigues, *Cylindraspis peltastes* (Duméril & Bibron 1835), *C. vosmaeri* (Suckow 1798), ?2000 to 200 yr BP.

TAXA OF AFRICAN CHELONIANS

Order Chelonii Brongniart, 1800 (Latreille 1800).

Linneaus did not erect an order for the group of chelonians: the taxon 'Testudines Linnaeus, 1758', currently employed after the incomplete analysis of Hunt (1958), does not exist because Linneaus, writing in latin, employed 'Testudines' as a plural form for the genus *Testudo*. Brongniart (1800) was the first to expressly erect an order for chelonians, 'Chéloniens' immediatly translated in Latin 'Chelonii' by Latreille (1800) (see Bour & Dubois 1985). The 'ordnung Testudines' exists, but it is due to Treviranus and not to Linneaus (1758). Actually, Treviranus (1802: 260) was the first to explicitly employ 'Testudines' (in Latin) for the order of 'Schildkröten' (in German), but after Chelonii and referring to Brogniart (sic) (1800). The same year McCartney (1802) erected the order Chelonia. Evidently, Treviranus (probably as also McCartney) ignored Latreille's translation. For chelonian nomenclature and references, see Bour & Dubois (1985, 1986).

INFRAORDER INDET.

Australochelyidae Gaffney & Kitching 1994

Australochelys africanus Gaffney & Kitching 1994, **Bormansdrift**, Orange Free State, Karoo, South Africa, Early Jurassic, Hettangian (Raath pers. comm.).

INFRAORDER PLEURODIRA COPE 1868

Araripemydidae Price, 1973: Plesion to hyperfamilia Pelomedusoides (sensu Broin 1988a,b)

Araripemys Price 1973, sp.: **Gadoufaoua**, Niger, **Aoulef, Timimoun**, (Gourara, Foggara Amerhaïer, Algeria, Late Aptian; **Timimoun, Gara Samani, Garet Touidjine** close to Oued Boudjihane, Algeria; **Erfoud area**, Hamada du Guir, **Kem Kem (Gara Tabroumit)**, Morocco, Albian-Cenomanian - prior to Cenomanian transgression.

Aff. *Araripemys* sp.: **Timimoun**, Algeria; **In Abangarit**, Mali, **Abay River Basin,** Ethiopia, Early Cretaceous, Albian-Cenomanian - prior to Cenomanian transgression.

?Araripemydidae

Taquetochelys decorata Broin 1980, **Gadoufaoua**, Niger, Late Aptian.

Cf. *Taquetochelys* sp.: **Anoual**, Morocco, Early Cretaceous, (Valanginian-Barremian), **Touil Dehibat**, Tunisia, Late Aptian.

Pelomedusoides Cope 1868

PELOMEDUSOIDEA COPE 1868

Pelomedusidae Cope 1868

Plesions to still extant genera of Pelomedusidae

Platycheloides nyasae Haughton 1928: **'Nyasaland'**, Malawi, Early Cretaceous.

Teneremys lapparenti Broin 1980: **Gadoufaoua**, Niger, Late Aptian.

'*Platycheloides* cf. *nyasae*' in Broin (1980) (Lapparent & Cooper in prep.): **Gadoufaoua**, Niger, Late Aptian.

Pelomedusidae indet.: **Hamadas du Guir-Erfoud area, Kem Kem**, Morocco, Albian-prior to Cenomanian transgression and prior to Cenomanian of Baharija.

Pelomedusidae (still extant genera).

Extant *Pelomedusa* Wagler 1830, Africa except Maghreb; Saudi Arabia; Madagascar; neighbouring islands (in particular Seychelles).

Pelomedusa subrufa (Lacépède 1788: **Haaskraal**, South Africa, Late Holocene.

P. subrufa olivacea (Schweigger 1812), **El Kadada,** Nile Valley, Sudan, Holocene, ca. 4800 yr BP.

P. cf. *subrufa*: **Ti-n Hanakaten**, NE Hoggar, Djanet Province, Algeria, Holocene, around 7000 yr BP.

Pelomedusa sp.: **Taungs (=Taung)**, South Africa, Plio-Pleistocene, ca. 2 or 2,5 myr.

Pelomedusa n. sp.: **Langental**, SW Namibia, Early Miocene, ca. 19 myr.

?*Pelomedusa* sp.: **Langebaanweg,** N Cape Town, South Africa, PPM, Pliocene, ca. 4-4,5 myr.

Extant *Pelusios* Wagler 1830, Africa except Maghreb, Madagascar; neighbouring islands.

P. adansonii (Schweigger1812) group:

P. adansonii: **Omo River Basin,** Ethiopia, Omo 75 (G4-13) and G4-27 to H Late, Late Pliocene-Early Pleistocene, ca. 1,7-1,9 myr; **Hassi el Abiod, Mali,** Holocene, 6970±130 yr BP; **Azaouak Valley**, Pr Baumhauer site, Niger, Holocene; **Saggai** 1, ca. 6500 yr BP, **Geili**, ca. 45 km N Khartoum, Nile right bank, ca. 5500 yr BP, **Debbat Bangdit**, UN 25, ca. 400-1000 AD, **Debbat El Eheima**, UN 24, ca. 1600-1000 BC, S Khartoum, 600 km N Malakal, at Er Renk, Nile Valley, **Wadi Howar**, ca. 5200 yr BP: Sudan, Holocene; **Umm Marihi**, Khartoum area, Nile Valley, Sudan, ca. 6700 yr BP; **Lake Chad**, S Shore, Cameroons, Protohistoric (1000 yr BP); **Sou, Lake Chad**, 75 km S Middle South shore, Cameroons, 7th-19th Century; **Koyom**, S Chad, Historic, ca. 19th Cry.

P. castaneus (Schweigger 1812):

P. castaneus: **Hassi el Abiod**, 6970±130 yr BP, **Erg Ine Sakane**, 9500-6400 years yr BP: Holocene, Mali; **Adrar Bous**, ca. 9030 yr BP, **Azaouak Valley, Pr Baumhauer site** : Niger, Holocene; **Wadi Howar**, Sudan, Holocene, ca. 5200 yr BP.

P. cf. *castaneus*: **In Aruinat, Azaouak Valley**, Niger, Holocene; **Geili**, ca. 45 km N Khartoum, right Nile bank, Sudan, Holocene, ca. 5500 yr BP; **Puits Tirenno**, Tibesti, Chad, Pleistocene-Holocene .

P. castaneus sub-group, sp. A: **Nkondo-Kaiso**, Early Pliocene, sp. B, **Kisegi-Nyabusosi**: Uganda, Late Pliocene.

Pelusios sp., *P. castaneus* sub-group: **?Cyrenaïca**, Libya, Holocene.

P. gabonensis (Duméril 1856):

P. gabonensis: **Awash River Basin, Central Afar, Hadar Formation** (SH-SH3, DD1-DD3), Pliocene, 3,40 to 3,18 myr, **Central Ledi Basin, West of Central Ledi Basin**: Pliocene, Ethiopia.

P. nanus Laurent 1965:

P. nanus: *'Pelusios* sp.': Van Neer (1978) = **Upemba depression**, Democratic Republic of Congo, Protohistoric, Iron Age (1200 yr BP).

P. sinuatus (A. Smith 1838):

P. sinuatus: **Wadi Natrun, Garet el Muluk**, Egypt, Late Miocene, MN 13+; **Nkondo-Kaiso**, Early and Middle Pliocene, **Kisegi-Nyabusosi area**, Late Pliocene: Uganda; **East LakeTurkana**, Kenya, Koobi Algi Formation, Early Pliocene, ca. 3,9-4,5 myr, Lower and Upper Koobi Fora Formation, Plio-Pleistocene, below KBS tuff (above Tulu Bor, 3, 35 myr), below to above KBS tuff, and between KBS and 'Okote tuff', ca. 1, 88 to 1,57 myr or more below Chari tuff (ca. 1,39 myr); **Ouadi Derdemy**, Chad, Pliocene, ca. 3-3,2 myr; **Chiwondo beds**, Malawi, Middle Pliocene, 2,5-4,8 myr; **Olduvai Gorge**, beds 1-2, Pleistocene, ca. 1,70-1,75 myr, **Njarasa Gorge = Lake Eyasi**, Late Pleistocene: Tanzania; **Omo River Basin**, Ethiopia, beds B9-10, C 8-9, E4, E4*, F1 to F3, G lower 1-9 and 11-13, ca. 3,79 to 1, 9 myr, Pliocene.

Cf. *P. sinuatus*: **Upper Semliki-Senga Rivers**, Lusso beds, Democratic republic of Congo, West Lake Albert, Pliocene.

P. cf. *sinuatus*: **Baringo Basin**, Ngorora F., Middle Miocene, Kenya; **Omo River Basin**, Ethiopia, Yellow Sands, A1, D2, E-E3, G3, Pliocene, 4 myr to 1,8 myr; **Republic of Djibouti**, Pliocene; **El Djour,** Yayo, Chad, Pliocene-Holocene.

Pelusios, indet. group:

P. rusingae Williams 1954a: **Rusinga Island**, NE Lake Victioria, Kenya, Early Miocene, ca. 18 myr.

Pelusios sp.: **Napak**, Uganda, Early Miocene, ca. 19-20 myr; **Hadar Formation, Ledi Basin, Awash River Basin, Central Afar**, Ethiopia, Pliocene; Chad Basin, Nigeria, Holocene, ca. 3000 yr BP; Sao de **Mdaga**, Chad, 425 BC to 1780 years AD.

Cf. *Pelusios* sp. (possibly *P. adansonii*): **Jebel Shaqadud**, S Atbara, towards Kiteiyab, N Khartoum, Atbara River Valley, Sudan, site A, cave deposits, Holocene, ca. 4200 to 4900 yr BP,

?*Pelusios* sp.: **Khashm el Girba**, Atbara River Valley, ca. 80 km S Kassala, E Khartoum, KG 68, Sudan, Holocene, ca. 7700 yr BP.

Pelomedusidae indet.

Aff. *Pelomedusa* sp.: **Ilimzi**, High Atlas, N Ouarzazate Basin, Morocco, Paleocene, Thanetian.

Pelomedusidae indet. (including *Pelusios*, possibly *P.* cf. *sinuatus*): **Baringo Basin**, Kenya Ngorora, Mpesida, Lukeino, Aterir, Chemoigut F., Mio-Pleistocene.

Podocnemidoidea Cope 1868

Bothremydidae Baur 1891

Apertotemporalis baharijensis Stromer 1934: **Baharija**, Egypt, Cretaceous, Early Cenomanian.

Bothremys Leidy 1865 group:

Zolhafah bella Lapparent de Broin & Werner, 1998: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian;

Bothremydidae indet. of *Bothremys* group, **Ammonite Hills**, Western Desert, Egypt, Late Cretaceous, Maastrichtian, aff. *Bothremys somaliensis* (Walker 1966); **Las Daban**, ca. 23 km ESE Berbera, Somalia, Lutetian.

Nigeremys Broin 1977 group:
Nigeremys gigantea (Bergounioux & Crouzel1968): **Ibeceten 2**, Niger, Maastrichtian.
Arenila krebsi Lapparent de Broin & Werner, 1998, ?cf. *Arenila krebsi*: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian.
Sokotochelys ummarumohammedi Halstead 1979, and *S. lawanbungudui* Halstead 1979: **SE Gilbedi village, Sokoto state,** Nigeria, Maastrichtian.
Indet. Aff. *Arenila* sp.: **Tagnout Chaggeret**, Mali A, Maastrichtian, **Wurno, Gada, Kworre, Gilbedi, Sokoto state,** Nigeria, Maastrichtian.
Bothremydidae indet., possible *Nigeremys* group: **Ibeceten 2**, Niger, Maastrichtian; **Jabal Umm Himar**, Saudi Arabia, Palaeocene.

Taphrosphys Cope 1869, group:
Taphrosphys congolensis (Dollo 1913): **Landana cliffs**, Cabinda, Angola, Palaeocene.
Group *T. phosphaticus* (De Stefano 1903) (= *'Gafsachelys' phosphaticus* De Stefano 1903) - *T. rotundiformis* (Bergounioux 1952) (= '*Eusarkia' rotundiformis* Bergounioux 1952) (synonyms '*Gafsachelys neurriregularis*' Bergounioux 1952 = *'Crassachelys' neurriregularis* in Moody 1872, '*G. moularensis*', Bergounioux 1955, '*Euclastochelys interrupta*' Bergounioux 1955): **Gafsa-Metlaoui** phosphates, Tunisia, Ypresian.
T. cf. *sulcatus* Leidy 1856: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian.
Taphrosphys sp.: **Tilemsi**, Mali C; **Phosphates**, Morocco, Maastrichtian-Ypresian.
Cf. *Taphrosphys* sp.: **Ammonite Hills**, Western desert, Egypt, Late Cretaceous, Maastrichtian; Popenguine, Senegal, Ypresian.
Aff. *Taphrosphys* sp.: **Benguerir**, Morocco, Palaeocene.

Bothremydidae indet.
Djoua, Gara Samani, Algeria; **In Abangarit**, Mali; **Erfoud area**, Hammada du Guir, Morocco; ?: **area of Remada**, Tunisia; 'Continental Intercalaire' of Sahara, late upper part, Albian-Cenomanian - prior to Cenomanian transgression.
Bothremydidae indet.: form A indet., ?*Bothremys* sp.: **Betioky**, Madagascar, Cenomanian; form B. indet. (a bothremydid quadrate): **Berivotro**, Madagascar B, Campanian; **Ambrizette**, 1 km S, around 7°15' S, Angola, Late Senonian (ca. Campanian); **In Farghas**, Cheit Keni, Tilemsi, Mali, Palaeocene; **Oued Zem**, Phosphates, Morocco, Palaeocene-Ypresian; **Samit**, Tilemsi, Mali B, Ypresian; **Tamaguilelt**, Tilemsi, Mali, Lutetian; new indet.: **Ghaba**, Sultanate of Huqf, Oman, Early Miocene-earlier Middle Miocene, Orleanian, ar. 18 myr; genus indet. (*'Podocnemis') lata* Ristori 1894: **Malta**, Miocene.
Bothremydidae indet.: *'Eusarkia'* sp. *in* Bergounioux & Crouzel 1968, **Tikarkas**, Mali D, Albian-Cenomanian - prior to Cenomanian transgression.

Podocnemididae Cope 1868
Erymnochelyinae Broin 1988a
Erymnochelys Baur 1888 group:
Extant *Erymnochelys* in Madagascar only.
Erymnochelys madagascariensis (Grandidier 1867): **Dembeni 1**, Mayotte Island, Comoros islands, 850-880 AD, introduced from Madagascar.
Dacquemys fajumensis (Andrews 1903) (= *Podocnemis fajumensis* Andrews 1903, + *Dacquemys palaeomorpha* Williams 1954b = *Podocnemis blanckenhorni* Reinach 1903): **Birket El Kurun beds, Fayum**, Egypt, Early Oligocene.
Aff. *Erymnochelys* sp. a and b: **Taqah**, Dhofar, Sultanate of Oman, Oligocene.
Aff. *Erymnochelys aegyptiaca* (Andrews 1900): **Moghara**, Egypt, Early Miocene, ca. 18 myr.
Aff. *Erymnochelys* sp., young: **Karungu**, NE Lake Victoria, Kachuku beds, Early Miocene, ca. 18 myr.
Aff. or cf. *Erymnochelys*: **El Arag**, Egypt, Neogene.
Kenyemys williamsi Wood 1983: **Lothagam 1**, Kerio River Basin, Kenya, Late Miocene, ca. 6 myr.
Aff. *Erymnochelys* sp. A: **Kerio River Basin**, Kenya, **Lothagam 1, 3, Kanapoi, Ekora**, Late Miocene-Pliocene.
Aff. *Erymnochelys* sp.: **Sinda-Mohari** Rivers Region, Lower Semliki river, West Lake Albert, Democratic Republic of Congo: Sinda beds, Ongoliba Horizon, site 11, Late Miocene; sites 3, 7 and 15, Middle and upper Members, Mio-Pliocene.
Erymnochelys group: **Ibeceten** 1, Niger, Senonian; **Moghara**, Egypt, Early Miocene, MN 3+, ca. 18 myr.
Pelomedusoides indet., possible aff. *Erymnochelys* sp.: **Kaiso Village**, Uganda, Pliocene, Kaiso Beds, 2 to 2,3 myr.
Erymnochelyidae indet.: **Wadi Abou Hashim**, N Sudan, Wadi Milk Formation and a **new loc.**, Shendi Formation, Sudan, Albian-Senonian.

Stereogenys Andrews 1901- *Schweboemys* Swinton 1939:
Stereogenys cromeri Andrews 1901: **Fayum, Qasr El Sagha beds,** Egypt, Late Eocene. *S. libyca* Andrews 1903: Fayum, Birket El Kurun beds, Egypt, Early Oligocene.
?*Stereogenys* sp.: **Djebel Zelten**, Egypt, Miocene, Orleanian, MN 4+, ca. 16,5 myr.
Schweboemys antiqua (Andrews 1903): **Fayum**, Qasr El Sagha beds, Egypt, Late Eocene.
Schweboemys sp.: **As Sarrar**, Eastern Province, Saudi Arabia, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr.
Aff. or cf. *Schweboemys*: **Taqah**, Dhofar, Sultanate of Oman, Early Oligocene; **Ghaba**, Huqf, Sultanate of Oman, lowe Middle-earlier Middle Miocene, Orleanian, ar. 18 myr.
Podocnemididae indet., *Stereogenys* group?: **Thaytiniti**, Dhofar, Sultanate of Oman, Early Oligocene.
Genus indet. (*?Schweboemys* = '*Podocnemis*') *bramlyi* Fourtau 1920: **Moghara**, Egypt, Early Miocene, ca. 17,5 myr.

Erymnochelyinae indet.: **Auchas**, ca. 18 myr, **Arrisdrift**, ca. 17 myr., N Orange River, S Namibia, Early Miocene.
Genus indet. (*Neochelys* group?: '*Stereogenys') podocnemoides* Reinach 1903: **Qasr El Sagha beds, Fayum**, Egypt, Late Eocene.
Genus indet. (*Schweboemys-Stereogenys* group?: *'Sternothaerus') blanckenhorni* Dacqué 1912: **Moghara**, Egypt, Early Miocene, ca. 17,5 myr.

Indet. sub-family:
Hammadachelys escuillei Tong & Buffetaut 1996: **Hammada du Guir**, Morocco, Albian-Cenomanian, prior to Cenomanian of Baharija and to Cenomanian transgression.

Podocnemididae indet.
In Akhamil, Algeria, **Hammada du Guir**, **Kem Kem**, Morocco, Early Cretaceous, Albian-Cenomanian, prior to Cenomanian transgression and to Cenomanian of Baharija and prior. **Djebel Zelten**, Libya, Early Miocene, ca. 16,5 myr (*?Stereogenys* sp.).

Podocemidoidea indet.
Gara Samani, Djoua, Algeria, **Hammada du Guir, Kem Kem**, Morocco, Early Cretaceous, Albian-Cenomanian, prior to Cenomanian of Baharija and to Cenomanian. **Abay River Basin**, Ethiopia, Early Cretaceous. **Dhor et Talha**, Libya, Late Eocene-Early Oligocene? (possible Podocnemididae). **As-Sarrar**, Eastern Province, Saudi Arabia, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr (aff. *Stereogenys* sp. or /± a Bothremydidae).

Pelomedusoides indet. incertae familiae, ?Pelomedusidae
Latisternon microsulcae Auffenberg 1981: **Olduvai Gorge**, Tanzania, Bed II (or Bed I, upper member?), Pleistocene, ca. 1,70 myr.

Pelomedusoides indet.
Primitive forms: **Djoua, 120 km E Fort Flatters, 17 km S Alrar**, Algeria, **Kem Kem, Hammada du Guir,** Morocco, **Remada Bir Kamboute, Dehibat Gara Er Rehi, Guermessa, Er Ronda Chenini trail,** Tunisia, Early Albian-Cenomanian, prior to Cenomanian of Baharija and to Cenomanian transgression.
Algeria: El Kohol, S Oran Province, Late Eocene ('Paludine turtle'). **Democratic Republic of Congo**: **Lower Semliki River**, Sinda-Mohari rivers, West Lake Albert lake: Ongoliba Beds: sites 5, 11, Late Miocene; **Upper Semliki-Senga rivers**, Lusso beds, West Lake Albert, Pliocene (Pelomedusidae?, Podocnemididae?). **Kenya: Baringo Basin**, Lukeino, Aterir and Chemoigut F., Mio-Pliocene; **Lothagam Hill**, beds 1, Pliocene (abnormal *Pelusios*?). **Libya: Dhor et Talha**, Idam Unit, ?Early Oligocene; **Zella Oasis**, Oligocene ('paludine turtles'). **Morocco**: **Adrar Mgorn, Ilimzi**, High Atlas, N Ouarzazate Basin, Thanetian. **Niger**: **Ebrechko**, Barremian-Aptian; **In Abangarit**, Early Albian-Cenomanian; **Ibeceten 1**, Senonian. **Sudan, North, loc. F 1/89 - F 2/89**, Wadi Milk Formation, Early Cretaceous, ca. Cenomanian; **Wadi Abou Hashim** and **new loc. Shendi Formation**, Cenomano-Turonian.
?Pelomedusoides indet.: **Anoual**, Morocco, Early Cretaceous, Valanginian-Barremian.

Pleurodira, probably Pelomedusoides indet.
Gokwe area, 18°21' S, 28°42' E, Zimbabwe, ?Cretaceous.

INFRAORDER CRYPTODIRA COPE, 1868

Dermochelyoidea Baur1888 (marine)
Dermochelyidae Baur1888
Extant *Dermochelys* Blainville 1816
Egyptemys eocaenus (Andrews 1901): **Qasr El Sagha beds, Fayum**, Egypt, Late Eocene.
Cosmochelys dolloi Andrews 1919: **Ameki**, Ombialla District, South Nigeria, Ameki Formation, Eocene (Lutetian).
Genus indet. ('*Thalassochelys*') *testei* Bergounioux 1956: **Gafsa-Metlaoui Phosphates**, Tunisia, Ypresian; new undescribed possible Dermochelyidae (private coll.) **Oued Zem**, Morocco, Palaeocene-Ypresian.

CHELONIOIDEA OPPEL 1811 (MARINE)
Toxochelyidae Baur 1895
?Toxochelyidae indet. (*Bantuchelys* Dollo 1924, *ex parte*): **Landana cliffs**, Cabinda, Angola, Palaeocene.

Osteopygidae Zangerl 1953
Aff. *Euclastes* Cope 1867 sp.: **Benguerir**, Phosphates, Morocco, Maastrichtian.
Osteopygidae indet.: **Oued Zem**, Phosphates, Palaeocene-Ypresian, Morocco.

Cheloniidae Oppel 1811
Extant *Caretta* Rafinesque 1814, *Chelonia* Latreille 1802, *Eretmochelys* Fitzinger 1843, *Lepidochelys* Fitzinger 1843, all African sea coasts.
C. mydas (Linneus 1758): **Berenike**, Egypt, Holocene, ca. 2000-1500 yr BP.
Cf. *Chelonia mydas*: **Dembeni 1**, Mayotte Island, Comoros islands, 850-880 Y after JC, introduced from Madagascar.
Genus indet. ('*Thalassochelys*') *libyca* Andrews 1901: **Qasr El Sagha beds, Fayum**, Egypt, Late Eocene.
Genus indet. *('Trachyaspis')* cf. *aegyptiaca* Lydekker 1889: **Qasr El Sagha** beds, Fayum, Egypt, Late Eocene.
Trachyaspis aegyptiaca Lydekker 1889: **Suez Canal**, Egypt, Tertiary indet., probable Miocene; erroneous attribution to *Syllomus* Cope, 1896, by Weems (1974, 1980), instead of *Trachyaspis* Meyer 1843; *Trachyaspis* cf. *aegyptiaca*, **Wadi Natrun** (Djebel El Muluk, Garet El Muluk), Late Miocene, MN 13+.
Cheloniidae, n. g. indet., '*Euclastes*' *douvillei* De Stefano 1902: **Gafsa-Metlaoui** Phosphates, Tunisia, Ypresian.
Cheloniidae indet.: **Faboura**, Senegal, Protohistoric, between 1360 and 1940 ±80 yr BP.
Incertae familiae
Genus indet. (Osteopyginae?: '*Thalassochelys*') *phosphatica* De Stefano 1903: **Gafsa-Metlaoui** Phosphates, Tunisia, Ypresian.
Aff. **Tasbacka** Nessov 1986, sp.: **Ammonite Hills**, Egypt, Late Cretaceous, Maastrichtian.
Cheloniidae?: genus indet. (*'Thalassochelys') libyca* Andrews, 1901'; *'Trachyaspis* cf. *aegyptiaca* Lydekker 1889': **Fayum**, Qasr El Sagha beds, Egypt, Late Eocene.
Chelonioidea indet., giant pre-cheloniid: **Ouled Adoun**, between Kouribga and Oued Zem, Phosphates, Morocco, Maastrichtian.

Dermochelyoidea or Chelonioidea indet.
Dermochelyoidea or Chelonioidea indet.,**Umtata River mouth**, South Africa, Albian-Cenomanian.
'Chelonioidea' indet., **Benguerir, Oued Zem**, Phosphates, Morocco, Maastrichtian-Ypresian.

Trionychoidea Fitzinger 1826
Carettochelyidae Boulenger1887
Aff. *Allaeochelys* Noulet 1867, sp. (see Broin 1977): **Moghara?, Wadi Faregh**, Egypt, Early Miocene, MN 3+, ca. 18 myr; **Ghaba**, Huqf, Sultanate of Oman, Early Miocene-earlier Middle Miocene, Orleanian, ar. 18 myr; **As-Sarrar**, Eastern Province, Saudi Arabia, Early Middle Miocene, Orleanian, MN 5, ca. 16 myr.
Carettochelyidae indet.; **Sinda Mohari Rivers Region**, Lower Semliki river, Democratic Republic of Congo, West Lake Albert, Sinda Beds, site 3, middle member, Mio-Pliocene.

Trionychidae Fitzinger 1826
Trionychinae Fitzinger 1826
Extant *Trionyx* Geoffroy 1809, eastern and partial Central Africa.
Trionyx triunguis (Forskål 1775): Sahabi, Libya, Late Miocene, MN 13+; **East Lake Turkana**, Kenya, Koobi Fora Formation, Pleistocene above KBS tuff, ca. 'Okote tuff', complex tuff KF, ca. 1,57 myr?; **Araouan-Guir area, Hassi el Abiod**,Taoudenni, Mali, Holocene, 6970±130 yr BP; **Neo Bochianga**, Chad, Holocene, Stone Age with harpoons, Pleistocene-Holocene ca. 5500 yr BP; **Saggai 1**, ca. 6500 yr BP, Geili, ca. 5500 yr BP, **El Kadada**, ca. 4800 yr BP, Holocene, Nile Valley: Sudan; **Toukh**, Egypt, Neolothic (Amratian and Gerzean); **Fayum**, Egypt, Holocene; **Adaïma**, Egypt, Neolothic; **Faboura**, Senegal, Protohistoric, between 1360 and 1940 ±80 yr BP.
Trionyx cf. *triunguis*, *Trionyx* sp.: **Low Lands of Chad, Eguei, Kanem, El Djour, Djourab, Borkou, Tibesti**, Chad, Pliocene, Pleistocene-Holocene; **Debbat Bangdit**, UN 25, Nile Valley, ca. 400-1000 BC, **Khashm el Girba,** Atbara River Valley, KG 55, ca. 7500 yr BP, Holocene, Sudan; **Kobadi**, KBD 84, E Nampala, S Mali, Holocene; **Takane Barva** and **Azaouk Valley**, Pr Baumhauer site, Niger, Holocene.
Trionyx s.s . sp.: **Wadi Natrun**, Egypt, Late Miocene, MN 13+; **Ichkeul**, Tunisia, Pliocene, MN15-, ca. 3,5 myr; **Rabat 6, coast from Rabat to Temara**, Morocco, Temara Formation, Late Pleistocene, Tyrrhenian.
Cf. *Trionyx* sp.: **Omo River Basin**, Ethiopia, bed A3, Pliocene, ca. 3 myr; **Ouadi Derdemi**, Chad, Pliocene, 3 to 3,2 myr.
'*Trionyx* sp.' (possibly a true *Trionyx* s.s.): **Aïn Boucherit**, Constantine Province, Algeria, Pliocene, Ruscinian, MN15; **Bled Douarah**, Tunisia, Late Miocene, Vallesian, MN 9-, ca. 11 myr; Bahr el Ghazal, E. Koro-Toro, KT 12 site, Chad, Pliocene, ca. 3-3,5 myr. ?*Trionyx* sp.: **Anteopolis** (Siout, Asyut) tomb, Egypt, Pleistocene-Holocene.
Trionyx s.l. sp., indet. group (not a *Trionyx* s.s.): Western Region, Emirate of Abu Dhabi, **Baynunah Formation**, Late Middle Miocene, ca. 8 myr.

Cyclanorbinae Lydekker 1889
Extant *Cyclanorbis* Gray 1835, partial Central Africa.

Cyclanorbis senegalensis (Duméril & Bibron 1835) group:
C. senegalensis (large and small forms): **East Lake Turkana,** Kenya, Koobi Fora Formation, lower member, area 105, 20 m

below tuff KBS (before 1,88 myr), Late Pliocene; **Bochianga, Puits Tirenno**, Chad, Pleistocene-Holocene (small form); **Hassi el Abiod**, 6970±130 yr BP, **Erg Ine Sakane**, 9500-6400 years yr BP, Guir, Taoudenni, Mali, Holocene, **Azaouak Valley, Ikawaten, In Aruinat**, Niger, Holocene (small form); **Saggai 1**, ca. 5500 yr BP (small form), **El Kadada**, ca. 4800 yr BP, **Debbat Bangdit**, ca. 400-1000 BC, **Debbat El Eheima**, UN 24, ca. 1600-1000 BC, Nile Valley, Sudan, Holocene; **Djebel Zelten**, Cyrenaica desert, Libya, Holocene (small form); **Mole National park**, Ghana, Protohistoric; **Sintiou Bara**, Senegambia, Senegal, Protohistoric, 400 to 1050 yr BP (small form); Sou, Lake Chad, 75 km S middle South shore, 7th-19th Century, Cameroons (small form); **Senegal middle Valley**, Senegal, IVth-Vth Ctry; **Koyom**, S Chad, Historic, ca. 19th Century.
C. turkanensis Meylan *et al.* 1990: **Kanapoi, Kerio River Basin**, Kenya, bed E, Pliocene, 4,2 to 5 myr.
Cyclanorbis sp. A.: **Kisegi-Nyabusosi area**, Uganda, Oluka Formation, lower member, Late Miocene, ca. 7-7,5 myr.
Cf. *Cyclanorbis* sp. B.: **Nkondo-Kaiso**, Uganda, Nkondo Formation, Nyaweiga member, Early Pliocene, ca. 5,5 Ma.
Cyclanorbis sp. C: **Kisegi-Nyabusosi area**, Uganda, Nyakabingo Formation, Late Pliocene (2,5-3 myr), Lake Baringo, Kenya, Chemeron beds (*Cycloderma* sp., in Meylan *et al.* 1990), Late Pliocene, ca. 2-2,5 myr ?
Cyclanorbis sp.: **Sinda-Mohari Rivers area**, Lower Semliki River, sites 1, 3, 5, Ongoliba beds, Democratic Republic of Congo, Miocene, ca. 6 myr.
?*Cyclanorbis senegalensis*: **Wadi Halfa**, Nile, Sudan, Pleistocene, **Anteopolis** (Siout, Asyut) tomb, Egypt, Pleistocene-Holocene.

Cyclanorbis elegans (Gray 1869) group:
C. elegans: **Omo River Basin**, Ethiopia, B9-10, ca. 2,9 myr, Pliocene; **East Lake Turkana**, Kenya, Koobi Fora Formation, area 102, below KBS tuff, Pliocene and undefined horizon; **El Kadada**, ca. 4800 yr BP, **Debbat El Eheima**, UN 24, ca. 160-1000 BC, **Debbat Bangdit**, UN 25, ca. 400-1000 BC, Nile Valley, **Khashm el Girba**, KG 55, ca. 7500 yr BP, Atbara River Valley, Sudan, Holocene.
C. cf. *elegans*: **Omo River Basin**, Ethiopia, Yellow Sands, ca. 4-myr, Pliocene; Geili, Nile Valley, Sudan, Holocne, ca. 5500 yr BP; **Mole National park**, Ghana, Protohistoric.

Cyclanorbis sp.: indet. group., **Wadi Howar**, Sudan, Holocene, 5200 yr BP.
Cyclanorbis sp. (*elegans* or *turkanensis*): **East Lake Turkana**, Kenya, 20 m below tuff KBS (before 1,8 myr), Late Pliocene and unknown horizon.
?Cyclanorbis sp.: bed A1, **Omo River Basin**, Ethiopia, Pliocene, ca. 3,6 myr.

Extant *Cycloderma* Peters 1854, partial Central Africa.
Cycloderma frenatum Peters 1854 group:
C. frenatum: Lothagam 3, **Kerio River Basin**, Kenya, Pliocene, ca. 1,8 myr; Chiwondo beds, Malawi, Pliocene, ca. 2,5-4,8 myr; **Omo River Basin**, Ethiopia, beds A1, ca. 3,6+ myr, B2, ca. 3,3 myr, E (E3, E4*), ca. 2,12 myr, G27, ca. 1,9 myr, Pliocene; **Awash River Basin, Central Afar** and **Central Ledi Basin**, **West of Central Ledi Basin**, Ethiopia, Pliocene; **East Lake Turkana**, Kenya, Koobi Fora Formation, area 105, 20 m below KBS tuff, before 1,88 myr, Pliocene; **Lake Malawi**, Malawi, Chiwondo beds, 'Pliocene'.
Cycloderma cf. *frenatum*: **East Lake Turkana**, Kenya, Koobi Fora Formation, between KBS and 'KF, Okote tuff', 1,88 to ?1, 57 myr, Plio-Pleistocene.
Cf. *Cycloderma* frenatum: **Tributary of Zambesi**, Mozambique, Pleistocene-Holocene.
Cf. *Cycloderma* sp.: **Awash River Basin**, Central Afar and **Geraru Basin**, Ethiopia, Pliocene.

Attributed to *C. frenatum* group
Aff. *Cycloderma victoriae* (Andrews 1914): **Karungu**, Kachuku beds, Kenya, Early Miocene, ca. 18 myr.
Aff. *C. debroinae* (Meylan *et al.* 1990): **Lothagam 1**, Kerio River Basin, Kenya, Late Miocene, ca. 6 myr.
Cycloderma aubryi (A. Duméril 1856):
Koyom, S Chad, Protohistoric, ca. 19 th Ctry.

Undefined group
Aff. *Cycloderma melitensis* (Lydekker 1891): **Malta**, Miocene.
'*Cycloderma* sp.': **Kaiso**, East Lake Albert, Uganda, Pliocene, ca. 4,8 myr.
Cf. *Cycloderma* sp. (or *Cyclanorbis* sp.?): **Upper Semliki-Senga rivers**, Democratic Republic of Congo, Lusso beds, Pliocene, ca. 2,4-2,5 myr.
Aff. *Cycloderma*, new primitive form: **Ghaba**, Huqf, Sultanate of Oman, Early Miocene-earlier Middle Miocene, Orleanian, ca. 18 myr; **As-Sarrar**, Eastern Province, Saudi Arabia, Early Middle Miocene, MN 5, ca. 16 myr.

Cyclanorbinae indet.:
Moghara (possible *Cyclanorbis senegalensis* group, Reinach 1903, pl. 17, fig. 6): **Wadi Faregh?**, Egypt, Early Miocene, MN 3+, ca. 18 myr; **Ombo**, Lake Victoria, Kenya Early-Middle Miocene, ca. 15-16 myr; Chalon, Saudi Arabia, Early Middle Miocene, ca. 16 myr; **Kanapoi**, Kerio River Basin, Kenya, Pliocene, ca. 4,2 myr; **Omo River Basin**, Ethiopia, beds A3, E, F1-F3, G27, Pliocene, ca. 3 to 1,8 myr; Kaiso Village, Uganda, Pliocene, ca. 2 to 2,3 myr.
?Cyclanorbinae indet. ('Trionychidae' indet.): **Koru**, Kenya, Early Miocene, ca. 20 myr; **Lake Victoria area**, Early-Middle Miocene, **Lake Baringo Basin**, Ngorora, Mpesida, Lukeino, Chemeron, Chemoigut Formations, Mio-Pleistocene, ca. 12,5 to 1,2 myr, **Lothagam 3**, ca. 3,8 myr and **Kanapoi**, just <4 myr, Kerio River Basin, Pliocene and **East Lake Turkana**, Koobi Fora Formation, 20 m below KBS tuf, before 1,88 myr and around 20 m below or above KBS tuff and undefined horizon, Plio-Pleistocene: Kenya; **Sinda-Mohari Rivers Region**, Lower Semliki river, Sinda Beds, Democratic Republic of Congo, Sinda beds, middle and upper Member, site 1, 3, 15, Mio-Pliocene; **Koyom**, S Chad, Protohistoric, ca. 19th Century.

Trionychidae indet.:
East Lake Turkana, Kenya, Koobi-Fora Formation, area 105, 20 m below KBS tuff, ca. 1,88 myr,
Khashm el Girba, ca. 80 km S Kassala, E Khartoum, Atbara River Valley, site KG 29N, Sudan, Holocene, 4500 yr BP.

?Trionychinae indet.
Upper beds of **Baringo Basin**, **Homa Peninsula** of Lake Victoria, Late Pliocene ('Trionychidae' indet.), **East Lake Turkana**, Koobi Fora Formation, Plio-Pleistocene: Kenya.
Trionychoidea indet.:
Baringo Basin, **Homa Peninsula**, Late Miocene-Early Pliocene, Kenya: 'Trionychidae' = Trionychidae / Carettochelyidae.

TESTUDINOIDEA BATSCH 1788
Emydidae Gray1825 (1815)
Extant *Emys orbicularis* (Linnaeus 1758), Maghreb, Palaearctic fauna.
?Algeria, ?Tunisia, various localities of Early Holocene, Capsian?: no proove or even indication of the presence of *Emys* is given *in* Roubet (1966) and Vaufrey (1955). The specimen attributed to *Emys* from Malta, Zebbug Cavern, Pleistocene (Leith-Adams 1877) is of *Mauremys leprosa.*

Testudinidae Batsch 1788
Geoemydinei Theobald 1868
Mauremys, Gray 1869, circum-Mediterranean Palaearctic fauna.
Extant *Mauremys caspica* (Gmelin 1774), eastern Mediterranea, Saudi Arabia.
Extant *Mauremys leprosa* (Schweigger 1812), Maghreb, western Mediterranea.
M. leprosa: **Aïn Boucherit**, Constantine Province, Pliocene, Ruscinian, MN 14-15, Tighenif (Ternifine, Palikao), Oran Province, Middle Pleistocene, Villanyan: Algeria; **Doukkala II**, Late Pleistocene, Soltanian, to Holocene, Rharbian, Taforalt, 55

km NW Oujda, Late Pleistocene, Aterian: Morocco; **Zebbug Cavern**, Malta, Pleistocene. Various other localities **Algeria, Tunisia?**, Early Holocene, Capsian (Vaufrey 1955).
Mauremys sp.: **Wadi Natrun**, Egypt, Late Miocene, MN 13+, **Dar Es Soltane**, Morocco, Late Pleistocene, Soltanian, or Holocene, Rharbian.
Mauremys sp.: probable *leprosa* group, **Mansourah**, Constantine Province, Algeria, Pleistocene.
? *Mauremys* sp.('*Emys*'): **Bou Hanifia**, Oran Province, Algeria, Late Miocene, Vallesian, MN 9+, ca. 10,5 myr; **Ichkeul**, Tunisia, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr.
?*Mauremys* sp.: **Hamada Damous**, Tunisia, Pliocene, Ruscinian, MN 14, ca. 4,5 myr.
Mauremys sp.: (not *leprosa* group), Western region, **Baynunah Formation**, Emirate of Abu Dhabi, Middle-Miocene, ca. 8 myr.

Testudininei Batsch 1788 (terrestrial)
Ethiopian - African endemic groups (sensu Williams 1952, emend. Bour 1980a; emend. *in* this work):
Small Ethiopian endemics:
Extant *Chersina* Gray, 1831, southern Africa.
C. angulata (Schweigger 1812): **Die Kelders 1**, middle Stone Age, ca. 75 000 to 50 000 yr BP, **Byneskranskop Cave 1**, later Stone Age, 13 000 to 250 yr BP, southern Cape Province, **Klipfonteinrand Cave**, Clanwilliam District, later Stone Age, **Elands Bay Cave and nearby sites**, between 18 000 and 300 yr BP, Pleistocene-Holocene: South Africa. **Edgehill** and **Welgeluk**, South Africa, Konaap River near Adelaide, eastern Cape, Holocene, from 6000 yr BP to the present.
Chersina sp.: **Langebaanweg**, N Cape Town, PPM, Pliocene, ca. 4-4,5 myr, **Hopefield**, N. Cape Town, Late Pleistocene, ca. 100 000 Y, southern Cape Province, Pleistocene-Holocene: South Africa.

Extant Homopus Duméril & Bibron 1835, southern Africa.
H. femoralis Boulenger 1888, *H. boulengeri* Duerden 1906: **Haaskraal**, South Africa, Late Holocene, Hantam Mountains, north-west of Calvinia, South Africa, Holocene 3119 BC.
H. areolatus Thunberg 1787, **Edgehill** and **Welgeluk**, South Africa, Konaap River near Adelaide, eastern Cape, Holocene, from 6000 yr BP to the present,
H. fenestratus Cooper & Broadley 1990: **Carlisle Bridge**, Cape Province, South Africa, probable Late Neogene.

Extant *Kinixys* Bell 1827, Africa, south of Sahel.
K. erosa (Schweigger 1812): **Songhor**, Kenya, Early Miocene, ca. 20 myr. **Matupi Cave**, northeastern Zaïre, Democratic Republic of Congo, late Stone Age, between 22000-2000 yr BP, Iron Age, before 2000 yr BP.
K. belliana Gray 1831: **Khashm el Girba**, Atbara River, Sudan, Holocene, KG 68, ca. 7700 yr BP, Koyom, S Chad, Protohistoric site.
Kinixys sp.: **Napak**, Uganda, Early Miocene, ca. 19-20 myr, **Khashm el Girba**, KG 0 (large form), ca. 2800 yr BP, KG 55, ca. 7500 yr BP, Atbara River, Sudan, Holocene.
?*Kinixys* sp.: **Ntadi Yomba**, Tsitolian Abri, People's Republic of Congo, Holocene, ca. 7000 years yr BP; **Jebel Shaqadud** (possibly *K. belliana*), site B, in front of cave, ca. 6500 to 7500 yr BP, **Khashm el Girba**, KG 23, ca. 4400 yr BP, Atbara River: Sudan, Holocene.
Cf. *Kinixys* sp.: **Umm Marihi**, Khartoum area Nile Valley, Sudan, ca. 6700 yr BP.

Extant *Malacochersus* Lindholm 1929, central-eastern Africa.
No fossil known.

Extant *Psammobates* Fitzinger 1835, southern part of Africa.
P. tentorius (Bell 1828): **Haaskraal**, South Africa, Late Holocene.
P. antiquorum Broadley 1997c: **Drimolen**, Gauteng Province, South Africa, Plio-Pleistocene, ca. 2 to 1,8-1,6 myr.

Other Ethiopian/African endemics:
Gigantochersina ammon (Andrews 1903) ('*Testudo ammon* Andrews and Beadnell 1903'), = *T. isis*, Andrews 1906? = *T. beadnelli* Andrews, 1906?): **NW Birket el Kurun**, Fayum, Egypt, Early Oligocene (Andrews 1904).
Testudininei indet. ('*Geochelone* s.l. sp', possible aff. *Gigantochersina*?): **Taqah**, **Thaytiniti**, Dhofar, Sultanate of Oman, Early Oligocene.
Impregnochelys pachytectis Meylan & Auffenberg 1986: **Rusinga Island**, NE Lake Victoria, Upper Katwanga serie, Early Miocene, ca. 18 myr.
Testudininei indet. small and medium sized forms: **Napak**, Uganda, Early Miocene, ca. 19-20 myr.
Testudininei n. g. a (large form): *'Testudo' namaquensis* Stromer, 1926: **Elisabethfeld**, SW Namibia, Early Miocene, ca. 19-20 myr.
Same Testudininei n. g . a (large form), several n. sp.: **Fiskus, Grillental**, **Langental**, **Glastal**, SW Namibia, Early Miocene, 19-20 myr; **Auchas**, **Arrisdrift**, **Karingarab**, wardi level, **North of Gypsum Plate Pan**, ca. wardi level, **Rooilepel**, wardi and laini levels, N Orange River, S Namibia, Early to Middle Miocene, ca. 18 to 8 myr.
Testudininei n. g. b (small form), several n. sp. including '*Chersina*' sp. in Meylan & Auffenberg (1986): **Langental**, SW Namibia, ca. 19 myr, **Arrisdrift**, N Orange River, S Namibia, ca. 17 myr, Early Miocene.
Testudininei nov. gen., *'Geochelone' stromeri* Meylan & Auffenberg 1986: **Langebaanweg**, N Cape Town, South Africa, Pliocene, ca. 4-4,5 myr, **'Namib Desert'**(=?age, ?locality), paratypes of *'Geochelone' stromeri* Meylan & Auffenberg 1986
Testudininei indet.: **Upper Semliki-Senga Rivers**, Lusso beds, Democratic Republic of Congo, Pliocene, ca. 2,4-2,5 myr; **Lake Victoria area**, **Nyakach area**, Early-Middle Miocene, **Baringo Basin area**, Mio-Pliocene, Kenya; **Matupi Cave**, eastern Zaïre, Democratic Republic of Congo, late Stone Age and Iron Age; **Oakleigh** near Queenstown, South Africa, levels 3-4, Late Holocene, 500-400 yr BP; **Tloutle**, north-western Lesotho, 6140 ±100 yr BP; **Sehonghong Rockshelter**, Qacha's nek District, western Lesotho, Late Holocene, 1400±50 yr BP; **Hololo Crossing**, 28°44'S; 28°27'E, Lesotho, Late Holocene, 330-260 yr BP.

African large endemics:
Extant *Centrochelys* Gray 1872: *C. sulcata* (Miller 1779), Sahel-northern Tropical Africa.
C. sulcata: **Awash River Basin**, Central Afar, Ethiopia, Hadar Formation, Pliocene (SH-SH3); **Tin Ouaffadene**, Niger, Holocene, ca. 9220 yr BP; **Ti-n Hanakaten**, NE Hoggar, Djanet Province, Algeria, Holocene, ca. 7000 yr BP; **Jebel Shaqadud**, Atbara River Valley, site A, cave deposits, Sudan, Holocene, ca. 4200 to 4900 yr BP; **Pedra de Lume Crater**, Sal Island, Cape Verde islands, Middle Quaternary (not verified).
C. cf. *sulcata*: **Ouadi Derdemi**, Chad, Pliocene, ca. 3-3,2 myr; **An Nafud**, northern Saudi Arabia, Pleistocene; **Chami**, Mauritania, Holocene, ca. 2100-3500 yr BP; **Burg et Tuyur** 80/73, Sudan, Holocene, 6000 yr BP; ?*Centrochelys sulcata*: **Berenike**, Egypt 2000 to 1500 yr BP.
C. aff. *sulcata*: **Baynunah Formation**, Western Region, Emirate of Abu Dhabi, Middle-Miocene, ca. 8 myr; **Sahabi**, Libya, Late Miocene, MN 13+.
Centrochelys sp.: **El Djour**, Chad, Plio-Pleistocene; **Goz Kerki Recent**, Chad, Holocene.
Cf. *Centrochelys* sp.: **Puits Tirenno**, Tibesti, Chad, Pleistocene-Holocene.
?*Centrochelys* ('*Geochelone* sp.'); **Bahr el Ghazal**, E. Koro-Toro, KT 12 site, Pliocene, ca. 3-3,5 myr.
Large cf. *Centrochelys* sp. and very large cf. *Centrochelys* sp.: **Djebel Zelten**, Libya, Early Miocene, ca. 16,5 myr.
?cf. *Centrochelys* sp.: **Ghaba**, Huqf, Sultanate of Oman, Early Miocene-earlier Middle Miocene, Orleanian, ar. 18 myr.

Extant *Stigmochelys* Gray 1873: *S. pardalis* (Bell 1828), eastern-southern part of Africa.
S. pardalis: **Brandberg**, Namibia, 1600-1750 AD, Historic site; **Haaskraal**, South Africa, Late Holocene; **Edgehill** and

Welgeluk, South Africa, Koonap River near Adelaide, Eastern Cape, Holocene, from 6000 yr BP to the present; **Makapansgat**, South Africa, Pliocene, 2,5 to 3 myr; **Olduvai Gorge**, Tanzania, Bed I, lower part of upper member, bed II, upper part, Pleistocene, ca. 1,70 to 1,75 myr; **Ndolanya beds**, Laetoli beds, Tanzania, Pliocene;
S. brachygularis (Meylan & Auffenberg 1987): **Laetoli beds, Endulen,** 8 km W, loc 2, top tuff 6, **Garussi area** Tanzania, Pliocene, ca. 3,59 to 3, 77 myr;
Large *Stigmochelys* sp. or aff. *Stigmochelys* sp: **Omo River Basin**, Ethiopia, Pliocene (beds B9-12, C5-9, D3), ca. 2,9 to 2,3 myr; **Awash River Basin**, Central Afar, Ethiopia, Pliocene, Hadar Formation: D-D2, >3, 22 < 3,18 myr; SH1-SH3, ca. 3,40 to < 3,28 myr; **Olduvai Gorge**, Tanzania, Bed IV, Pleistocene, 0,4 to 0,7 myr.
Testudininei indet. ('*Geochelone* s.l. sp. B'): **Olduvai Gorge**, Tanzania, Bed I, Middle part of upper member, Pleistocene, ca. 1,75 myr.
Testudininei indet. (*Stigmochelys*?): **Sterkfontein**, Member 5, ca. 2,5 (2,6 to 2,8) myr, **Kromdraai A, B**, ca. 2 myr, **Swartkrans**, Member 2, 2 to 1,8 myr, Plio-Pleistocene, South Africa.
?Aff. *Stigmochelys laetoliensis* Meylan & Auffenberg 1987, (probably a *Stigmochelys* group member): **Laetoli beds**, Tanzania, Endulen, 5 km W, loc. 5, between tuffs 2 and 5 and 0,50 m below tuff 6, loc. 6, tuff 7 and loc. 10 W, below tuff 3, Pliocene, ca. 3,59 to 3, 77 myr .
Large Testudininei indet. (*Centrochelys* or *Stigmochelys* or other African endemics):
? cf. *Centrochelys* sp.: **As-Sarrar**, Eastern Province, Saudi Arabia, Early-Middle Miocene, Orleanian, MN 5, ca. 16 myr; **Al-Jadidah**, Hasa Province, Saudi Arabia, Middle Miocene, Early Astaracian, MN 6, ca. 13 myr; **Annabokoma site**, Gobaad, Republic of Djibouti, Plio-Pleistocene; **Holocene Delta, Awash River basin**, Central Afar, Ethiopia.
Testudininei indet. (*Stigmochelys* group? Or synonym of *Impregnochelys*?) (*'Testudo* cf. *crassa* Andrews 1914'): **Rusinga Island**, NE Lake Victoria, Kenya, Early Miocene, ca. 18 myr.
Giant forms, ?cf. *Centrochelys*: **Djebel Krechem El Artsouma**, Tunisia, Miocene, Late Vallesian, MN 10, ('*Geochelone* sp.', in Geraads 1989), **Ichkeul**, Tunisia, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr (*'Testudo' punica* Arambourg 1979).
Testudininei indet.: **Malta**, giant tortoise, (*'Testudo' robusta* Leith-Adams 1877), Ossiferous Caverns: Benghisa Gap, Mnaidra Gap, Zebbug Cavern, Pleistocene.
Testudininei indet. (*Stigmochelys* group?): **Lothagam 1**, Kerio River Basin, Kenya, Late Miocene; **Kanapoi** ['*Geochelone crassa* (Andrews 1914)': Meylan & Auffenberg 1986], **Ekora, Kerio River Basin,** Kenya, Early and Middle Pliocene; **East Lake Turkana**, Kenya, Koobi Fora Formation, upper member, Plio-Pleistocene: between KBS and Chari tuffs ca. 'Okote tuff', ?1,57 myr?.
Testudininei indet., aff. *Stigmochelys*? (*'Testudo' crassa* Andrews 1914): **Karungu**, NE Lake Victoria, Kenya, Kachuku beds, ca. 18 myr, Early Miocene.
Testudininei indet.: **Baringo Basin**, Kenya, Ngorora (including a giant Tortoise, member D, Loc. 2/106, ca. 11,7 myr, pers. comm. M. Pickford), Mpesida, Lukeino Formations, ca. 11-12 myr to 5,8-6 myr, Mio-Pliocene; **Lothagam 1, 3, Kanapoi, Ekora, Kerio River Basin**, SW Lake Lake Turkana, Kenya, Mio-Pliocene, ca. 6 to 4 myr; **East Lake Turkana**, Kenya, Koobi Fora Formation, between KBS and 'KF' tuffs, 1,88 to 1,57 myr or upper and undefined horizon, Late Pliocene-Pleistocene; **Upper Semliki-Senga rivers,** Lusso beds, Pliocene, ca. 2,4-2,5 myr, and **Sinda-Mohari Rivers**, Lower Semliki River, Pliocene, W Lake Albert, Democratic Republic of Congo; **Mumba Cave**, N.E. of Lake Eyasi, Tanzania, Pleistocene, *'Testudo pardalis' in* Lehmann (1957); **Abu Balias**, Egypt, Holocene, 8300-6800 yr BP.
Giant new form, ?aff. *Stigmochelys* sp.: **Rawi**, Kenya, Early Pleistocene.
Gigantic Testudininei indet.: **Kaiso Village**, Uganda, Pliocene, ca. 2-2,3 myr, **East Lake Turkana**, (J. Harris pers. comm.; not collected), undefined level.

Malagasy-Indian Ocean islands fauna
Extant *Pyxis* Bell 1827, in Madagascar only.
Pyxis sp.: **Dembeni 1**, Mayotte island, Comoros islands, 850-880 AD, introduced from Madagascar.

Extant *Astrochelys* Gray 1873, in Madagascar only.
A. yniphora (Vaillant 1885): **Dembeni 1**, Mayotte Island, Comoros islands, 850-880 Y after JC, introduced from Madagascar.
A. radiata (Shaw 1802): **Ambato, Ankevo, Antsirabe,** < 10 000 yr BP, **Ambolisatra, Andrahomana,** < 1000 yr BP, Madagascar.

Dipsochelys Bour 1982, extant in Aldabra atoll: *D. e. elephantina* (Duméril & Bibron 1835).
D. grandidieri (Vaillant 1885), *D. abrupta* (Grandidier 1868): **Mahajanga area, southwestern-southern area between Ambato (Morondava) and Andrahomana (Taolanaro),** Madagascar (detailed **38 localities** in Bour 1994), <3000 to ca. 750 yr BP.
D. daudini (Duméril & Bibron 1835), *D. arnoldi* Bour 1982, *D. hololissa*, Günther 1877, **Granitic Seychelles**, < ?10 000 to 150 yr BP (for the supposed Present presence of the two latter, see Granitic Seychelles, in the country section above).
D. e. elephantina (Duméril & Bibron 1835), < 10 000 yr BP : *D. dussumieri* (Gray 1831) is a senior synonym; but it has not been revived - the type being a juvenile - in order to respect the stability of the nomenclature because it is a *nomen oblitum* (Bour 1995). *D. e. sumerei* (Sauzier 1892), ?10 000 to ?150 yr BP (maybe still extant, introduced in **Mauritius**), Seychelles atolls, including **Aldabra.**
Dipsochelys sp.: **Aldabra,** 100 000 yr BP, **Gloriosa**, 125 000 yr BP.

Cylindraspis Fitzinger 1835
C. borbonica Bour 1978: **La Réunion**, Mascarene islands, 2000 to 200 yr BP.
C. inepta (Günther 1873), *C. triserrata* (Günther 1873) = ?*C. graii* (Duméril & Bibron 1835): **Mauritius**, Mascarene islands, ca. 1700 to 300 yr BP.
C. peltastes (Duméril & Bibron 1835), *C. vosmaeri* (Suckow 1798): **Rodrigues**, Mascarene islands, ?2000 to 200 yr BP.

Extant *Testudo* Linnaeus 1758 s.s., Palaearctic fauna, most southern Spain, northern part of Africa and eastern Mediterranenan fauna.
Testudo g. graeca Linnaeus 1758: **Oualidia**, Soltanian, **Taforalt**, 55 km NW Oujda, Roche, 1953, Late Pleistocene; **Doukkala II**, Late Pleistocene-Holocene, Soltanian-Rharbian, Morocco.
T. graeca: **Jebel Irhoud**, Late Pleistocene, Soltanian; **Carrière Thomas I**, (Thomas Quarry I), **Coast from Rabat to Temara** (small dune of Choubert & Marçais 1947), Late Pleistocene, Tensiftian, ca. 400 000 yr BP, Morocco.
T. cf. *graeca*: **Abri Bou Guennouna**, Holocene, Neolithic; **Mehdia**, probable Neolithic; **Toulkine-Bou Ben Adam**, Holocene, Neolithic, Morocco.
T. cf. *graeca*: **Dar Es Soltane**, Late Pleistocene-Holocene, Soltanian-Rharbian, Morocco.
'T. g. graeca' (fide Roubet 1966): **Cubitus** and **Aïn Keda**, near Tiaret, **Abri Alain**, Algeria, **El Khenzira**, near Cap Blanc, Morocco, **Abri Clariond**, near Aïn Moularès, **Oued Bou Haya**, near Feriana, Tunisia: Epipalaeolithic, Capsian, Early Holocene. **Abri du Relilaï, Col des Kifène, Damous el Amar, Khanguet Si Mohamed Tahar Cave, Djebel Fartas, Djebel Marhsel, Hyènes Cave, Bou Zabaouine Cave, Ours Cave, Hadrar Gueldaman, Columnata, Rhar Oum el Fernan, Cascades Cave, Oued Saida, Troglodytes Cave, Polygone Cave, Cuartel Cave, Ciel Ouvert Cave, Forêt Cave, Chabet Sardi Cave, El Bachir Cave, Coralès fireplaces-Escargots cemetery, Aïn Guedara**, upper cave, Dahar, **Hassi Mouilah** (Ouargia), Algeria, Neolithic; **Kheneg Kenadsa**, Tendrara, Morocco, Neolithic; **Abri de Redeyef**, W Gafsa, **Djebel Hamra**, S Haïdra, **Kef el Agab**, near

Souk el Arba, Tunisia, Neolithic: Late Holocene.
T. kenitrensis Gmira 1992: **Kenitra**, Morocco, Middle Pleistocene, Inter Amirian-Tensiftian.
T. aff. *kenitrensis*: **Ahl Al Oughlam**, carrière Déprez, Casablanca, Morocco, Pliocene, ca. 2 to 2,5 myr.
Testudo s.l. sp.: **Ichkeul**, Tunisia, Pliocene, Ruscinian, MN 15-, ca. 3,5 myr; Tighenif (Ternifine, Palikao), Oran Province, Algeria, Middle Pleistocene.
Testudo s.l. sp.: **Aïn Boucherit**, Constantine Province, Algeria, Pliocene, Ruscinian, MN 14-15.
Testudinidae indet. (*T. g. graeca* alone, or also *Mauremys leprosa*?): **Bouknadel** and **Aïn Rohr**, Late Pleistocene, Early Soltanian; **Aïn Bahya**, Late Pleistocene, Soltanian,
Rhafas Cave, Late Pleistocene, Soltanian, and Middle Holocene; **El Heriga**, Abri Rhirane, Late Pleistocene and Holocene; **Oued el Haij Terrace, Jorf el Anngra**, Holocene: Morocco.
?Testudininei, possible *Testudo*: **Hamada Damous**, Tunisia, Pliocene, Ruscinian, MN 14, ca. 4,5 myr.
T. s.l. semenensis (circum-mediterranean *Testudo* s.l.): **Djebel Semene** mine, or **Djebel Semama**, SW Tunisia, Late Miocene, Early Vallesian, MN9+, ca. 10 myr.
Testudininei indet., either small *Testudo* or northern large Testudininei.
'*Testudo* ': **Bou Hanifia**, Oran Province, Algeria, Miocene, Vallesian, MN 9+, ca. 10,5 myr.

Cryptodira indeterminata

Chelonians: **Puits Karoubi**, 2 km SW Eckmühl, Oran Province, Algeria, Pliocene (Testudinidae, *Trionyx*?).
Indet. eggs (round eggs: Cyclanorbinae or Testudininei?): **Awash River Basin, Central Afar**, Ethiopia, Hadar Formation (DD3), Pliocene, >3,22 to < 3,18 myr.
Possible Trionychidae: ?*Cyclanorbis senegalensis*, ?*Trionyx* sp., **Wadi Halfa**, Nile, Sudan, ca. 80 km S Abou Sinbel, Pleistocene; ?*Cyclanorbis senegalensis*, **Anteopolis** (Siout, Assiout) tomb, Egypt, Pleistocene.

Chelonii indeterminata

El Mers, Morocco, Middle Jurassic, Bathonian, **Anoual**, Morocco, Early Cretaceous, (Berriasian-Valanginian), **Algoa Basin**, South Africa, Early Cretaceous (Valanginian), **Koum Basin**, Mayo Rey River, loc. KB6, North Cameroons, Barremian-Aptian, **Idfu**, Egypt, Turonian-Early Senonian, **Kababish Formation**, Sudan, Campanian-Maastrichtian, **Oued Erguita**, Phosphates, Morocco, Maastrichtian; **El Kohol**, S Oran Province, Algeria, Late Eocene ('Paludine turtle' = possible Pelomedusoides); **Napak**, Iriri Member, ca. 18-19 myr, Moroto II, ca. 14,3 myr and **Moroto I**, ca. 12,5 myr, Early Miocene: Uganda ('Chelonians' = Testudininei?, Pelomedusoides?). **Mteitei area**, Early Miocene, ca. 19-20 myr, **Mfwangano Island** in Walangani and Higeni Formations, **Rusinga Island** in Wayondo, Hiwegi and Kulu Formations, **Uyoma Peninsula**, Kenya, Early Miocene, ca. 18 myr, **Ombo**, Maboko Formation, **Nyakach Area**, Nyakach Formation, Early Middle Miocene, ca. 15-16 myr, **Gwasi Peninsula**, Early Miocene, **Baringo Basin**, Early-Middle Miocene: Kenya (including possible Pelomedusoides, Cyclanorbinae and Testudininei with giant forms of tortoises and a giant freshwater turtle at Ngeringuerwa); **Homa Peninsula: Kanam** (1), Kenya, Pliocene, ca. 4 myr (including possible Pelomedusoides and Trionychoidea), **Lothagam, Lothagam 2**, Kenya, Lake Baringo, Kerio River Basin, Pliocene; **El Arag**, Egypt, Neogene; **Bahr el Ghazal** area, Chad, E. Koro-Toro, Pliocene, ca. 3-3,5 myr; **Kanam** (2), Kenya, Plio-Pleistocene (including possible Pelomedusoides); **Wadi Halfa**, Nile, S Abou Sinbel, close Egypt fronteer, Sudan, Pleistocene and **Anteopolis** (Siout), Egypt, Pleistocene (?*Cyclanorbis sengalensis*); **Algeria, Tunisia** (see Vaufrey 1955), Early Holocene, Capsian, possible *Mauremys leprosa*. **Ntloana Tsoana**, north-western Lesotho, Holocene, 8780 ±80, 12110 ±120 yr BP. **Leliehoek Shelter**, eastern Orange Free State, South Africa, Holocene.

ABBREVIATIONS

AUH	Emirate of Abu Dhabi Museum, United Arab Emirates.
CM	Cairo Museum.
DMD	Direction des Mines, Dakar, Senegal.
CMN	Canadian Museum of Nature, Ottawa.
FSR	Faculty of Sciences, Rabat University, Morocco.
GU	Gent University, Belgium.
INSAP	Institut National des Sciences de l'Archéologie et du Patrimoine, Département de Préhisoire, Rabat, Morocco.
MSGN	Museum of the Geological Survey of Namibia, Windhoeck.
MMB	Musée du Mali-Bamako.
MHNT	Muséum d'Histoire naturelle de Toulouse, France.
MNHB	Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Germany.
MNHN	Muséum national d'histoire naturelle, Paris, France.
MRAC	Musée Royal d'Afrique Centrale, Tervuren, Belgium.
NHM	BM(NH), Natural History Museum, London, United Kingdom.
NME	National Museum of Ethiopia, Addis Abeba.
NMK	National Museums of Kenya, Nairobi.
SAM	South African Museum, CapeTown, South Africa.
OMS	Sperrgebiet Museum, Oranjemund, Namibia.
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany.
TUB	Technische Universität Berlin, Germany.
UM	Uganda Museum, Kampala.

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NOTES ON THE SYSTEMATICS OF MICROMAMMALS FROM STERKFONTEIN, GAUTENG, SOUTH AFRICA

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ABSTRACT

The micromammalian fauna from Sterkfontein Members 4, 5E and 6 comprises 34 species. These include six insectivores, three bats, three elephant shrews and 22 rodents. Most of these taxa, or their equivalents, have been previously recorded. Four or five new additions were recovered from deposits probably belonging to Late Pleistocene Member 6, which have previously received little or no attention. Some previously recorded taxa were not found, but this was probably due to differences in identification rather than to the absence of these forms from the sample.

KEYWORDS: micromammals, Pleistocene, Sterkfontein, systematics

INTRODUCTION

Sterkfontein (26°01'S; 27°44'E) is one of the best known South African palaeoanthropological sites, having produced a wealth of hominid remains ascribed to at least three genera (Clarke 1994). The site has been excavated and described almost continuously since the first hominid specimen was published by Broom (1939). Initially, Member 5 collections were treated as contemporary, but Clarke (1994) and Kuman (1994, 1996) have shown that Member 5E includes earlier deposits containing Oldowan artefacts underlying deposits with Early Acheulean material. Their detailed work has further revealed that solution of the breccia in Member 5E led to mixing of material in the upper parts, particularly above 15 ft (4.6 m) but to a lesser extent down to 22 ft (6.7 m) (Kuman 1996). The site continues to be excavated in imperial measurements because the grid system was laid out in feet. In the present report the original measurements are given with metric equivalents in brackets. Current age estimates are: 2.8 to 2.6 my for Member 4; 2.0 to 1.7 my for the Oldowan deposits; about 1.5 my for the Early Acheulean sample; and >0.10 my for Member 6 (Clarke 1994, Clarke & Tobias 1995, Kuman pers. comm.) (Table 1).

Previous micromammalian samples, belonging to A.R. Hughes's pre-1969 collections from the Sterkfontein Type Site (STS), Dumps 1 & 2, Dump 8 and STW/H2, have been described by Pocock (1969, 1987). These were all considered to have come from Member 5, which is the second youngest of six members identified by Partridge (1978). Other material from the Type Site, which was described by De Graaff (1960), may have come from Member 4 (Brain 1981). Denys (1990) listed taxa found in a sample from the Sterkfontein Extension Site (SE), which lies within Member 5 West. The material reported here was collected by R.J. Clarke and K. Kuman since 1991 in Member 5 and comes mainly from Member 5 East. There are small samples from the adjacent Member 4 and from the Middle Stone Age (MSA), which is designated Member 6 (Tobias *et al.* 1993) and is a later infill that divides Member 5 East from Member 5 West. A final, possibly contaminated, sample derives from Member 5 West in the area previously excavated by Robinson (1962).

There is generally little difference in the micromammals from Sterkfontein and Swartkrans even though the former includes material that is both older and younger than that from Swartkrans, which has been discussed recently (Avery 1998). This paper is therefore confined to providing information on species not present at Swartkrans, and other supplementary remarks where appropriate. A separate study of the environmental implications of the Sterkfontein micromammalian fauna is in progress (Avery in prep.).

MATERIAL AND METHODS

Basic excavation units were 3 ft (0.9 m) square and generally 1 ft (0.3 m) deep. In the following discussion the material has been lumped into seven larger groups of units. Table 1 provides a general description of the grouped units and details of the assignments of individual units are available on request. Species represented are given in Table 2, together with the units in which they occur. Mandibles and maxillae were employed for identifications and computation of minimum numbers of individuals. Length and breadth of the lower first molar in *Steatomys* were measured (Figure 1) and unpaired *t*-tests were performed to determine whether more than one species was represented (Table 3). Percentage length of M_1 to M_2 in Sterkfontein *Mus* sp. was used as a basis for unpaired *t*-tests to compare the fossil material with modern *M. minutoides* and *M. musculus* (Table 4).

TABLE 1
Excavation units at Sterkfontein that yielded micromammalian material.

Member	Code*	Culture	Distribution+	Depth§	Comments	my B.P
6	M6	MSA	N59-60, Q58	18-28 ft (5.5-8.5 m)	Infill into M5	± 0.10
5	M5	ESA/MSA ?mixed	M63, N63-64,O64	12-16ft (3.7-4.9 m)	?decalcified deposit	
6/5	M6/5	ESA/MAS ?mixed	O59-61,O64/64, p59-61	13-13 ft (4.0-7.0 M)	possible mixing with M5	
5 East	M5E-A	Early Acheulean, ?mixed with MSA	O58, P53-54, P57-58, Q51-57, R50, R52-57, S52-57, T53-56	16-22 ft (4.9-6.7 m)	above 22 ft	± 1.5
5East	M5E-O	Oldowan	P53-54,P57-58, Q52-57, R52-57, S52-56, T55-56	22-34 ft (6.7-10.4 m)	Oldowan Infill below 22 ft	± 2.0-1.7
5East/4	M5E/4		Q49-52, R49, S51, T52-54	14-29 ft (4.3-8.8 m)	boundary between members	
4	M4		N46/O45/P45L, Q48-50, R49-51, S50	13-30 ft (4.0-9.1 m)		± 2.8-2.6

* Code: abbreviation used in other tables and figures + Distribution: horizontal distribution of samples
§ Depth: vertical distribution of samples

SYSTEMATICS
Insectivora

Chrysochloridae
Amblysomus Pomel, 1848 (golden mole)

For the present all smaller specimens are assigned to *Amblysomus*, as they were at Swartkrans (Avery 1998). It is possible that two taxa are represented but Bronner (1996) has demonstrated that there can be considerable intra-populational variation within *Amblysomus*. In the Sterkfontein material, all specimens show an alveolus for M_3 although not all alveoli are the same size. The number of teeth is variable in modern chrysochlorids (Ellerman et al. 1953, Bronner 1996). This could be part of an evolutionary trend or it could be due to the unusual sequence of tooth replacement, as suggested by Bronner (1996). There is also variation in the extent to which talonids occur in the fossil material. However, the situation is not as clear as it is at Swartkrans, where there is generally a talonid on P_4 but not on M_1 (Avery 1998). Of the four examples of P_4, one each from M5E-A and M5 have talonids while another from M5E-A and one from M6 do not. One M_1, from M5E-A, has a slight talonid whereas the other, from M5E/M6, has none. It could be inferred that the earlier specimens represent a population in which this feature was in the process of disappearing and that by about

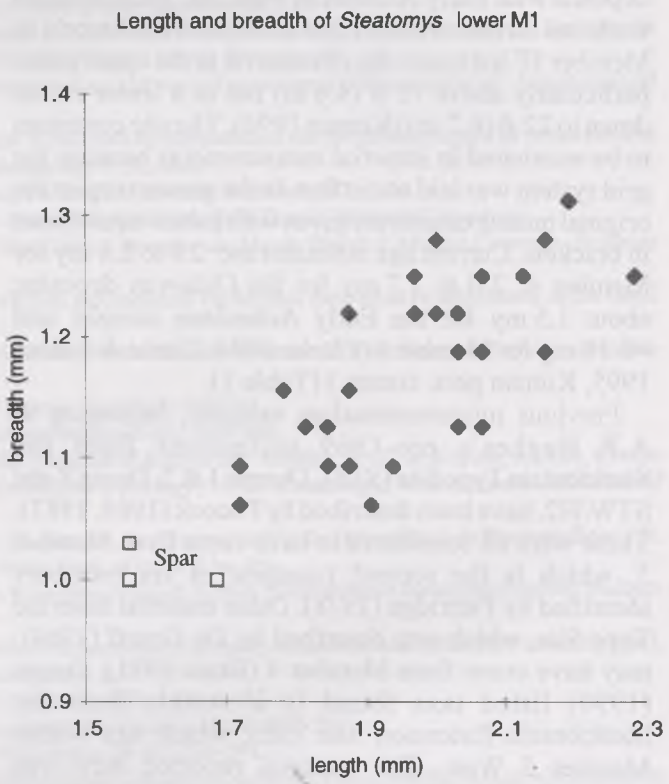


Figure 1. Variation in length and breadth of lower M1 in *Steatomys* from Sterkfontein. Spar — putative *Steatomys parvus*.

120 000 years ago the process had been completed. Many more specimens will, of course, be required to determine the correctness of this proposition. It will also be necessary to compare the fossil specimens with Bronner's (1996) detailed database.

Chlorotalpa sclateri (Broom, 1907) (Sclater's golden mole)

One mandible that may be referable to *Chlorotalpa sclateri* was recovered from M5E-O. The genus was listed by Pocock (1987) and the extinct form *C. spelea* was recorded by De Graaff (1960). The fossil and modern forms are separated solely on cranial proportions (Broom 1941) and there is no *a priori* reason to propose that the present mandible belongs to an extinct species. The absence of *Chlorotalpa sclateri* from later samples and from the area today indicates that this taxon has not inhabited the region for a considerable period.

Soricidae

Crocidura silacea Thomas, 1895 (lesser grey-brown musk shrew)

Broom (1948) mentioned the occurrence of *Crocidura* sp. at Sterkfontein but subsequent workers failed to confirm the presence of this genus. As a result it has been accepted that *Crocidura* did not occur in the Sterkfontein Valley (Meester 1955; Pocock 1987; Avery 1998). It would appear, however, that the reason previous workers did not find it was that they were examining Early Pleistocene material. The present sample includes two mandibles from M6 and a palate from M6/M5, which suggests that it was a late arrival in the valley. The palate includes alveoli for only three teeth between I^1 and P^4, thereby clearly identifying the specimen as *Crocidura* rather than either *Myosorex* or *Suncus*, and the left P^4 belongs to *Crocidura* and not *Myosorex*. The body of a right mandible includes a P_4 that lacks both the protostylid and the metaconid typical of *Myosorex* (Butler & Greenwood 1979). The buccal cingulum of the molars is anteriorly broad, and the M_3 has an entoconid, which is a feature of *Crocidura silacea* (Meester 1963). The mandible is comparable in size with the *Myosorex* material, which suggests that it belongs with *C. silacea* rather than the considerably smaller *Suncus* material. The posterior half of a left mandible exhibits various features indicative of *Crocidura* rather than *Myosorex*. These include the shape of the condyle, the location of the muscle attachment on the condyle, and M_1 with the posterolingual rib and buccal cingulum as in *Crocidura*.

TABLE 2

Species of micromammals represented in Sterkfontein samples with total minimum number of individuals. † indicates extinct species. Modern species listed according to Wilson & Reeder (1993). See Table 1 for details of excavation units.

Family	Species	Common Name	M6	M5	M6/ M5E	M5E -A	M5E -O	M5E /M4	M4
Chrysochloridae	*Amblysomus* sp.	golden mole	x	x	x	x	x	x	
	Chlorotalpa cf. *sclateri*	Sclater's golden mole					x		
	Chrysospalax villosus	rough-haired golden mole			x	x		x	x
Soricidae	*Crocidura* cf. *silacea*	grey musk shrew	x		x				
	Myosorex tenuis	forest shrew	x		x	x	x	x	x
	Suncus varilla	lesser dwarf shrew	x		x	x	x	x	
Rhinolophidae	*Rhinolophus* cf. *capensis*	Cape horseshoe bat	x		x		x		
	Rhinolophus cf. *clivosus*	Geoffroy's horseshoe bat	x	x	x	x	x		
Vespertilionidae	*Myotis tricolor*	Temminck's hairy bat	x		x	x	x		
Muridae	*Saccostomus campestris*	pouched mouse			x				
	Dendromus melanotis	grey climbing mouse	x	x	x	x	x	x	x
	Malacothrix typica	large-eared mouse	x	x	x		x		
	Steatomys parvus	tiny fat mouse	x	x					
	Steatomys pratensis	fat mouse	x	x	x	x	x		
	Tatera cf. *leucogaster*	bushveld rat	x	x	x	x	x		
	Acomys cf. *spinosissimus*	common spiny mouse					x		
	Aethomys chrysophilus	red veld rat	x	x	x		x		
	†?*Dasymys* sp.	swamp rat	x	x	x	x	x	x	x
	Mastomys natalensis s.l.	multimammate mouse	x		x	x	x		
	Mus sp.	pygmy mouse	x		x	x	x		
	Rhabdomys pumilio	striped mouse	x	x	x	x	x		x
	Thallomys cf. *paedulcus*	tree rat	x						
	Zelotomys cf. *woosnami*	Woosman's desert rat	x	x	x	x	x		
	Mystromys albicaudatus	white-tailed rat	x	x	x	x	x	x	x
	†*Proodontomys cookei*				x	x	x	x	x
	Otomys irroratus	vlei rat	x	x	x	x	x		
	Otomys saundersiae	Saunders's vlei rat	x	x	x	x	x	x	x
	Otomys sloggetti	Sloggett's rat		x	x	x	x		x
Myoxidae	*Graphiurus* sp.	dormouse	x		x	x	x		
Bathyergidae	*Cryptomys hottentotus*	common molerat	x	x	x	x	x	x	x
	Georychus capensis	Cape molerat		x			x		
Macroscelididae	*Elephantulus intufi*	bushveld elephant-shrew	x	x	x	x	x	x	x
	Elephantulus fuscus	Peters's short-snouted elephant-shrew				x		x	
	Macroscelides proboscideus	round-eared elephant shrew	x						
	Minimum number of individuals represented		308	138	430	371	866	42	36

Myosorex tenuis Thomas and Schwann, 1905 (dark-footed forest shrew)

Most of the soricid material is referable to *Myosorex* and there is no reason to suggest that a different species is represented at Sterkfontein from that occurring at Swartkrans. Material has previously been assigned to the extinct *M. robinsoni* (De Graaff 1960), which was at one time said to be an ancestral form of *M. varius* (Brain 1981, based on an implied relationship in Meester [1958] but not an explicit relationship in the original diagnosis [Meester 1955]). Butler & Greenwood (1979), on the other hand, consider *M. robinsoni* to be a close relative of modern *M. cafer tenuls*, as understood by Heim de Balsac & Meester (1977) and Meester *et al.* (1986), or *M. tenuis*, as recognized by Hutterer (1993) and accepted here. The disposition of the anterior palatal foramina has been discussed previously (Avery 1998). It therefore needs only to be pointed out here that the pattern in the two Sterkfontein specimens (one each from M5E-A and M6) where it is visible is closer to *M. varius* than *M. cafer*, as shown by Meester (1958). It conforms, however, to the pattern in *M. cafer tenuis* shown by Butler & Greenwood (1979) so that it would appear that the Sterkfontein material should be assigned to *M. tenuis sensu* Hutterer (1993).

CHIROPTERA

Rhinolophidae

Rhinolophus Lacépède, 1799 (horseshoe bat)

Present evidence agrees with Pocock's (1987) findings that two species of *Rhinolophus* are represented and tends to support his assignment of the larger specimens to *R. clivosus*. This identification is based on the fact that, in the four specimens where it is preserved, the P_3 alveolus is located outside the toothrow as it is in *R. clivosus*. It is not possible to determine whether the smaller specimens should be assigned to *R. darlingi*, as suggested by Pocock (1987), or to *R. capensis*, as proposed for Swartkrans (Avery 1998).

RODENTIA

Muridae

Saccostomus campestris Peters, 1846 (pouched mouse)

Saccostomus campestris, as presently understood (Musser & Carleton 1993), may well comprise more than one species in southern Africa (Gordon 1986; Gordon & Rautenbach 1980). However, until additional species are formally recognized and their morphological characteristics are established, it is necessary to refer material to *S. campestris sensu lato*, as was previously discussed for Gladysvale (Avery 1995). Four mandibles referable to *S. campestris* have been recovered from adjacent squares O59 and O60 at depths from 17 ft (5.2 m) to 19 ft (5.8 m). These constitute the first *S. campestris* specimens recorded from the Sterkfontein Valley australopithecine sites. It is significant that the deposits that yielded this material are Upper Pleistocene (K. Kuman, pers. comm.). Moreover, the apparent absence of *S. campestris* from earlier deposits supports Denys's (1990) hypothesis that the taxon migrated south some time after about 1.6 my.

Three lower first molars from Sterkfontein measure 2.2 x 1.3 mm, 2.1 x 1.3 mm and 2.1 x 1.4 mm. These measurements lie within the range of *S. campestris* as given by Denys (1990) whereas two molars from the Cave of Hearths fall within the size range of East African *S. mearnsi* (Denys 1990). What is more important, the Sterkfontein specimens should be referred to *S. campestris* rather than to *S. mearnsi* using the various features in M_1 listed by Denys (1988) to distinguish the two species. Only an indication of a link between the anterior two cusps (a-lab, a-ling) (cusp terminology after Musser 1981) and the central two cusps (pd, md) was found in the more worn specimen while no link existed in the less worn specimens. Conversely, in the two less worn individuals the cusps pd, md and hd, ed (the central and posterior rows respectively) are already joined, thereby indicating that the two pairs of cusps are not deeply separated.

Saccostomus campestris occurs in some units at Gladysvale (Avery 1995). It could be argued that its presence suggests that these units are younger than those that have not yielded the taxon. The presence of *S. campestris* with one possible *Proodontomys cookei* in the Pink Breccia appeared to nullify this hypothesis. However, re-examination of the specimens concerned (both right mandibles without cheek teeth) has led to the conclusion that they should be assigned to *Mastomys* sp. rather than *S. campestris*. Measurements of two *S. campestris* lower first molars (2.2 x 1.4 mm and 2.1 x 1.4 mm), from units S18.E6 and S19.E6, fall within the range of *S. campestris*, as given by Denys (1990). These specimens also accord with Denys's (1988) description of *S. campestris* rather than that of *S. mearnsi*.

Steatomys parvus Rhoads, 1896 (tiny fat mouse)

Previously, only one species of *Steatomys* has been recorded from the Sterkfontein Valley (Pocock 1987, Denys 1990, Avery 1998). The present study revealed three mandibles (one from M6 and two from M5) that belong to a second, smaller species than the rest of the specimens. Length and breadth of M1 in these mandibles are lower than they are in all other samples (Figure 1). Unpaired *t*-tests of length and breadth of lower M1 show that there is a significant difference between the small individuals and both the earlier M5E-O material and, more significantly, the apparently contemporary sample from M6 (Table 3).

All three mandibles contain M_{1-2} but the teeth in one mandible are little worn while the others are in a more advanced state of wear. The unworn first molar of the small species has a maximum length of 1.7 mm whereas four specimens of the larger species from the same sample have an average length of 2.0 mm. The teeth in the Sterkfontein mandibles are more closely comparable with *S. krebsii* than with *S. pratensis*. The unworn first molar shows no trace of a cingular conule and is

TABLE 3

Results of unpaired t-tests to determine whether samples of *Steatomys* sp. belong to different species, based on maximum length and breadth of lower M1. Spar is modern *S. parvus*. *t*-values are significant at the at the 1% (**) or 0.1% (***) level.

Maximum Length			Maximum Breadth		
Samples	df	*t*	Samples	df	*t*
M5E-O, M6	9	-3.65**	M5E-O, M6	9	-3.41**
M5E-O, M6/5	20	-2.61*	M5E-O, M6/5	20	-3.05**
M5E-O, Spar	5	2.46	M5E-O, Spar	5	4.79**
M6, M6/5	23	-0.39***	M6, M6/5	23	-0.33
			M6, Spar	8	4.49**
M6/5, Spar	19	3.98***	M6/5, Spar	19	4.05***

relatively narrow, although this is difficult to quantify. Examples of modern *S. parvus* were not available for study. However, Thomas & Wroughton (1905) remark that the closest relative of *S. minutus* (now included in *S. parvus* [Musser & Carleton 1993]) appears to be *S. pentonyx* (now *S. krebsii* [Musser & Carleton 1993]). This view seems to be implicitly supported by Roberts (1931) in his descriptions of *S. chiversi* (now *S. krebsii* [Musser & Carleton 1993]) and *S. c. tongensis* (now *S. parvus* [Musser & Carleton 1993]). It seems probable therefore that the small Sterkfontein specimens should be referred to *S. parvus*.

Steatomys parvus does not currently occur closer than northern KwaZulu-Natal, which is some 500 km to the east of Sterkfontein. On geographical grounds it could therefore be considered more reasonable to assign the material to *S. krebsii*, which does occur in the region today. Moreover, in some areas (e.g. the Western Cape) some mandibles of *S. krebsii* are close in size to some of *S. parvus*. However, modern specimens from nearer Sterkfontein are larger and very similar in size to the nearest *S. pratensis* (Roberts 1951). Besides, *Steatomys krebsii* and *S. pratensis* are not found together in northeastern South Africa today (Rautenbach 1982) although they do occur together elsewhere (Skinner & Smithers 1990). On balance it seems most likely that the species represented is *S. parvus* but the matter requires further investigation.

Dasymys Peters, 1875 (water rat)

The status of *Dasymys* has been discussed at some length elsewhere (Avery 1998) where it was concluded that two species are probably represented at Swartkrans. The sample from Sterkfontein is much smaller but supports the previous contention (Avery 1998) that this genus requires attention. At Swartkrans the two putative species are represented approximately equally. The two taxa were separated initially on the presence or absence of a crest between the anterolingual cusp and metaconid on the lower first molar. In the Sterkfontein sample there is a crest in 15 out of 16 specimens where the feature is visible; the exception may not show the feature because it belonged to a young individual. This age difference could, however, be significant because there is some evidence at Swartkrans that age, or degree of tooth wear, may have caused an artificial distinction between the two forms. If the difference is real, it is of interest that the young specimen was recovered from Member 4 whereas the other specimens came from later members, including M6. This would indicate that two putative species apparently co-existed for a considerable period. It would further suggest that modern *Dasymys incomtus* (represented by the species without the crest) was already present more than two million years ago whereas the second species, if it is extinct, became so within the last 120 000 years. Denys (1990) and Misonne (1969) both considered that the Pleistocene *Dasymys* (presumably the crested form) possessed some features that are more advanced than those found in *D. incomtus* and the Sterkfontein specimen may support their contention. Crawford-Cabral (1983) found *D. incomtus* and *D. nudipes* to be sympatric in one region of Angola, which provides a modern analogue for the co-occurrence of two species in the Sterkfontein Valley. However, the molars of *D. nudipes* are very similar to those of *D. incomtus* and do not exhibit the crest found in the fossil material (Crawford-Cabral & Pacheco 1989; pers. obs.).

TABLE 4

Results of unpaired *t*-tests to determine whether samples of *Mus* spp. are separable based on percentage length of lower M1 to lower M2. *t*-values are significant at the 5% (*) or 0.1% (***) level.

Samples	df	*t*
M. minutoides, M. musculus	28	5.45***
M. minutoides, Mus sp.	18	4.01***
M. musculus, Mus sp.	14	1.33*

TABLE 5

Micromammalian taxa recorded from Sterkfontein by various workers, with the units examined. † indicates extinct species. STS is the Type Site, STW the West Pit, and SE the Extension.

			This paper	Denys 1990	Pocock 1987	Pocock 1969	De Graaff 1961	De Graaff 1960
				SE	STS & STW	Dump 8*	?STS	STS**
Insectivora	Chrysochloridae	*Amblysomus* sp.	x					
		Chlorotalpa sclateri	x					
		†*Chlorotalpa spelea*						x
		Chlorotalpa sp.			x			
		Chrysospalax villosus	x					
		Chrysospalax sp.			x			
		Gen. nov.			x			
	Soricidae	*Crocidura silacea*	x					
		†*Myosorex robinsoni*						x
		Myosorex tenuis	x					
		Myosorex sp.			x	x		
		Suncus infinitesimus			cf.	x		
		Suncus varilla	x		cf.	x		
		Suncus sp.						x
Chiroptera	Rhinolophidae	*Rhinolophus capensis*	cf.					
		Rhinolophus clivosus	cf.		cf.	cf.		
		Rhinolophus darlingi			x	cf.		
	Vespertilionidae	*Myotis tricolor*	x		cf.			
		Miniopterus schreibersi			cf.			
Rodentia	Muridae	*Saccostomus campestris*	x					
		Dendromus melanotis	x			cf.		
		Dendromus mesomelas					x	cf.
		Dendromus sp.		x	x			
		Malacothrix typica	x					
		Malacothrix sp.		x	x	x		
		Steatomys parvus	x					
		Steatomys pratensis	x					
		Steatomys sp.		x	x	x		
		Tatera brantsii					cf.	cf.
		Tatera leucogaster	cf.		cf.			
		Tatera sp.		x		x		
		Acomys spinosissimus	cf.					
		Acomys sp.		x	x			
		Aethomys chrysophilus	x		x	cf.		
		Aethomys namaquensis					cf.	cf.
		Aethomys sp.		x				
		Arvicanthis sp.					?	?
		Dasymys incomtus					x	cf.
		?†*Dasymys* sp.	x	x	x	x		
		Grammomys sp.		x				
		Lemniscomys sp.		x				
		Mastomys coucha					x	
		Mastomys natalensis	s.l.			cf.		cf.
		Mastomys sp.		x	x	x		
		Mus minutoides						cf.
		Mus musculus				cf.		
		Mus sp.	x	x	x			
		Pelomys fallax					cf.	cf.?
		†*Rhabdomys 'minor'*				x		
		Rhabdomys pumilio	x				cf.	cf.
		Rhabdomys sp.		x	x			
		Thallomys paedulcus	cf.					
		Zelotomys woosnami	cf.					
		Zelotomys sp.		x	x			
		Mystromys albicaudatus	x					
		†*Mystromys hausleitneri*		x	x	x	x	x
		†*Proodontomys cookei*	x		x			
		†*Otomys gracilis*		x	x	cf.	x	x
		Otomys irroratus	x					
		Otomys saundersiae	x					
		Otomys sloggetti	x					
	Myoxidae	*Graphiurus* sp.	x		x	x		
	Bathyergidae	*Cryptomys hottentotus*	x		x	cf.		
		†*Cryptomys robertsi*			x		x	x
		Georychus capensis	x					
Macroscelidea	Macroscelididae	†*Elephantulus antiquus*			x			
		Elephantulus brachyrhynchus			cf.			
		Elephantulus fuscus	x					
		Elephantulus intufi	x					
		†*Elephantulus langi (= broomi)*						x
		Macroscelides proboscideus	x		cf.			
		†*Mylogale spiersi*						?
		No. of taxa recognized	34	15+	30	19	11	17

* M5 (Brain 1981) ** probably M4 (Brain 1981) + Muridae only

Mus Linnaeus, 1758 (mouse)

There are seven mandibles referable to *Mus* from Sterkfontein, two each from M6, M5E/M6 and M5E-O, and one from M5E-A. All specimens possess the first molar while three also have the second molar. Neither of the M6 lower first molars has an anterocentral cusp, which is present in the others. All have a posterior cingulum but only two have posterolingual cusplets. This variation is similar to that found at Swartkrans and is not useful in determining the species involved. The amount of reduction in three preserved third-molar alveoli suggests *M. minutoides* but the percentage length of M_1 to that of M_2 indicates a significant difference from modern *M. minutoides* and *M. triton* (Figure 2). In this feature both the Sterkfontein and the Swartkrans material is closest to *Mus musculus* , which probably implies the presence of the same or closely allied species at both sites.

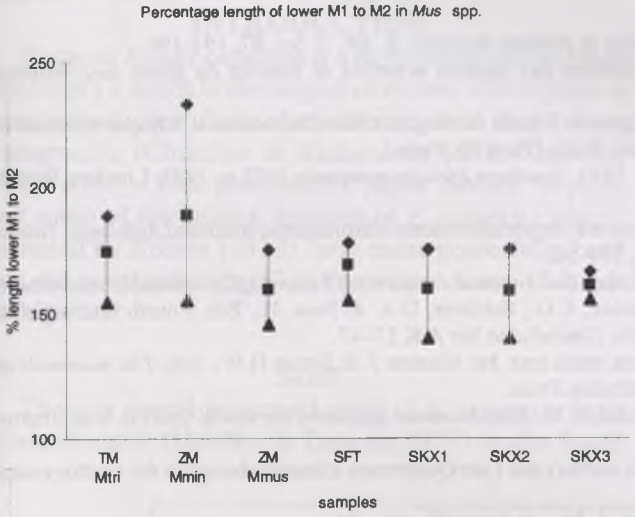


Figure 2. Mean, maximum and minimum percentage length of M_1 to M_2 in modern *M.triton* (TMMtri) from the Transvaal Museum, and *M.minutoides* (ZM Mmin) and *M.musculus* (ZM Mmus) in the South African Museum compared with fossil *Mus*. sp. from Sterkfontein (SAFT) and Swartkrans (SKX1, 2 and 3). Sample size: TM Mtri - 9; ZM Mmin - 16; ZM Mmus - 10: SFT - 3; SKX1 - 16; SKX2 - 9; SKX3 - 2

DISCUSSION

The list of species from Sterkfontein appears to be long (Table 5) when the work of De Graaff (1960, 1961), Pocock (1969, 1987) and Denys (1990) is combined with the results of the present study. However, there are many cases of alternative specific identifications and the maximum number of taxa identified in one sample is 34. A further 11 were either not found or not accepted. Reasons for differences in specific identifications vary. In some instances one of two closely related modern species may be represented. Examples are *Rhinolophus capensis* and *R. darlingi, Dendromus melanotis* and *D. mesomelas*, and *Aethomys chrysophilus* and *A. namaquensis*. There are also several possible chronospecies and it is perhaps a matter of opinion whether the extant form or a fossil antecedent is represented at Sterkfontein. These include *Myosorex robinsoni— tenuis* and *Elephantulus broomi — intufi* (see Corbet & Hanks 1978). Finally, genera such as *Arvicanthis, Pelomys* and *Mylogale* were at one time considered to be represented (De Graaff 1960) but have not been reported more recently. Conversely, genera such as *Chrysospalax, Grammomys, Lemniscomys* and *Zelotomys* were later added to the list (Pocock 1987, Denys 1990) and still other additions are proposed in this report. It is therefore clear that there is a critical need for a re-examination of all available material based on current taxonomy. Such a consistent examination should eliminate duplications and inaccuracies, and can be expected to reduce the list still further.

Some of the new additions listed in this report almost certainly result from the inclusion of Late Pleistocene samples for the first time rather than from differences of taxonomic opinion. This is suggested by the exclusive occurrence of four genera and one species in the later samples (Table 2), where only *Macroscelides proboscideus* was previously listed (Table 5). It will thus be important in future work to distinguish between samples of such different ages when compiling faunal lists. By providing intermediate examples, later material from Sterkfontein will also be important for evaluating the likelihood that species found in the Early Pleistocene levels are distinct from modern taxa. Early Pleistocene forms seem previously to have been considered extinct solely because of their age but there is no intrinsic reason why a species may not exist for two million years. It is also worth emphasizing that size alone is not a good criterion for distinguishing non-contemporary taxa. Thus, the two species of *Steatomys* in M6 can be distinguished on size because they are contemporary. Conversely, asynchronous samples cannot be separated on this basis even if they have a significantly different mean size (Table 3) because extraneous factors such as climate may influence size (Klein 1991).

The present samples confirm the richness of the Sterkfontein micromammalian fauna shown by Pocock (1987). At the same time, they highlight the amount of work that still needs to be done before the fauna is properly understood.

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Dr K. Kuman of the University of the Witwatersrand made the material available for study and answered many questions about the stratigraphy of the site. This work comprises part of a larger project that is supported by the Foundation for Research and the South African Museum. An anonymous referee provided useful constructive criticism.

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EQUUS CAPENSIS (MAMMALIA, PERISSODACTYLA) FROM ELANDSFONTEIN

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ABSTRACT

The skull and limb bones collected at Elandsfontein, Cape indicate that *E. capensis* was different from a Grevy's zebra. The body proportions were similar to those of an extant draft horse *(E. caballus)* and the skull resembled those of true Cape quaggas and a fossil Algerian plains zebra, *E. mauritanicus*.

KEYWORDS: Pleistocene, Elandsfontein, *Equus capensis*, zebras.

INTRODUCTION

Because *Equus capensis* is a large equid and because the Grevy's zebra is the largest of extant wild equids, it has sometimes been considered that they were conspecific (Churcher & Richardson 1978; Churcher 1986, 1993). This preliminary paper intends to point out some of the general features of *E. capensis* which, as noted by Broom (1913) "was more powerfully built but did not stand so high" as "a modern horse 15 hands in high".

Skull

There is a well preserved skull of *E. capensis* from Elandsfontein (Hendey & Deacon 1977) in the South African Museum Cape Town (E21025). It is very large, but quite unlike a Grevy's zebra skull. Grevy's zebras have very long distances between the posterior border of the palate and the posterior border of the vomer, and their muzzles are narrow (Eisenmann 1980 Plate 1). In the skull of *E. capensis* mentioned above, the muzzle is much wider and the distance between palate and vomer (vomerine length) is relatively short. A scatter diagram of these dimensions in Grevy's zebras, plains zebras, and true Cape quaggas (Figure 1) shows that the *E. capensis* skull has proportions similar to true Cape quaggas although it is larger. On the same diagram, *E. mauritanicus* from Tighenif (Ternifine), Algeria, plots between true quaggas and *E. capensis*.

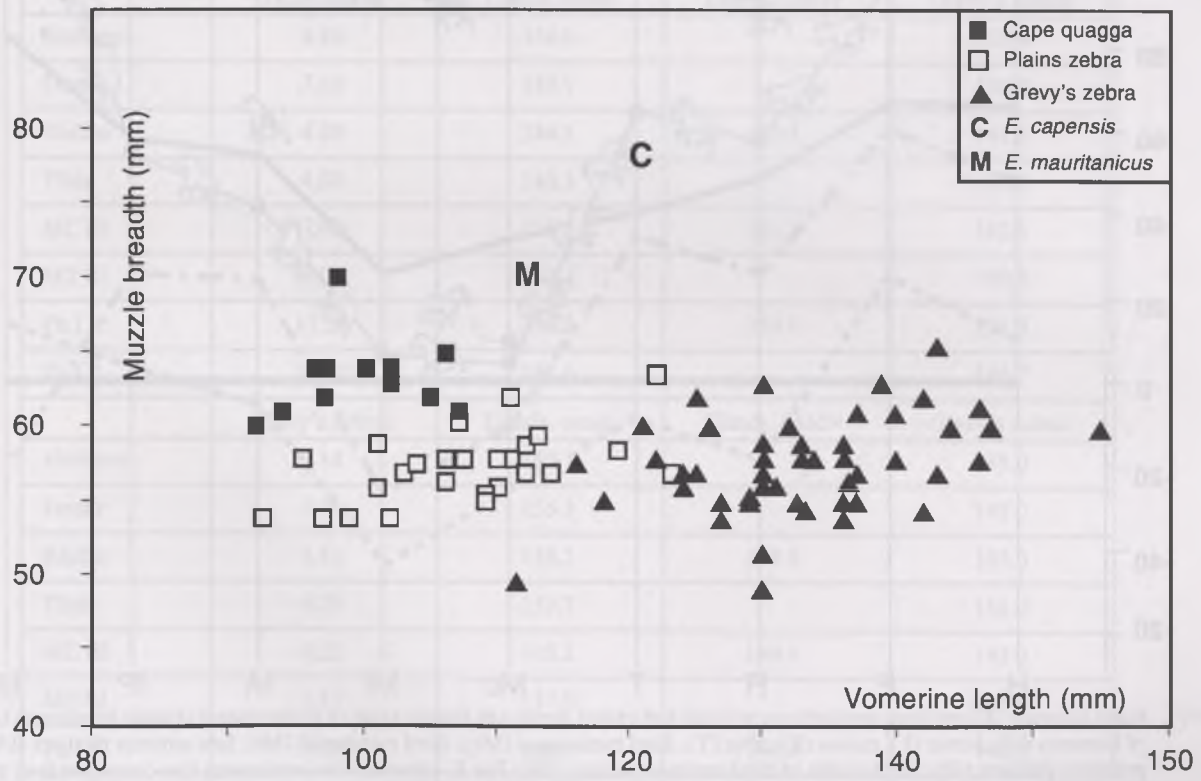


Figure 1. Scatter diagram in millimeters of muzzle breadths versus vomerine lengths in skulls of fossil and extant species of *Equus*.

The middle Pleistocene (Geraads *et al.* 1986) *E. mauritanicus* is probably a close relative to quaggas and plains zebras (Eisenmann 1979). Not shown on the diagram, horses plot near true quaggas while mountain zebras plot near plains zebras.

General body build

In cursorial animals, the proximal limb bones (humerus, femur, radius, tibia) tend to be relatively short while more distal limb bones, in particular metapodials, tend to be long (Gregory 1912; Osborn 1929).

Simpson's (1941) ratio diagrams of limb bone dimensions make comparisons of sizes and proportions very easy (Table 1). In Figure 2 the onager (*Equus hemionus onager*) – a very cursorial equid – is taken as the reference (horizontal line). Both mountain zebras and plains zebras have longer humeri and femora, but shorter third metacarpals and metatarsals since their body build is less cursorial. The mountain zebras, as usual in climbing animals, have narrower hooves than plains zebras, and even shorter third metapodials relative to the lengths of the tibia and radius. Moreover, mountain zebras and plains zebras have relatively long

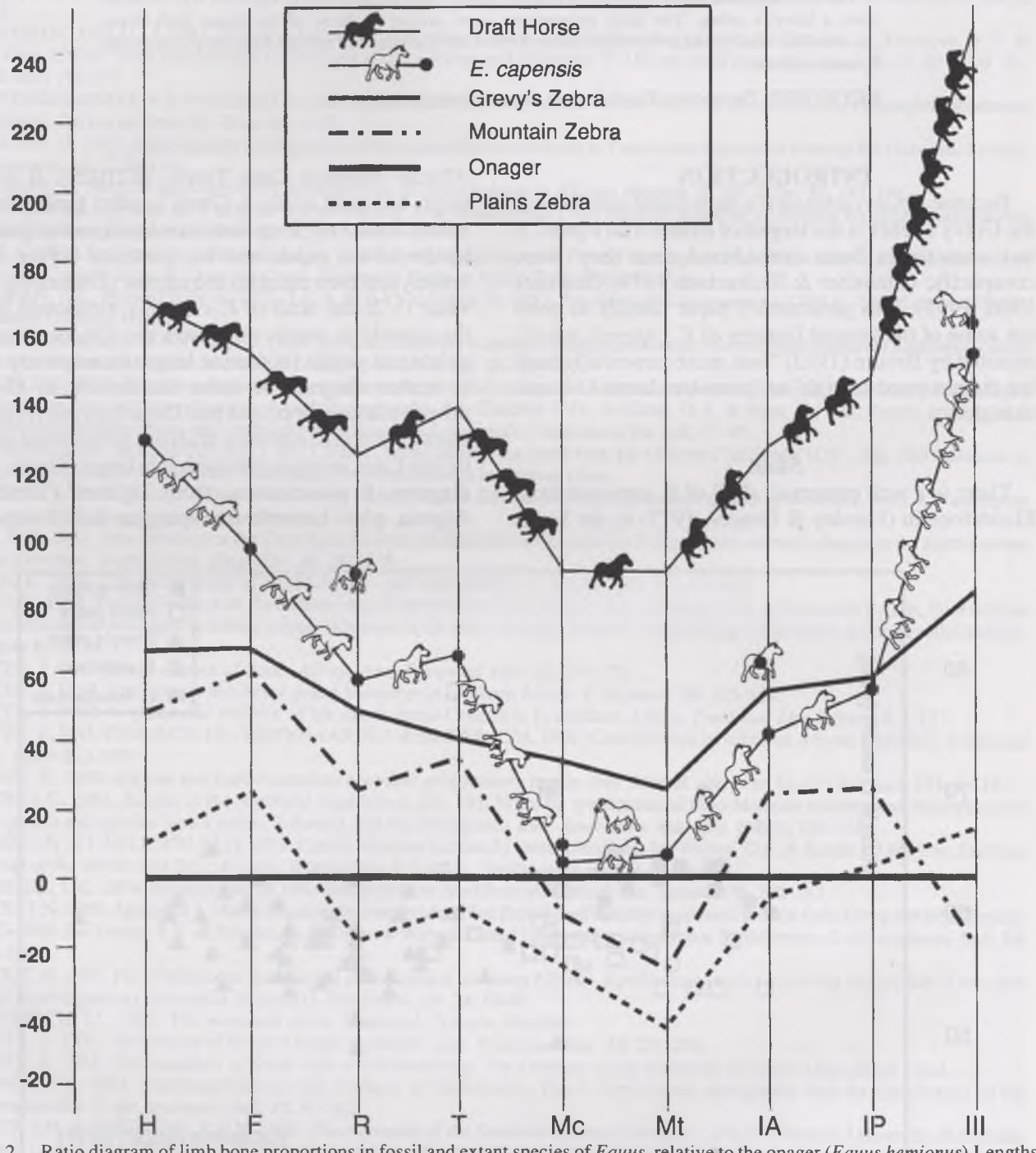


Figure 2. Ratio diagram of limb bone proportions in fossil and extant species of *Equus*, relative to the onager (*Equus hemionus*).Lengths of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (Mc), third metatarsal (Mt), first anterior phalanx (IA), first posterior phalanx (IP), and breadth of third anterior phalanx (III). For *E. capensis*, the continuous line corresponds to average values while the isolated spots correspond to associated bones of a front limb (E 16659).

femora and tibiae. Grevy's zebras appear less cursorial than the onagers but more so than mountain and plains zebras.

An associated front limb of *E. capensis* was found at Elandsfontein (South African Museum, E16659). It has a very long radius relative to the third metacarpal (Table 1). These proportions are unlike those of Grevy's zebras (Figure 2), and quite uncommon in extant equids. Unfortunately, there are not many entire proximal limb bones at Elandsfontein, but the

TABLE 1.

Limb bone dimensions in millimeters (all are maximal lengths except for the third anterior phalanx where the dimension is the maximal width). MC III = third metacarpal; MT III = third metatarsal; Ph I = first phalanx; Ph III = third phalanx; A = anterior; P = posterior. The numbers of specimens on which the means were calculated are in brackets. In the last column are the values concerning associated bones of a front limb (E 16659).

	E. hemionus onager	Grevy's zebra	Plains zebra	Hartmann's zebra	Draft horse	Elandsfontein mean	Elandsfontein 16659
Humerus	241,3 (10)	282 (19)	247 (25)	270 (12)	356 (2)	325 (1)	
Femur	329,7 (10)	385.5 (19)	349.2 (25)	378.4 (12)	467.5 (2)	413 (2)	
Radius	293,5 (10)	329 (20)	280 (25)	312 (12)	387.5 (2)	336 (3)	360
Tibia	313 (10)	342.9 (20)	305.3 (25)	338.9 (12)	425 (2)	363.31 (10)	
MC III	214,1 (10)	232 (21)	201.7 (25)	209 (14)	263 (2)	216.3 (47)	219
Mt III	250,8 (10)	266.5 (21)	226.4 (25)	235.1 (15)	308 (2)	253.9 (64)	
Ph I A	76,3 (10)	86.4 (21)	75.3 (21)	80.6 (13)	101.5 (2)	83.6 (49)	88
Ph I P	71,2 (10)	81.5 (20)	71.3 (21)	75.6 (14)	99 (2)	80.9 (58)	
Ph III A	54 (8)	65.3 (18)	55.6 (13)	51.6 (13)	95 (2)	76.7 (19)	79

TABLE 2.

Estimations of the height at the withers in centimeters in heavy horses and *E. capensis* and in the much more cursorial Grevy's zebra. Withers heights are obtained by multiplying the length of a limb bone (Table 1) by the corresponding 'index'. Indices differ in heavy and cursorial forms.

	Indices	Withers height	Withers height	Withers height
	Draft horses	Elands. mean	Elands. 16659	Grevy's zebras
Humerus	4.80	156.0		135.4
Femur	3.60	148.7		138.8
Radius	4.30	144.5	154.8	141.5
Tibia	4.00	145.3		137.2
MC III	7.00	151.4	153.3	162.4
MT III	6.00	152,3		159.9
Ph I A	17.50	146,3	154.0	151.2
Ph I P	18.00	145,6		146.7
	Grevy's zebras	Elands. mean	Elands. 16659	Grevy's zebras
Humerus	5.14	167.1		145.0
Femur	3.76	155.3		145.0
Radius	4.41	148.2	158.8	145.0
Tibia	4.23	153.7		145.0
MC III	6.25	135.2	136.9	145.0
MT III	5.43	137.9		145.0
Ph I A	16.86	140.9	148,4	145.0
Ph I P	17.68	143.0		145.0

available data (Table 1) indicate that *E.capensis* was rather like a draft horse in its general build, although smaller (Figure 2).

Estimation of the height at the withers

The height at the withers of a horse used to be expressed in "hands" (one hand = 4 inches) or in "inches" (one inch = 25,4 millimeters). Thus, a horse "15 hands high" measures 152,4 cm at the withers. The height at the withers can be estimated by multiplying the length of a limb bone by an adequate number. The best known numbers for horses (average and range of variation) are those proposed by Kiesewalter in 1889 ('Kiesewalter's indices' of Gromova, 1949, p.14). However, as already pointed by Gromova and by Mourer-Chauviré (1980), the estimations based on the average indices are often not concordant, while the use of the range of variation makes them so approximate that they become useless. It is indeed natural that numbers adequate for a cursorial form will not give a correct estimation for a draft horse. Using my own data on limb bone lengths of heavy horses, and previously published average heights, I have calculated 'indices' (Table 2) that may reasonably be applied to *E. capensis*. At least, they give relatively concordant indications, whatever the bone used. The estimated heights range between 144 and 156cm, confirming Broom's (1913) opinion: on average, *E. capensis* 'did not stand so high as a modern horse 15 hands high'. The same table shows the indices calculated for Grevy's zebra, assuming an average withers height of 145cm (Kingdon 1979).

If applied to the associated front limb of *E.capensis*, the Grevy's indices would provide estimations of 137cm (using the third metacarpal) to 159cm (using the radius) Conversely, if *E. capensis* indices were applied to the average Grevey's zebra, the estimations would range from 135 to 162cm (Table 2). These discordances are another expression of the fact that *E. capensis* was not a kind of Grevy's zebra.

Estimation of weight

Several ways have been proposed to estimate the body weight of an equid (Alberdi *et al.* 1995). For instance, the occlusal surface of an upper cheek tooth can be taken as a base (Figure 3). Unfortunately, some equids (*E. caballus* in particular) have relatively larger teeth than others. Thus, the occlusal surface of an upper first molar (M1) measures about 500 square millimeters in a horse which weighed about 150 kilos, but about the same surface is the minimum for Grevy's zebras whose minimal weight is about 350 kilos (Kingdon 1979). Obviously, the relationship between tooth surface and body weight is not the same in all equids. It is possible, however, to determine a relationship using regression analyses (Eisenmann & Sondaar 1998): Ln of the weight = -6.388 + 1.873 (Ln surface M1). For *E. capensis* of Elandsfontein, the average upper molar occlusal surface area of M1 is 796 square millimeters (n=50) and the average weight can be estimated at 450 kg.

A better way is to use the product of a limb bone depth (antero-posterior diameter) by its width (transverse diameter). For instance, using the distal end of the third metacarpal, Ln of the weight = -4.525 + 1.434 (Ln of the product of articular width by minimal depth of the medial condyle). In *E. capensis* of Elandsfontein, the average distal depth for 47 third metacarpals is 30.2 (maximum 32mm); the average

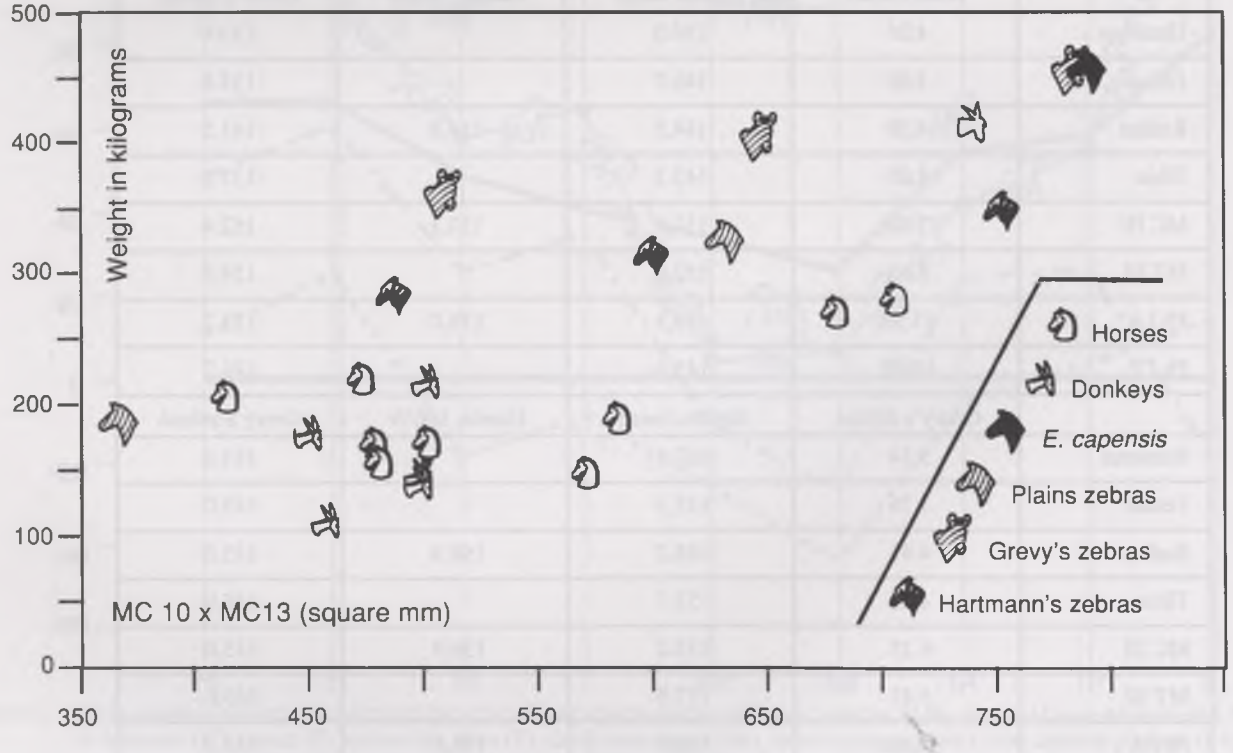


Figure 3. Scatter diagram of weights versus occlusal surfaces of upper M1 of extant *Equus*. The weight of *E. capensis* was calculated according to the regression: Ln of the weight = -6.388 + 1.873 (Ln product occlusal length by occlusal width of M1).

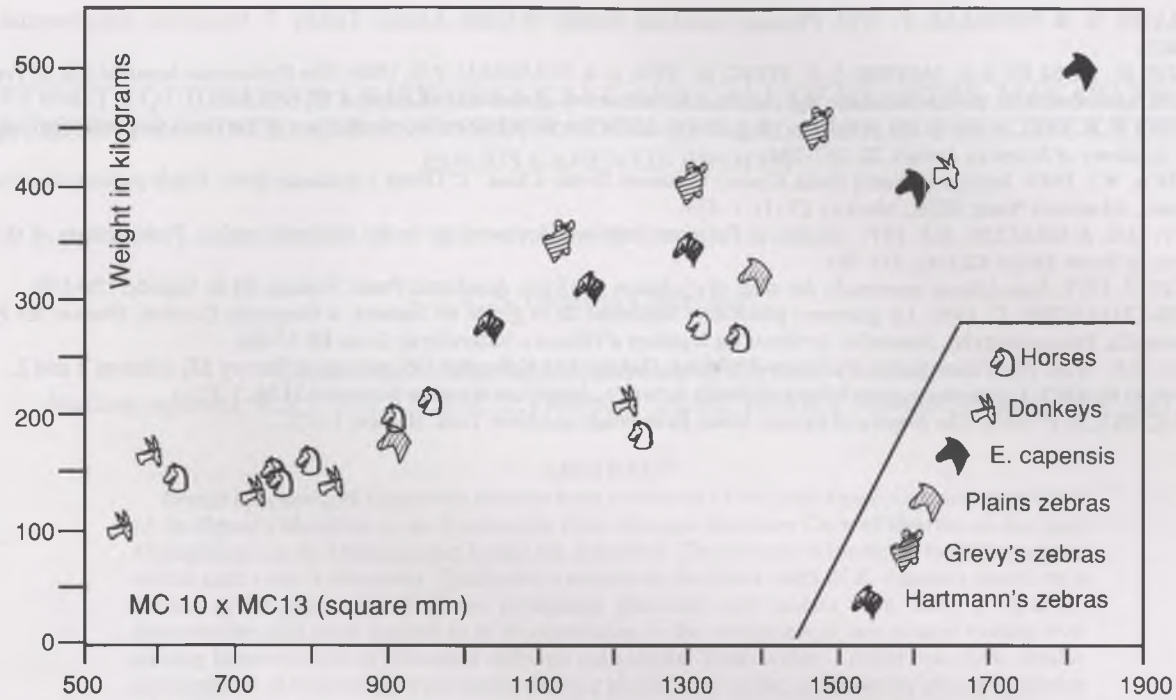


Figure 4. Scatter diagram of weights versus sections of third metacarpals of extant *Equus*. The average and maximal weights of *E. capensis* were calculated according to the regression: Ln of the weight = -4.525 + 1.434 (Ln product of articular width by minimal depth of the medial condyle).

distal width is 51.4 (maximum 57mm); the product of average distal depth by distal width is 1552.3 (maximum 1824). These parameters indicate (Figure 4) an average weight of about 400 kg, and a maximum weight of about 500 kg.

CONCLUSIONS

On the basis of fossils of *E. capensis* collected at Elandsfontein, one can conclude that this species resembled, in its general body build, a heavy horse (*E. caballus*) more than any other extant equid. By comparison with extant heavy horses, the height at the withers of *E. capensis* can be estimated at about 150cm, which is in accordance with Broom's estimation. Judging by the width and depth of its third metacarpals, the average weight would have been about 400 kg. Skull proportions resemble true Cape quaggas more than any other extant species, and also *E. mauritanicus*, a probable relative of plains zebras, represented in the Middle Pleistocene of Tighenif, Algeria.

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EXTINCT EQUIDS FROM LIMEWORKS CAVE AND CAVE OF HEARTHS, MAKAPANSGAT, NORTHERN PROVINCE, AND A CONSIDERATION OF VARIATION IN THE CHEEK TEETH OF *EQUUS CAPENSIS* BROOM

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ABSTRACT

Dental specimens of *Hipparion libycum* from Limeworks Cave, and *Equus capensis* from Cave of the Horse's Mandible in the Limeworks Cave entrance and from Cave of Hearths on the farm Makapansgat in the Makapansgat Valley are described. The concept of restricted local formations within each cave is discussed. Qualitative variation in the cheek teeth of *E. capensis*, based on a sample of 40 upper and 60 lower permanent premolars and molars from Cave of Hearths, demonstrates that there appears to be no correlation in the occurrence of one enamel feature with another between teeth of presumed different individuals. Teeth within a molar row show similar development of features between teeth, whether premolar or molar, as shown by plis, progressive migration of the protocone isthmus along the row, and penetration of the buccal valley to between the enamel loops of the metaconid and metastylid. Consequently, earlier descriptions of species of large Pleistocene *Equus* in Southern Africa founded on isolated teeth and, using such qualitative variation, are inept, unsuitable and inappropriate, and modern taxonomies synonymising them under *E. capensis* are supported. The Cave of Hearths 'loose breccia' (Beds 1-3 of Mason, 1988) containing earlier Stone Age/Later Acheulean artifacts, is circumstantially dated between 300 000 and 200 000 years BP.

KEY WORDS: Makapansgat Valley, Late Pleistocene, Cave of Hearths, Limeworks Cave, *Hipparion lybicum*, *Equus capensis*, dental variation.

HISTORICAL INTRODUCTION

The Makapan caves lie on the farms 'Makapansgat' and 'Swartkrans' in both south and north walls of the valley of the Mwaridzi stream (also known as the 'Makapan River' or'Makapanspruit'), about 16 km east of Potgietersrus, Northern Province (Figure 1). The Mwaridzi drains part of the Strydpoortberge and is a tributary of the Mogalakwena River ('Magalakwyn' on some maps), which it enters west of Potgietersrus. The caves are located at about latitude 24°08′ south, longitude 29°16′ east, and at an altitude of about 1500 masl. The caves formed from the combined effects of subsidence and solution in the Malmani Dolomite of the Transvaal Supergroup (Partridge, 1975) and have been refilled by stratified deposits of travertine, cave earth, soil, fragments of dolomite from the roof, and biological remains.

Seven named caves are located within the Makapansgat valley - Peppercorn Cave, Buffalo Cave, Swartkrans Prospects, Limeworks Cave (including Cave of the Horse's Mandible), Historic or Makapan's Cave, Cave of Hearths, and Rainbow Cave - respectively from west to east. Buffalo and Limeworks Cave and Cave of Hearths have yielded extinct equids, but only Limeworks Cave and Cave of Hearths will be considered here. Buffalo Cave has yielded both *Hipparion* cf. *lybicum* and *Equus* cf. *capensis* (Kuykendall *et al.*, 1995), with *E. capensis* first recorded by Broom (1937).

Limeworks Cave was first reported to be fossiliferous by W.I. Eitzman (Dart, 1925), a school teacher in Pietersburg, who began collecting fossils in the Makapansgat Valley. Some of these fossils were donated to the Department of Anatomy, University of the Witwatersrand by Dart (1925) who published a short note on the 'Limeworks' occurrence. After 1927 Dart was responsible for the collection of the many additional specimens from Limeworks Cave (Malan, 1988). Cooke (1952) and Oakley (1954a, 1954b) discussed the significance of the fossil faunas obtained by James W. Kitching in the 1940s and 1950s. Wells & Cooke (1956) first reported the three-toed equid *Stylohipparion* sp. from Limeworks Cave and Ewer (1958) referred it to '*Stylohipparion van Hoepeni* spp.' Boné & Singer (1965) recorded '?*Stylohipparion steytleri*' from Makapansgat and justified this taxonomic identity as 'after Cooke (1963).' Churcher (1970, Table 8) recognised *Hipparion steytleri* and ?*Equus capensis* from Limeworks Cave and *E. capensis*, *E. burchelli* and *E. plicatus* (since considered conspecific with *E. capensis*) from Cave of Hearths. Churcher & Richardson (1978, Table 20.1) revised the species to *H. libycum* and *E. (Dolichohippus) capensis*. Churcher & Watson (1993) recombine this hipparion's name as *H. l. steytleri*.

Cave of Hearths was recognised as containing fossils in 1925 when Eitzman collected fossils from it. Dart (1925) also noted it as fossiliferous and was

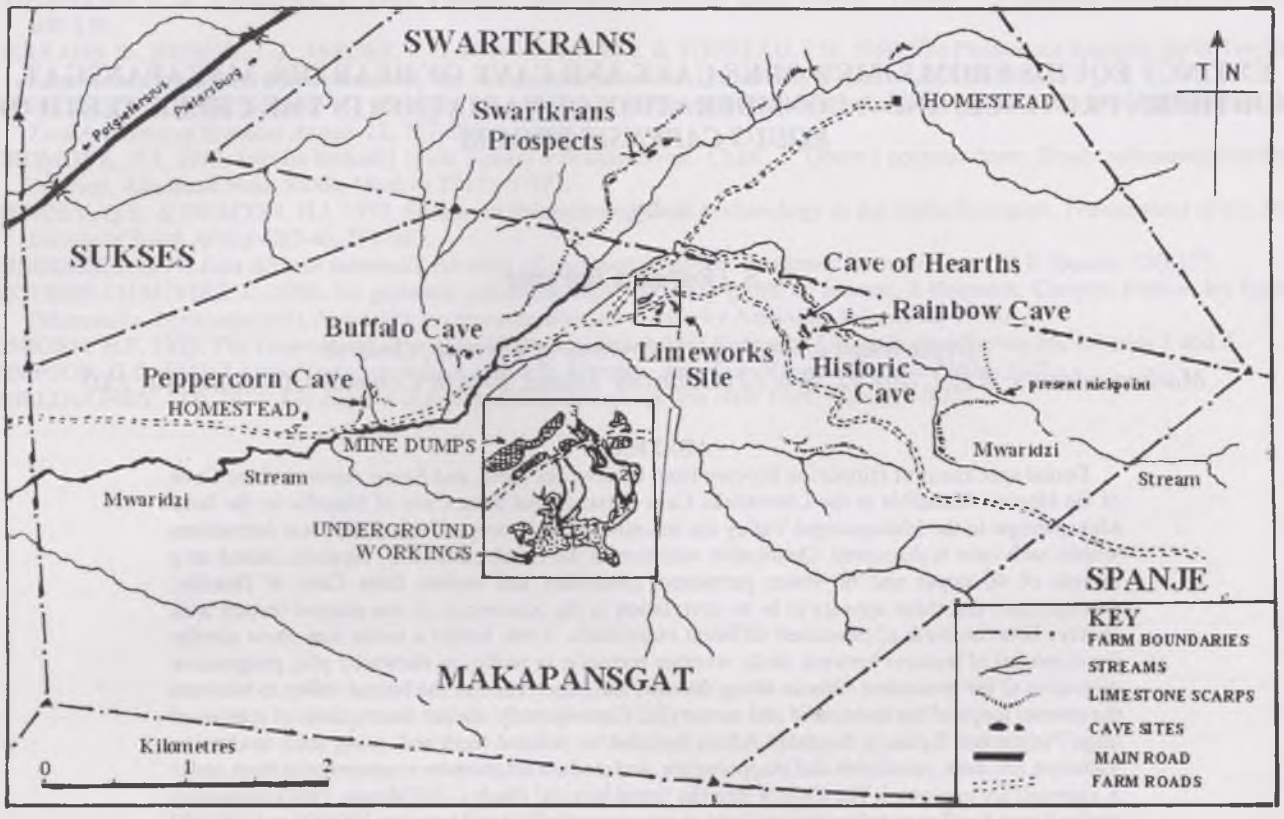


Figure 1. Map of the Makapansgat Valley and Makapansgat Farm with named cave sites.

responsible for the collection of additional fossils after 1927. Only *Equus burchelli* and *E. capensis* are reported from this cave (Churcher & Richardson, 1978; Cooke, 1988). Because of the cave's early history of exploration for mineral lime and the removal of most of the breccias by the miners, its stratigraphy and interpretation are unclear and its palaeontological importance less manifest than that revealed in Limeworks Cave.

GEOLOGY OF THE DEPOSITS AND CONTAINING STRATA

Breccias are recorded within Limeworks Quarry or Cave, the north side of Buffalo Cave, Rainbow Cave, Cave of Hearths and Swartkrans Prospects. Wells & Cooke (1956:4) discussed the basic history of cavern formation, infilling, sapping and thinning of the roof, and solution of the breccias, and conclude that 'similar lithological sequences of detrital cave deposits may vary widely in age.' As the nickpoint of the Mwaridzi Stream Makapan River in the Malmani Dolomite migrated eastwards, water tables would have progressively lowered within the dolomite and surface erosion increased on the downstream slopes below the nickpoint. Thus the caves might reflect a crude older to younger west to east sequence. Assuming that the caves formed at similar depths due to equivalent hydrological circumstances and with comparable thicknesses of overlying dolomite roofs, and that surface erosion progressed at similar rates above each cave, connection of the cavities to the surface may also have been sequential from west to east. Thus the basal faunas within the caves may be older in the western caves (Peppercorn and Buffalo caves) and younger in the eastern caves (Cave of Hearths and Rainbow Cave). Later stratigraphic units might therefore contain faunal elements that could be much later than the time of penetration of the roof and could be later than basal faunas in the younger eastern caves.

As the fillings of the different caves at Makapansgat are spatially disjunct and are probably temporally asynchronous, at least at the times that the cavities became connected with the surface, it is unwise to consider all the breccias and other deposits within Limeworks Cave, Cave of Hearths, Rainbow Cave, etc., as comprising a single formation. It is even less likely that Sterkfontein Cave or other Krugersdorp caves would also have developed in parallel synchronism. In effect, each cave's infilling constitutes a much restricted local formation and the term 'Makapansgat Formation' (of Partridge, 1975) is appropriate only for the fillings within Limeworks Cave to which Partridge applied it. The stratified deposits within each cave should logically be termed a formation named from the cave, with those within Makapansgat or Historic Cave the 'Makapan Cave Formation' and those within Limeworks Cave the Limeworks Cave Formation (=Makapansgat Formation), etc. The term 'Makapansgat Caves' Group' might be suitable to embrace all the deposits in the caves within the valley. Recently, McKee (1995) demonstrated a faunal seriation in selected southern

African caves that supports asynchronous fossiliferous deposits between the Makapansgat caves, specifically Makapansgat Members 3 and 4, and Cave of Hearths, as well as between the Krugersdorp caves.

MATERIALS

All specimens are housed in the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, Gauteng, South Africa and are accessioned with the prefix 'LM' for Limeworks Cave, Makapan, materials or 'COH' for Cave of Hearths specimens. The *Hipparion lybicum* remains mainly comprise isolated whole or partial cheek teeth lacking roots and from which most of the outer cementum has spalled. Only three specimens (LM 197, 181-488, and one unnumbered) comprise dental series within fragments of dentaries. Two milk teeth (M 2480 & 2481) may be associated on the evidence of occlusal wear and interdental facets and derive from an individual hipparion. A few additional hipparion specimens, including some metapodials, are also conserved in the Bernard Price Institute's collections (M.A. Raath, *pers. comm.*, Feb., 1999), but they were unavailable to me when I carried out my examinations. These had evidently been included among unidentified bovid elements from the cave.

The specimens are stained in various hues of red, brown and yellow from iron oxides and black from manganese dioxide. Calcium carbonate crystals occur within some pulp cavities or within bones and over some enamel surfaces. The matrix preserved on the crowns of the teeth and in spaces between portions of the dentaries of LM 197 and the unnumbered specimen is coarse and red from haematite.

Identification of specimens to position in the jaw and tooth row may be difficult for isolated equid cheek teeth. Second premolars (P2s) are identified from their prolonged mesial areas (often broken), but the third and fourth premolars are considered indistinguishable because sizes and enamel patterns overlap. Similarly, only third molars are identifiable on their distal conformation and firsts and seconds are

MALMANI DOLOMITE (roof)	
MEMBER 5	Locally stratified brownish-red silty sand matrix with abundant chert and dolomite fragments: formerly Brain's (1958) 'Phase II Red Breccia'. Contains scattered bone; *Australopithecus* jaw, *Papio* skeletal and dental remains; two *Equus capensis* jaw fragments from Cave of the Horse's Mandible at the northwest entrance to the adit into the eastern quarry (Figure 1 and Wells & Cooke, 1956, fig. 2).
Erosional Unconformity	
MEMBER 4	Pink, thick, silty sand matrix with angular chert and dolomite fragments and some bone clusters: formerly Brain's (1958) 'Upper Phase I Pink Breccia'. *Oreotragus, Tragelaphus* (kudu), small *Parapapio, Gigantohyrax, Procavia transvaalensis, P. capensis/antiqua.*
Unconformity	
MEMBER 3	Thin layer of closely packed bone bed cemented by calcite: generally equivalent to Brain's (1958) 'Lower Phase I Grey Breccia.' Highly fossiliferous and has produced most of the Limeworks local fauna including Bovinae, rhinoceros, small *Hyaena*, bushpig, *Hipparion lybicum.*
MEMBER 2	Brownish-red, bedded, fossiliferous silt to fine sand, with angular chert and dolomite fragments, deposited subaqueously: formerly basal part of Brain's (1958) 'Lower Phase I' unit. Birds, pig and rhinoceros.
MEMBER 1	White travertine, frequently banded very pale brown, and brown laminated, crystalline calcite, frequently containing bones, either isolated or in articulation as full or partial skeletons.
MALMANI DOLOMITE (floor)	

Figure 2. Stratigraphic sequence of infilling deposits at Limeworks Cave, Makapansgat (Makapansgat Formation, Partridge, 1975; after Brock *et al.*,1977).

indistinguishable by patterns, There are no other qualitative distinguishing characters, and crown heights are similar and thus uninformative. Interdental facets and inclinations of the worn dental surfaces to the occlusal plane may assist in placing fourth premolars posterior to third, or second molars posterior to first molars. However, permanent lower molars are usually reliably distinguished from premolars because their buccal mesial valleys do not penetrate lingually between the bases of the enamel loops of the metaconids and metastylids (Figure 3). In newly erupted teeth these criteria are undeveloped because of immature stages of wear. Figure 3 illustrates the features in the enamel patterns of worn upper and lower cheekteeth. The named features are those referred to in the text. The terminology follows Churcher & Richardson (1978, 387, Figure 20.5).

Not all specimens were fit for line illustration and only those sufficiently complete and with clearly visible enamel patterns are depicted in Figures 4-7.

Specimens listed in Tables 1-10 (Appendix 1) are those that were sufficiently complete for measurement or recording of qualitative features. Not all specimens were recorded in both manners for various reasons including breakage, worn dimension points, worn surfaces, or form obscured by still adhering matrix, etc.

LIMEWORKS CAVE

Depositional History and Stratigraphy

The Limeworks Cave lies on the south side of the Makapansgat Valley (Figure 1), west of the Historic Cave and Cave of Hearths and east of Peppercorn and Buffalo caves on the north side of the valley. The cave originally formed as a solution cavity at a lower level than the present cave. The original roof collapsed to move the cavity upwards. The enlarged cavity then became filled by travertine and cave earth, brought in through seepage, solution and fluviatile transport and, after an opening to the surface was established, by windblown dust and water transported soil and rock fragments, and by additional dolomite blocks fallen from the roof (Brain, 1956; Partridge, 1975). Fossil bones, teeth and coprolites are incorporated in this complex later breccia.

Brain (1956) was the first to classify the sediments contained within Limeworks Cave based on a detailed analysis of their variations. He recognised five sedimentological units, numbered 1 to 5 from bottom to top. Butzer (1971) criticised Brain's palaeo-environmental deductions, considered his basic premises ambiguous and that the time spans and external depositional influences were downplayed or ignored. Partridge (1975) agreed with Butzer and erected a new schema for the deposits. He named the Limeworks Cave infillings within the Malmani Dolomite the 'Makapansgat Formation', with an areal extent of some 230 by 100 m (see comments earlier). The sequence of members, based on Brock *et al.* (1977), from the basal disconformity over the Malmani Dolomite, and with faunal elements included, is given in Figure 2.

Materials and List of Specimens

The Limeworks *H. lybicum* dental sample comprises the crowns of two upper milk incisors, 33 isolated whole or partial upper milk premolars, one isolated permanent second premolar (LM 193), 11 isolated whole or partial lower milk premolars, and one fragment of a right juvenile dentary with p_{2-4} (181-488; Table 1). *E. capensis* is represented by two crushed horizontal rami with damaged and well worn (LM 197) and newly worn dentitions (181-488), respectively, and a lower molar series embedded on matrix (No Number), all from Cave of the Horse's Mandible (Table 2). No postcranial elements from *Equus* have been recognised from Limeworks Cave. Some assorted hipparion postcranial elements from Limeworks Cave are in the collections of the BPI (M.A. Raath, *pers. comm.*, Feb., 1999) but were not examined by me.

In the account that follows, teeth will be identified as permanent or milk by capital and lower case letters respectively, with numbers written superscript for upper and subscript for lower teeth, and L and R indicating left and right side of the animal, e.g., Lp^4 for left milk fourth upper premolar, and RM_3 for right permanent third lower molar.

The *Hipparion lybicum* teeth derive from juveniles in which the teeth are either unworn or only newly worn, except for LM 2475, which is from a late juvenile in which the permanent premolars are well developed with P^2 entering wear (Figure 4). All specimens derive from Member 3.

The informative *Equus capensis* jaw fragments represent a single mature individual (LM 197) with well-developed enamel patterns on the molars (Figure 5), and a young individual (181-488) in which wear has scarcely revealed an enamel pattern. The *E. capensis* specimens derive from the breccia in the Cave of the Horse's Mandible at the entrance to the east adit. The cave gains its name from the mandible LM 197.

The specimens are listed under *Hipparion lybicum* (Table 1) and *Equus capensis* (Table 2), and the teeth of the former by incisors and upper and lower premolars. Many of the *H. lybicum* teeth have lost all or most of the outer cement, a few have calcite crystals formed on them, and most are some shade of brown. All measurements are given in millimetres (mm).

Descriptions of the milk premolars of *Hipparion lybicum*

The premolar specimens are generally unworn and the enamel patterns obscured by cement or not fully developed by wear (Figure 4). Measurements of measurable specimens are given in Table 3. Among the upper milk premolars, only LM 2483 (Lp^2), 2481 (Lp^3), 2480 (Lp^4) and 2496 (LP^3) show stages of early wear (Figure 3). No definite plis caballine are present in any milk premolars but promontories reaching towards the protocone confuse their recognition: 1 or 2 plis protoloph, 2 or 3 plis protoconule, 2 or 4 plis prefossette, 1-3 plis postfossette, and 0-2 plis hypoloph may be seen. However, as wear is just beginning, characters and pli

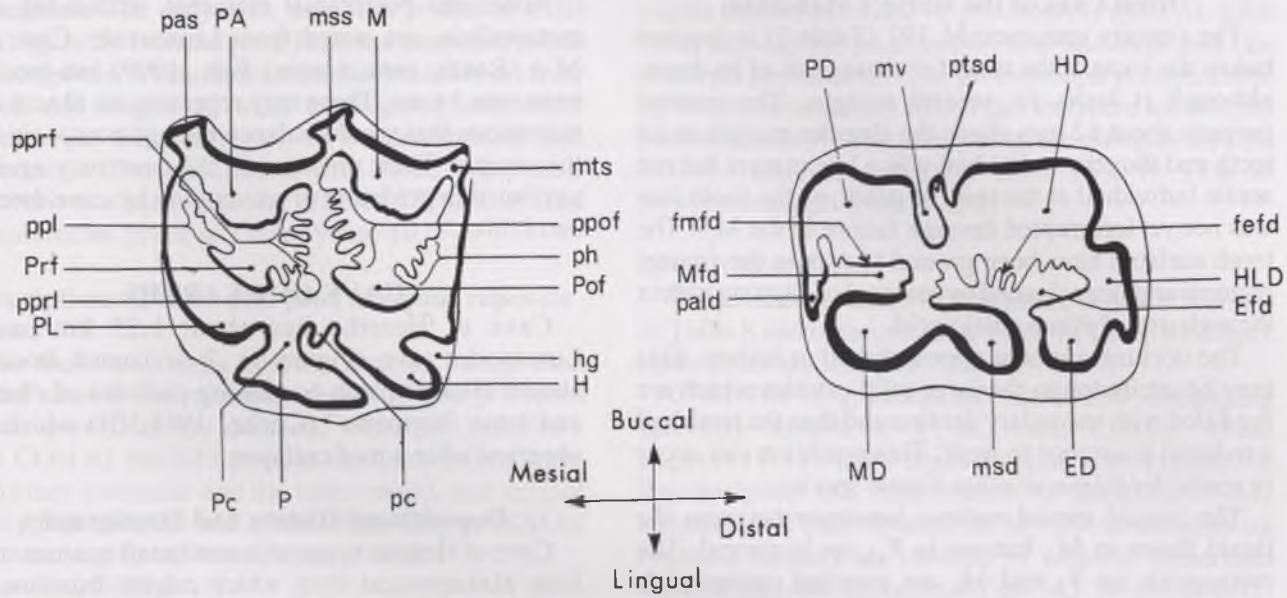


Figure 3. Generalised enamel patterns of upper and lower cheekteeth of advanced equids.

counts are probably unreliable because of small sample size and poor pattern development. No attempt has been made to review the qualitative characters of these upper and lower milk cheek teeth.

The permanent upper right fourth premolar (LM 2475, Figure 4) has been sectioned as the crown is unworn. The revealed enamel pattern shows a separate oval protocone, a double isthmus or commissure, and a rudimentary pli caballine. The paraconule is bulbous and rounded, and separated from the main protoloph by strong valley or glyph. There are two plis protoconule, a complex pli protocone, two plis prefossette (one large and one small), two plis postfossette (one large and one squarish), and one pli hypoloph. The parastyle is simply rounded and the mesostyle a smooth rise. Most of the cement ring has spalled away from the outer enamel walls.

The sectioned permanent right upper second premolar (LM 193, Figure 4) shows a double isthmus, a large pli protoloph with an incipient rise buccally, one medium and two small plis protoconule, one pli prefossette, two plis postfossette and a buccal thickening, and a small pli hypoloph. An additional small pli lies mesial to the isthmus and may represent the pli caballine.

The lower milk premolars are also generally unworn, and enamel patterns are revealed only in early stages of wear in LM 2505 ($Lp_{3/4}$) and 2474 ($Rp_{3/4}$). The typically elongate sectioned buccal pillars are present on all milk premolars and lie just distal to the buccal mesial valley with their mesial edges about level with the valley. LM 2173 has an additional oval distal buccal pillar placed off the distobuccal angle of the hypoconid and oriented nearly transversely. The floor of the entoflexid is sinuous in LM 2474 and less so in 2505.

Measurements of the milk premolars (Table 3) appear larger than those recorded for *H. lybicum* (cf. Table 4), although the lower premolars are small. Unfortunately only permanent premolars are recognised from Kromdraai (KA 729+1351, LP^2; Churcher, 1970) and Swartkrans (SK 3278, LP^3; 3982, LP^4; 2307, RP^4; Churcher, 1970: SKX 1706+1708, RP^2; Churcher & Watson, 1993) so comparisons with *H. lybicum* from other Transvaal cave deposits is restricted to comparison of LM 2475 RP^2 with KA 729+1351 and SKX 1706+1708; the latter is too damaged for meaningful comparison. The enamel patterns are similar, size is comparable, and the protocones similarly compressed (cf. Tables 3 and 4). There is no specimen comparable to that recorded from Swartkrans Member 3 which yielded a five tooth P_3-M_3 fully adult row that lacks its ventral margin (Churcher & Watson, 1993).

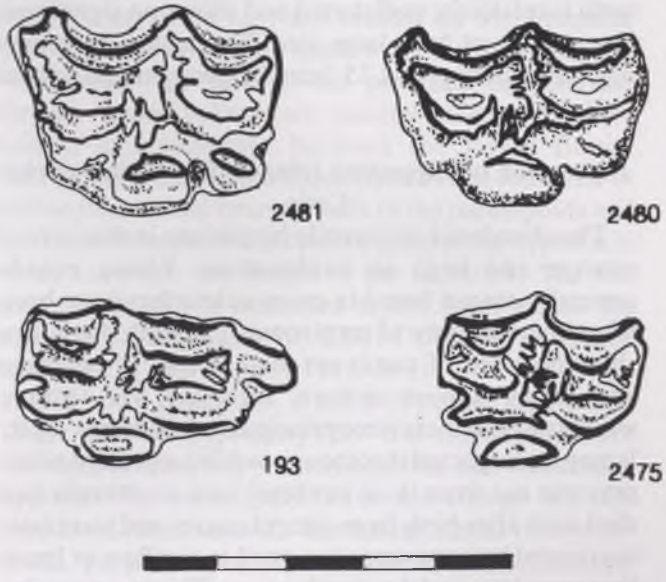


Figure 4. Crown enamel patterns of cheek teeth of *Hipparion lybicum* and *Equus capensis* from Limeworks Cave.

Descriptions of teeth and jaws of *Equus capensis* (from Cave of the Horse's Mandible)

The dentary specimen M 197 (Table 2) is crushed below the roots of the teeth for about 60% of its depth, although it lacks its ventral margin. The enamel projects about 12 mm above the alveolar margin on all teeth and thus the individual was a late mature but not senile individual at the time of death, as the tooth row was not yet interrupted through failure of the M_1s. The tooth surfaces have been ground to expose the enamel patterns and later cleaned by removal of capping matrix through use of dilute acetic acid.

The occlusal surfaces appear dished or hollow. This may be attributed to the large pulp cavities which are not filled with secondary dentine and thus the teeth had a reduced resistance to wear. This condition can occur in senile dentitions of other *Equus* species.

The buccal mesial valleys penetrate between the flexid floors in M_1, but not in P_{3-4}, as is normal. The metaconids on P_3 and M_1 are rounded, metastylids pointed but not strongly inflated, entoconids squarely inflated, and no hypoconid spur is visible. Measurements of these teeth (Table 5) are normal for those reported in the literature (cf. Churcher, 1970; Churcher & Watson, 1993) and compare well with those reported below for *E. capensis* from the Cave of Hearths (see below and Table 10).

The juvenile left lower dentition p_{2-4} LM 181-488 is newly worn and slightly damaged. The cusps are all proportionately elongate, as is normal in milk cheek teeth, especially when in early wear, as is p_4. The characters of the cusps are not fully developed and inflation is reduced by lateral compression of the pattern. However, the metaconids are rounded, metastylids pointed distolingually and entoconids elongatedly oval in p_{2-3} and squarely rounded in p_4. The distal parts of the floors of the entoflexids are smooth but in p_{3-4} the mesial parts are bent. There are no ptychostylids. The dentary fragment which bears these teeth is relatively undistorted and shows no significant character apart from large size. The dentary measures 33.5mm below p_2 and 35.5mm below p_3 on the lingual face.

Discussion of *Hipparion lybicum* from Limeworks Cave

The abundance of juvenile hipparions in this cave is strange and begs an explanation. Young equids generally are not found in caves unless they have been taken there as prey of carnivores. The milk premolars show no signs of carnivore tooth marks or breakage and, being almost unworn, represent very young animals whose diets were principally their mares' milk. It may be suspected that these juveniles represent either prey cut out from their mothers' care or animals that died soon after birth from natural causes and were later scavenged by carnivores too small to swallow or break the premolars, and thus not hyaenas. This suggests that a carnivore which could not destroy bones, e.g., a felid, such as a leopard, may have been responsible for the accumulation of the animals whose teeth are preserved.

Additional postcranial elements, includidng some metapodials, are noted from Limeworks Cave (*fide* M.A. Raath, *pers. comm.*, Feb., 1999) but have not been seen by me. These may represent the absent adult hipparions that would balance the age composition of the sample. Their presence in the cave may again be attributed to predation or scavenging by cave dwelling carnivores.

CAVE OF HEARTHS

Cave of Hearths lies about 1.25 km east of Limeworks cave (Figure 1). It is named from "an almost circular patch containing particles of charcoal and bone fragments" (Cooke, 1988:507) which was observed after a roof collapse.

Depositional History and Stratigraphy

Cave of Hearths is one of a number of quarries on the farm Makapansgat from which calcite dripstone was excavated for lime. These excavations exposed much breccia, in which many bones and hand-axes were included, and which exposed the larger circular patch of charcoal and bone fragments from which it gained its name (Cooke, 1988; Mason, 1988). Most of the breccia was too poor in calcite to warrant burning for lime and was removed and stacked outside the adits (Figure 1, insert). The cavity is an elongate hall that was divided by a travertine septum into the eastern Cave of Hearths and western Hyaena Cave; to the east it connects with the Historic Cave (Brain, 1988).

Most of the fossils were obtained from the breccia dumps and thus lack adequate stratigraphic provenance. These breccia blocks are termed 'loose breccia' in many publications, and almost certainly derive from the Early Stone Age/Later Acheulean horizons, designated Beds 1 to 3 by Mason (1988:67), and equivalent to the 'Fauresmith' stage of other writers (e.g., Cooke, 1988). About two-thirds of the breccia derives from a pipe-like trap called the 'Swallow Hole', which perhaps connected with the passage linking to the Historic Cave to the east.

Materials and List of Specimens

Cooke (1988:514) noted that 'equine teeth are very abundant' and that 'the majority (more than 500) cannot be distinguished from corresponding teeth of the living bontequagga, *Equus burchelli* ...' He also recorded 'some 65 specimens that are of much larger size and these are referred to the extinct *Equus capensis*.' Only these will be considered here.

The *Equus capensis* sample from the Cave of Hearths includes two maxillary fragments with P^4-M^1 (COH 41) and P^4-M^2 (No Number), six mandibular fragments with one series of P_2-M_3 (415), two series of P_{3-4} (537 & 557), and one each of p_3-M_2 (550), P_3-M_1 (OQ/25-25/14-16') and P_3-M_3 (404). Isolated teeth comprise three permanent incisors and 89 isolated cheek teeth (Tables 5-7). All are catalogued with the prefix 'COH'. Field numbers, levels, horizons or

square designations, where known, are given in parentheses. The only milk dentition is that of COH 550 (Figure 5). Isolated teeth from the same individual are recognised when interdental facets, occlusal wear angles and stages of wear correspond and allow positions in the tooth row to be determined (see Materials). The specimens are listed with their qualitative characters in Tables 7 and 8 and measurements given in Tables 9 and 10.

Descriptions of teeth and jaws of *Equus capensis*

Incisors

The incisive crowns possess heavier buccal than lingual enamel and resemble those of Grevy's zebra (*Equus grevyi*) or the domestic horse (*E. caballus*). Both COH 62 and 623 possess marks or infundibula, the former lenticular and the latter round, and located mainly in the lingual half of the tooth. That in COH 62 has a wavy or fluted buccal enamel wall.

Upper Cheek Teeth

These are listed in Table 6, qualitative dental features are summarised in Table 7, and measurements given in Table 9.

COH 41 is a small maxillary fragment containing P^4-M^1 with buccal surfaces damaged on P^4 and ectoloph missing on M^1 (Figure 6). Single plis prefossette occur in both teeth and a single pli hypoloph in M^1. The fossettes in M^1 have pits in the cement.

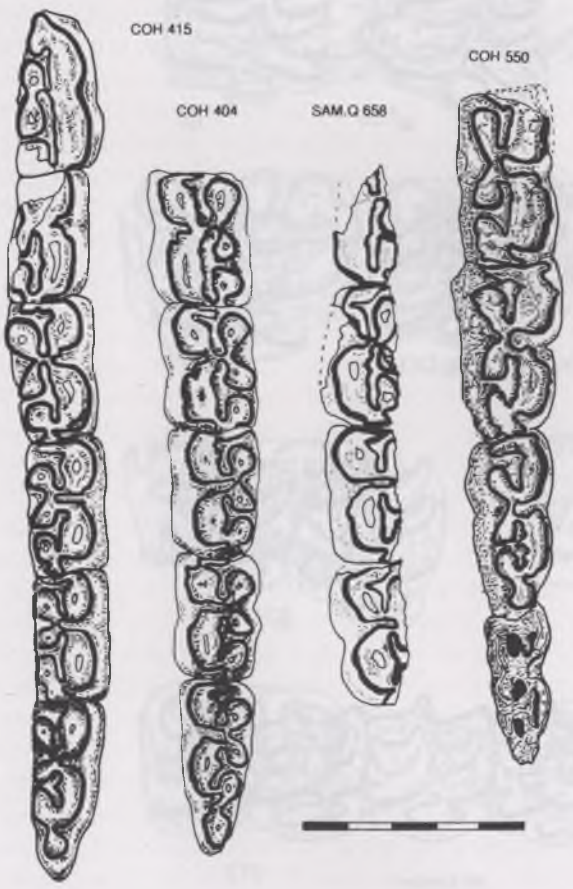


Figure 5. Crown enamel patterns of mandibular cheek teeth of *Equus capensis* COH 415, 404, 550 compared with that of the holotype SAM Q.658.

The No Number maxillary specimen with P^4-M^2 shows no plis caballine or protoloph (Figure 6). Each tooth has one pli protoconule, and one large and one small pli postfossette. The pli hypoloph is represented by small waves only in the molars and there are two plis prefossette in P^4. The protocones are elongate and the isthmus migrates mesially from 25% to 15% of protocone length from P^4 to M^2.

Lower Cheek Teeth

These teeth are listed with qualitative dental features in Table 8 and measurements given in Table 10. Cheek teeth series are listed in Table 6.

COH 404 is a partial left tooth row comprising laterally displaced P_3-M_3 (see Cooke, 1988, Figure111.1) and reassembled in Figure 5. Ptychostylids are represented by kinks in P_3-M_3, strongest on P_3 and weakest on M_1. The metaconids are rounded, metastylids rounded or pointed, entoconids squared and the hypoconulid on M3 'acorn shaped'. The floors of the metaflexids are smoothly curved (P_3-M_1) or bent ($M_{2\text{-}3}$) and of the entoflexids lightly wavy ($P_{3\text{-}4}$) or crested ($M_{1\text{-}3}$). The buccal mesial valleys are broad, parallel sided and terminally rounded, but square in M_3. Those of $P_{2\text{-}3}$ approach the isthmus between the flexid floors but those of $M_{1\text{-}3}$ penetrate into the metaconid-metastylid junction and meet the lingual valley wall. Interdental wear by the hypoconulids has abraded the paraconid-paralophid areas resulting in a reduced length to the toothrow.

COH 415 (F/2/15) is a slightly warped but worn entire right lower cheek tooth row with damage to the lingual and mesial surfaces of P_3 and the entoconid of P_2 (Figure 5). Ptychostylids are represented by kinks in P_2-M_2, but not in M_3. The metaconids are rounded, metastylids round pointed, entoconids squared, and the hypoconulid on M_3 rounded. The floors of the metaflexids are bent or strongly curved in P_4-M_3 and flat in P_2, and of entoflexids shallowly wavy on premolars, slightly curved on $M_{1\text{-}2}$ and crested on M_3. Premolar buccal mesial valleys are shallow (almost absent on P_2), with broad 'Vs' and do not penetrate between the flexids; molar valleys are parallel sided and round ended, and penetrate between the flexid floors. Interdental wear by the hypoconulids has removed or thinned the mesial enamel walls of the paralophids and by the protoconids some cement distal to the hypoconid so as to reduce the length of the toothrow. The full toothrow length is estimated at 201.9mm versus the measured 192.5 (Table 10). COH 415 is also illustrated by Cooke (1988, Figures 111.2 & 3).

COH 537 comprises a left P_3-P_4 pair (Figure 7a). There are no ptychostylids; the metaconids are rounded, metastylids pointed deltoids, and entoconids squared. The metaflexid floors are curved and the entoflexid floors smooth. The buccal mesial valleys are broad, parallel sided, with rounded ends and incline mesially. This specimen derives from an aged individual and the teeth are very worn.

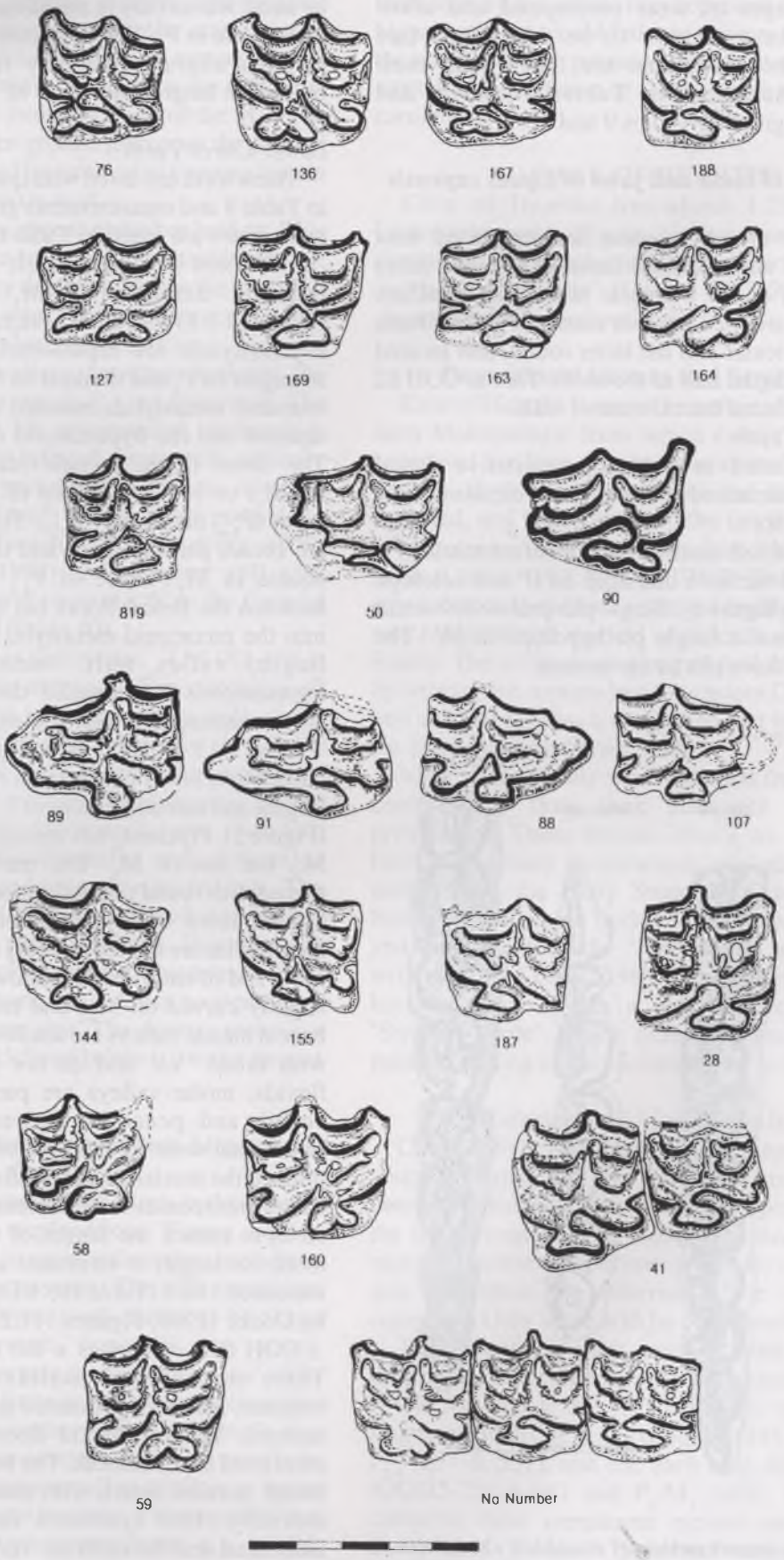


Figure 6. Crown enamel patterns of maxillary cheek teeth of *Equus capensis* from Cave of Hearths.

COH 550 comprises associated right milk p_{3-4} and permanent M_1 in an early stage of wear, with M_2 emerging (Figure 5). Ptychostylids are short and robust on p_3-M_1. In p_{3-4}, the milk metaconids are rounded, metastylids squarely pointed, and entoconids rounded wedges: the hypoconulid is prominent in p_4 and compressed in p_2. In M_1, the metaconid is elongate and not as rounded as in p_3-p_4, the entoconid pointed, and hypoconulid squared. The floors of the metaflexids are smooth or shallowly arced in p_3-p_4 and irregularly wavy in M_1.

COH 557 comprises associated left P_3-P_4 (Figure7). Ptychostylids are absent. The metaconids are rounded, metastylids pointed, and hypoconids squared. The metaflexid floors are curved or bent and entoflexid floors smooth. The buccal mesial valleys are wide, inclined mesially, and penetrate to the level of the medial wall of the protoconid (100%) in P_4.

The left dentary fragment OQ/25-25/14-16' contains a partial tooth row with P_3-M_1 (Figure 7). Ptychostylids are represented by kinks. The metaconids are rounded, metastylids pointed and entoconids squarish. The metaflexid floors are bent and entoflexid floors crested, slightly more so in M_1 than in P_{3-4}. The buccal valleys are broad, V-shaped in P_3 and parallel sided in P_4-M_1, and penetrate 80% of the width of the protocone in P_3, 100% in P_4, and 130% in M_1.

Discussion of *E. capensis* from Cave of Hearths

Cooke (1988) briefly considers the Perissodactyla from Cave of Hearths. Apart from the major sample of some 450 teeth assigned to *E. burchelli*, he noted 65 specimens identified as or ascribed to *E. capensis*. COH 415 is noted as from Bed 2 in the Acheulean deposits and COH 404 as from the 'swallow hole'. Both of these are considered closely comparable to specimens from

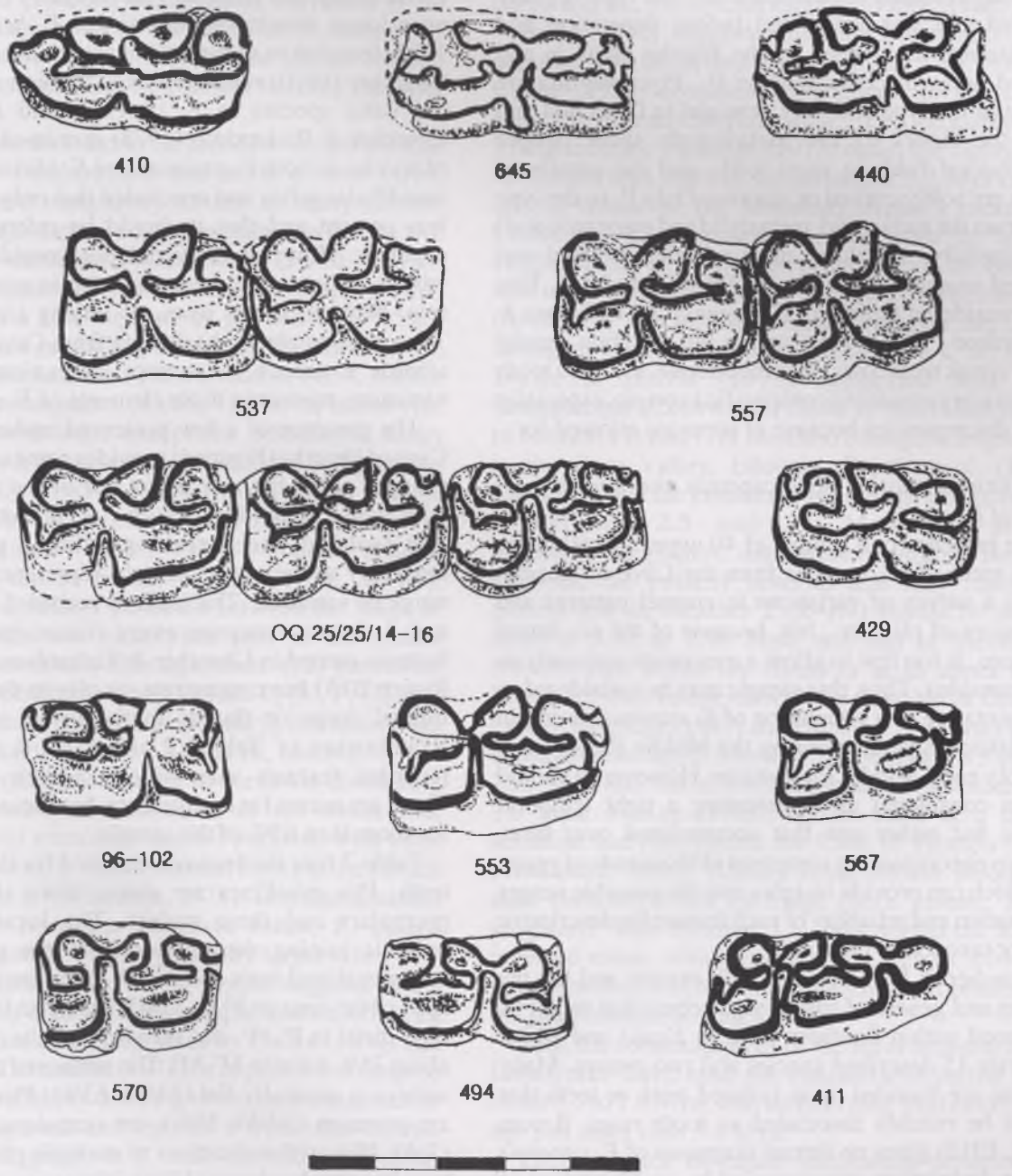


Figure 7. Crown enamel patterns of mandibular cheek teeth of *Equus capensis* from Cave of Hearths.

COH 550 comprises associated right milk p_{3-4} and permanent M_1 in an early stage of wear, with M_2 emerging (Figure 5). Ptychostylids are short and robust on p_3-M_1. In p_{3-4}, the milk metaconids are rounded, metastylids squarely pointed, and entoconids rounded wedges: the hypoconulid is prominent in p_4 and compressed in p_2. In M_1, the metaconid is elongate and not as rounded as in p_3-p_4, the entoconid pointed, and hypoconulid squared. The floors of the metaflexids are smooth or shallowly arced in p_3-p_4 and irregularly wavy in M_1.

COH 557 comprises associated left P_3-P_4 (Figure7). Ptychostylids are absent. The metaconids are rounded, metastylids pointed, and hypoconids squared. The metaflexid floors are curved or bent and entoflexid floors smooth. The buccal mesial valleys are wide, inclined mesially, and penetrate to the level of the medial wall of the protoconid (100%) in P_4.

The left dentary fragment OQ/25-25/14-16' contains a partial tooth row with P_3-M_1 (Figure 7). Ptychostylids are represented by kinks. The metaconids are rounded, metastylids pointed and entoconids squarish. The metaflexid floors are bent and entoflexid floors crested, slightly more so in M_1 than in P_{3-4}. The buccal valleys are broad, V-shaped in P_3 and parallel sided in P_4-M_1, and penetrate 80% of the width of the protocone in P_3, 100% in P_4, and 130% in M_1.

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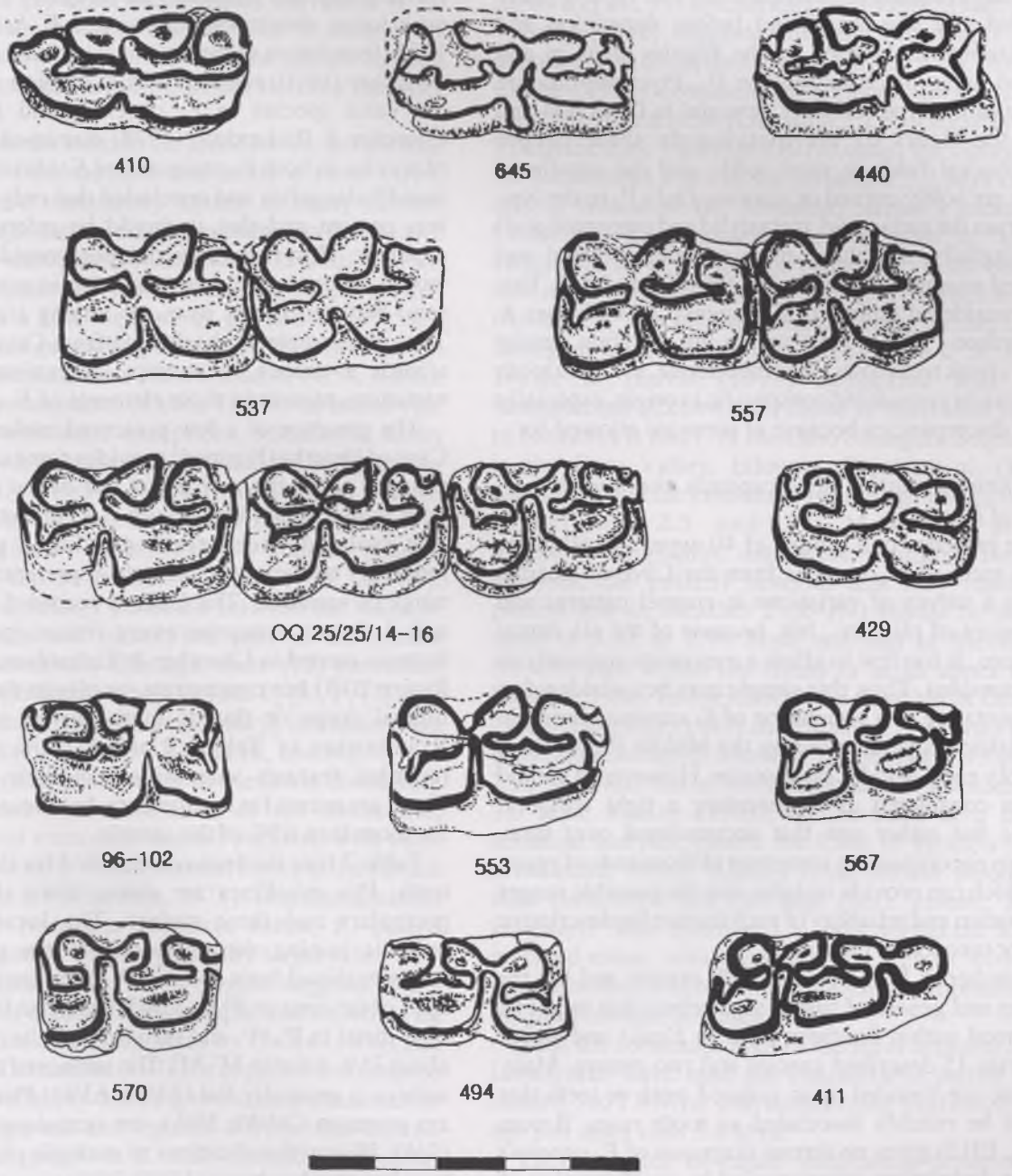


Figure 7. Crown enamel patterns of mandibular cheek teeth of *Equus capensis* from Cave of Hearths.

Vlakkraal (Wells *et al.*, 1942) and Florisbad (Dreyer, 1931).

Cooke (1988, Table 2) lists the fauna from Cave of Hearths by Early (ESA or Pietersburg) or Middle Stone Age (MSA or Acheulean), or mixed categories. Both *E. capensis* and *E. burchelli* are present in all three categories. Because of the paucity of materials known certainly to originate from these layers, and the majority of the materials originating from mixed or statrigraphically unknown horizons, Cooke (1988, 518) is unsure whether 'the differences between the ESA and MSA assmblages as listed are real or are the consequences of inadequate diagnosis.'

Comparison of the full right dental row of COH 415 with the type specimen SAM.Q 658 of *E. capensis* (Broom, 1909), a damaged partial left row P_3-M_2 (Figure 5), from Ysterplaats, near Cape Town, shows two rows of similar size and portions of the crown enamel patterns of P_3-M_2 available for comparison. The type is badly abraded and was weathered before deposition and fossilisation; as evinced by the angular break in and spalled areas of cementum on P_4. Ptychostylids are absent in the type and only vestigial in COH 404 and 415, the floors of the metaflexids show deeper mesiobuccal folds in most teeth, and the entoflexid floors are softly curved or sinuous. Only P_4 in the type preserves the metaconid, metastylid and entoconid at all meaningfully, and these show rounded, pointed and squared enamel outlines as in COH 404 and 415. This was considered typical of *E. capensis* by Churcher & Richardson (1978). Thus within the variation among lower cheek teeth rows described above, the three tooth rows can be considered conspecific in origin, especially when discrepancies because of wear are allowed for.

Qualitative variation in E. capensis *cheek teeth from Cave of Hearths*

The presence of a sample of 40 upper and 60 lower cheek teeth of *E. capensis* from the Cave of Hearths allows a survey of variations in enamel patterns and incidences of plis, etc., but, because of the six dental positions, is too few to allow a mensurational analysis of dimensions. Thus, this sample may be considered as representative of a population of *E. capensis* living in the Makapansgat area during the Middle Pleistocene, possibly early Middle Pleistocene. However, it should not be considered as representing a tight temporal sample but rather one that accumulated over time, perhaps encompassing some tens of thousands of years, but which can provide insights into the possible ranges of variation and reliablity of each feature for descriptive and for taxonomic purposes.

Churcher & Richardson (1978) review and list the species and genera of fossil large zebras that might be subsumed within Southern African *Equus* and which comprise 15 described species and two genera. Many of these are founded upon isolated teeth or teeth that cannot be reliably associated as tooth rows. Broom (1909, 1913) gives no formal diagnosis of *E. capensis* but his description, accompanied by an illustration of the jaw fragment, effectively allows identification of the taxon, despite Wells' (1959) opinion that *E. capensis* is indeterminable. Broom's founding of *E. capensis* on a lower jaw fragment requires associated upper and lower molar rows, of which the lower resemble that of the type, to allow a diagnosis for the upper dentition. Cooke (1950) provided this but did not consider either variation along a molar row or variation between teeth of different individuals, and instead provided a description of the features of an average upper cheek tooth. However, he originally recognised as separate eight of the then described 14 species but, in an appendix added just prior to publication, noted Broom's (1948) description of a further species and reduced it and three others to synonymy within a surviving five species. Later, he (1963) accepted Wells' (1959) decision of the invalidity of the type specimen of *E. capensis* and recognised only *E. (= Kolpohippus) plicatus* Van Hoepen 1930 (founded on a lower cheektooth series) and *E. helmei* Dreyer 1931 (founded on apparently unassociated cheekteeth). Churcher (1970) rejected Wells' opinion and reduced the valid species to *E. capensis* and *E. plicatus*. Churcher & Richardson (1978) discussed this duality of species as both *E. capensis* and *E. plicatus* represent mandibular series and concluded that only one species was present and that it should be referred to as *E. capensis*. However, they did not consider variation within a population, between teeth in a single molar row, between molar rows, or among isolated teeth. Thus, the sample of cheek teeth from Cave of Hearths affords a chance to attempt an evaluation of the variations present in these elements of *E. capensis*.

The presence of a few preserved molar rows from Cave of Hearths (Figure 4) provides some control in the changes along the row and a test of the randomness with which individual features occur between teeth. The isolated cheek teeth provide a presumedly randomly accumulated sample representative of the range of variation. The features recorded in Tables 7 and 8 do not comprise every feature possible (see features named in Churcher & Richardson, 1978, 387, Figure 20.5) but concentrate on plis in the upper and lingual cusps or flexids in the lower cheek teeth. Examination of Tables 7 and 8 show that all the recorded features vary widely in their expression. There are norms for each feature, but these are unusual for more than 65% of the sample.

Table 7 lists the features recorded for the maxillary teeth. Plis caballines are absent from all but three premolars and three molars. The location of the isthmus joining the protocone to the protoconule migrates distad from about 10% distal from the mesial apex of the cone on P^2, to 35-45% distal in P^3, and to 45-50% distal in P^4-M^1, and then reverses its migration to about 35% distal in M^2-M^3. The surface of the ectoloph valleys is generally flat (24/38, 63%). Plis protolophs are common (20/40, 50%), are occasionally twinned (2/40, 5%), with indications of multiple plis in another two, but may be absent (12/40, 30%) or vestigial (7/40,

17.5%). Plis protocones are also comon (25/40, 62.5%) or absent (13/40, 32.5%), but twinned in two (2/40, 5%). Plis prefossettes occur (16/40, 40%), are absent (13/40, 32.5%), twinned (5/40, 12.5%), triple in one, or vestigial (6/40, 15%). Plis postfossettes are very common (31/40, 77.5%), twinned (6/40, 15%) with others (12/40, 30%) showing indications of additional plis, absent (4/40, 10%), and vestigial in one. Plis hypolophs are present (15/40, 35.5%), twinned in one, absent (16/40, 40%), or vestigial (6/40, 15%).

From these summations from Table 7, plis prefossettes occur most frequently and are twinned most often, plis protolophs, protoconules and prefossettes are about as frequently present as absent, plis postfossettes are the most likely to be multiple, and all plis can be twinned or multiple. Within a single animal, e.g., COH 41 or No Number (Figure 6), the teeth all tend to reflect a dominant molar morphology throughout a premolar-molar field, but there is no obvious linkage between the presence or absence of different features, e.g., plis protocone and prefossette are both present in COH No Number but only the latter in COH 41.

Table 8 lists the features recorded for the mandibular cheek teeth. Ptychostylids are rarely present (4/60, 6.6%) and are completely absent in many (24/60, 40%), although there are kinks or bumps in the smooth curve of the shoulder in many others (29/60, 48.3%). Metaconids generally have a rounded shape (51/57, 89.5%) with a few wedged or pointed (3/57, 5%). Metastylids are generally pointed (53/58, 91.4%), with a round conformation as the alternative (4/58, 6.8%). Entoconids are squared (43/60, 71.7%) or round (16/60, 26.7%) with some exceptions. Metaflexid floors are bent, arced, or curved, with the distal end pointing bucccodistally (43/54, 79.6%), with a few flat or smooth (9/54, 16.7%). Entoflexid floors are mostly wavy or sinuous (24/56, 42.9%), smooth (12/56, 21.4%), but can be crested or bent (17/56, 30.4%). Buccal mesial valleys penetrate between the bases of the metaconids and metastylids only in the molars (>100% penetration), although some (12) premolars attain 100% penetration, and include P_4 (8), P_3 (3), and P_2 (1). Penetration of the buccal valleys increases from mesial to distal, with 120-130% in M_2 and M_3.

The most reliable character of the lower cheekteeth of *E. capensis* is the inflation of the metaconid, metastylid and entoconid enamel outlines, with thick enamel, and usually simple enamel floors to the flexids (see Churcher & Richardson, 1978). This distinguishes *E. capensis* from the common zebra, *E. quaga burchelli*, together with its generally larger size.

This assessment of a small sample suggests that a broader survey of an enlarged sample, and including all characters considered important by Cooke (1950) and Churcher & Richardson (1978), is required to attempt to evaluate the reliabilty of trying to use such characters to identify *E. capensis* and separate it from other zebras, particularly *E. grevyi* or *E. oldowayensis*. At present, these large grevyine zebras are recognised on size, robustness of their teeth, and perhaps the degree of inflation of the lingual enamel outlines in the lower molars and the robust ectoloph, flattened or grooved crests to the ectostyles, especially the mesostyle, and the broader protocone and hypocone in the upper molars.

DISCUSSION AND CONCLUSIONS

Hipparion lybicum ethiopicum is reported in Shungura Formation Members F-L in the Omo sequence (Hooijer & Churcher 1985, 100) although "the documentation is not as good as one would wish."

Equus oldowayensis first appears in the Omo sequence in Shungura Formation Member G (Churcher & Hooijer, 1980). It also appears in Members H and J-L and in the Kalam Outcrop. Member G corresponds to Bed I in Olduvai Gorge and both cover the times from earliest Early Pleistocene (G) to late Early Pleistocene (K-L). These are dated between 1.93 and 1.34 Mya (Brown *et al.*, 1978; Churcher & Hooijer, 1980: 279).

Brain (1956) suggested that the Limeworks Cave deposits span the period from 3.5 to 2.5 Mya. Wells & Cooke (1956) considered the faunas to be 'Latest Kageran or earliest Kamasian', i.e., probably late Villafranchian. Partridge (1973) dated the opening of the Limeworks Cave to the surface at 3.7 Mya on the rate of retreat of the Mwadziri stream's nickpoint. Cooke (1970) suggested that the fauna is "in the vicinity of 2.5 to 3.0 million years old" on the basis of suid morphology and, on the presence of *Notochoerus capensis*, a species intermediate between the upper Shungura B *N. euilus* and the Shungura C *N. scotti*. White & Harris (1977) suggested that "the Makapansgat [Limeworks] fauna is equivalent in age to Members B and C of the Omo Shungura Sequence" in the Omo Valley, Ethiopia. Brock *et al.* (1977) concluded that the consensus for the age of Member 3 is between 2.5 and 3.0 Mya but, as no magnetostratigraphic data were available for this member, the polarity reversal that they report as present low in Member 2 (R→N) should be one of those at 3.32 or 2.94 Mya, and that in Member 4 (N→R) high within the Gauss or at its upper limit. Member 5 may be coeval with the Réunion or Olduvai events. Partridge (1983) and Partridge & Talma (1986) considered the age of Member 3 to be between 3.40 and 2.92 Mya, and that of lower Member 4 to be older than 2.0 Mya. McKee (1995), on the basis of a faunal seriation analysis, placed the Cave of Hearths fauna penultimate before Klasies River Mouth among 18 sites considered and Partridge (*pers. comm.*, 1998) suggested "that Member 3 ... falls within the Kaena reversed event, which lasted from 3.11 to 3.04 myr (based on the most recent astronomical calibrations of the palaeomagnetic timescale)".

Thus the consensus ages of the infill deposits in the Limeworks Cave span the considerable period from about 3.5 to 1.8 Mya, with an emerging likelihood of an age just older than 3.0 Mya.

The sequence of equid succession reported by Churcher & Watson (1993) in which *H. lybicum* and *E.*

capensis exist together before *E. burchelli* appears in the Swartkrans sequence suggests that the Limeworks Cave's record with only the hipparion is very early and earlier than the deposit in the Cave of the Horse's Mandible, where only *E. capensis* is present. *E. capensis* probably entered southern Africa slightly later than in East Africa (1.8 Mya in Bed 1, Olduvai Gorge and 1.9 Mya in Member G, Shungura Formation, Omo Valley; Churcher, 1981), possibly about 1.8-1.75 Mya or ealiest Pleistocene. Thus the Cave of the Horse's Mandible may be at oldest 1.8 Mya while the body of Limeworks cave with only *H. lybicum* is older and possibly about 3.0 My.

The Cave of Hearths has provided a reasonable sample of *E. capensis* and many *E. burchelli* specimens, most of which derive from a Later Acheulean (= 'Fauresmith') horizon considered to be Mason's (1988) Beds 1-3. The presence of both monodactylous equids coexisting in this site suggests an age less than about 2.0 or 1.8 Mya, dates at which *E. burchelli* is first recorded from Laetoli and Olduvai Gorge, respectively (Churcher & Richardson, 1978, 414/415, Figure 20.7) or when *E. capensis* is first recorded in East Africa (Churcher, 1981). However, *E. burchelli* is not known from coeval beds in the Omo sequence. Cave of Hearths Beds 1-3 lie beneath a debris layer some 6 m deep and perhaps representing passage of a hundred thousands years. Bed 4 records the change from unifacial to bifacial tools and may be dated at about 100 000 BP or more (see below). Thus the equid fossils are minimally at least 200 000 years old.

More recent dates for the 'Fauresmith' Late (Terminal) Acheulean (e.g., from Florisbad, Grün *et al.*, 1996) indicate the actual age may well be of the order of 300 000 yr. BP or even older. Upper Acheulean tools from Refruf Pass (Wadi el-Refruf) in the Libyan Escarpment to the northeast of Kharga Oasis, Egypt (Caton-Thompson, 1952, Locus V) are dated at $\geq$ 400 000 BP and 'Lower Levalloisian' (= older Middle Stone Age, Caton-Thompson, 1952, Locus IV) at 220 000 $\pm$ 20 000 BP (Isotope stage 7) (Kleindienst *et al.*, 1996). Recent recoveries of early Middle Stone Age tools and associated fauna from Dakhleh Oasis, Egypt (Churcher *et al.*, in press) also associate a fauna containing a northern *E. capensis* population and other mammals with earlier Middle Stone Age lithics. These are estimated on geomorphological evidence and by correlation with the Kharga record to date from about 250 000 yr BP.

The Twin Rivers Cave site (Barham, 1998), near Lusaka, Zambia, contains a breccia with artifacts and bones, which was sealed by roof collapse in the late Middle Pleistocene. The tools comprise a combination of flake and core forms which place the doposit early in the Middle Stone Age. $^{230}Th/^{234}U$ analysis of a sample of speleothem (F Block) from the top of the breccia gave an age of 230 000 +35 000/-28 000 yr BP. Analysis by mass spectrometer also supports a late Middle Pleistocene age for the speleothem (F Block) at 195 000 $\pm$ 19 000 yr BP (error at 2 sigma). A second but weathered speleothem sample (A Block) yielded an infinite mass spectrometer date (>350 000 yr BP) which, after removal of a source of error, has a minimum age of 300 000 years. Barham (1998) concludes that the Acheulean-Middle Stone Age transformation as shown in Twin Rivers Cave occurred earlier than 200 000 yr BP. As all the 'real' Acheulean in the Western Desert is beyond U-series dating range (>400 000 Uyrs), the Early to Middle Stone Age transformation may be earlier than 300 000 yr BP (M.R. Kleindienst, *pers. comm.*, June 1999) .

The recovery of the Cave of Hearth equids from the blocks of breccia mined and stacked outside the adit makes any attempt at a stratigraphic separation of *E. capensis* and *E. burchelli* at this site wasted effort. As both species existed into Recent times, a date close to the present of 17 000 years, proposed by Mason (1962), is possible but unlikely as the evidence from Florisbad (South Africa), Twin Rivers (Zambia) and Karga and Daklhleh Oases (Egypt) suggests that the early Middle Stone Age transition occurred between 300 000 and 200 000 years ago. The relatively greater abundance of *E. burchelli* fossils compared to those of *E. capensis* may reflect a coexistant herding behaviour between the two species similar to that between the extant *E. grevyi* and *E. burchelli* observable to-day (Churcher, 1982, 1993), and thus that this behaviour has an ancient source. The greater frequency of common zebra should not be taken to indicate a date towards the end of a replacement process of *E.capensis* by *E.burchelli.*

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TABLE 1.
Specimens of *Hipparion lybicum* from Limeworks Cave, Makapansgat.
(LM prefix to accession numbers)

Specimen No.	Tooth	Description
Incisors		
196	L i^2 or R i_2	rootless, unworn
2478	R i^2 or L i^2	rootless, unworn
Upper Premolars		
187	R p^3	rootless, unworn
188	L p^4	rootless, unworn
190	R p4	lacking paracone and roots, unworn
192	R p^2 or P^2	lacking mesial half and distolingual corner, in jaw fragment
193	R P^2	newly worn, buccal cement damaged
546	R p^3	damaged on hypoglyph, rootless, unworn
2167	R p?	paracone only, rootless, unworn, cement
2168	R p^4	rootless, unworn
2169	L p^3	lacking mesial half of paracone and protoconule, rootless, unworn
2171	L $p^{2/3}$	central fragment, rootless, unworn
2185	L p^3	rootless, unworn
2475	R P^4	rootless, newly worn, cement (sectioned)
2480	L p^4	rootless, early wear, complete cement
2481	L p^3	rootless, worn, cemented. M 2480 and 2481 derive from one individual as they share matching interdental facets
2483	L p^2	damaged on mesial style, rootless, early wear, cement
2485	R p^2	damaged on mesial style and protoconule, rootless, unworn
2486	L p^2	rootless, unworn, little cement
2487	R p^4	damaged on protocone and protoconule, rootless, unworn
2488	L p^4	damaged, protocone absent, rootless, early wear
2490	L $p^?$	protocone, hypocone and fossettes only, rootless, unworn, calcite crystals in pulp cavities
2491	R p^4	damaged metacone, rootless, unworn
2492	R p^4	rootless, unworn
2494	L p^3	damaged buccally, rootless, newly worn, cement
2495	R $p^?$	buccal area and prefossette only, rootless, unworn
2496	L p^3	rootless, early wear, cement
2497	L p^2	lacks mesial process, rootless, unworn, some cement
2498	R p^4	damaged distally and on parastyle, rootless, unworn, some cement
2499	L $p^?$	lacking paracone and protoconule, rootless, unworn
2500	R p^4	lacking distal half of hypocone and metacone, broken on paracone and hypocone cusps, unworn, calcite crystals in pulp cavities
2501	R p^4	enamel damaged buccally and distally near margin, rootless, unworn
2502	R p^4	damaged mesial half of paracone and on metacone cusps, rootless, unworn, cement
2509	R $p^{2?}$	damaged on crown and lingually, rootless, unworn, some cement
No number	R p^4	rootless, unworn, little cement
No number	R p^2	rootless, unworn, little cement, calcite encrusted
No number	L p^3	mesial halves of metacone and hypocone only, rootless, worn, cement
Lower Premolars		
182	R p_2	damaged mesially, rootless, unworn, additional long enamel pillar on buccal surface near valley
2166	R p^{3-4}	abraded and damaged crown, buccal face absent, rootless, calcite encrusted
2170	L $p_{3/4}$	lacking distal halves of hypoconid and entoconid, rootless, unworn, little cement, calcite encrusted
2172	L $p_{3/4}$	protoconid, paraconid and mesial metastylid only, rootless, calcite encrusted
2173	R $p_{2/3}$	lacking distal halves of metaconid and hypoconid, rootless, calcite encrusted, with additional pillar buccal to mesiobuccal angle separate from protoconid
2474	L p_4	mesial protoconid, paraconid and metastylid only, and roots of p_3, in dentary fragment, with calcite infillings, early wear
2503	L $p_{3/4}$	rootless, unworn, little cement
2504	R $p_{3/4}$	rootless, newly worn, little cement, calcite in pulp cavities
2505	L $p_{3/4}$	rootless, newly worn, little cement, calcite in pulp cavities, fused pillar
2506	L $p_{3/4}$	rootless, newly worn, little cement, calcite in pulp cavities, pillar broken
2508	L $p_{3/4}$	rootless, unworn, little cement, calcite in pulp cavities
2510	L $p_{3/4}$	rootless, unworn, little cement, calcite in pulp cavities, damaged
2511	R $p_{3/4}$	rootless, unworn, little cement, calcite in pulp cavities
2512	–	Five equid (2 upper and 3 lower) tooth fragments, and 2 bovid (possibly alcelaphine) tooth fragments

TABLE 2.
Specimens of *Equus capensis* from Cave of the Horse's Mandible, Limeworks Site, Makapansgat.
(LM prefix to accession numbers)

Specimen No.	Description of Specimen
197	Left dentary fragment with distal portion of P_3, P_4–M_1, and damaged crowns of M_2–M_3. Dentary crushed below teeth, and thus individual is late mature to old.
181– 488	Right dentary fragment with slightly damaged p_2–p_4; damaged protoconids on p_2 and p_4, and some damage buccally on p_3; unworn, cement, juvenile.
No Number	Left M_{1-3}, in dentary fragment, with matrix over crown.

TABLE 3.
Measurements of isolated premolars of *Hipparion libycum* from Limeworks Cave, Level 3, Makapansgat.
(LM prefix to accession numbers)

Abbreviations: MDD - mesiodistal diameter midway between enamel and occlusal margins on upper and just above enamel margin on lower premolars; BLD - buccolingual diameter over enamel only; PaH - height of paracone; PrH - height of protocone or protoconid; PrL - greater diameter of protoconid pillar. e - estimated measurement, w - measurement reduced because of wear, + indicates a minimal value due to damage PrD - lesser diameter of protoconid pillar.

Specimen No.	Tooth	MDD	BLD	PaH	PrH	PrL
Upper dentition						
Permanent premolar						
193	R P^2	37.9	22e	56.5e	53e	10.8
2475	R P^4	Unrecorded				
Milk premolars						
2483	L p^2	39.2+	27.0	30.2	21.4	11.0
2485	R p^2	45.3+	22.2+	–	21.7	9.4
2486	L p^2	43.8	23.1	29.3	21.6	9.2
No Number	R p^2	47.5	19.5	27.2	22.9	10.7
187	R $p^{3/4}$	33.1	25.2	33.6	25.1	9.1
188	L $p^{3/4}$	32.5	25.5	32.7	21.3	10.2
190	R $p^{3/4}$	–	–	31.0	23.0	11.9
546	R $p^{3/4}$	31.3	19.3	–	27.5e	10.2
2165	L $p^{3/4}$	34.2	25.8	–	27.2	10.4
2168	R $p^{3/4}$	32.9	25.1	31.4	25.1	10.8
2480	L $p^{3/4}$	32.3	28.9	29.2w	22.3w	11.2
2481	L $p^{3/4}$	29.6	27.9	35.7w	27.5w	12.3
2487	R $p^{3/4}$	33.2	24.8	29.6e	27.8	11.0
2492	R $p^{3/4}$	33.8	23.0	27.8	24.8	10.2
2494	L $p^{3/4}$	34.6	21.5	34.5e	28.0	12.6
2496	L $p^{3/4}$	31.5	25.5	30.0w	21.3w	8.4
2498	R $p^{3/4}$	33.0	24.2	32.0	22.9	10.6
2501	R $p^{3/4}$	32.5	24.4	34.5e	25.9	11.2
No Number	R $p^{3/4}$	33.3	23.0	35.1	26.5e	10.6

Lower dentition

Specimen No.	Tooth	MDD	BLD	PrH	PrL	PrD
Milk premolars						
2503	L $p_{3/4}$	33.1	14.9	33.8	20.4	8.6
2504	R $p_{3/4}$	33.5	15.2	31e	20.5	9.8
2505	L $p_{3/4}$	34.9	15.2	33.9	15.9	7.8
2506	L $p_{3/4}$	33.7	11e	30.5	17.7e	8.9
2508	L $p_{3/4}$	33.8	16.6	–	23.3	8.8
2511	L $p_{3/4}$	33.7	14.1	29.8	21.5	7.1

TABLE 4.

Measurements of permanent maxillary teeth of *Hipparion lybicum* from Kromdraai (KA) and Swartkrans (SK) Caves.

Abbreviations: MDL - mesiodisal length; BLD -bucclingual diameter; PaH - paracone height; PH -protocone height; PL - protocone mesiodistal length. e - estimated measurement, + - minimal measurement, (1) data from Churcher (1970) or (2) from Churcher & Watson (1993) with revised measurements '*'.

Specimen No	Tooth	MDL	BLD	PaH	PH	PL	Source
KA 729–1351	L P^2	38.8	28.2	78.0+	59.2+	11.8	(1)
SK 3982	L P^4	24.2	26.0	61.4+	56.4+	9.0	(2)
SK 2307	R P^4	24.0*	27.3*	47e+	40.2+	9.0	(2)
SK 3278	L P^3	24.9	24e	43e+	41.0+	10.6	(2)

TABLE 5.

Measurements of mandibular cheek teeth of *Equus capensis* from Cave of the Horse's Mandible, Limeworks Site, Makapansgat.

(LM prefix to accession numbers).

Specimen No	Tooth	MDD	BLD	PrH	PrL	PrD
197	L P_2	–	–	17.7e	–	–
L P_3	30.7	–	18.7	18.9e	11.9e	
L P_4	30.2	20.1	18.5	17.9	9.9	
L M_1	26.1	18.8	16.4	14.0	7.4e	
L M_2	24.3e	–	14.9e	–	–	
L M_3		(roots only)				
		(mesiodistal length P_3-M_1 = 85.3e)				
181–488	L p_2	38.9	17.5e	12.4	17.6	15.4
L p_3	32.7	16.9	11.4	17.4	14.5	
L p_4	33.1	15.3	11.0	15.2	12.8	
		(mesiodistal length p_2-p_4 = 110.2)				

TABLE 6

Incisors and associated tooth rows of *Equus capensis* from Cave of Hearths, Makapansgat.

(COH prefix to accession numbers)

Abbreviations: MMD - mesiodistal diameter of protocone; BLD - buccolingual diameter over enamel only; PrH - height of protoconid; PrL - mesiodistal length of protoconid; PrD - buccolingual diameter of protonid.

Specimen No	Description
Incisors	
62	R I^1, in matrix sample. Mark present.
210	L I^3 or R I_3. Crown and root broken, no mark.
623	R I^1, but labelled 'lower I_1'. Root broken, mark present.
Maxillary Series	
41	Left maxillary fragment with P^4-M^1, damaged, and ectoloph of M^1 absent. No field data.
No Number	Left maxillary fragment with P^4-M^2. No field data.
Mandibular Series	
404 (KH 12)	Left dentary with series P_3-M_3, separated but in one matrix block; teeth well worn and preserved. No associated P_1 or P_2, but fragments of crushed bone *in situ* both against sides of teeth and in the matrix (Fig. 5).
415 (F/2/15)	Right dentary fragment with P_2-M_3; P_3 damaged mesiolingually, all well worn. Cement spalling on buccal faces. Acheulean level, Bed 2 (Fig. 5).
537	Left dentary fragment with P_{3-4}; well worn. No field data.
550 (K/14/14'-16')	Right p_{3-4}, M_{1-2}. Milk teeth maturely worn; M_1 worn just to reveal enamel pattern, but not fully developed, M_2 unworn (Fig. 5).
557	Left dentary fragment with P_{3-4}. Cement spalled from teeth, teeth rooted, old individual.
OQ/25-25/14-16'	Left dentary with series P_3-M_1; P_3 damaged mesiobuccally, teeth possibly rooted.

TABLE 7.

Maxillary cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.
(COH prefix to accession numbers)

Annotated for qualitative characters. Abbreviations: PC - pli caballin; PI % - position of protocone isthmus from mesial extremity of protocone; Ectstyl - shape of enamel between ectostyles; Ppl - pli protoloph; Ppc - pli protocone; Ppf - pli prefossette; Pof - pli postfossette; PH - pli hypoloph. 0 - not developed , VS - very small, S, M, L, and XL - short, medium, long and very long mesiodistal lengths to the protocone, ? - partially expressed, numbers indicate number of plis, + indicates indication of pli only. Nos. 136 and 160 derive from the 'Swallow Hole' (SH) and 90 is noted as from an Acheulian (A) context.

Specimen No.	Tooth	PC	PI	Ectstyl	Ppl	Ppc	Ppf	Pof	PH
41	L P^4	0	M 45%	flat	0	0	0	1	bump
	L M^1	0	M 25%	missing	0	kink	0	1	0
No number	L P^4	0	M 25%	arc	0	1	2	1+	0
	L M^1	0	M 20%	missing	0	1	0	1+	wave
	L M^2	0	L 15%	flat	0	1	bump	1+	wave
Isolated teeth									
45	R P^2	0	S 10%	slight rise	?	0	?	?	?
79	R P^2	0	S 10%	flat	1	0	?	?	?
88	R P^2	0	S 10%	flat	1	0	1	1-wavy	0
89	L P^2	0	S 10%	ridge	1	0	1	2	1
91	L P^2	0	S 10%	concave	kink	0	1	1	bump
107	R P^2	1	S 35%	flat	1	1	0	bump	1
132	R P^2	0	M 15%	flat	0	bump	0	0	0
2179	R P^2	0	M 10%	ridge	0	1	0	1	1
28	R P^3	0	M 35%	flat	1	1	0	1	1
58	R P^3	1+	M 30%	arc	1	1	0	1	1
83	L P^3	missing	missing	flat	1	0	1	?	0
135	L P^3	0	S 50%	flat	1	0	1?	1	?
144	L P^3	0	M 45%	flat	1	1	2	1	0
155	L P^3	0	M 30%	flat	wavy	1	1	1+	1
160	R P^3	1	M 30%	flat	1	1	2+	1+	1
187	L P^3	1	M 30%	ridge	wavy	1	1	1+	bump
69	R P^4	0	L 30%	curve	2	1	1	2	1
106	R P^4	VS	S 50%	flat	1	1	bump	2	0
136 (SH)	L P^4	0	M 45%	flat	1	2	2	2+	0
76	L M^1	0	L 50%	flat	1+	1	wavy	1+	1
127	R M^1	bump	M 45%	arc	wavy	1	bump	1+	0
136	L M^1	1	L 45%	flat	2	1	bump	2	1
167	L M^1	1	L 40%	flat	1++	1	0	2	0
169	R M^1	0	L 30%	flat	0	0	1	1+	1
188	L M^1	bump	M 40%	flat	0	1	wavy	1	0
30	R M^2	0	M 45%	arc	?	0	0	0	0
141	L M^2	+	XL 45%	arc	1	2	2	1	2
160 (SH)	R M^2	0	M 40%	round	1	1	wavy	1	1
163	R M^2	0	L 35%	flat	0	1	wavy	1	1
164	R M^2	1	L 35%	flat	bump	1	wavy	1	0
819	L M^2	bump	L 35%	flat	bump	1	0	1+	0
No number	R M^2	bump	XL 30%	flat	0	1	3	1+	bump
(Tu/15-19/28-30 inscribed on this tooth)									
50	R M^3	0	XL 35%	low ridge	bump	0	0	0	0
90 (A)	R M^3	0	XL 30%	flat	1	0	1	?	1
129	R M^3	0	XL 35%	arc	0	0	0	0	0

TABLE 8.

Mandibular cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.

(COH prefix to acession numbers)

Annotated for qualitative characters. PC - pli caballinid, Mc - metaconid shape, Ms - metastylid, Ent - entoconid, Mf - metaflexid floor, Ef - entoflexid floor, BMV - penetration of buccal mesial valley past protoconid (buccolingual diameter of protoconid = 100%). O - not developed or VS - very small, S, M, L, and XL - short, medium, long and very long mesiodistal lengths of the protocone, ? - partially expressed, numbers indicate number of plis, + indicates indication of pli only.

Specimen No.	Tooth	PC	Mc	Ms	Ent	Mf	Ef	BMV
404	L P_3	kink	round	point	square	arc	wavy	50%
	L P_4	kink	round?	point?	round	bent	wavy	50%
	L M_1	kink	round	point?	round	bent	wavy	110%
	L M_2	0	round	point	square	bent	crest	110%
	L M_3	kink	round	point	square	bent	wavy	110%
415	R P_2	0	round	point	square	flat	wavy	0%
	R P_3	bump	–	–	square?	–	dip	50%
	R P_4	bump	round	point	square	crest	wavy	90%
	R M_1	bump	round	point	round?	rise	crest	110%
	R M_2	bump	round	round	oblong	arc	rise	110%
	R M_3	0	round	round	point	arc	crest	105%
537	L P_3	0	round	point	square	curve	smooth	100%
	L P_4	0	round	point	square	curve	smooth	100%
550	R p_3	1	round	point	round	data unrecorded		
	R p_4	1	round	point	round	"	"	"
	R M_1	1	long	point	square	"	"	"
557	L P_3	0	round	point	square	crest	flat	90%
	L P_4	0	round	point	square	crest	rise	90%
OQ/25	L P_3	kink	round	point	round	crest	wavy	90%
-25/	L P_4	bump	round	point	round	crest	wavy	100%
14/16'	L M_1	bump	round	point	square	rise	rise	120%
Isolated teeth								
410	L P_2	kink	round	point	square	wavy	wavy	30%
432	R P_2	?	–	–	round?	–	wavy	–
449	R P_2	0	round?	point	round	flat	smooth	30%
513	R P_2	+	wedge?	point	round	smooth	crest	50%
576	L P_2	0	round	point	square	smooth	smooth	50%
412	L P_2	1	wedge	point	round	crest	wavy	100%
485	L P_2	kink	round	point	square	crest	smooth	60%
586	L P_2	kink	wedge	point	square?	flat	smooth	40%
645	R P_2?	Unrecorded						
No number	L P_2	0	round	point	square	curve	wavy	–
440	R P_3	+	round?	point	square	angle	wavy	90%
488	R P_3	?	point	point	round	angle	wavy	60%
492	L P_3	0	round	point	square	smooth	wavy	100%
524	L P_3	0	round	point	square	smooth	smooth	100%
558	L P_3	0	round	point	square	curve	smooth	–
4512	R $P_{3/4}$	+	round	point	round	angle	wavy	100%
429	R P_4	kink	round	point	square	curve	wavy	80%
433	L P_4	kink	–	point	square?	–	wavy	80%
444	L P_4	0	round	point	square	curve	crest	100%
458	L P_4	0	round	point	square	angle	wavy	100%
487	R P_4	kink	round	point	square	curve	wavy	100%
497	L P_4	+	round	point	square	angle	smooth	90%
498	L P_4	kink	round	point	square	crest	wavy	90%
512	R P_4	0	round	point	square	crest	smooth	80%
540	R P_4	kink	square	point	square	crest	wavy	100%
616	R P_4	kink	round	point	square	curve	crest	90%
640	R P_4	kink	round	point	square	angle	smooth	60%
651	R P_4	kink	round	point	square	curve	crest	80%
652		Unrecorded						
96-102	R P_4/M_1	+	round	point	square	curve	wavy	100%
413	L M_1	0	round	point	square	crest	wavy	115%
453	L M_1	0	round	point	square	crest	crest	110%
553	L M_1	kink	round	point	round	crest	crest	110%
567	L M_1	0	round	round	square	crest	rise	115%
570	L M_1	0	round	point	square	flat	rise	130%
494	R M_2	0	round	point	square	curve	crest	120%
496	L M_2	0	round	point	square	curve	wavy	125%
538	R M_2	0	round	point	square	crest	crest	110%
645	R M_2	1	round	blunt	square	flat	–	110%
411	L M_3	kink	round	point	square	arc	crest	120%

TABLE 9.

Measurements of incisors and maxillary cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.

COH prefix to accession numbers.

Abbreviations: BLD - buccolingual diameter, over cement below occulsal surface on cheekteeth; BLDE - buccolingual diameter over enamel of ectoloph and protocone; BLDM - buccolingual diameter of mark; MDD - mesiodistal diameter; MDDM - mesiodistal diameter of mark; PL - protocone length. e - estimated measurement, + indicates a minimal value due to damage. Specimen 819 (R M^2) is marked 'To/15-19/28-30' and 160 derives from the 'Swallow Hole' (SH).

Incisors

Specimen No.	**Tooth**	**BLD**	**MDD**	**BLDM**	**MDDM**	**Comment**
62	RI_1?	12.1	17e	5.8	10.2	Mark
210	LI^3 or RI_3	–	13.2	–	–	Mark absent
623	RI^1	15.6	18.7	7.7	8.0	Round mark

Upper Cheekteeth

Specimen No.	Tooth	BLD	MDD	BLDE	PL
41	L P^4	30.4	32.8+	31.9	13.7
	L M^1	25.7	28+	28.0	11.8
No number	L P^4	27.3	28.7	27.9	11.8
	L M^1	24.7	27.6	26.3	12.0
	L M^2	25.2	28.0	24.0	13.3
	Mesiodistal length P^4-M^2 = 77.7				

Isolated teeth

45	R P^2	Unrecorded			
79	R P^2	Unrecorded			
88	R P^2	36.3	25.5	25.0	7.1
89	L P^2	38.4	29.9	28.8	10.3
91	L P^2	39.1	26.5	24.6	9.3
107	R P^2	46.5e	25.8	25.3	9.9
132	R P^2	Unrecorded			
2179	R P^2	41.5	30.3	29.7	10.3
28	R P^3	30.3	34.7	32.6	12.4
58	R P^3	27.7	27.5	26.0	11.9
83	L P^3	Unrecorded			
135	L P^3	30.3	32.7+	32.7	11.5
144	L P^3	32.1	29.6	28.4	10.2
155	L P^3	27.8	28.5	27.5	10.0
160	R P^3	32.1	30.3	29.0	11.1
187	L P^3	27.4	26.4	25.2	10.0
69	R P^4	31.4	30.8	28.9	13.5
106	R P^4	Unrecorded			
76	L M^1	28.8	29.6	28.2	16.0
127	R M^1	29.1	27.4	24.4	13.5
136	L M^1	31.8	30.9	28.2	13.6
167	L M^1	28.3	28.7	26.3	13.7
169	R M^1	28.5	28.2	27.5	13.3
188	L M^1	25.7	26.9	25.4	12.5
30	R M^2	Unrecorded			
141	L M^2	Unrecorded			
160 (SH)	R M^2	Unrecorded			
163	R M^2	28.4	28.3	26.0	15.2
164	R M^2	28.4	27.4	26.4	13.9
819	R M^2	29.0	29.0	26.6	14.3
50	R M^3	30.6	31.3	28.1	18.5
90	R M^3	26.7	31.0	24.7	15.8
129	R M^3	Unrecorded			

TABLE 10.

Measurements of mandibular cheek teeth of *Equus capensis* from Cave of Hearths, Makapansgat.

COH prefix to accession numbers.

Abbreviations: BLD - buccolingual diameter over cement below occlusal surface; BLDE - buccolingual diameter over enamel of ectoloph and protocone; EfxL - mesiodistal length of entoflexid; McMsL - mesiodistal length of metaconid-metastylid knot; MDD - mesiodistal diameter. e-estimated measurement, w - measurement reduced because of wear, + indicates a minimal value due to damage.

Specimen No.	Tooth	MDD	BLD	BLDE	McMsL	EfxL	Comment
404	L P_3	31.8	22.7	18.5	19.8	17.9	
	L P_4	31.3	22.4	17.6	17.6	15.0	
	L M_1	28.3	21.8	16.0	15.5	10.6	
	L M_2	28.3	19.8	15.6	15.2	11.0	
	L M_3	36.5	17.2	14.8	15.5	10.0	
	Mesiodistal lengths P_{2-4} = 95.6e; M_{1-3} = 93.3e; P_2-M_3 = 189e: all based on lengths of individual teeth.						
415	R P_2	36.3	21.7	17.9	19.7	18.8	
	R P_3	30.7	21.2	18.7	–	15.4	
	R P_4	34.1	23.7	17.5	18.9	14.6	
	R M_1	31.8	21.8	18.0	15.6	10.1	
	R M_2	31.6	21.0	15.3	16.3	10.9	
	R M_3	37.4	19.8	15.9	16.0	11.0	
	Mesiodistal lengths P_{2-4} = 100.0; M_{1-3} = 95.3; P_2-M_3 = 192.5.						
537	L P_3	30.1	19.4+	19.4	20.5	13.6	
	L P_4	29.2	19.3+	19.3	18.5	11.8	
550	R p_3	35.1	20.5	19.0	21.7	11.4	
	R p_4	37.2	22.5	19.5	20.2	11.2	
	R M_1	37.0	18.5+	18.5	17.9	9.7	
557	L P_3	31.2	20+	20.0	20.2	13.7	
	L P_4	29.2	20.2+	19.3	18.0	12.0	
OQ/25	L P_3	33.1	21.1	18.5	20.0	18.0	
25/	L P_4	33.3	19.9	17.7	17.9	15.5	
14-16	L M_1	28.9	19.2	16.5	15.8	9.5	
Isolated teeth							
410	L P_2	36.8	21.5	17.3	20.0	17.8	
412	L P_2	39.3	20.5	17.3	15.2	17.0	
485	L P_2	–	19.7	17.2	16.8	18.0	
576	L P_2	33.4	18.1+	18.1	16.0	15.9	
586	L P_2	Unrecorded					
645	R P_2?	38+	16.4	15.0	19.7	–	
No number	L P_2	38.0	17.1+	17.1	18.2	15.7	
440	R P_3	37.1	19.0	16.1	20.6	15.5	
472?	R P_3	32.6	20.1	16.1	17.4	16.6	
488	R P_3	35.0	19.2	16.5	21.8	18.7	
492	L P_3	28.9	17.9	14.4	16.7	12.1	
524	L P_3	28.1	17.7+	13.5	16.7	12.4	
558	L P_3	Unrecorded					
4512	R $P_3/_4$	Unrecorded					
429	R P_4	29.1	20.9	17.1	18.3	14.9	
433	L P_4	Unrecorded					
444	L P_4	26.7	21.1	16.8	16.5	11.7	*?burchelli*
458	L P_4	26.5	18.8	17.3	12.3	13.3	
487	R P_4	30.7	22.1	18.9	18.3	13.6	
497	L P_4	32.4	21.4	15.0	20.4	16.0	?P_3
512	R P_4	29.9	19.7	15.9	18.5	16.5	
540	R P_4	29.7	19.9	15.4	16.9	16.4	
616	R P_4	29.0	19.4	15.7	17.9	14.9	
640	R P_4	27.7	18.6	17.6	17.5	13.5	
652	R P_4	29.5	21.0	16.5	16.0	13.7	
96-102	R P_4 or M_1	30.4	19.6	16.4	19.0	14.7	
413	L M_1	Unrecorded					
453	L M_1	30.0	16.9+	16.9	15.8	12.3	
553	L M_1	33.3	20.4	18.0	20.4	13.7	
567	L M_1	28.7	19.6	16.5	14.8	11.3	*?burchelli*
570	L M_1	28.9	22.5	17.6	15.3	12.0	
494	R M_2	30.7	19.9	15.2	16.8	11.9	
496	L M_2	33.5	22.6	16.2	17.5	11.3	
538	R M_2	32.4	18.8	14.5	14.5	10.3	
411	L M_3	38.1	18.8	16.7	15.1	11.4	

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THE NEOGENE RHINOCEROSES OF NAMIBIA

by

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ABSTRACT:

Since 1991 the Namibia Palaeontology Expedition has excavated four Miocene sites in the Sperrgebiet, three of which (Arrisdrift, Fiskus and Auchas Mine) are new.

Only the material from Arrisdrift and a single bone from Langental are specifically determinable. All but one of the 81 rhinocerotid fossils from Arrisdrift constitute a homogeneous sample pertaining to a very large species of cursorial rhino. The exception is an isolated magnum which suggests a small to medium-sized short legged form, perhaps *Chilotheridium pattersoni*.

A magnum from Langental probably represents *Brachypotherium heinzelini*.

The large form from Arrisdrift seems to be the largest of the Miocene African Rhinos; the size and proportions of the metapodials and the other limb bones suggest an analogy with *Diceros* gr. *pachygnathus-neumayri* of the Upper Miocene of the Near East; the type of construction of the upper cheek teeth, namely the fourth premolar, is of Dicerotine type 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. This Rhino is *Diceros australis* nov. sp., so far the oldest known species of the subfamily.

KEYWORDS: Neogene, Namibia, Sperrgebiet, Arrisdrift, Perissodactyla, Rhinocerotidae, *Diceros australis* sp. nov.

INTRODUCTION

Since 1991 the Namibia Paleontology Expedition, led by B. Senut and M. Pickford, has excavated Miocene sites in the Sperrgebiet (Pickford *et al.* 1995). Rhinos were found at four sites, one of them, Arrisdrift, being very important. I had the good luck to find among about 85 fossils three specimens of the same carpal bone, the magnum, showing that three different species are present, one at Langental and two at Arrisdrift (Figure 1: 3-5; Figure 2). The bulk of the Arrisdrift material (80 pieces) belongs to a new species, *Diceros australis*. *D. australis* is the oldest species of the Dicerotine subfamily, whose present day representatives are the black and the white rhinos of Africa.

Previously, some mammalian remains were recovered from South West Africa and sent to Germany, where they were studied by E. Stromer (1926); the only published fossil rhino was assigned to "Rhinocerine g. et sp. indet". Several papers were later published reassessing some mammalian species and describing others. Hamilton & Van Couvering (1977) synthesized the preceding works and brought the faunal list up to date. In that list the only identified rhinocerotid was *Brachypotherium heinzelini*, based on a report by K. Heissig (1971) on the half-mandible found at Langental and described without determination by E. Stromer.

Among the undescribed rhino fossils from Namibia found prior to the work of the Namibia Palaeontology Expedition, there is a weathered but complete metatarsal III from a large *Brachypotherium* housed in the



Figure 1. 1: right calcaneum (AD 50'97) of *Diceros australis* nov. sp.; 2: left astragalus (AD 619'94) of *Diceros australis* nov. sp.; 3-5: the three magnums of the Miocene rhinoceroses from Namibia: 3: cf. *Chilotheridium pattersoni* (AD 618'97), 4: *Diceros australis* nov. sp. (AD 638'97); both from Arrisdrift, 5: *Brachypotherium heinzelini* from Langental (LT 384'96). Scale bar is 3 cm.

collections of the South African Museum (SAM PQ 2517) and recovered 8 km southeast of Bogenfels (probably the sites of Glastal 1 or 2) by J. Schneider in 1983.

Finally some Quaternary rhino remains also are known from Namibia: an M3/ of *Ceratotherium* (South African Museum SAM PQ 2126) was found in 1978 by G. Corvinus in the "brown grits in the Upper Grillental". A skull, a mandible and some rhinoceros tracks attributed to *Diceros bicornis* were recovered near Kolmannskuppe (= Kolmanskop) and Charlottenthal and briefly described by R. Heinz (1933) and reviewed by C. Guérin & G. Demathieu (1993).

THE SITES

Four lower or middle Miocene rhino sites were worked by the Namibia Paleontology Expedition in the Sperrgebiet, three of which are new : Arrisdrift, Fiskus and Auchas Mine.

Arrisdrift

This very rich site, near the Orange River, 35 km east of Oranjemund, is about 17 Ma old and yielded numerous vertebrate remains (Pickford *et al.* 1996). All but one of the 81 fossil rhino specimens from Arrisdrift constitute a homogeneous sample pertaining to a very large species of cursorial rhino, *Diceros australis*. The exception is an isolated magnum which is totally different from the magnum assigned to *D. australis*: it is shallow and very wide and suggests a small to medium sized short-legged form, perhaps *Chilotheridium pattersoni*, which was defined at Loperot, Kenya, the age of which is about the same as that of Arrisdrift.

Langental

In this 18 to 19 Ma old site one rhino specimen, a complete magnum, was recovered. This fossil probably represents *Brachypotherium heinzelini* which was recognized by Heissig in 1971 on the basis of half a mandible found at the same site.

Fiskus

A deeply worn upper premolar was found in Fiskus, with an age of about 20 Ma.

Auchas Mine

Auchas Mine is an alluvial diamond-bearing deposit 50 km upstream from Oranjemund (Pickford *et al.* 1995), about 19 to 20 Ma old. Among seven mammalian species found in pit AM 02 is an undetermined rhinoceros of which two specimens were recovered: an atlas vertebra and a mandible fragment.

MIOCENE RHINOS OF AFRICA

Six rhino lineages (comprising a total of seven genera and eleven species) are so far known from the African Miocene (Hooijer 1973, 1978; Guérin 1980 b, 1989; Prothero *et al.* 1989). The ages of numerous African sites are based on the results of M. Pickford (pers. comm.).

Aceratheres

Aceratheres are medium to large-sized, hornless, tapir-like cursorial rhinos with four toes in the forelimb. They possess strong lower tusks, and their cheek-teeth are very brachyodont with the upper ones possessing an outer wall which is more or less flat. They are recorded from East and North Africa:

Aceratherium acutirostratum (Deraniyagala 1951) is medium-sized: It is known from the Alengerr Beds (14 to 12 Ma), Chemeron Formation-Northern Extension (5 to 4.5 Ma), Karungu (18 Ma), Moruaret Hill near Losidok (ca 16 Ma), Ngorora Formation (11 to 12 Ma), Ombo (15 Ma), and Rusinga (18 Ma) in Kenya; Napak (19.5 Ma) in Uganda; Karugamania (older than 7 Ma) and Sinda (more than 6 Ma) in Congo.

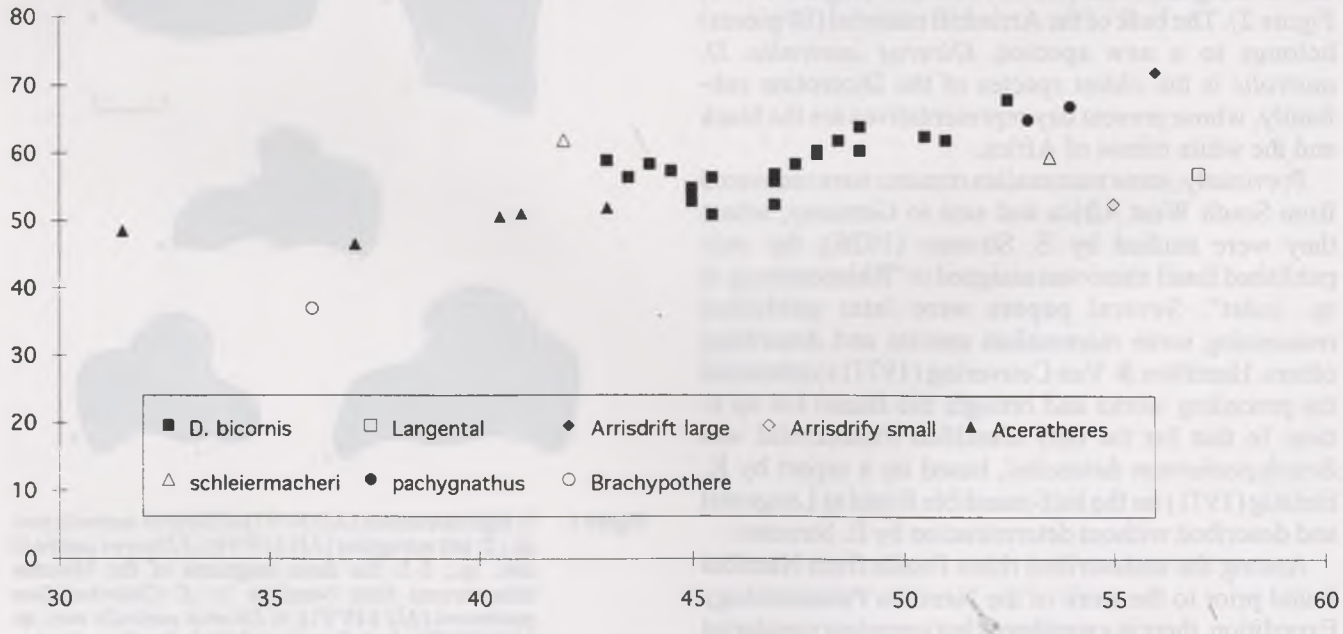


Figure 2: Scatter diagram of the anterior width (Y axis) versus the sus-articular height (X axis) of the three magums of Miocene rhinoceroses from Namibia, other Miocene rhinoceroses and the present day *Diceros bicornis*.

Aceratherium campbelli Hamilton 1973 is very large: it is recorded from Jebel Zelten (ca 16 to 17 Ma) in Libya.

Dicerorhines

Dicerorhines are two-horned medium- to large-sized cursorial rhinos with well developed lower tusks; the upper cheek teeth are relatively brachyodont with an outer wall presenting (especially in the two last premolars) two powerful vertical folds (paracone and metacone folds). They possess long faces. It is known from East Africa:

Dicerorhinus leakeyi Hooijer 1966 is medium-sized: it has been recorded from the Alengerr Beds (14 to 12 Ma), Chemeron Northern Extension (ca 5 Ma), Karungu (18 Ma), Maboko (15.5 Ma), Ombo (15 Ma), Rusinga (18 Ma) in Kenya and Napak (19.5 Ma) in Uganda. Note that in most of these sites *D. leakeyi* is sympatric with *Aceratherium acutirostratum*.

An Upper Miocene Algerian species, *Dicerorhinus primaevus* Arambourg 1959, has a controversial generic status (Geraads 1986).

Large species of *Dicerorhinus* are so far unknown in the African Miocene but are present in Europe with *D. schleiermacheri* and others (Guérin 1980).

Dicerotines

This subfamily includes the two extant African rhinos *Diceros bicornis* ("black" rhino) and *Ceratotherium simum* ("white" rhino). *Ceratotherium* is much more evolved and dates from the Uppermost Miocene. Species of the less specialized genus *Diceros*, which appears during the Middle Miocene, are large and heavily-built two-horned rhinos. The face is short; they possess short mandibular symphysis and there are no incisors. The outer wall of the brachyodont upper cheek teeth possesses only one marked vertical fold, the paracone. Miocene forms are known from Northern Africa, Southern Spain, Italy and the Near East (Guérin 1980):

Diceros douariensis Guérin, 1966: This species has been reported from Douaria (9.5 Ma), and possibly Djebel Krechem el Artsouma (Upper Miocene) in Tunisia (Geraads 1989), and Baccinello V3 (zone MN 13) in Italy (Guérin 1980). Material from Gravitelli (Upper Miocene) in Sicily (Italy), Cenes de la Vega and Los Hornillos (both MN 13) in the Granada Basin (Spain) clearly represents *Diceros* but is not sufficient for a determination at the specific level. The two Near-East Upper Miocene *Diceros* species, whose discrimination and affinities are somewhat controversial, are *D. pachygnathus* from Pikermi (Greece) and *D. neumayri* from Turkey. All these species of *Diceros* are much younger than the Arrisdrift fauna.

Paradiceros mukirii Hooijer 1968 is a small rhino of the Dicerotine group known from Fort Ternan (about 13 Ma) and perhaps Maralal in Kenya, Kisegi (13 to 14 Ma) in Uganda, and Beni Mellal (12.5 Ma) in Morocco (Hooijer 1968; Guérin 1994).

Iranotheres

Iranotheres are very large and heavily built rhinos from Eurasia with (for the time) extremely hypsodont cheek-teeth whose folded enamel is characteristic. Only one species has so far been found in Africa, and it is poorly known (Aguirre & Guérin 1974):

Kenyatherium bishopi Aguirre & Guérin 1974 is recorded from Nakali (9.5 Ma) and Samburu Hills in Kenya (9.5 Ma) (Nakaya *et al.* 1999).

Brachypotheres

Brachypotheres are large hippopotamus-like hornless rhinos with very shortened but powerful legs. The outer wall of the upper cheek teeth show a trend to flattening. The tusks are large. The way of life was hippopotamus-like. As noted by M. Pickford *et al.* (1993, p. 109) the African species need revision. They are known from North, East and South Africa:

Brachypotherium snowi (Fourtau 1920) is known from Wadi Moghara, Egypt and Jebel Zelten (17 to 16 Ma) in Libya.

Brachypotherium heinzelini Hooijer, 1963 is reported from Arongo Uyoma (Early Miocene), Chemeron Formation-Northern Extension (5 to 4.5 Ma), Karungu (18 Ma) and Rusinga (18 Ma) in Kenya; Bukwa (between 17.5 and 18.5 Ma) and Napak (19.5 Ma) in Uganda; Karugamania (older than 7 Ma) and Sinda (more than 6 Ma) in Congo and Langental (18 Ma) in Namibia.

Brachypotherium lewisi Hooijer & Patterson, 1972 is recorded from Kanapoi (4.5 Ma), Lothagam (7 Ma), Mpesida (6.5 Ma), Ngorora (12 to 11 Ma) in Kenya and Sahabi (6.5 Ma) in Libya.

Chilotheres

Although pertaining to a different subfamily *Chilotheridium* presents many convergences with the preceding group. It is a small short-legged rhino with small tusks, but there is one small horn in both sexes, and the manus is four-toed. The cheek teeth are hypsodont. It is known from East Africa (Hooijer 1971).

Chilotheridium pattersoni Hooijer 1971 is present at Kirimum (15 Ma), Loperot (17 Ma), Ngorora (12 to 11 Ma), Ombo (16 Ma) and Rusinga (18 Ma) in Kenya; and Bukwa (ca 18 Ma) in Uganda.

Reference material

I had the opportunity to study a great number of specimens of Miocene rhinos from Africa, particularly material preserved in the Natural History Museum, London. I had the possibility to study all the known material of *Chilotheridium pattersoni* from Loperot when it was in Holland. The holotype of *Diceros douariensis* is in Lyon, and the material from Baccinello V3 is preserved in Basle, Switzerland. Among the material in London there are different pieces from the three African species of *Brachypotherium*, good casts of skulls and teeth of *Paradiceros mukirii*, some specimens of *Aceratherium campbelli*, skulls and mandibles of *Aceratherium acutirostratum* and *Dicerorhinus leakeyi*.

Unfortunately, in the original description of *Dicerorhinus leakeyi*, D.A. Hooijer (1966, 1973) wrote that it is impossible to distinguish the postcranial material of that species from *Aceratherium acutirostratum*. Consequently postcranial bones of the two species are not separated in the London collections, and they are not numerous enough to enable distinction. But, although I have not seen it, I am convinced that such a distinction will be possible on the original material housed in the National Museums of Kenya in Nairobi. In the following tables the undifferenciated *D. leakeyi/A. acutirostrartum* material is named MSUR. To cover up the absence of references for the postcranials of medium-sized African *Aceratherium*, I thus use a mixture of measurements taken on the European species *Aceratherium tetradactylum* (Middle Miocene) and *A. incisivum* (Upper Miocene), which pertain to the same lineage, for comparison; in the tables the mixture is labelled Aceratheres. Because large species of *Dicerorhinus* are so far unknown in the Miocene of Africa, I utilise *Dicerorhinus schleiermacheri* from the Upper Miocene of Europe for comparisons. Finally, to have a sample of large Miocene *Diceros*, I used the material from Pikermi (widely scattered in all the Natural History Museums of Europe) which is *D. pachygnathus*, and the material from Turkey which is housed in the Museum of Munich, Germany; the last one belongs to *Diceros neumayri*. In order to avoid the problems of disorder in the nomenclatural designation of *D. pachygnathus*, and of the differentiation between *D. pachygnathus* and *D. neumayri* (in my opinion close to but somewhat distinct from each other) I will refer to the regrouped material by the name *Diceros* gr. *pachygnathus-neumayri*.

THE LARGE RHINOCEROS FROM ARRISDRIFT,

Diceros australis sp. nov

Material

2 large and 5 small fragments of mandibles with more or less important elements of their respective tooth-rows;
2 lower incisors;
10 isolated upper cheek-teeeth;
13 isolated lower cheek-teeth;
1 radius;
3 ulnae (including 1 complete);
6 carpals (2 magnums, 2 pyramidals, 1 semilunar, 1 pisiform);
4 metacarpals (1 Mc II, 2 Mc III, 1 Mc IV);
1 tibia;

TABLE 1.
Compared dimensions of the mandible of *Diceros australis* nov. sp.
ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

ARRISDRIFT							*Diceros douariensis*			
n°	AD 556'94	AD 300'97	AD 313'98	AD 437'97	AD 223'97	AD 478'95	n	mean	min.	max.
symmetry	R	L	R	R	R					
Distance symphysis-heel		462					1	396		
Depth horiz. ramus P2-P3		67		67.5			1	82.00		
Depth horiz. ramus P3-P4		80			77		2	84.50	80	89
Depth horiz. ramus P4-M1	87.5	81					2	96.50	95	98
Depth horiz. ramus M1-M2	93.5	93					2	108.00	106	110
Depth horiz. ramus M2-M3	99	102.5	108				1	100.00		
Depth horiz. ramus M3	107	105					1	107.00		
Width horiz. ramus P4-M1		60			about 43,5		2	49.75	49.5	50
Width horiz. ramus M3	67	60.5	50				2	57.50	57	58
AP diam. ascending ramus	167									
Transv. diam. condyle						125.5				

Chilotheridium pattersoni					*P. mukirii*	*B. heinzelini*	MSUR
	n	mean	min.	max.	Fort Ternan	Langental	Karungu
Distance symphysis-heel	2	423.00	404	442			
Depth horiz. ramus P2-P3	1	92.00			59.5		60
Depth horiz. ramus P3-P4	3	84.50	71	98	64		59
Depth horiz. ramus P4-M1	3	89.00	77	99	70		64
Depth horiz. ramus M1-M2	3	91.67	77	104	82.5		66
Depth horiz. ramus M2-M3	3	91.67	85	103	88.5	est. 82	70
Depth horiz. ramus M3	2	101.75	101.5	102	92		78
Width horiz. ramus P4-M1					45		37
Width horiz. ramus M3					47	54	41.5
AP diam. ascending ramus							
Transv. diam. condyle							98

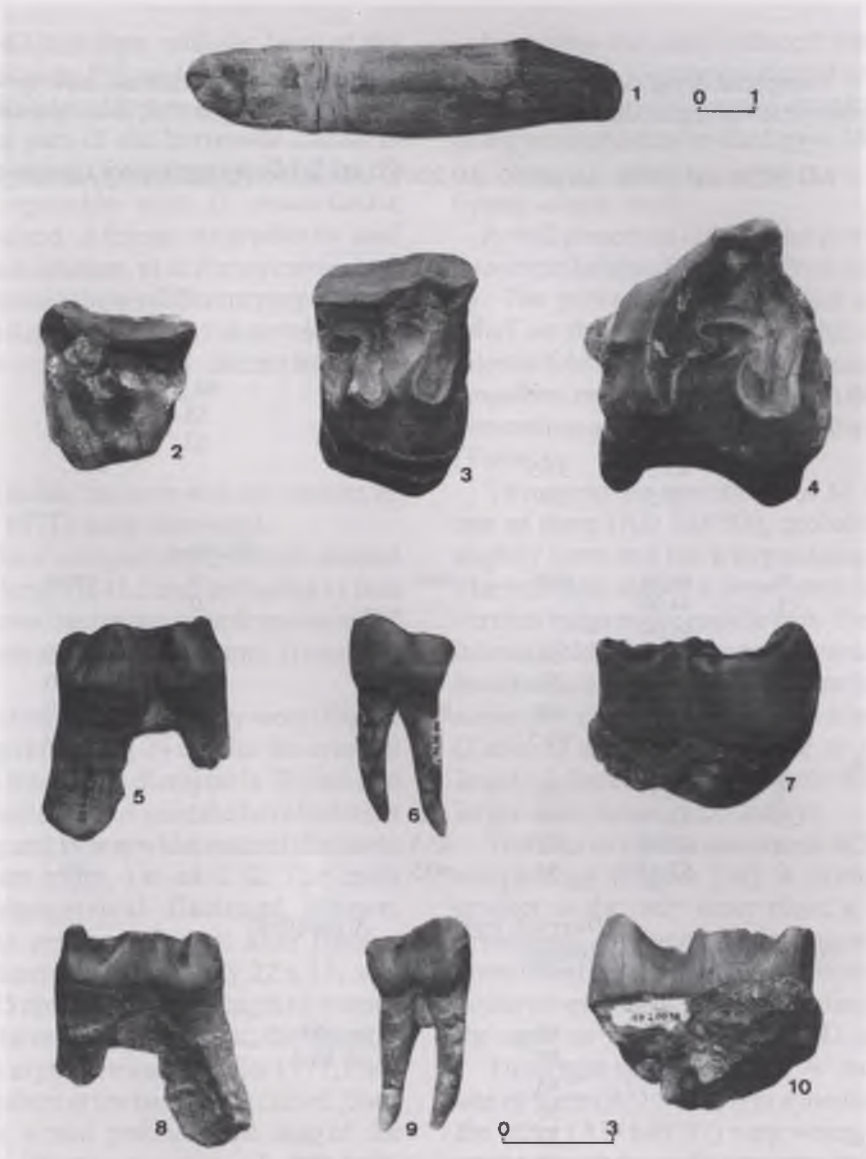


Figure 3: Teeth of *Diceros australis* nov. sp. 1: lower tusk AD 87'98 (photo V. Eisenmann); 2: Left D 4/ AD 292'94; 3: Right P 4/ AD 578'98; 4: Right M 3/ PQ AD 339; 5 and 8: Left D /3 PQ AD 635 (respectively labial and lingual view); 6 and 9: Left P /2 AD 86'98 (respectively labial and lingual view); 7 and 10: Left M /3 AD 200'98 (respectively labial and lingual view). Scale bar is 1 cm for the tusk and 3 cm for the cheek-teeth.

1 patella;

11 tarsals (3 tali, 4 calcanea, 1 cuboid, 2 naviculars, 1 first cuneiform);

9 metatarsals (4 Mt II including 2 complete, 4 complete or subcomplete Mt III, 1 complete Mt IV);

9 phalanges;

3 sesamoids.

Systematic Palaeontology

All but one of the 81 fossil rhino specimens from Arrisdrift constitute a homogeneous sample pertaining to a very large species of cursorial rhino. The large rhino from Arrisdrift can be characterized as follows:

- with the possible exception of *Kenyatherium*, whose teeth are totally different, it is the largest of the known African Miocene rhinos;
- size and proportions of the metapodials and the other limb bones suggest an analogy especially with the *Diceros* gr. *pachygnathus-neumayri* of the Upper Miocene of the Near East, and to a lesser extent with *Dicerorhinus schleiermacheri* from the Upper Miocene of Europe;
- the type of construction of the upper cheek teeth, especially the fourth premolar, is of Dicerotine type and presents strong resemblances to *Diceros douariensis* of the Upper Miocene of North Africa and Italy;
- the mandible shows analogies with the Dicerotines, especially the apparently short symphysis.
- the small reduced lower tusk could represent an evolutionary stage prior to the loss of the entire anterior dentition.

Thus this rhino is a large new species of Dicerotine, which I name *Diceros australis* nov. sp.; it is so far the oldest known species of the sub-family. Its definition is as follows:

TABLE 2.

Compared dimensions of the upper cheek teeth of *Diceros australis* nov. sp

ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

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 PD	AD 1103
D 4/	ap	47								
	tr	47								
M 1/	ap				59					
	tr				56.5					
M 2/	ap					58				
	tr					62.5				
M 3/	absolute length						64.5	65.5	66.5	65.5
	anat. length						55	53	52	54
	tr						62	62	61	60
P 4/	ap		43.5	37.5						
	tr		60.5	54						

D. douariensis		n	mean	min.	max.	*B. snowi* n	mean	min.	max.
D 4/	ap	1	44.00			0			
	tr	1	49.00			0			
M 1/	ap	2	60.25	59	61.5	2	61.50	55	68
	tr	3	61.33	59	64	1	71.00		
M 2/	ap	3	62.83	60	67.5	2	67.00	63	71
	tr	2	68.75	66.5	71	2	76.50	74	79
M 3/	absolute length	1	63.00			0			
	anat. length	3	57.33	50	64	1	63.00		
	tr	3	61.17	59	64	0			
P 4/	ap	2	40.50	37.5	43.5	1	49		
	tr	2	57.25	54	60.5	1	69		

Paradiceros mukirii		Fort Ternan	*Dicerorh. leakeyi* Rusinga	*A. campbelli*
D 4/	ap			
	tr			
M 1/	ap		40	58
	tr		50	68.5
M 2/	ap		48	
	tr		56	
M 3/	absolute length		53	54
	anat. length		43	47.5
	tr		56.5	49.5
P 4/	ap	31.5		48
	tr	45		63

Diagnosis: a very large cursorial rhinoceros of the Dicerotine type. Upper cheek teeth brachyodont, with a more or less continuous crenellated inner cingulum, and a crochet as the only or main internal fold. Ectoloph of the upper premolars with a strong parastyle, paracone fold thick but not very prominent and no mesostyle nor metacone fold. Upper molars possess on their ectoloph a large paracone fold and a weak vertical bulge in the middle of it, and a protocone weakly constricted on its anterior face. Tall and slim but sturdy limb bones. Lateral and medial metapodials very long with respect to the central one.

Locus typicus and Stratum typicum: Arrisdrift, Sperrgebiet, Southern Namibia; Lower Middle Miocene, about 17 Ma.

Derivatio nominis: from «austral» = southern; *D. australis* is the most southern Tertiary *Diceros* ever found.

Holotype: Left third metacarpal AD 52'97 (Figure 5: 3 and 4).

Ascribed material: Left half mandible AD 300'97; right upper fourth premolar AD 578'98 (Figure 3: 3); left upper fourth milk molar AD 292'94 (Figure 3: 2); right upper third molar PQ AD 339 (Figure 3: 4); left lower second premolar AD 86'98 (Figure 3: 6 and 9); left lower third molar AD 200'98 (Figure 3: 7 and 10); left lower third milk molar PQ AD 635 (Figure 3: 5 and 8); left radius PQ AD 3099; AD 52'97; left astragalus AD 619'94 (Figure 1: 2); right calcaneum AD 50'97 (Figure 1: 1); right third metatarsal AD 618'94 (Figure 5: 1 and 2).

The material is housed in the Geological Survey of Namibia in Windhoek.

Description

Mandible

Of the six specimens which are all incomplete, two possess an important part of the horizontal ramus, with probably a very short symphysis (none showing the anterior end) whose maximum height is 35 mm. In the two cases the posterior border of the symphysis at the middle P /2 level; for *Diceros douariensis* the symphysis

is 100 mm long and 43 mm high, with the level of the posterior border is between P /2 and P /3; the posterior border is at the anterior part of P /4 in *D. pachygnathus*. Whereas the anterior part of the horizontal ramus is shallower, the posterior part (from about the M /2 level) has dimensions comparable with *D. douariensis* (Table 1). Middle-sized African Aceratheres and Dicerorhines are much smaller, as is *Paradiceros*, and *Chilotheridium pattersoni* shows different proportions. Symphysis shortness suggests a very weak development or an absence of lower incisors, a character of the Dicerotine group.

Lower incisors

Two lower tusks (in fact incisors and not canines as reported by Hooijer 1971) were recovered.

AD 88'98 looks like a vestigial tooth, is knob-shaped and unworn. Its total length is 41.5 mm including 11 mm for the crown, the crown base transverse diameter is 9.5 mm, and its dorso-ventral diameter is 11 mm. It could be a dI /1.

AD 87'98 is a right lower incisor, feebly worn (Figure 3:1), it is 84 mm long (including 24 mm for the crown); at the crown base the transverse diameter is 19 mm, and its dorso-ventral diameter is 13.5 mm; the bevelled wear surface is 11 mm long and 10 mm wide; enamel thickness indicates a permanent tooth, i.e. an I /2. The cross section is an asymmetrical flattened ellipse. *Chilotheridium* tusks are much larger: after Hooijer 1971, the cross sections are respectively 22 x 17, 30 x 18, 30 x 15 and 40 x 25 mm, with crown length (for much worn specimens) between 44 and 55 mm; the shape is different, being more asymmetrical (Hooijer 1971, Plate 6), and there is a cingulum at the base of the crown. Such reduced dimensions would preclude the use of the Arrisdrift tusk as an effective weapon, whereas tusk-bearing living (and thus fossil) rhinos have much larger tusks and use them as bayonets.

I consider the small reduced lower adult tusk from Arrisdrift to be a representative of an evolutionary stage prior to the loss of the entire anterior dentition, the loss being accomplished in the Upper Miocene Dicerotine.

Upper cheek teeth

A well preserved D 4/ is weakly worn (Figure 3:1): its maximum height of 38 mm gives it a hypsodonty index of 81. The powerful paracone fold constitutes the sole relief on the outer wall, and the crochet is the only internal fold. There is a discontinuous crenellated lingual cingulum, mainly under the mouth of the inner valley. Its dimensions are about the same as these of *D. douariensis* (Table 2).

Two complete specimens of M 1/ or 2/ are known; one of them (AD 228'97), probably an M 1/, is only slightly worn and has a hypsodonty index of about 85. The ectoloph shows a large paracone fold and a weak vertical bulge in the middle of it. The crochet is the only internal fold. The protocone is weakly constricted on its anterior face. There is a weak crenellated inner cingulum under the mouth of the inner valley. The dimensions (Table 2) are slightly inferior to *D. douariensis* and largely inferior to *A. campbelli* but the two teeth are larger than those of *D. leakeyi*.

The four available specimens of M 3/ show the same morphology (Figure 3:4): a strong paracone fold, a crochet as the only inner pleat, a weakly constricted protocone, an incomplete lingual cingulum and a crenellated postero-labial cingulum extending onto the posterior quarter of the outer surface. Its dimensions are the same as for three M 3/ of *D. douariensis*.

Two right specimens of P 4/ have been recovered, one of them (AD 578'98) in a medium state of wear and the other (AD 649'97) very worn. The ectoloph has a strong parastyle, and a paracone fold which is thick but not very prominent; there is no mesostyle nor metacone fold. The sole inner fold is a strong crochet (but AD

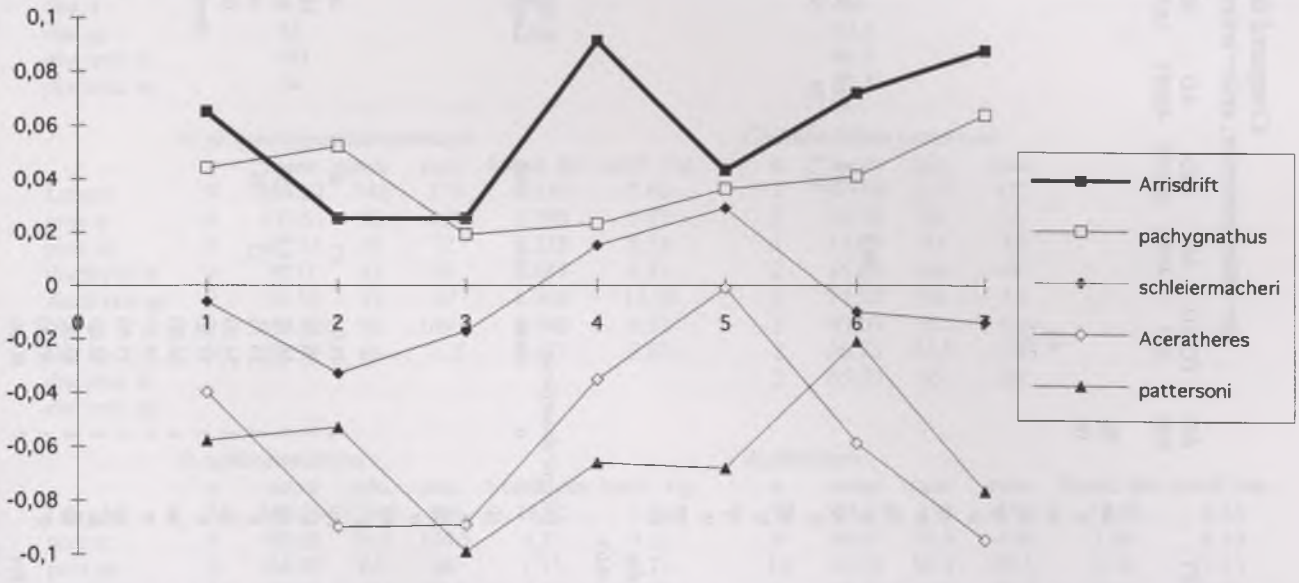


Figure 4: *Diceros australis* nov. sp: Simpson diagram of the radius compared with that of other Miocene rhinoceroses. Reference is *Diceros bicornis*. 1: Length; 2: proximal transverse diameter; 3: proximal anteroposterior diameter; 4: diaphysis transverse diameter; 5: diaphysis anteroposterior diameter; 6: distal transverse diameter; 7: distal anteroposterior diameter.

TABLE3

Compared dimensions of the lower cheek teeth of *Diceros australis* nov. sp

ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

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	PQ AD 330	AD 556'94	AD 300'97	AD 313'98	AD 437'97	AD 223'97
D /2	ap	30																	
	tr	18																	
D /3	ap		45																
	tr		25.5																
D /4	ap																		
	tr																		
M /1	ap														45	46.5			
	tr															37.5			
M /2	ap														50.5	55	58		
	tr			38.5											37	39	33.5		
M /3	ap				59	52.5	60								59	about 60			
	tr				36.5	39	35								35.5				
P /2	ap							31.5	33	30								32	
	tr							20.5		19.5								22	
P /3	ap										38	39	38			39		43	
	tr										28	29	27.5			29			
P /4	ap													40.5	40	44.5			46
	tr														32.5	35.5			37
Length P/3-P/4																83			
Length M/1-M/3															156.5	157			

		Diceros douariensis				*B. heinzelini*	*B. snowi*	*Chil. pattersoni*				MSUR	*P. mukirii*
		n	mean	min.	max.	Langental		n	mean	min.	max.	East Africa	Fort Ternan
D /2	ap											28.50	
	tr											16.00	
D /3	ap												
	tr												
D /4	ap												
	tr												
M /1	ap	2	48.00	47	49	48		2	42.00	40.5	43.5	39.00	35
	tr	1	30.50			34.5		2	30.00	27	33	30.00	27
M /2	ap	2	56.75	55.5	58	50	51.50	3	54.50	50.5	57	47.00	42
	tr	2	33.75	32	35.5	36	35.00	3	31.00	29.5	32.5	32.00	26
M /3	ap	1	54.00			60	58.00	2	59.50	56	63	54.00	43.5
	tr	1	31.50			about 38	36.50	2	30.75	27.5	34	31.00	25
P /2	ap	1	26.00				30.00	4	23.12	20	25	22.00	24
	tr	1	18.50				22.00	2	16.00	14	18		14
P /3	ap	1	35.50				36.50	4	33.62	25.5	38.5	32.50	27.5
	tr	1	33.00				26.50	4	21.12	18.5	24	23.50	19.5
P /4	ap	1	43.00				44.50	4	37.50	34	39	37.50	30.5
	tr	1	30.00				31.50	3	26.17	25.5	27	27.50	24.5
Length P/3-P/4		1	80.00					3	67.00	53	74.5	66.00	59
Length M/1-M/3		1	155.00			about 154	169.00	4	152.25	144	159	130.00	121

649'97 shows a closed medifossette). There is a strong, continuous and crenellated lingual cingulum, and no trace of constriction of the protocone (Figure 3:3). Such a morphology, especially that of the outer wall - the best odontological character for rhino determinations, see Guérin 1980 a - is very close to that seen in *Diceros douariensis* and *D.* gr. *pachygnathus-neumayri* from Pikermi, as are the dimensions (Table 2).

Lower cheek teeth

Lower deciduous molars include one D /2 and one D /3. The latter tooth, which is weakly worn, shows sharp V-shaped internal valleys with no difference in level; traces of a labial cingulum are to be seen on the posterior lobe (Figure 3: 5 and 8). Dimensions (Table 3) are very similar to those (43 x 24 mm) of an isolated D /3 from Pikermi (Museum of Bologna, Italy).

There is one incomplete isolated M /2, and there are three isolated M /3, the latter in a good state of preservation (Figure 3: 7 and 10). These are wider than the only known M /3 of *D. douariensis*, and are about as large as those of *Brachypoptherium heinzelini* and *B. snowi*, but much wider than *Chilotheridium*, *Paradiceros* and the medium-sized African Acerathere and Dicerorhinine (Table 3). The internal valleys have, for the anterior one, a sharp V-shaped transverse profile; the posterior valley is V-shaped in one case, U-shaped in the other two, the difference of level being moderate or strong. There are no lingual or labial cingula, but all the M /3 present a crenellated posterior cingulum of a very diverse shape.

Two isolated specimens of P /2, three of P /3 and one of P /4 were available for study. The P /3 n° AD 157'95 shows no trace of wear and possesses a hypsodonty index of 108; the two internal valleys are V-shaped with a strong level difference; there are no labial nor lingual cingula but the anterior and posterior ones run slightly onto the labial surface, as also observed in the P /2 (Figure 3: 5 and 8).

Lower cheek teeth included in tooth rows present the same characters; the most complete row (AD 300'97) has the lengths of the molar segment and of the two last premolars very close to the values observed in *D. douariensis* (Table 3) and *D.* gr. *pachygnathus-neumayri*.

Radius and ulna

The radius is longer than those of the largest *D.* gr. *pachygnathus-neumayri* and *D. schleiermacheri*, the last being more slender. The undifferentiated Acerathere/ Dicerorhine from Rusinga, which possesses the same dimensions and proportions as the middle-sized Upper Miocene Aceratheres of Europe, is smaller and with different proportions. The radius of *Chilotheridium* and especially *B. snowi* is stockier and much shorter (Table 4; Figure 4).

TABLE 4.

Compared dimensions of the radius of *Diceros australis* nov. sp
ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	ARRISDRIFT PQ AD 3099	MSUR Rusinga	*B. snowi* Jebel Zelten
Length	435	305	286.5
prox tr	113	95	86.5
prox ap	70.5	57.5	51.5
diaphysis tr	64.5	51.5	48.5
diaphysis ap	42	47.5	40
dist tr	115	92	86
dist ap	83	69	53.5
dist artic tr	103		80.5
dist artic ap	54		41.5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*			
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.
Length	9	364.22	342	375	9.536	2.62	1	327.00	327	327
prox tr	9	100.61	95	107	3.790	3.77	2	94.50	94	95
prox ap	9	65.00	55	72	5.315	8.18	1	53.00	53	53
diaphysis tr	9	59.11	55	63	2.667	4.51	2	45.00	44	46
diaphysis ap	9	38.78	33	47	4.402	11.35	2	32.50	32	33
dist tr	9	104.00	95	109.5	4.488	4.32	2	93.00	91	95
dist ap	9	65.78	60	71.5	3.833	5.83	2	56.75	54.5	59
dist artic tr							2	85.50	85	86
dist artic ap										

	D. schleiermacheri					Aceratheres					
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	5	369.30	351.5	396	18.62	5.04	6	341.17	316	348	12.46	3.65
prox tr	4	99.38	94.5	104.5	4.33	4.35	9	86.67	78.5	100	7.96	9.19
prox ap	3	64.00	63	66	1.73	2.71	10	54.25	50.5	59.5	2.78	5.13
diaphysis tr	5	54.20	48	57.5	3.78	6.98	6	48.33	44	52.5	3.66	7.56
diaphysis ap	5	40.60	38	43	1.78	4.39	6	37.92	33	42.5	3.65	9.63
dist tr	5	95.20	87	100	5.71	6.00	6	85.17	75	103.5	10.61	12.45
dist ap	5	65.60	61	69	3.99	6.08	7	54.50	50	61	3.93	7.20
dist artic tr	4	82.12	79	88.5	4.39	5.34	5	72.60	68.5	79.5	4.89	6.74
dist artic ap	4	44.75	44	45	0.50	1.12	5	38.70	36.5	42.5	2.41	6.24

The proximal articulation does not possesses the very undulating anterior border nor the large re-entrant angle at the level of the coronoid process which characterize the genus *Ceratotherium*. But it shows a transversely elongated lateral facet the anterior border of which is only slightly retracted in relation to the anterior edge of the medial facet, and whose posterior border, regularly concave, constitutes moreover an obtuse angle with the posterior edge of the medial facet. These last characters speak in favour of the proximity of the large Arrisdrift rhino to the Dicerotine subfamily.

Three ulnae have been recovered from Arrisdrift of which one only (AD 273'97) is complete; for a total length of 533 mm its proximal articular diameter is 95 mm and the proximal antero-posterior diameter is 157 mm. The other two pieces are a distal epiphysis of an adult specimen and the proximal end of a juvenile one.

Carpus

The semilunar presents an anterior surface whose width (42 mm) is similar to the height. The distal point of that surface, sited near the midline, is rounded. The length is 69.5 mm.

One of the two known pyramidals (= cuneiforms) is well preserved; it is very large, and markedly wider (71.5 mm) than tall (63 mm).

The only pisiform in the collection has a length of 70 mm, and is 29 mm wide; the height is 52 mm.

One only of the two magnums found at Arrisdrift (AD 538'97) is attributable to the large rhino species. Its dimensions are as follows:

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

Such dimensions and proportions differ from those of *D. schleiermacheri* but are close to those of three magnums of *Diceros* gr. *pachygnathus-neumayri;* they are totally different from that of the other magnum recovered in the same site (Figure 1: 3-5 and Figure 2). In anterior view the bone presents a rhomboidal outline, rounded distally, and is higher than wide; the distal articulation is about as wide in its fore part as in its posterior part.

Metacarpal II

The only known specimen, a left one, is longer than the largest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, and is distinctly slender. That of *Chilotheridium* is very short and stocky, and that of true Aceratheres is shorter and shows very different proportions (Table 5).

The proximal articulation is long and narrow, crescent-shaped with a distinct notch on its posterior edge. On the lateral surface of the proximal epiphysis there is only one

TABLE 5.

Compared dimensions of the second metacarpal of *Diceros australis* nov. sp
ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	ARRISDRIFT AD 536'97
Length	188
prox tr	41
prox ap	54
diaphysis tr	32.5
diaphysis ap	25
dist max tr	43
dist tr artic	42
dist ap	45.5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*			
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.
Length	9	156.33	140.5	169	8.842	5.66	2	129.50	129.5	129.5
prox tr	9	44.67	37	54	5.385	12.06	2	43.00	42	44
prox ap	4	46.50	40	51	4.231	9.10	2	37.25	37	37.5
diaphysis tr	9	40.78	33.5	44.5	4.374	10.73	2	31.75	31	32.5
diaphysis ap	9	24.33	20	26	1.750	7.19	2	16.50	16	17
dist max tr	9	48.89	40	54	5.355	10.95	2	39.75	37	42.5
dist tr artic	9	43.17	34.5	48.5	4.644	10.76	2	34.00	31	37
dist ap	9	42.39	38.5	46	4.583	6.09	2	36.25	36	36.5

	D. schleiermacheri						Aceratheres					
	n	mean	min.	max.	Stand dev.	coeff. var.	n	mean	min.	max.	Stand	coeff.
Length	3	168.83	156.5	179	11.41	6.76	5	133.20	120.5	148	13.30	9.98
prox tr	3	43.00	40	47	3.61	8.39	3	33.67	32	36	2.08	6.18
prox ap	3	42.50	40	44	2.18	5.13	3	33.17	29.5	40	5.92	17.86
diaphysis tr	4	36.88	34	40.5	2.72	7.37	4	32.38	28.5	36	3.09	9.55
diaphysis ap	4	22.50	18.5	27	3.54	15.71	4	19.00	17	21.5	1.96	10.30
dist max tr	3	44.67	40	47	4.04	9.05	4	37.75	36	40	1.66	4.39
dist tr artic	3	40.17	39	41	1.04	2.59	4	34.38	32.5	36	1.49	4.34
dist ap	3	40.33	39.5	41.5	1.04	2.58	4	35.62	32	38.5	2.69	7.55



Figure 5. Third metapodials of *Diceros australis* nov. sp. 1: Mt III AD 618'94, front view; 2: Mt III AD 618'94, posterior view; 3: Mc III AD 52'97, front view; 4: Mc III AD 52'97, posterior view. Scale bar is 3 cm.

articular facet, constricted in its medium part and expanding onto the whole height of the bone. The transverse section of the diaphysis is a rounded triangle.

Metacarpal III

Two left Mc III have been recovered complete and the largest is marginally longer than the largest known specimens of *Diceros gr. pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but are a little more slender. *Brachypotherium snowi* and *B. heizelini* are shorter and stockier, as is *Chilotheridium*. True Aceratheres show more or less analogous proportions but are much smaller.

The Simpson diagram shows that the Arrisdrift Mc III does not belong to a Brachypothere, nor to an Acerathere, whereas analogies with *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri* are noticeable (Table 6, Figures 5 and 6).

The proximal articulation is very wide, triangular, and with a rectilinear anterior edge. There are two articular facets on the lateral surface of the proximal epiphysis; the anterior one is pentagonal with two parts, the lowest of which is more or less expanded anteroposteriorly according to the observed specimen; the posterior facet, located lower than the anterior one, is a rounded triangle whose width varies on each specimen. On the medial surface of the epiphysis there is a small inverted S-shaped facet whose height is variable. The transverse section of the diaphysis is trapezoidal, with a slightly convex anterior edge and a slightly concave posterior one; the lateral edge is straight and longer than the medial edge whose profile is more or less straight.

Metacarpal IV

This bone is much more longer and more slender than the largest measured specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri* (Table 7).

The proximal articulation is triangular, a little longer than broad; such a width/height ratio is inverted for short-legged rhinos such as *Brachypotherium* and *Chilotheridium*. On the medial surface of the proximal epiphysis there are two articular facets; the anterior one is long and low, and semi-elliptical, while the posterior one is a vertical ellipse, much taller than broad.

Tibia

Only one tibia was found, and it is badly damaged especially the proximal epiphysis, but the total length can nevertheless be measured. As for the Mc IIIs the tibia is marginally longer than the largest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, and is more slender (Table 8). Surprisingly enough, the dimensions of a broken distal epiphysis of a *Diceros* cf. *douariensis* from Baccinello V3 are identical to those of Arrisdrift!

Astragalus

Three astragali have been recovered of which two are complete (Figure 1: 2). Dimensions (Table 9) and proportions (Figure 4) are close to those of *Diceros* gr. *pachygnathus-neumayri*, and do not differ much from *Dicerorhinus schleiermacheri*. The astragalus of *Brachypotherium snowi* is slightly larger but markedly lower, and it is proportionally the same for

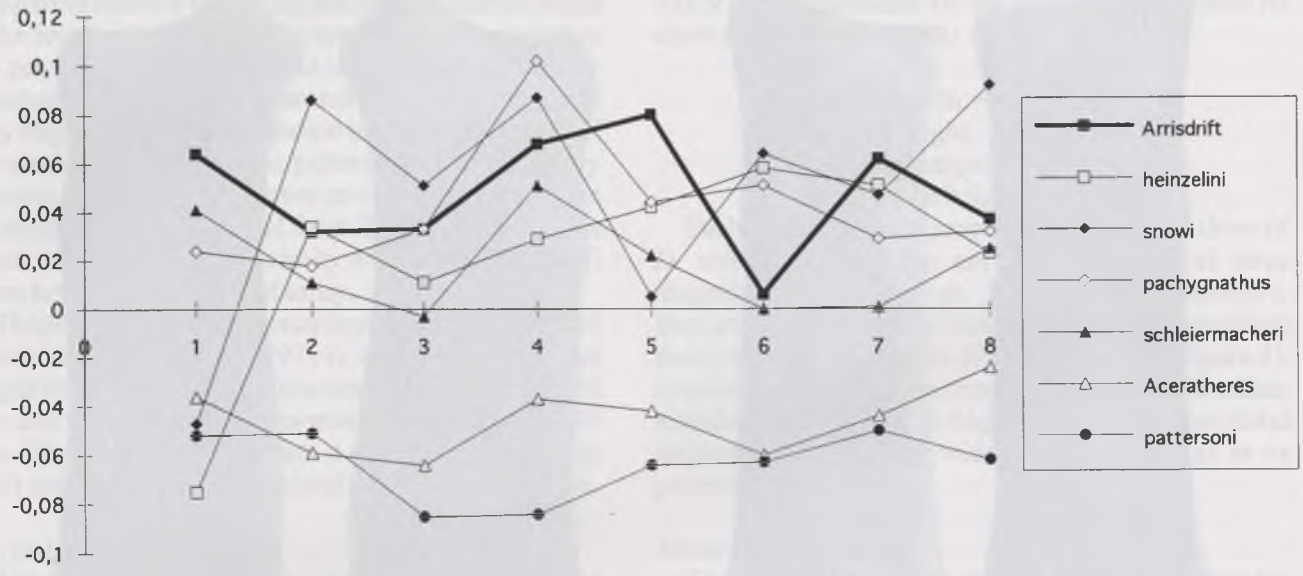


Figure 6: *Diceros australis* nov. sp: Simpson diagram of the third metacarpal compared with that of other Miocene rhinoceroses. Reference is *Diceros bicornis*. 1: length; 2: proximal transverse diameter; 3: proximal anteroposterior diameter; 4: diaphysis transverse diameter; 5: diaphysis anteroposterior diameter; 6: distal maximal transverse transverse diameter; 7: distal transverse articular diameter; 8: distal anteroposterior articular diameter diameter.

TABLE 6.

Compared dimensions of the third metacarpal of *Diceros australis* nov. sp.

ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	ARRISDRIFT		*B. snowi*	*B. heinzelini*
	AD 52 '97	AD 243 '95	Jebel Zelten	Rusinga
Length	200	212	159.5	149.5
prox tr	68	63.5	74.5	66
prox ap	58	51.5	57	52
diaphysis tr	57.5	58.5	60.5	53
diaphysis ap	27	26.5	22.5	24.5
dist max tr	65	63.5	73.5	72.5
dist tr artic	60	60	58	58.5
dist ap	48		54.5	46.5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*			
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.
Length	9	187.17	181	198	5.668	3.03	3	157.67	150	169
prox tr	6	65.50	62.5	74.5	4.461	6.81	3	54.33	50	61
prox ap	8	54.94	52	59	2.427	4.42	3	41.67	37	45
diaphysis tr	11	63.55	59	69	3.020	4,75	3	40.83	39	43
diaphysis ap	9	24.56	22	26.5	1.333	5.43	3	19.17	17.5	21.5
dist max tr	9	71.22	66.5	76	2.705	3.80	3	54.83	51	61
dist tr artic	10	56.15	52	59	2.174	3.87	3	46.33	44.5	49.5
dist ap	10	48.05	45	53	2.619	5.45	3	38.17	37.5	39

	D. schleiermacheri						Aceratheres					
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	6	195.42	181	204	8.55	4.37	10	163.75	139.5	181	13.38	8.17
prox tr	9	62.67	58	69	3.70	5.90	10	53.35	50	59.5	3.09	5.80
prox ap	5	50.30	47.5	52	1.99	3.95	10	43.80	40	47.5	2.41	5.49
diaphysis tr	9	55.78	49.5	66	5.36	9.61	11	45.55	42	49	2.25	4.95
diaphysis ap	8	23.38	22	25.5	1.19	5.08	10	20.20	17	24.5	2.16	10.71
dist max tr	7	63.50	60	69	3.15	4.96	10	55.25	49.5	60.5	3.68	6.65
dist tr artic	7	52.14	49	56	2.48	4.75	10	47.00	38.5	52	3.89	8.29
dist ap	7	46.71	45	49	1.41	3.02	7	41.71	38	44.5	2.56	6.15

TABLE 7:

Compared dimensions of the fourth metacarpal of *Diceros australis* nov. sp.

ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	ARRISDRIFT AD 404'97
Length	about 188
prox tr	55
prox ap	51.5
diaphysis tr	37.5
diaphysis ap	27
dist max tr	51
dist tr artic	45
dist ap	53

	MSUR			
	N	moyenne	mini	maxi
Length	2	158.75	152.5	165
prox tr	1	52.00		
prox ap	1	46.00		
diaphysis tr	2	34.00	34	34
diaphysis ap	2	21.25	20.5	22
dist max tr	2	46.25	42	50.5
dist tr artic	2	43.00	40	46
dist ap	2	38.75	37	40.5

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*				
	n	mean	min.	max.	Stand. dev. coeff. var.	n	mean	min.	max.	Stand. dev.
Length	8	144.81	134	156	9.059 6.26	3	125.17	121.5	129.5	4.04
prox tr	8	47.81	43	53	3.535 7.39	2	35.50	34	37	2.12
prox ap	8	42.12	37	47,5	3.410 8.09	2	38.00	32	44	8.49
diaphysis tr	8	37.69	31.5	41	3.162 8.39	3	26.17	23	30.5	3.88
diaphysis ap	8	24.75	20	29	2.726 11.01	3	18.00	17.5	18.5	0.50
dist max tr	8	46.69	39	52.5	4.166 8.92	3	42.17	37	47.5	5.25
dist tr artic	8	43.06	37.5	47	3.590 8.34	3	35.50	33.5	37	1.80
dist ap	8	41.00	37.5	46	2.712 6.62	3	34.33	33	37	2.31

	D. schleiermacheri				Aceratheres					
	n	mean	min.	max.	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	1	145.00			5	144.50	141.5	147.5	2.48	1.71
prox tr	2	49.25	47.5	51	7	42.86	38.5	48	3.58	8.35
prox ap	1	43.00			7	39.21	32	42	3.32	8.45
diaphysis tr	2	32.50	32.5	32.5	5	30.10	27.5	32.5	2.38	7.91
diaphysis ap	2	21.50	21	22	5	22.40	19	25	2.33	10.40
dist max tr	2	45.25	43	47.5	5	39.00	37.5	40	0.94	2.40
dist tr artic	2	42.25	38.5	46	5	38.90	36	43	2.90	7.46
dist ap	2	40.50	40	41	5	37.60	34	40	2.38	6.34

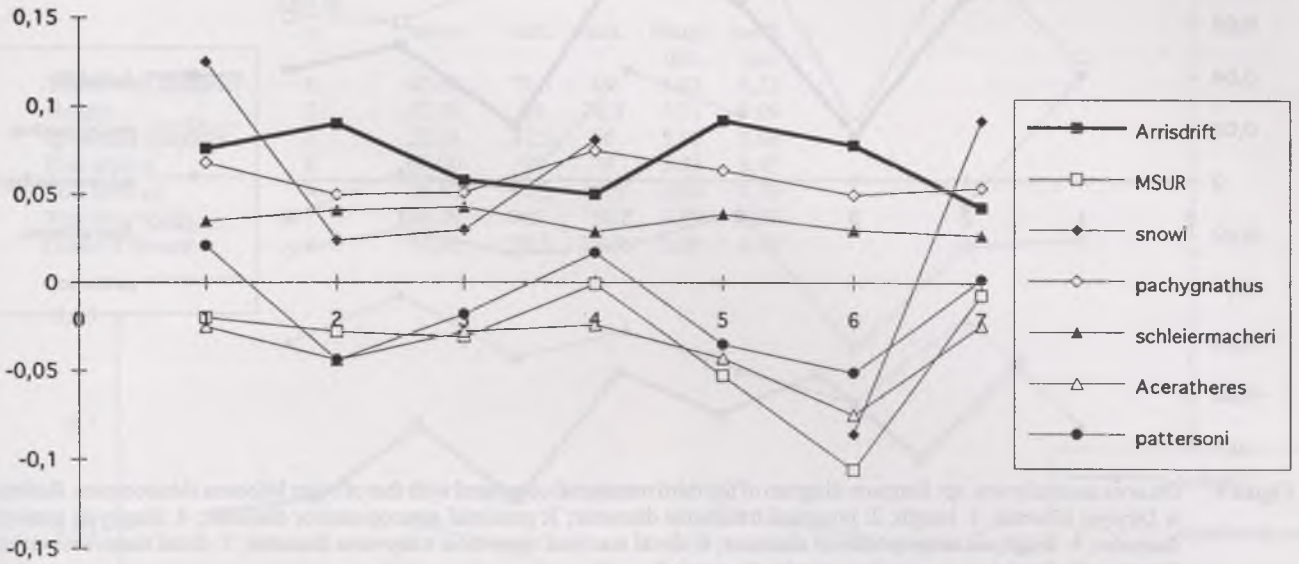


Figure 7: *Diceros australis* nov. sp: Simpson diagram of the astragalus compared with that of other Miocene rhinoceroses. Reference is *Diceros bicornis*.1: transverse diameter; 2: height; 3: anteroposterior medial diameter; 4: distal articular transverse diameter; 5: distal articular anteroposterior diameter; 6: trochlea upper width; 7: distal maximal transverse diameter.

Chilotheridium. The dimensions are inferior and the proportions are different for the true Aceratheres, and also for the undifferenciated sample of *D. leakeyi-A. acutirostratum*, whose similarity with true Aceratheres is noticeable.

Among the qualitative characters, the tubercle on the lower part of the medial surface is located in the middle, well above the articular edge. Individual variation observed in the three astragali from Arrisdrift concerns mainly the height of the neck, the obliquity of the medial edge of the distal articulation, and the posterior development of the upper end of the medial lip.

Calcaneum

A damaged juvenile and three adult calcanei are known, of which two are complete (Figure 1: 1). As for the astragalus, their dimensions (Table 10) and proportions are close to *Diceros* gr. *pachygnathus-neumayri* and

TABLE 8.

Compared dimensions of the tibia of *Diceros australis* nov. sp

ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

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

	D. gr. pachygnathus/neumayri n	mean	min.	max.	Stand. dev.	coeff. var.	*D. cf. douariensis* Baccinello V3
Length	5	390.40	368	420	19.97	5.12	
diaphysis ap	7	58.36	49	73	8.80	15.07	58
dist tr	6	107.92	99	115	7.09	6.57	101
dist ap	7	79.00	71	99	10.72	13.57	80
dist artic tr							
dist artic ap							

	D. schleiermacheri n	mean	min.	max.	Aceratheres n	mean	min.	max.	Stand. dev.	coeff. var.
Length	2	398.00	386	410	9	361.22	328	383	20.66	5.72
diaphysis ap	2	58.25	57.5	59	9	47.39	38	53	5.82	12.28
dist tr	2	103.50	101	106	9	86.17	72.5	91.5	6.26	7.26
dist ap	2	72.25	69	75.5	11	62.55	53	68	5.01	8.01
dist artic tr	1	82.50			3	71.00	60	79	9.85	
dist artic ap	1	60.00			3	50.67	46	55	4.51	

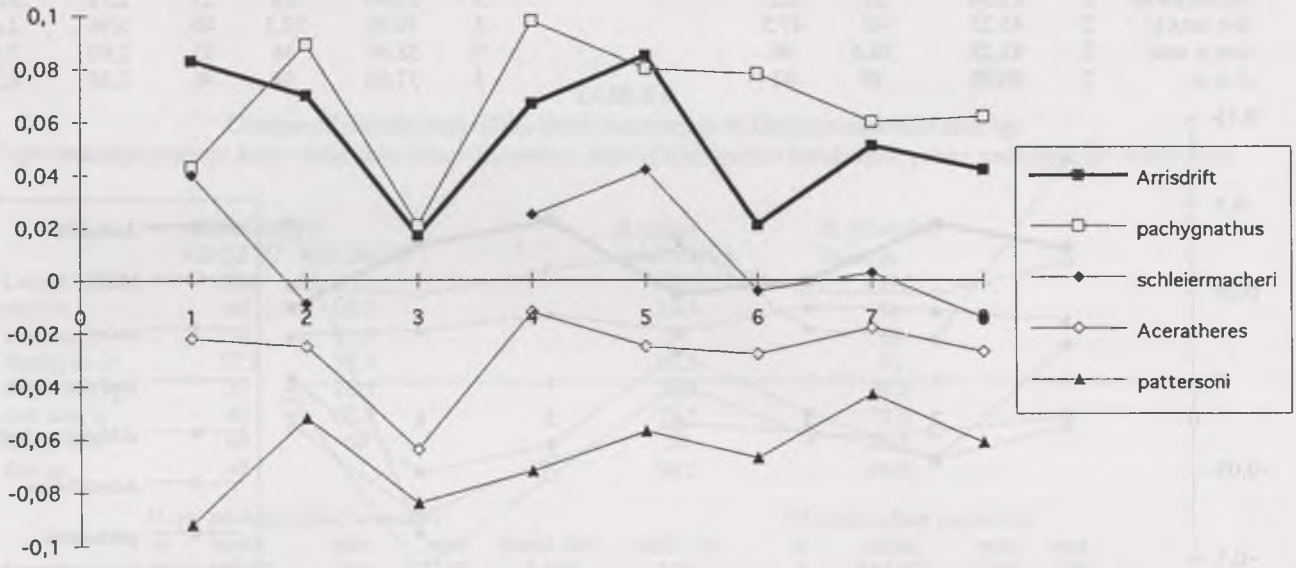


Figure 8: *Diceros australis* nov. sp: Simpson diagram of the third metatarsal compared with that of other Miocene rhinoceroses. Reference is *Diceros bicornis*. 1: length; 2: proximal transverse diameter; 3: proximal anteroposterior diameter; 4: diaphysis transverse diameter; 5: diaphysis anteroposterior diameter; 6: distal maximal transverse transverse diameter; 7: distal transverse articular diameter; 8: distal anteroposterior articular diameter diameter.

D. schleiermacheri, having nothing to do with those of *Paradiceros*, *Chilotheridium* nor Aceratheres.

In posterior view the sustentaculum axis makes a right angle with the axis of the body of the bone.

In lateral view the front of the tuberosity is situated well behind the beak (= foremost part of the bone), the anterior edge between the two points being oblique and slightly concave. The posterior edge of the surface is globular for the upper two thirds of its height, and depressed for the last third, especially in specimen PQ AD 601.

Individual variation is noticeable in the proximal part of the bone when observed from the posterior surface: shaped as an inverted V for PQ AD 601, it is flat for AD 50'97.

Other tarsals

The cuboid is very large: its total length is 77 mm, its total height 61 mm, and maximum width 52.5 mm. The anterior surface is much taller than broad (53 and 41.5 mm), and its lateral edge is longer than the medial one.

Two naviculars have been recovered, and are broader

TABLE 9.

Compared dimensions of the astragalus of *Diceros australis* nov. sp.
ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	Arrisdrift AD 619'94	Arrisdrift PQ AD 1219	*D. gr. pachygnathus/neumayri* n	mean	min.	max.	Stand. dev.	coeff. var.
Transverse diameter	101	100	7	98.57	94	104	3.65	3.70
Height	95	96	6	87.17	84	92	3.55	4.07
ap medial diameter	63.5	64.5	6	63.00	61	65	1.90	3.01
Dist artic tr	75	78	7	81.07	76.5	86	3.10	3.83
Dist artic ap	55	53.5	7	50.86	45	53.5	3.33	6.54
Trochlea width	72	77	6	69.83	61	77.5	5.77	8.26
Distal tr diameter	80.5	85	5	84.90	82	90.5	3.47	4.09

	D. schleiermacheri n	mean	min.	max.	Stand. dev.	coeff. var.	*Brachypotherium snowi* n	mean	min.	max.
Transverse diameter	11	91.45	86.5	99	3.60	3.93	2	108.75	105	112.5
Height	13	85.35	78.5	93	4.72	5.53	1	82.00		
ap medial diameter	12	61.79	55	70	4.13	6.68	2	59.00	58	60
Dist artic tr	8	73.00	62	82	6.65	9.11	2	82.25	80	84.5
Dist artic ap	10	47.95	44.5	55	2.83	5.91				
Trochlea width	12	66.63	61	75	3.73	5.60	1	51.00		
Distal tr diameter	10	79.75	76	86	3.81	4.78	2	92.75	90.5	95

	Aceratheres n	mean	min.	max.	Stand. dev.	coeff. var.	*Chilotheridium pattersoni* n	mean	min.	max.	Stand.. dev.
Transverse diameter	29	79.60	72	88.5	4.35	5.46	3	88.50	85.5	92	3.28
Height	30	70.07	62	81	4.58	6.54	3	70.17	68.5	71	1.44
ap medial diameter	26	52.44	45	59	3.59	6.85	3	53.67	52	55.5	1.76
Dist artic tr	29	64.59	56.5	73	3.88	6.01	3	71.00	64	79	7.55
Dist artic ap	25	39.68	35	47	2.69	6.77	2	40.50	38	43	3.54
Trochlea width	31	52.39	46	65	5.23	9.98	3	55.33	52	58	3.06
Distal tr diameter	28	70.95	65	76.5	3.12	4.40	3	75.33	73	79	3.22

	MSUR n	mean	min.	max.	Stand. dev.	coeff. var.
Transverse diameter	8	80.62	75.5	84	3.41	4.23
Height	7	72.79	69	78.5	3.71	5.09
ap medial diameter	7	52.14	47.5	56	3.16	6.06
Dist artic tr	8	68.00	65	74	3.02	4.45
Dist artic ap	6	38.83	33.5	43.5	3.80	9.79
Trochlea width	7	48.79	45	50	1.89	3.87
Distal tr diameter	8	73.81	70.5	78.5	3.09	4.19

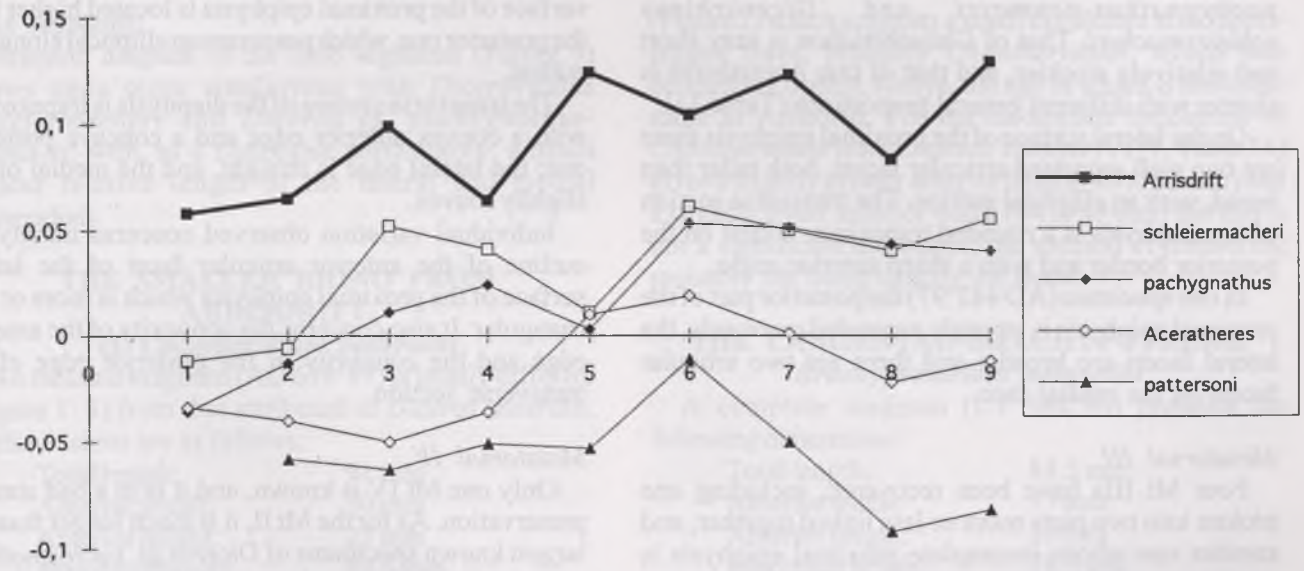


Figure 9. *Diceros australis* nov. sp: Simpson diagram of the limb segments compared with those of other Miocene rhinoceroses. Reference is *Diceros bicornis*. 1: ulna length; 2: radius length; 3: Mc II length; 4: Mc III length; 5: Mc IV length; 6: tibia length; 7: Mt II length; 8: Mt III length; 9: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

TABLE 10.

Compared dimensions of the calcaneum of *Diceros australis* nov. sp.
ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	ARRISDRIFT AD 50'97	ARRISDRIFT PQ AD 601	ARRISDRIFT AD 530'95	*Paradiceros* Kisegi	MSUR
Height	158.5	153	153	92.5	130.5
Head tr	58	55	64	36	52.5
Head ap	77	67		50	54
middle width	41.5	40		33	43
Sustentaculum tr	77.5	79	77	50	81
maximum width	81	81	80	55.5	85.5
maximum ap	84	75.5	about 75		63

	D. gr. pachygnathus/neumayri					*Chilotheridium pattersoni*				
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.	Stand. dev.	coeff. var.
Height	7	143.36	132	151.5	6.30	4.39	3	120.83	113	132	9.93	8.22
Head tr	6	58.42	54	63	3.64	6.23	3	44.33	42	48.5	3.62	8.16
Head ap	7	75.07	65	82	5.76	7.68	3	67.67	60	74	7.10	10.48
middle width	2	46.50	45	48	2.12	4.56						
Sustentaculum tr	7	82.07	74	87.5	4.64	5.65	2	70.00	70	70	0.00	0.00
maximum width												
maximum ap	5	77.90	72	83	5.03	6.46	3	59.17	57	62	2.57	4.34

	D. schleiermacheri					Acératheres				
	n	mean	min.	max.	Stand. dev.	coeff. var.	n	mean	min.	max.	Stand. dev.	coeff. var.
Height	5	142.10	134	149	6.71	4.72	20	108.82	98.5	123.5	6.66	6.12
Head tr	6	53.17	50.5	55	1.78	3.35	20	42.97	35	49	3.93	9.13
Head ap	6	72.67	68.5	79.5	5.97	9.01	19	61.03	49.5	79	6.55	10.73
middle width	4	40.13	37	43.5	2.78	6.93	6	33.75	26	41	6.03	17.87
Sustentaculum tr	5	80.90	72.5	88	6.37	7.87	15	70.33	61	78.5	4.14	5.88
maximum width												
maximum ap	6	74.50	69	86	6.72	9.01	20	59.58	51	70	5.10	8.55

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.

The only big cuneiform preserved is 44.5 mm long, 26 mm wide, and 35.5 mm high.

Metatarsal II

Four Mt IIs were found, of which two are complete or nearly so (during fossilisation they were broken but knitted again into place). They are much longer but more slender than the largest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*. That of *Chilotheridium* is very short and relatively stockier, and that of true Aceratheres is shorter with different general proportions (Table 11).

On the lateral surface of the proximal epiphysis there are two well separated articular facets, both taller than broad, with an elliptical outline. The transverse section of the diaphysis is a rounded trapezium, widest on the posterior border and with a sharp anterior angle.

In one specimen (AD 442'97) the posterior part of the proximal epiphysis is strongly expanded rearwards, the lateral facets are broader and there are two articular facets on the medial face.

Metatarsal III

Four Mt IIIs have been recovered, including one broken into two parts more or less linked together, and another one whose incomplete proximal epiphysis is partly preserved in gypsum.

The bone (Figure 5: 1-2) is about as long as the largest known specimens of *Diceros* gr. *pachygnathus-neumayri* and has about the same proportions except the sus-articular transverse distal diameter. It is significantly longer than those of *Dicerorhinus schleiermacheri*. *Chilotheridium* is much shorter and relatively stockier. True Aceratheres show different proportions and are smaller (Table 12, Figure 8).

The proximal articulation is very wide, triangular, with a convex anterior edge whose point of bending is laterally offset; the antero-lateral angle is pointed; the medial edge begins with a cant followed by a shallow depression. The anterior articular facet on the lateral surface of the proximal epiphysis is located higher than the posterior one, which possesses an elliptical elongated outline.

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

Individual variation observed concerns mainly the outline of the anterior articular facet of the lateral surface of the proximal epiphysis which is more or less triangular. It also concerns the convexity of the anterior edge and the concavity of the posterior edge of the transverse section.

Metatarsal IV

Only one Mt IV is known, and it is in a bad state of preservation. As for the Mt II, it is much longer than the largest known specimens of *Diceros* gr. *pachygnathus-neumayri* and *Dicerorhinus schleiermacheri*, but is not especially slender. That of *Chilotheridium* is very short, and that of true Aceratheres is shorter with different general proportions (Table 13).

TABLE 11.

Compared dimensions of the second metarsal of *Diceros australis* nov. sp.
ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	Arrisdrift AD 744'97	Arrisdrift PQ AD 251	Arrisdrift AD 442'97	Arrisdrift AD 348'95	*Chilotheridium pattersoni* Loperot	Loperot	MSUR Kiboko
Length	182.5	181			129	115	153
prox tr	30	31	32	31	about 36	30	27
prox ap	51	47	57	51		37.5	34.5
diaphysis tr	31	30	31.5			23	19.5
diaphysis ap	30	25.5	29			21	18.5
dist max tr	40.5	39			42	35	29
dist tr artic	38.5	37.5			38.5	32.5	28
dist ap	46	40			43	36.5	30

D. schleiermacheri

	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	3	153.33	150	156	3.06	1.99
prox tr	3	33.83	27	40.5	6.75	19.96
prox ap	3	45.67	43	50.5	4.19	9.18
diaphysis tr	2	27.00	26	28	1.41	5.24
diaphysis ap	2	27.75	27	28.5	1.06	3.82
dist max tr	3	37.17	35.5	39	1.76	4.72
dist tr artic	3	35.00	33	37	2.00	5.71
dist ap	3	39.17	37	40.5	1.89	4.83

D. gr. pachygnathus/neumayri

	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	5	153.70	147.5	157.5	4.04	2.63
prox tr	5	33.60	30.5	37	3.03	9.01
prox ap	5	45.70	42.5	49	2.73	5.97
diaphysis tr	5	34.80	32	37.5	2.08	5.98
diaphysis ap	5	25.20	23.5	27	1.48	5.89
dist max tr	4	43.50	40	45	2.38	5.47
dist tr artic	5	39.30	36.5	41	1.75	4.46
dist ap	5	43.50	39	47	2.96	6.80

Aceratheres

	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	8	137.06	117.5	165.5	14.37	10.49
prox tr	9	28.00	25.5	31	1.70	6.06
prox ap	9	39.17	35	41.5	2.26	5.78
diaphysis tr	7	26.57	23.5	32	2.99	11.26
diaphysis ap	7	21.93	19	25	2.13	9.71
dist max tr	7	36.07	31	40	3.18	8.82
dist tr artic	8	32.88	26	40	4.60	14.00
dist ap	7	36.50	33	40.5	2.80	7.67

Limb segments:

Simpson diagram of the limb segments (Figure 9) shows once more similarities with *Dicerorhinus schleiermacheri* and *Diceros* gr. *pachygnathus-neumayri*, with, as a noticeable particularity, a much greater relative length of the lateral and medial metapodials.

THE SMALLER RHINO FROM ARRISDRIFT, cf. *Chilotheridium pattersoni*

An isolated magnum (AD 618'97) is totally different (Figure 1: 3) from that attributed to *Diceros australis*. Its dimensions are as follows:

Total length:	91 mm
Anterior width:	50 mm
Anterior height:	27 mm
Maximum height:	54.5 mm
Sus-articular height:	52.5 mm

Shallow and very wide, with a flattened and oblique anterior surface, it shows an inverted width/height ratio (Figure 2) which suggests a small to medium sized short-legged form, probably *Chilotheridium*, which was defined at Loperot, Kenya, the age of which is about the same as Arrisdrift. For ten incomplete specimens of *Chilotheridium* from Loperot, Hooijer (1971, Table 14) gives a slightly greater anterior height (30 to 33 mm) and a slightly lesser anterior width (44 to 49 mm) but this is not a significant difference, the method of measuring probably not being exactly the same.

THE LANGENTAL BRACHYPOTHERE, *Brachypotherium heinzelini*

A complete magnum (LT 384'96) presents the following dimensions:

Total length:	84.5 mm
Anterior width:	57 mm
Anterior height:	39 mm
Maximum height:	58.5 mm
Sus-articular height:	57 mm

The Langental magnum (Figure 1: 5) is thus much larger than the smaller specimen from Arrisdrift but

TABLE 12.

Compared dimensions of the third metatarsal of Diceros australis nov. sp. ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	Arrisdrift AD 618'94	Arrisdrift PQ AD 249	Arrisdrift PQ AD 119	Arrisdrift PQ AD 183		*C. pattersoni* Loperot
Length	197.5	197	about 180	about 178		128
prox tr	57.5	61		54		43.5
prox ap	52			49		40
diaphysis tr	50	51.5	52.5	44		36
diaphysis ap	26	25.5		25.5		18.5
dist max tr	61.5	60.5	57.5	55.5		48
dist tr artic	53	57	52.5	51		43
dist ap	46	47.5	42	42		35
	D. schleiermacheri					
	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	2	173.25	171.5	175	2.48	1.43
prox tr	1	48.00				
prox ap	1	40.00				
diaphysis tr	2	45.00	43.5	46.5	2.12	4.71
diaphysis ap	2	23.25	23	23.5	0.35	1.52
dist max tr	2	55.50	53.5	57.5	2.83	5.10
dist tr artic	2	47.75	46	49.5	2.48	5.18
dist ap	2	39.00	33	45	8.49	21.76
	D. gr. pachygnathus/neumayri					
	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	9	174.56	165	194.5	8.56	4.90
prox tr	8	60.06	57	64.5	2.32	3.86
prox ap	8	50.88	45	57.5	4.96	9.74
diaphysis tr	9	53.22	51.5	55	1.23	2.31
diaphysis ap	9	25.33	22.5	28.5	1.97	7.77
dist max tr	7	66.93	60.5	71.5	3.76	5.61
dist tr artic	8	54.50	49.5	60.5	3.65	6.69
dist ap	8	46.50	41.5	49	2.41	5.17
	Aceratheres					
	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	11	150.36	130	166	11.44	7.61
prox tr	10	46.25	40	53.5	4.63	10.00
prox ap	10	41.90	38	46	2.76	6.58
diaphysis tr	11	41.32	37.5	46.5	2.70	6.55
diaphysis ap	10	19.90	16.5	24.5	2.76	13.85
dist max tr	11	52.45	47	60.5	4.12	7.85
dist tr artic	11	45.45	40.5	51.5	3.23	7.10
dist ap	11	37.82	32	42.5	3.47	9.17

presents the same kind of width/height ratio (Figure 2), which is typical of Brachypotheres and Chilotheres. I thus assign it to *Brachypotherium heinzelini*, a large brachypothere whose magnum remains undescribed but the presence of which is already known at the site since the study of K. Heissig (1971).

UNDETERMINED RHINOS FROM FISKUS AND AUCHAS MINE

From Fiskus a very worn and poorly preserved upper right premolar (P 3/ or P 4/) was recovered. Its total length is 42 mm for a collar width of 52 mm. The ectoloph seems flat. Dimensions are compatible with the P 3/ of a Brachypothere or the P 4/ of a large true Acerathere.

From Auchas Mine there is an atlas not completely cleared from the sediment, and a totally encrusted mandibular fragment which was found during the field trip following the 1998 PSSA meeting at Windhoek.

CONCLUSIONS

Four mammal-bearing Miocene sites excavated since 1991 by the Namibia Paleontology Expedition have yielded rhinoceros remains: Langental, Fiskus, Auchas Mine and Arrisdrift, the last three being new.

At Langental a well preserved magnum was found. It probably pertains to *Brachypotherium heinzelini*, a half mandible of which was recovered from the site before the First World War and which was identified by K. Heissig (1971).

From Fiskus there is a very worn upper premolar, perhaps from an Acerathere or a Brachypothere.

An atlas vertebra and a mandibular fragment, both encrusted with sediment and thus specifically undeterminable, have been recovered from Auchas Mine.

A great number of rhino specimens were found at Arrisdrift. All but one of the 81 fossil pieces constitute

TABLE 13.

Compared dimensions of the fourth metatarsal of Diceros australis nov. sp. ap= anteroposterior; artic= articular; diam= diameter; dist= distal; horiz= horizontal; prox= proximal; tr= transverse.

	Arrisdrift PQ AD 253	*Chilotheridium pattersoni* Loperot	Loperot
Length	about 182	111	113
prox tr	44	41	40.5
prox ap	42	40	about 38,5
diaphysis tr	35.5	22.5	22.5
diaphysis ap	22.5	20.5	20
dist max tr	42	33	30.5
dist tr artic	41	34.5	32
dist ap	about 36	35.5	34.5

D. schleiermacheri

	n	mean	min.	max.
Length	2	153.50	152	155
prox tr	2	42.25	37	47.5
prox ap	1	50.00	50	50
diaphysis tr	2	27.75	26.5	29
diaphysis ap	2	29.25	28	30.5
dist max tr	2	36.00	35.5	36.5
dist tr artic	2	36.50	35	38
dist ap	2	42.50	42	43

D. gr. pachygnathus/neumayri

	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	8	148.31	138.5	166.5	9.05	6.10
prox tr	8	48.63	43	53	3.15	6.47
prox ap	8	46.88	42.5	51	2.90	6.19
diaphysis tr	8	32.12	30	35	1.64	5.11
diaphysis ap	8	29.00	24.5	32	2.79	9.62
dist max tr	8	41.12	37	45	2.62	6.36
dist tr artic	8	39.75	35.5	43	2.78	6.99
dist ap	8	42.75	40	45	1.93	4.51

Aceratheres

	n	mean	min.	max.	Stand. dev.	coeff. var.
Length	10	131.40	117.5	144	9.02	6.87
prox tr	11	40.95	37	44.5	2.08	5.08
prox ap	11	38.09	32.5	42.5	3.59	9.43
diaphysis tr	10	26.85	23	30	2.08	7.76
diaphysis ap	10	24.85	21	28	2.21	8.90
dist max tr	9	31.56	29	34.5	1.98	6.26
dist tr artic	8	30.25	27.5	35.5	2.87	9.47
dist ap	10	35.15	31	37.5	2.48	7.07

a homogeneous sample pertaining to a very large species of cursorial rhino. The exception is an isolated magnum which suggests a small to medium sized short-legged form, perhaps *Chilotheridium pattersoni*, a species described from Loperot in Kenya, the age of which is about the same as Arrisdrift, i.e. 17 Ma. 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 type 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. This rhino is *Diceros australis* nov. sp., so far the oldest known species of the subfamily.

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SUPERIOR CERVICAL VERTEBRAE OF A MIOCENE HOMINOID AND A PLIO-PLEISTOCENE HOMINID FROM SOUTHERN AFRICA

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ABSTRACT

The Miocene hominoid and Plio-Pleistocene hominid vertebral record is poor. In 1994, a complete atlas of a hominoid was found in breccia at Berg Aukas in Namibia. Its age was estimated to be middle Miocene (13 myr) on the basis of microfauna. This locality yielded the holotype of *Otavipithecus namibiensis* and the atlas could belong to the same genus. The specimen exhibits clear hominoid traits such as a weakly salient retroglenoid tubercle at the superior articular facet of the lateral mass, and a horizontal transverse process. This morphology of the transverse process is close to that of pygmy chimpanzees, gibbons and African colobines, suggesting that *Otavipithecus* was arboreal. This confirms the conclusions drawn from other parts of the skeleton. From the size of the atlas, a body weight of 15-20 kg is estimated for the Berg Aukas hominoid, which accords with previous estimates based on its teeth.

The second fossil considered in this paper is an axis from Swartkrans, SK 854, dated to nearly 1,8 myr. This axis is compared with another Plio-Pleistocene axis from Ethiopia, AL 333.101. SK 854 shows a morphology different from that of humans and AL 333.101, and also of apes. The South African axis was attributed to *Paranthropus* by Robinson (1972), and its morphology is probably typical of bipedalism associated with climbing.

KEYWORDS: Cervical vertebrae, hominoid, hominid, Miocene, Plio-Pleistocene, Namibia, South Africa.

INTRODUCTION

Man differs from other primates by his orthograde posture and his permanent bipedal locomotion. All non-human hominoids also show these two characteristics, but only occasionally. Postcranial elements, especially the vertebral column, have tended to be neglected in the reconstruction of hominid and hominoid phylogeny. Nevertheless, several studies on the vertebral column of extant primates point to functional and systematic differences between apes and humans (Ankel 1967 & 1972; Gommery 1993, 1994, 1995, 1996, 1998b; Schultz 1961; Shapiro 1993). Some observations have been made on fossil hominoids and hominids (Benade 1990; Conroy *et al.*, 1996; Gommery 1995, 1996 & 1997; Harrison 1991; Johanson 1982; Köhler & Moyà-Solà 1997; Sanders & Bodenbender 1994; Senut & Gommery 1997; Ward 1990, 1993 ; Ward *et al.* 1993; Leutenegger 1977; Sanders1998; Schmid 1983 & 1991).

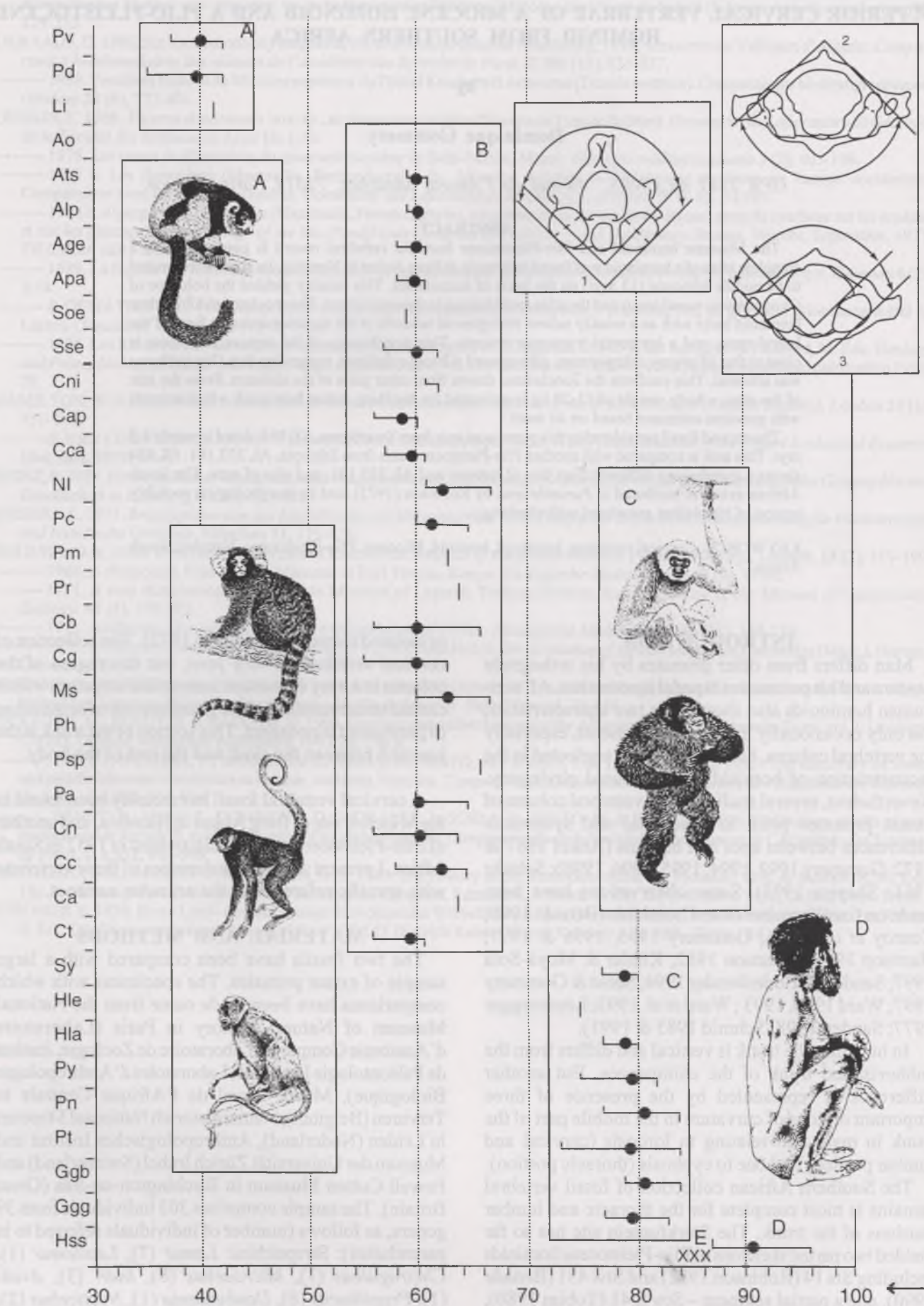
In humans, the trunk is vertical and differs from the subhorizontal trunk of the chimpanzee. But another difference is represented by the presence of three important regions of curvature in the mobile part of the trunk in man, two relating to lordosis (cervical and lumbar portion) and one to cyphosis (thoracic portion).

The Southern African collection of fossil vertebral remains is most complete for the thoracic and lumbar portions of the trunk. The Sterkfontein site has so far yielded two partial skeletons of Plio-Pleistocene hominids including Sts 14 (Robinson 1972) and Stw 431 (Benade 1990), and a partial segment – Stw 8/41 (Tobias 1980), or isolated elements (Robinson 1972). The collection of cervical vertebrae is very poor, but this region of the column is a very important anatomical structure which can aid understanding of the phenomenon of acquisition of permanent bipedalism. This section of the trunk is the junction between the skull and the rest of the body.

A cervical vertebral fossil has recently been found in the Miocene site of Berg Aukas in Namibia, and another of Plio-Pleistocene age was discovered in 1952 in South Africa. I present some characteristics of these vertebrae with specific reference to the articular surfaces.

MATERIAL AND METHODS

The two fossils have been compared with a large sample of extant primates. The specimens with which comparisons have been made come from the National Museum of Natural History in Paris (Laboratoire d'Anatomie Comparée, Laboratoire de Zoologie, Institut de Paléontologie Humaine, Laboratoire d'Anthropologie Biologique), Musée Royal de l'Afrique Centrale in Tervuren (Belgium), Natuurhistorich Nationaal Museum in Leiden (Nederland), Anthropologisches Institut und Museum der Universität Zürich Irchel (Switzerland) and Powell Cotton Museum in Birchington-on-Sea (Great Britain). The sample comprises 303 individuals from 39 genera, as follows (number of individuals referred to in parentheses): Strepsirhini: *Lemur* (7), *Lepilemur* (1), *Cheirogaleus* (1), *Microcebus* (8), *Indri* (3), *Avahi* (1), *Propithecus* (8), *Daubentonia* (1), *Nycticebus* (2),


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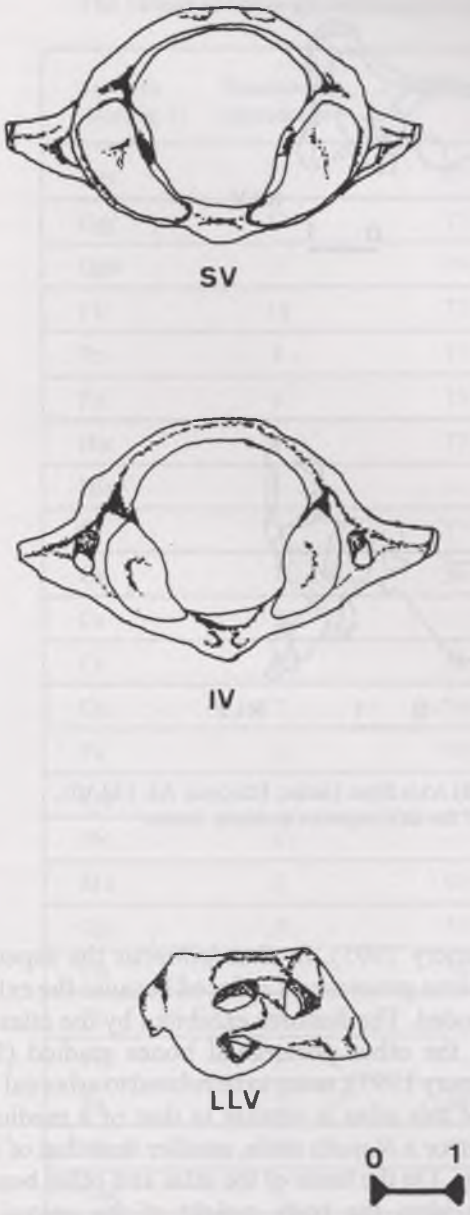


Figure 2. Atlas from Berg Aukas, Namibia. BA 104'91. SV: superior view; IV: inferior view; LLV: left lateral view.

Perodicticus (2), *Galago* (4); Tarsiers: *Tarsius* (1); Platyrrhini: *Callithrix* (1), *Leontopithecus* (1), *Aotus* (2), *Callicebus* (1), *Pithecia* (2), *Cacajao* (1), *Cebus* (16), *Saimiri* (6), *Ateles* (13), *Lagothrix* (2), *Alouatta* (11); Cercopithecoidea: *Cercopithecus* (24), *Cercocebus* (9), *Erythrocebus* (2), *Macaca* (9), *Papio* (9), *Mandrillus* (6), *Theropithecus* (2), *Nasalis* (4), *Colobus* (17), *Presbytis* (7); Hominoidea: *Hylobates* (15), *Symphalangus* (3), *Pongo* (6), *Pan* (35), *Gorilla* (29), *Homo* (37). This list includes an important sample of wild animals but the Strepsirhini listed include some zoo animals. The observations have been extended to other mammals such as rabbit, dog, cat, horse, cow, bear, lion, etc...

ANATOMICAL DIFFERENCES (Figure 1)

In previous studies (Gommery 1995 & 1997), I observed specific anatomical parts on the superior articular facet (*fovea articulares superiores atlantis*): the retro-glenoid tubercle. The distinction is based on the orientation of curvature of this part. The curvature is more or less cranial. The morphology permits one to distinguish four groups of extants primates: 1) Strepsirhini and *Tarsius*; 2) Platyrrhini and Cercopithecoidea; 3) apes and 4) humans. We observe the same morphological difference on the posterior part of the inferior atlas articular facet (*fovea articulares inferior atlantis*) and the superior axis articular facet (*facies articularis anterior*). We call these parts the homologous part of the atlas retro-glenoid tubercle (Gommery 1995, 1998a, 1999).

In this study we model three angles in different extant primates describing the orientation of the retro-glenoid tubercle and the homologous part on the atlas and axis (Figure 1 & Table 1). We have taken these measurements directly on the bones and also from X-Ray to confirm the data. The same four groups of extant primates show specific mean values: 1) 40° for Strepsirhini (range: 35° - 42°), 2) 60° for Platyrrhini (range : 55° - 67°) and Cercopithecoidea (range : 56° - 67°), 3) 80° for apes (range : 73° - 84°) and 4) 90° for humans (range : 87° - 96°).These angles represent different functional models: one, represented by Strepsirhini (e.g. Malagasy lemur),

Figure 1. The retro-glenoid angle (1) with the two homologous angles on the atlas (2) and axis (3).
Graph legend : Horizontal axis: values of angles in degrees; vertical axis: species of primates. For each species, the range is represented by the horizontal line, with the minimum data marked by the up-turned tick and the maximum data by the down-turned tick; the dot represents the mean.
Key to abbreviations: A) Strepsirhini: *Propithecus verreauxi* (Pv), *Propithecus diadema* (Pd), *Indri indri* (Ii). B) Platyrrhini: *Aotus trivirgatus* (Ao), *Alouatta seniculus* (Ats), *Alouatta palliata* (Alp), *Ateles geoffroyi* (Age), *Ateles paniscus* (Apa), *Saimiri oerstoedii* (Soe), *Saimiri sciureus* (Sse), *Cebus nigrivittatus* (Cni), *Cebus apella* (Cap), *Cebus capucinus* (Cca). - Cercopithecoidea: *Nasalis larvatus* (Nl), *Presbytis cristata* (Pc), *Presbytis melalophos* (Pm), *Presbytis rubicundra* (Pr), *Colobus badius* (Cb), *Colobus guereza* (Cg), *Mandrillus sphinx* (Ms), *Papio hamadryas* (Ph), *Papio sp.* (Psp), *Papio anubis* (Pa), *Cercopithecus nictitans* (Cn), *Cercopithecus cephus* (Cc), *Cercopithecus ascanius schmidti* (Ca), *Cercocebus torquatis* (Ct). C) Non-human Hominoidea: *Symphalangus syndactylus* (Sy), *Hylobates leuciscus* (Hle), *Hylobates lar lar* (Hla), *Pongo pygmaeus* (Py), *Pan paniscus* (Pn), *Pan troglodytes* (Pt), *Gorilla gorilla beringei* (Ggb), *Gorilla gorilla gorilla* (Ggg). D) Human: *Homo sapiens sapiens* (Hss). E) *Paranthropus*: SK 854
Measurement legends : 1 – angle of retroglenoid tubercule on atlas : dorsal angle corresponding to the lateral borders of retroglenoid tubercles. 2 – homologous angle of the inferior articular facets on atlas : ventral angle corresponding to lateral borders or inside borders on the posterior parts (homologous parts of retroglenoid tubercles) of inferior articular facets. 3 - homologous angle of the superior articular facets on axis : ventral angle corresponding to the lateral border or to the median axis on the posterior parts (homologous parts of retro-glenoid tubercles) of the superior articular facets.

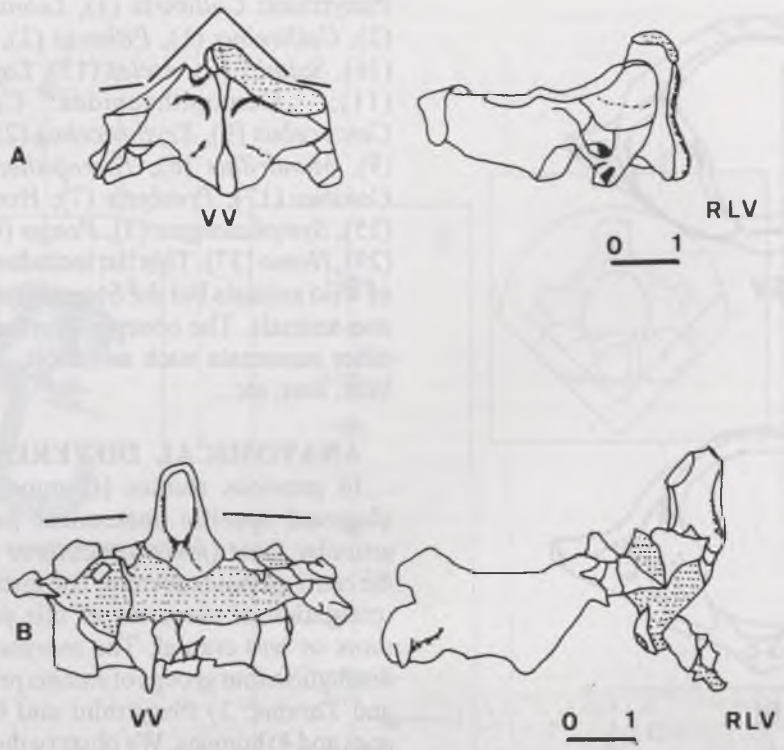


Figure 3. (A) Axis from Swartkrans, South Africa, SK 854; (B) Axis from Hadar, Ethiopia, AL 333.101. The line represent the transverse section of the different parts of the axis superior articular facets.
Abbreviations: VV, ventral view; RLV, right lateral view
Scale bar = 1 cm.

has low values and reveals a great capacity for flexion and extension movements; at the opposite extreme, the values for humans are high, and reveal a lesser capacity for flexion-extension movements.

Atlas BA 104'91 (Figure 2)

In northern Namibia, the fossiliferous breccia at Berg Aukas, near Grootfontein, dated by microfauna to the Middle Miocene (13 -12 myr), has yielded a hominoid, *Otavipithecus namibiensis* (Conroy & *et al.* 1992). The first remains, discovered in 1991 by a French-American team, consisted of a right partial mandible. In 1994, during acid preparation of a breccia block from this locality, Martin Pickford discovered a hominoid atlas BA 104'91 (Figure 2) (Conroy *et al.* 1996; Senut & Gommery 1997). On the atlas, the cranio-dorsal orientation of the glenoid cavities, especially the retroglenoid tubercles, suggest that movements of flexion-extension were powerful at the joint for the occipital condyles. The angle of the retroglenoid tubercle is 81°; the observed range for apes is 73° to 84° with a mean of 80° (Figure 1 & Table 1). The narrowed and elongated morphology of the transverse processes, close to that seen in *Pan paniscus* (the pygmy chimpanzee, or bonobo) and gibbons, would be related to a more extended lateral inclination of the head on the trunk. The aspect of the transverse processes is a long triangle in Bonobo, gibbons and African colobines and is different from the trapezoid transverse processes in terrestrial African cercopithecids (Gommery 1995). In *Otavipithecus* the aspect of the transverse processes is reduced because the extremities are eroded. The features exhibited by the atlas, as well as by the other postcranial bones studied (Senut & Gommery 1997), seem to be related to arboreal life. The size of this atlas is similar to that of a medium-sized baboon or a *Nasalis* male, smaller than that of a female bonobo. On the basis of the atlas and other bones, such as the ulna, the body weight of the animal can be estimated, compared with the same proportions of atlas and ulna of a medium size baboon and a *Nasalis* male, at roughly 15-20 kg (Jungers 1985). The same weight has been estimated based on the size of the molar on the mandible (Conroy *et al.* 1992).

Axis SK 854: Figures 3 & 4

The South African axis, SK 854 (Figure 3), was discovered at Swartkrans in Member 1, and its age is estimated at 1,8 million years (Robinson 1972; Brain 1993). We compare this axis with an Ethiopian axis AL 333-101 (Figure 3), dated to approximately 3,3 myr (from the DD2 and DD3 level of the Denen Dora Member of the Hadar locality AL 333 (Lovejoy *et al.* 1982; Walter 1994). These two axis specimens are the only ones known from the African Plio-Pleistocene hominid collection. The two specimens differ in the orientation of the superior articular facet which resembles a platform in the Ethiopian axis and is cone shaped near the odontoid process, and which describes a platform

TABLE 1.
The values of retro-glenoid angle with the homologous angles on the atlas and axis.

Species (See Fig. 1)	Number of specimens	Minimum	Maximum	Mean	Standard deviation
Hss	37	87	96	90.58	2.64
Ggg	12	77	83	79.67	1.92
Ggb	5	79	84	81.2	1.92
Pt	14	73	84	79.57	3.71
Pn	8	77	84	81	2.27
Py	6	75	82	78.83	2.79
Hla	5	77	80	78.6	1.34
Hle	1	—	—	75	—
Sy	5	77	80	78.6	1.34
Ct	7	56	61	59.28	1.8
Ca	1	—	—	64	—
Cc	7	58	65	61	2.94
Cn	7	56	64	60.14	2.54
Pa	3	60	65	62.67	2.52
Psp	1	—	—	66	—
Ph	1	—	—	62	—
Ms	2	60	67	63.5	4.95
Cg	5	55	63	60	3.39
Cb	7	56	66	60.43	3.41
Pr	1	—	—	64	—
Pm	1	—	—	63	—
Pc	2	60	65	62.5	3.53
Ni	3	61	67	63.67	3.05
Cca	5	57	61	59.2	1.48
Cap	2	56	60	58	2.83
Cni	3	61	62	61.33	0.58
Sse	3	57	62	60.33	1.53
Soe	1	—	—	59	—
Apa	2	58	61	59.5	2.12
Age	4	58	61	59.75	1.26
Alp	2	59	60	59.5	0.71
Ats	5	59	61	60.8	1.3
Ao	1	—	—	62	—
Ii	1	—	—	41	—
Pd	2	35	42	38.5	4.95
Pv	2	37	42	39.5	3.53

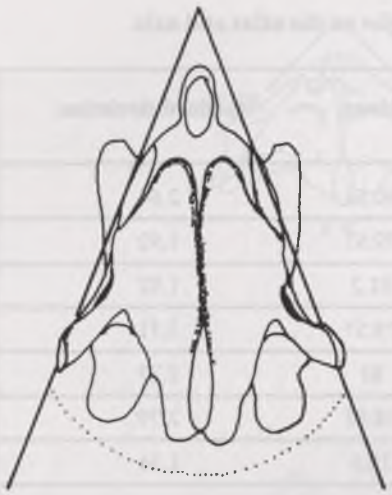


Figure 4:. Axis cone-shape (after Delattre 1924).
The superior articular facets are contained on a virtual cone-shape where the movements are localised in the articulation between atlas and axis. The cone shape axis is symbolized by the axis of the odontoid process

near the border in the South African axis. Another significant difference is the presence of a well-developed and sharp ventral crest on the vertebral body (*crista ventralis*) in the South African fossil. This crest ends in a prominent tubercle (*tuberculum anterius*). The ventral face on the vertebral body is very similar to the morphology in the bonobo, but unlike the Ethiopian fossil. The Ethiopian axis is more human in form.

Delattre (1924) described a cone-shaped superior articular surface of the axis in many mammals, especially primates, but with two isolated superior articular facets (Figure 4). The association of the superior articular facet with the odontoid process makes a functional plan of rotation but also an angulation with the vertebral body of the axis. The angulation of the odontoid is responsible for one component of the lordosis curvature of the spinal column. In the Ethiopian axis, the odontoid process is straight, whereas in the Swartkrans specimen, just the beginning of angulation of the odontoid process is observed. It seems that the odontoid process described a slight angulation.

The homologous angle of the superior articular facets of axis SK854 is 85° (Figure 1). This falls just between the apes (73° - 84°) and humans (87° - 96°). By comparison, the axis AL 333.101 has a homologous angle of 90°, the same value as the human mean.

The morphology of the vertebral body and superior articular surface of the axis reveal certain biomechanical constraints. The platform axis, as in AL 333.101, corresponds with compression forces typical of upright posture and permanent bipedy, as is the case in humans. The cone shaped axis corresponds with tensional forces associated with flexion-extension movements and the degree of opening depends on the particular systematic group. In extant hominoids, we consider two groups, one corresponding to man characteristed by permanent bipedy and the second group corresponding to apes, especially the great apes which are quadrupedal, have a semi-erect posture, practise knuckle-walking, climbing and very occasional bipedy. The Swartkrans specimen presents mixed characters, and suggests the presence of more flexion-extension movement than in humans and less than in great apes. This axis is perhaps more typical of bipedalism associated with climbing in the same way as some other Plio-Pleistocene hominid postcranial bones (Senut 1978, Senut & Tardieu 1985 & Tardieu 1979). The specimen was attributed to *Paranthropus* by Robinson (1972). In addition other Plio-Pleistocene superior cervical vertebrae confirms the presence of two locomotor groups in early hominids (Gommery 1995 & 1997).

CONCLUSION

The cervical vertebrae represent the junction between the head and the body. Understanding the evolution of the cervical trunk is very important for an understanding of the change from quadrupedalism to bipedalism. The only known African Miocene cervical vertebra is represented by BA 104'91 from Namibia. This atlas shows many characteristics found in arboreal hominoids and colobines. Some morphological characteristics resemble those seen in the pigmy chimpanzee, or bonobo. The conclusion, for the atlas accords with that based on other postcranial bones of *Otavipithecus* (Senut & Gommery 1997). In SK 854, a Plio-Pleistocene hominid, some characteristics are associated with one of the specific types of bipedalism of the first hominids. The South African axis presents the same locomotor characteristic as other East African Plio-Pleistocene superior cervical vertebrae. At the same time, another specimen presents the characteristics of permanent bipedalism as in humans. Although its systematic position is not clear, it may represent either *Homo* or *Praeanthropus* (Senut 1995 & 1996) or a specific Australopithecine lineage as *Australopithecus anamensis* (Coppens 1995).

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HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In:** Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of Mammal-like Reptiles*, 159-168. Washington, Smithsonian Institution Press.

ROMER, A.S. 1966. *Vertebrate Palaeontology* (3rd edn). Chicago, University of Chicago Press.

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in recognition of a lifetime of dedicated service to palaeontology

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