

Mio-Plio-Pleistocene geology and palaeobiology of the Etosha Pan, Namibia

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The Etosha Pan, northern Namibia, at nearly 5,000 km², is one of the largest in the world. A major hurdle to understanding the geological history of Etosha Pan has been the lack of dated horizons in the local stratigraphic record. We here report the discovery of fossil plants, invertebrates and vertebrates at several distinct horizons within the pan and its immediate vicinity, which reveal the presence of deposits ranging in age from Late Miocene to Late Pleistocene. Most of the floor of the pan consists of Late Miocene deposits whereas in islands and ridges within the pan and along its margins there occurs a discontinuous deposit of Pliocene, Pleistocene sediments up to 20 metres thick. Finally, there are discontinuous patches of green silts on Pelican Island at an altitude of ca 1093 metres, some 8-10 metres above the floor of the pan, which attest to a Late Pleistocene lacustrine episode. Similar aged deposits at the western end of Oshigambo Peninsula have yielded a rich and diverse mammalian fauna containing remains of the aquaphile bovid *Tragelaphus spekei* (the sitatunga).

The discovery of Mio-Pliocene fossils in Etosha is important as it helps to fill what used to be a large geographic gap in the African palaeontological map of this epoch. Late Miocene sites in particular, are poorly represented over much of the continent, being concentrated in the rift valleys of East Africa, the Chad basin, the Maghreb and north African littoral zone.

Introduction

The processes which led to the formation of Etosha Pan, northern Namibia, (Fig. 1, 2) are still a matter of debate, mainly due to a lack of dated stratigraphic horizons within the Tertiary and Quaternary sediments that blanket the Greater Etosha Basin (also known as the Owambo Basin) in which the pan occurs. At almost 5,000 km², Etosha Pan is one of the largest in the world, and it is accompanied by many smaller pans, especially on its western and northern sides. The immense dimensions of the pan have stimu-

lated discussions about its origins, because it has been argued that the usual processes which form small pans may not apply to such a huge one (Hutter, 1910; Jaeger, 1926; Jaeger & Waibel, 1921; Wellington, 1938, 1939).

Hipondoka (2005) wrote that « Etosha Pan is presently an aggradational landform, contrary to conclusions reached by recent studies. Aggradational phases alternated with erosive phases and phases of relative stability and soil formation ». In contrast, for Beugler-Bell & Buch, (1997) the pan's present day form was interpreted as being due to de-

flation.

In 2006 and 2007, Miocene and Pliocene fossils were found in the Etosha Basin, a discovery that provides constraints on the timing of geological activity within the depression. These age determinations will impact on the debate about the origins of Etosha Pan and its substrate. This paper is or-

ganised into several parts dealing first with the geological context of the Etosha Basin and its fossil record, followed by the palaeontology of the basin, examining the fauna and flora in stratigraphic order, by a discussion of the biochronological and palaeoenvironmental implications of the fossils, and completed by the conclusions.

Fossiliferous localities of Africa ranging in age from 8 to 4 Ma



Figure 1: Late Miocene and Early Pliocene fossiliferous localities of Africa. The Etosha occurrences help to fill out a huge gap that existed in the palaeontological map of the continent for this epoch. The Berg Aukas karst deposit near Etosha contains microfauna only, whereas the Etosha sites yield a rich and varied macrofauna.

Prior geological, geomorphological and palaeontological studies

The presence of Mio-Pliocene deposits (Andoni Formation) in the Etosha Basin (Hutter, 1910 ; Jaeger, 1926 ; Jaeger & Waibel, 1921 ; Wellington, 1938, 1939) has been reported on several occasions (Buch, 1996 ; Haddon, 2000 ; Hipondoka, 2005 ; Smith & Mason, 1991) but until recently there has been no direct evidence as to the age of the strata. In several papers the Andoni Formation has been broadly referred to the Oligo-Miocene (Buch, 1993 ; Smith & Mason, 1991).

The first fossils reported from the Etosha region were eggshell fragments of « *Struthio* » *oshanai* (now *Namornis oshanai*) (Sauer, 1966) from a borehole at Beisebvlakte (at a depth of 34 m) a few km northeast of the Etosha Pan (18°31'S : 17°04'E) . Similar struthious eggshells were subsequently found in the Namib Desert (Dauphin *et al.*, 1996 ; Mourer-Chauviré *et al.*, 1996 ; Pickford *et al.*, 1993 ; Senut & Pickford, 1995, Senut *et al.*, 1994, 1998) where they are restricted to basal Middle Miocene levels, and this is the likely age of the Beisebvlakte occurrence.

Subsequently stromatolites (oncolites) of unknown age were described (Martin & Wilczewski, 1972 ; Smith, 1980 ; Smith & Mason, 1991 ; Talma & Rust, 1997). Hipondoka (2005 ; Hipondoka *et al.*, 2006) reported the presence of Latest Pleistocene fossil vertebrates at Oshigambo Peninsula and of unknown age at the Ekuma River Delta area. Because the assemblages included remains of *sitatunga* and *Kobus* sp. the authors concluded that there must have existed perennial lacustrine conditions at the time of deposition. The latter interpretation obtains support from two additional lines of evidence ; a) the occurrence of raised beaches at Poacher's Point and in the Ekuma River valley, about 1.5 to 2 metres above the present day floor of the pan, and b) the presence of green silts on Pelican Island, 8-10 metres above the floor of the pan, where they unconformably overlie Plio-Pleistocene cal-

careous deposits (Poacher's Point Carbonate Member), and a widespread rubble horizon containing black sediment nodules (Miller, 2007) (Fig. 3).

The recent discovery of several fossiliferous levels spanning the Late Miocene, Middle Pliocene, Plio-Pleistocene and Holocene (Hipondoka, 2005 ; Hipondoka *et al.*, 2006) provides important constraints on interpretations of the stratigraphy, and therefore of the history, of the Greater Owambo Basin, and the Etosha Pan that occurs in it.

Geological context of the Etosha Basin

The regional geological context of the Etosha Depression (Fig. 2) has been extensively discussed on account of its petroleum potential (Haddon, 2000 ; Hedberg, 1979 ; Hipondoka, 2005 ; Miller, 1997) but most of the information about the subsurface deposits in the basin comes from seismic surveys and shallow boreholes (Miller, 1997).

Infilling a vast depression floored by Proterozoic rocks (the Great Etosha Basin or the Greater Owambo Basin as it is also known) extending from the Otavi Mountains, Namibia, in the south (Fig. 2), to Southern Angola in the north, is a thick sequence of Mesozoic deposits, in turn overlain by Tertiary and Quaternary sediments (Table 1). The Tertiary deposits are generally attributed to the Andoni Formation, an unknown thickness of greenish silts and clays with subordinate quartzite lenses. Miller (2007) formalised several names for subdivisions of the Andoni Formation, and in this contribution, we follow and extend his nomenclature.

Stratigraphy and age of sedimentary deposits exposed in Etosha Pan

The stratigraphy of sediments exposed in the Etosha Pan and around its margins has been summarised by Miller (2007) who subdivided the Andoni Formation of previous authors (Buch, 1996 ; Haddon, 2000 ; Hipondoka, 2005 ; Smith & Mason, 1991) into three members. The Etosha Pan Clay Mem-

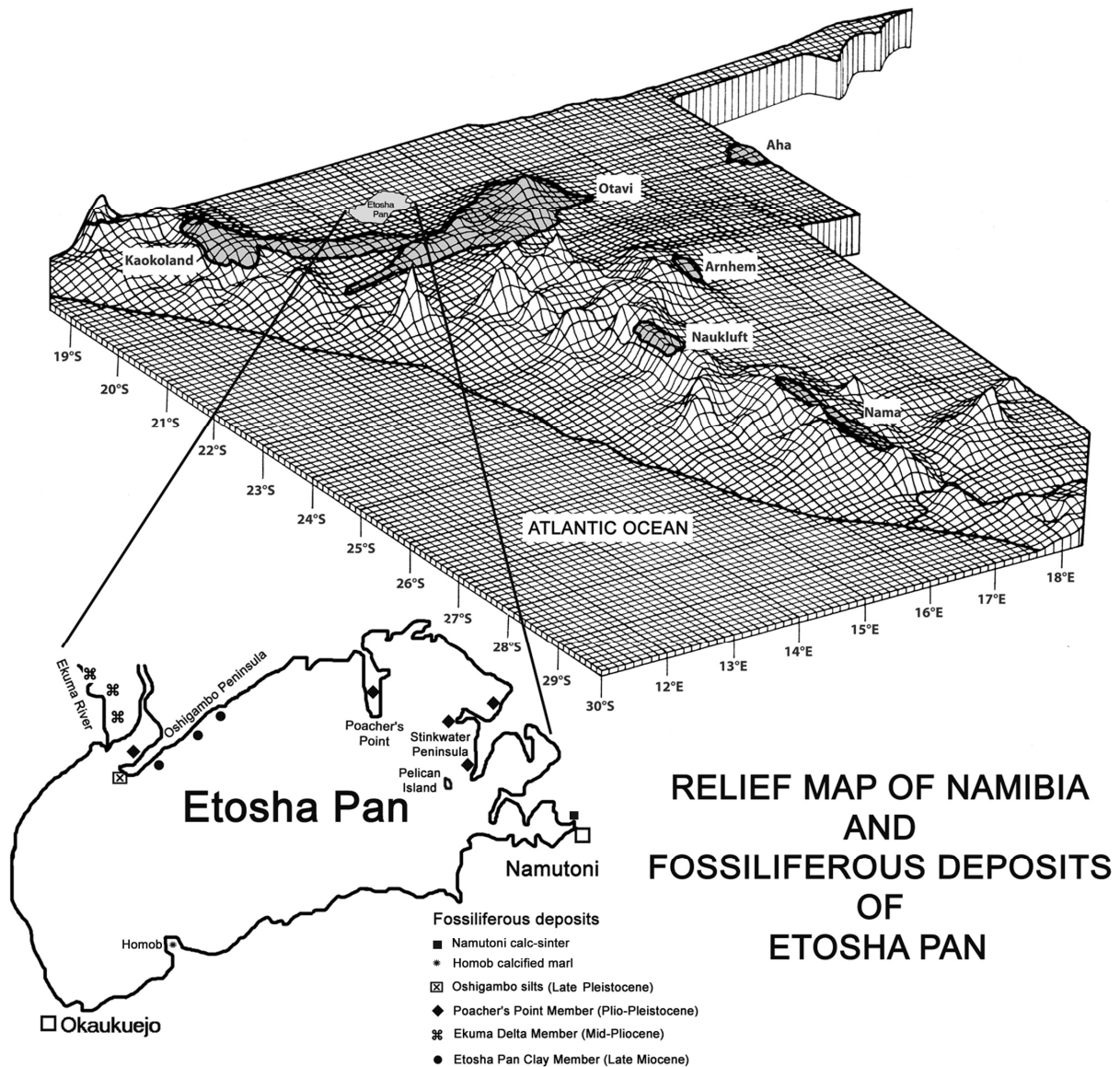


Figure 2: Location of the Etosha Pan, northern Namibia, and fossiliferous deposits discussed in the text. Dolomites of the Otavi Mountains and other parts of Namibia are highlighted by the thick line.

ber (EPCM) is exposed extensively in the floor of the pan, the Ekuma Delta Member (EDM) crops out widely in the Ekuma and Oshigambo drainages close to the pan, and the Poacher's Point Carbonate Member (PPCM) is exposed widely on steep ground along the northern flank of Oshigambo Peninsula, around the flanks of Poacher's Point, the Stinkwater Peninsula and Pelican Island. The PPCM is overlain by the Etosha Limestone, a calccrete of diverse origin, being a groundwater calccrete in the south, and a pedogenic calccrete in the north. Unconformably overlying the Etosha Limestone, is a

variety of poorly indurated to unindurated sediments comprising widespread but thin Oshigambo Pan-loess deposits, Okondeka lunette dunes, Pelican Island green silts, unnamed beach deposits about 1.5 – 2 metres above the present day pan floor (eg at Poacher's Point and in the Ekuma River Valley), calc-tufa deposits, calcified marls in water holes, and salt crusts. The geological sequence is summarised in Table 1.

The Poacher's Point Carbonate Member is overlain by the Etosha Limestone, a widespread calccrete up to 3 metres thick in the vicinity of the pan (Fig. 3), but consid-

Sediment unit	Thickness	Age	Fossil content
Aeolian sands (Okondeka lunette dunes), beach deposits, fans at river mouths, salt crusts	Up to 6 metres	Holocene to Present	Extant snails, <i>Struthio camelus</i> eggshells, Mammals
Unnamed calc-tufa at Namutoni	1 metre	Holocene	Planorbidae,
Unnamed calcified marl in Homob Waterhole depression	1 metre	Holocene	<i>Xerocerastus</i> , Planorbidae
Oshigambo Pan-loess	1-1.5 metres	Latest Pleistocene	Snails, <i>Struthio camelus</i> eggshells, Mammals
Pelican Island Green Silts	3 metres	Latest Pleistocene	
Elevated beach deposits (1.5-2 m above floor of pan)	0.5 – 2 metres	Latest Pleistocene	<i>Hodotermes</i> bio-constructions, reworked oncolites, <i>Melanoides tuberculata</i> , <i>Bellamyia unicolor</i> , <i>Mutela</i> sp.
Erosional unconformity	Incision of up to 20 metres	Middle to Late Pleistocene	
Etosha Limestone (fossiliferous calcrete and calcreted sands)	1-3 metres in the north, thicker in the south	Early Pleistocene	Oncolites (reworked), plant root networks, <i>Achatina</i> , <i>Xerocerastus</i>
Unnamed thin but widespread rubble horizon containing black sediment nodules (Ekuma and Oshigambo Valleys; Pelican Island)	10 cm	Early Pleistocene	Reworked fragments of fish and turtles from the Ekuma Delta Member
Poacher's Point Member (fossiliferous micro-oolitic strata becoming oolitic with Magadi-type chert on Pelican Island)	3-20 metres	Late Pliocene to Early Pleistocene	Oncolites, Ostracoda <i>Xerocerastus</i> , <i>Achatina</i> , <i>Succinea</i> , <i>Struthio camelus</i> eggshells
Ekuma Delta Member (cross-bedded clean quartzite with minor green clay)	50 cm to 2 metres	Middle Pliocene (ca 4 Ma)	<i>Bellamyia</i> , <i>Mutela</i> , <i>Clarias</i> , Cyclanorbinae, <i>Pelusios</i> , <i>Crocodylus</i> , Phoenicopteridae, <i>Struthio daberasensis</i> eggshells, Mammals
Etosha Pan Clay Member (green clay and silt with quartzite stringers)	At least 3 metres (probably considerably thicker)	Late Miocene (ca 6 Ma)	Oncolites, <i>Clarias</i> , Cyclanorbinae, <i>Pelusios</i> , <i>Crocodylus</i> , <i>Phoenicopterus</i> , Mammals
Beisebvlakte Borehole (?Andoni Formation)	At ca 34 metres depth	Base of the Middle Miocene (16 Ma)	<i>Namornis oshanaieggshells</i>
Subsurface mudstones, shales	--	Mesozoic	<i>Palynomorphs</i>
Subsurface dolomites, limestones	--	Proterozoic	<i>Stromatolites</i>

Table 1: Stratigraphic succession in the north and east parts of the Etosha Pan, Namibia.



Figure 3: Stratigraphic succession at Poacher's Point, Etosha Pan, Namibia.

erably thicker in the south towards the Otavi Mountains (Gevers, 1930 ; Miller, 2007). Unconformably overlying an eroded and deeply incised surface of calcrete and older rocks, there is a series of unindurated or weakly indurated lacustrine, marginal lacustrine, fluvial, aeolian and pedogenic deposits, and salt crust (Beugler-Bell & Buch, 1997 ; Buch, 1993 ; Buch & Zoller, 1992 ; Buch *et al.*, 1992 ; Rust, 1984).

The Late Pleistocene Oshigambo Peninsula fossils (Hipondoka, 2005 ; Hipondoka

et al., 2006) occur in grey to yellow clays and silts representing an accumulation of dust derived from the floor of Etosha Pan which was trapped and fixed by vegetation growing on its margins ; These are fine sand, and the ridges are essentially shorelines. These loess-like deposits are here named the Oshigambo Pan-loess, which is a widespread but thin horizon (up to 1.5 metres) that extends over much of the Greater Etosha Basin, but is absent from pans in the region. It unconformably overlies the Andoni Forma-

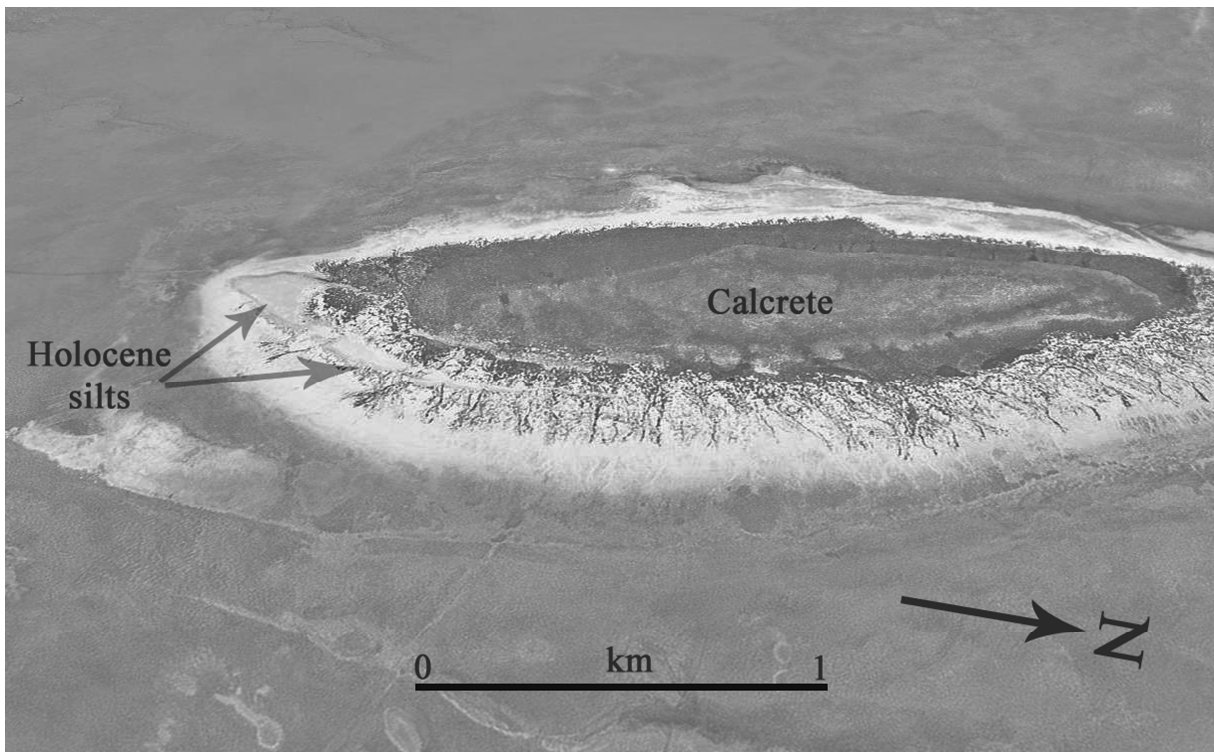


Figure 4: Oblique view of Pelican Island from the East, showing the distribution of the Pelican Island Green Silts (Holocene) on the southern end of the island. Note also the Etosha Calcrete which forms the resistant cap of the island. Image modified from Google Earth.

tion, the Etosha Limestone and the raised beach deposits and is of Latest Pleistocene age (Table 1). Another, more localised latest Pleistocene deposit occurs on the southern end of Pelican Island (Fig. 4) and consists of green silts which drape the incised margins of the island.

Geological processes active in the Etosha Basin

At present there is a complex interplay of erosion, sediment transportation, deposition and diagenesis within the Greater Etosha Basin, with a net loss of fine sediment and salts from Etosha Pan itself, principally by deflation accompanied by short to long distance aeolian transportation (Fig. 5) (Bittner & Plöthner, 2001 ; Bryant, 2003 ; Buch, 1997 ; Buch & Zoller, 1992 ; Buch *et al.*, 1992 ; Engert, 1997 ; Hipondoka, 2005 ;

Hipondoka *et al.*, 2004b, 2006; Kempf & Hipondoka, 2003 ; Lindeque & Archibald, 1991 ; Rahm & Buch, 1997 ; Rust, 1981, 1984, 1985 ; Stuart-Williams, 1992 ; Talma & Rust, 1997). There is also considerable aeolian and aquatic redistribution of sand and silt within the confines of the basin (Hipondoka *et al.*, 2004a ; Beugler-Bell & Buch, 1997) and much sediment is brought into the pan by seasonal rivers flowing in from the north and to a lesser extent from the south. The southern margins of the basin have experienced widespread, active groundwater calcrete genesis with the build-up of large, low angle, megadomes of dolomitic carbonate which often have a depression at the top in which water holes occur (Gevers, 1930 ; Rahm & Buch, 1997) whereas the northern parts of the basin experienced pedogenic calcrete formation, often with the preservation of extensive rhizolith networks.



Figure 5: Dust storm on Etosha Pan, 19th November, 2007. The storm front was about 40 km wide and the height of the advancing dust cloud was ca 1 km. Much dust settled onto vegetated ground (dark horizontal features in the background) but some was blown right out of the Etosha Basin towards the Atlantic Ocean.

Sedimentology and Palaeoenvironment

A comprehensive study of the Etosha palaeoenvironment was carried out by Hipondoka (2005) who was interested in the origins and development of the Etosha Pan. His studies revealed that many of the previous hypotheses about pan formation are debatable, even if much of the geological and

geomorphological observation upon which they were based is sound. Part of the uncertainty about the origins and history of the pan relates to the fact that the sedimentary deposits lacked precise geological age control, and this chronological uncertainty impacted on ideas concerning processes and rates of pan formation. Various dating methods have been tried, but most of the deposits

are beyond the range of the ^{14}C method or the methods used are inherently imprecise.

The Andoni Formation comprises lacustrine (green silts and quartzite lenses of the Etosha Pan Clay Member), fluvio-lacustrine (quartzite stringers and lenses in the Ekuma Delta Member) and shallow-water carbonates (micro-oids of the Poacher's Point Carbonate Member). This succession suggests a progressive infilling of a palaeolake in the Etosha Basin, resulting in a shallowing upwards sequence of deposits. The bulk of the fauna from this formation, in particular the fish, turtles and crocodiles, belongs to fresh water species, whereas the fla-

mingos indicate a saline or alkaline environment. The presence of chert nodules in certain localities at Poacher's Point and Pelican Island (Fig. 6) similar to those that formed in Lake Magadi, Kenya, suggests that at some stages of the lake basin development, there must have been hyper-alkaline conditions (pH greater than 12). These cherty deposits occur *in situ* in the Poacher's Point Carbonate Member at Pelican Island (Fig. 6). As the palaeolake became shallower and shallower, there was a progression from freshwater deposition in the Late Miocene to hyper-alkaline deposition during the Plio-Pleistocene.

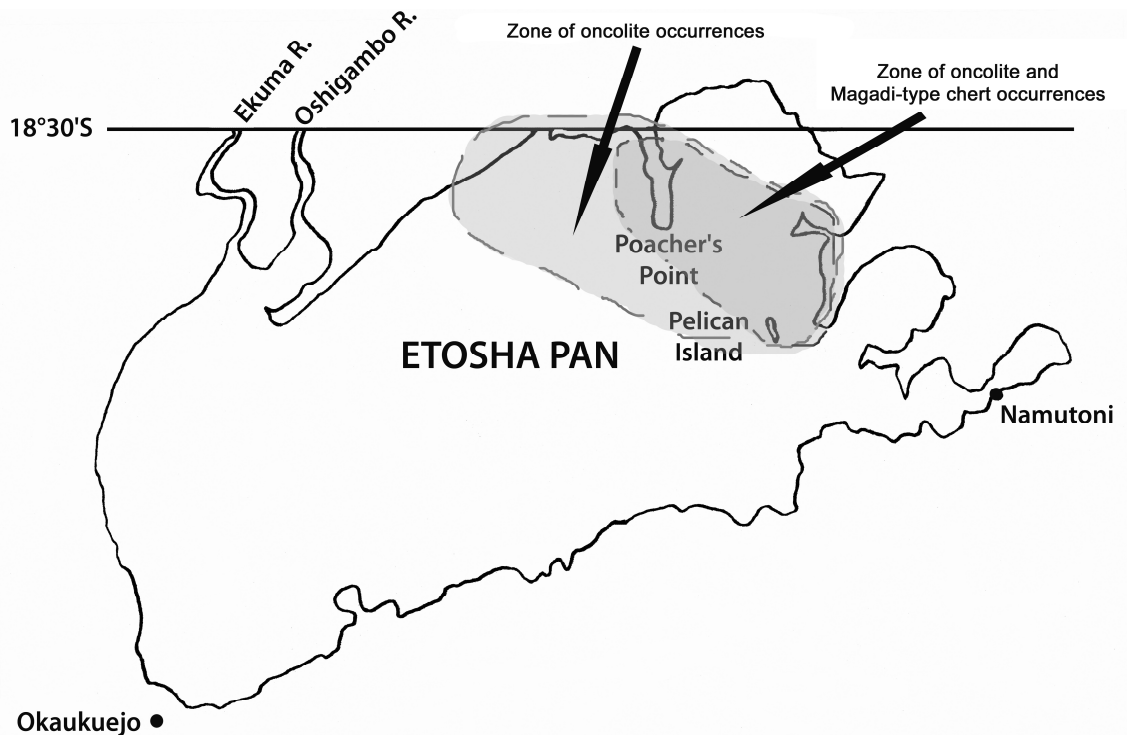


Figure 6: Distribution of oncolites and Magadi-type chert nodules in Etosha Pan. These deposits attest to a highly alkaline depositional environment during the Plio-Pleistocene.

The Etosha Pan Clay Member and the Poacher's Point Carbonate Member host abundant oncolites (Fig. 7, 8). The richest *in situ* occurrences of oncolites occur at the Stinkwater Peninsula and Pelican Island, but they occur widely in the pan (Fig. 6).

The Ekuma Delta quartzite and green silts contain rich assemblages of freshwater gastropods (*Bellamyia unicolor*) and bivalves (*Mutela* preserved as articulated couplets) which indicate freshwater deposition and

well oxygenated waters. The abundant presence of rhizoliths and casts of tree trunks *in situ* in the quartzites indicate shallow water deposition followed by subaerial exposure.

The Poacher's Point Member at Oshigambo and Poacher's Point comprises a 15-20 metre thick micro-oid horizon containing abundant arid-adapted terrestrial snails (small *Achatina*, *Xerocerastus* and *Succinea*) indicating a semi-arid to sub-humid regional environment. It also contains oncolites. At



Figure 7: Abundant oncolites occur in the Poacher's Point Carbonate Member on the northern margin of the Stinkwater Peninsula. The outcrop has been affected by calcrete pedogenesis.

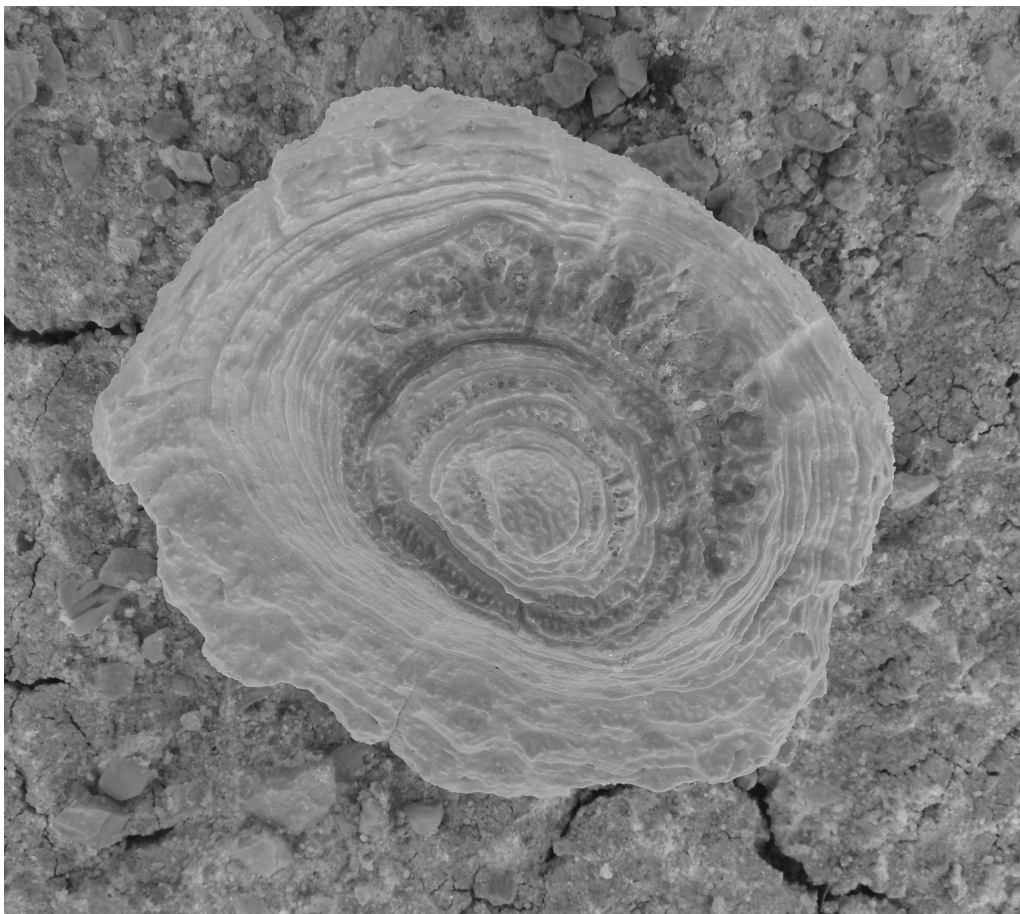


Figure 8: Naturally sectioned and slightly weathered oncolite from the western margin of Poacher's Point, showing multiple growth phases (diameter of specimen ca 25 cm).

Pelican Island, this unit contains limestone horizons comprised of ooliths up to 2 mm in diameter (Fig. 9), interbedded with horizons containing Magadi type chert plates. The latter deposits indicate highly alkaline condi-

tions in palaeolake Etosha during the early Pleistocene, contrasting with the fresher conditions that likely prevailed earlier in its history.

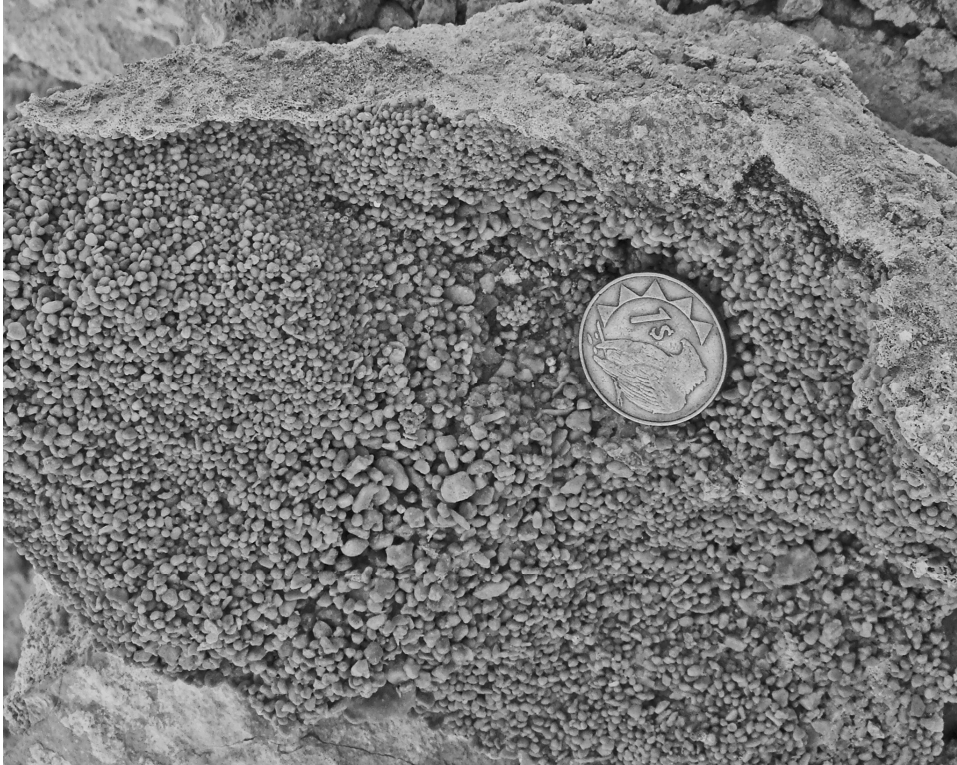


Figure 9: Oolitic limestone in the Poacher's Point Carbonate Member at Pelican Island, Etosha Pan, Namibia.

The Etosha Limestone (pedogenic and groundwater calcrete) contains termite hives (*Hodotermes*) and abundant terrestrial snails, similar to those that occur in the region today. The discovery of reworked oncolites in the calcrete that caps the cliffs at Poacher's Point, suggests that there was a lake at this altitude (1120 masl) well above the present day floor of the pan (1084 masl). Abundant oncolites occur along the edges of the Etosha Pan at Stinkwater Peninsula and at Pelican Island, associated with the Poacher's Point Carbonate Member of the Andoni Formation. Similar oncolites have been observed littering the floor of the Etosha Pan at various localities where they lie on green silts of the Etosha Pan Clay Member (Fig. 6).

Beach deposits are preserved on a terrace ca 1.5-2 metres above the present day floor of the pan at Poacher's Point and similar deposits occur in the Ekuma River Valley, stratigraphically between the Ekuma

Delta Member beneath, and the Oshigambo Pan-loess above. In both areas the beach deposits are fossiliferous, those at Poacher's Point yielding calcified termite hives in indurated sand which also contains quantities of reworked oncolites, and those at Ekuma containing abundant shells of *Melanoides tuberculata* and rarer shells of *Mutela* sp. and *Bellamyia unicolor*. These pale orange, partly calcified beach deposits underlie the Oshigambo Pan-loess deposits, and they attest to widespread lacustrine conditions at the time of deposition.

Tertiary and Quaternary Palaeontology of the Etosha Basin

The palaeontological descriptions that follow are arranged in stratigraphic order. This approach leads to some repetition, but it yields a better comprehension of the content of each fauna and thereby provides a surer



Figure 10: Section in the east bank of the Ekuma River Valley exposing at the base, quartzite of the Ekuma Delta Member, above which lies a pale orange silty sand horizon 1.5 metres thick (small eroded embayment surrounded by vegetation) rich in lacustrine molluscs. The top of the succession comprises 1 to 1.5 metres of Oshigambo Pan-loess, on which the vegetation is growing.

foundation for palaeoenvironmental and bio-chronological studies which flow from the faunal study.

Fauna from the Etosha Pan Clay Member of the Andoni Formation

In Etosha Pan, green silts and quartzites of the Etosha Pan Clay Member of the Andoni Formation have yielded abundant vertebrate fossils (Fig. 15-19) from several distinct localities along the northern rim of the pan. By far the most common fossils are cranial and skeletal fragments of clariid fish which are accompanied by scutes of freshwater turtles and crocodiles as well as leg bones of flamingos, and rarer terrestrial mammal remains. Deposition in shallow lacustrine conditions, near end points of rivers flowing into the palaeolake appears to have occurred.

Bivalvia (MP)

Internal and external molds of a large bivalve were found in quartzite of the EPCM on the south side of the Oshigambo Penin-

sula. The dimensions and shape of the specimens suggest a mutelid (Fig. 12). The specimens are poorly preserved but they probably belong to *Mutela* sp.

Pisces (HJ)

The fish bones collected in the green silts of the EPCM belong above all to the skull roof, ornamented in the characteristic fashion of Siluriformes, in which the shape and distribution of granules is typical of that of Clariidae (*Clarias*, *Heterobranchus*). Among the other skull bones, the commonest are articulars, dentaries and mesethmoids. The cleithral belt has yielded abundant pectoral spines and a few fragments of cleithrum. Vertebrae are abundant, but determining their position along the vertebral column necessitates a detailed comparison with extant Clariidae. Of these elements of the skeleton, only the pectoral spines permit an accurate identification. They possess well developed parallel striae along the cleithral articular surface, a character that is typical of the genus *Clarias* (Gayet & Van Neer; 1990). The sample is monospecific, without



Figure 11: Outcrops of Pelican Island Green Silt reposing unconformably on an incised rubble-covered erosional terrace at Pelican Island, Etosha. A) the silts (to left of the people) drape an incised topography some 10 metres above the floor of the pan (southeast edge of Pelican Island), B) the geologist is standing on Pelican Island green silts which drape a rubble covered slope beneath a cliff of Etosha Pan Clay Member locally rich in oncolites (the undercut in shadow) and Poacher's Point Carbonate Member (cliff forming strata) (southern end of Pelican Island).

any sign of another taxon. We therefore identify the Etosha fossils as Siluriformes, Clariidae, cf. *Clarias* sp.

Employing the equations developed for the genus *Clarias* by Van Neer & Lesur (2004), we can estimate the dimensions of individuals represented by fossil at Etosha, by measuring mesethmoids, dentaries, ar-

ticulars, quadrates, operculars, urohyals, cleithra and pectoral spines (Tab. 2, Fig. 13). Most of the specimens are large with the size profile centred on 70 cm, and the largest reaching a length of 110 cm. Individuals smaller than 50 cm are undoubtedly present at Etosha but would require fine screening to sample.



Figure 12: ET 55'07, internal and external molds of shells of *Mutela* sp., in quartzite of the Etosha Pan Clay Member, Etosha, Namibia.

Dimensions (cm) / Samples	40	50	60	70	80	90	100	110	120
ET16'07		1		2	1				
ET28'07			2	8	3	2	1	1	
ET35'07		4	5	4	2			1	
ET43'07			3	2	3	1	1		
ET47'07			1						
ETOSHA total	0	5	11	16	9	3	2	2	0

Table 2: Dimensions (in cm) calculated for individual specimens of *Clarias* sp.

Monospecific assemblages of *Clarias* are common in shallow, poorly oxygenated waters of Africa. *Clarias* are fish that can survive in anoxic waters thanks to a certain number of physiological and anatomical adaptations. They possess two respiratory organs derived from their pharyngeal cavity,

which permits them to obtain oxygen directly from the air. Assemblages comprising individuals of all sizes can be found together embedded in mud around desiccated water holes during the dry season (Paugy *et al.*, 2003).

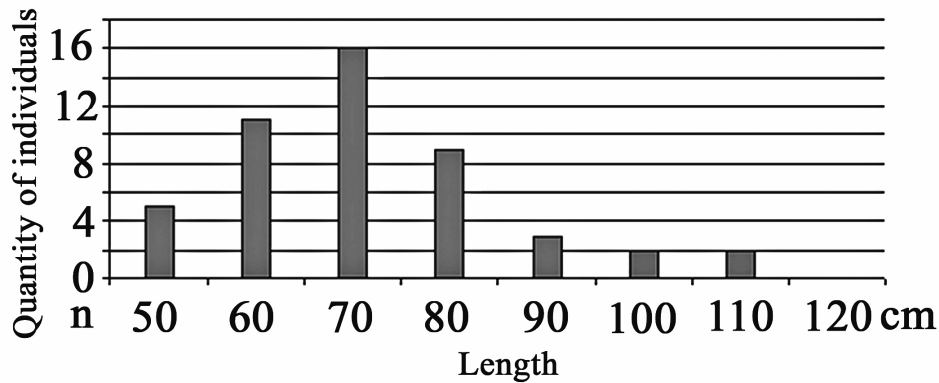


Figure 13: Profile of dimensions (preliminary) of *Clarias* sp. from the Etosha Pan Clay Member of the Andoni Formation, Etosha.

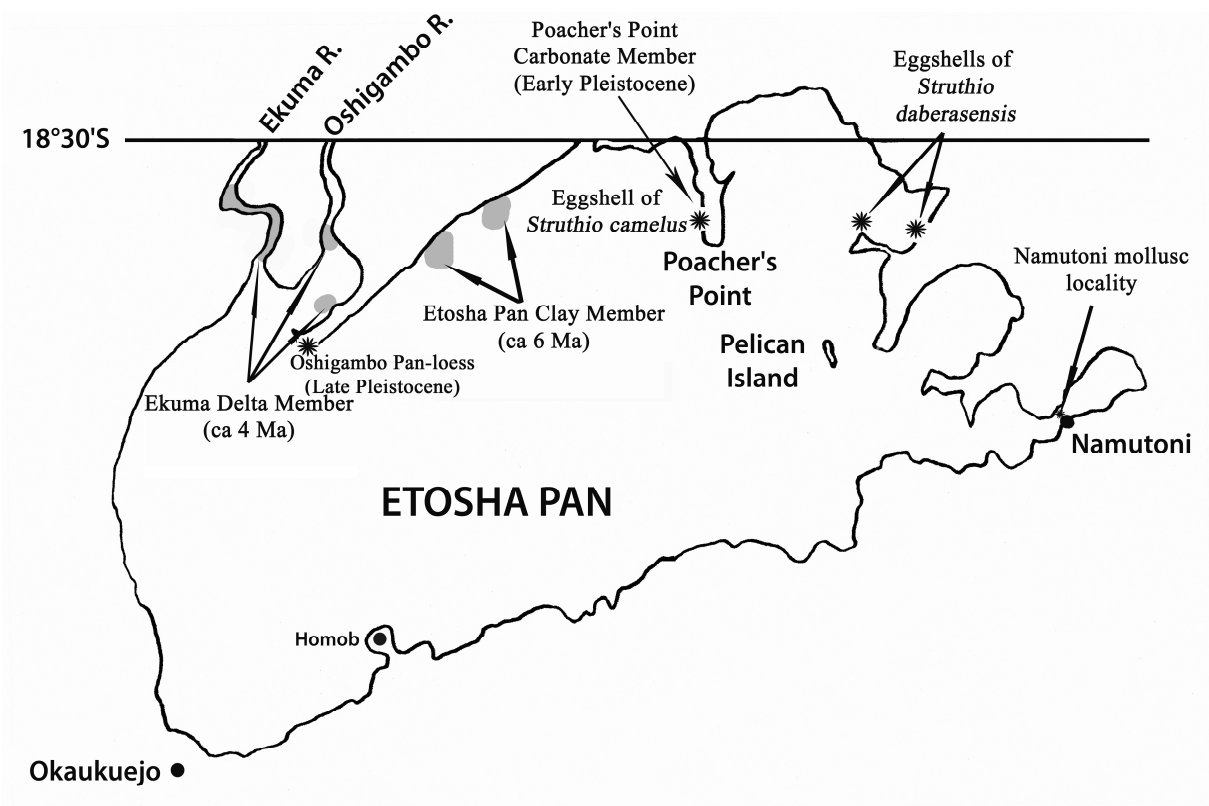


Figure 14: Main Late Miocene, Pliocene and Pleistocene vertebrate fossil localities at Etosha Pan.

Chelonia (de Lapparent de Broin, pers. comm.)

Pelusios is represented in the EPCM by several scutes (ET 34'07) (Fig. 15) with the characteristic surface texture of the genus, but without ridges and pustules. The grooves corresponding to the edges of the shell that overlies the scutes is clearly visible, as are growth ridges (Fig. 15 B).

Cyclanorbidae is represented in the EPCM by a characteristic scute (ET 33'07)

which is patterned with anastomosing worm-like ridges and bony pustules characteristic of this family (de Lapparent de Broin, pers. comm.) The scute is dorsally concavo-convex round its margin (Fig. 16 A) and possesses an apophysis at one corner.

The two chelonian taxa from the EPCM are freshwater turtles that are widespread in tropical Africa (de Lapparent de Broin, 2000).

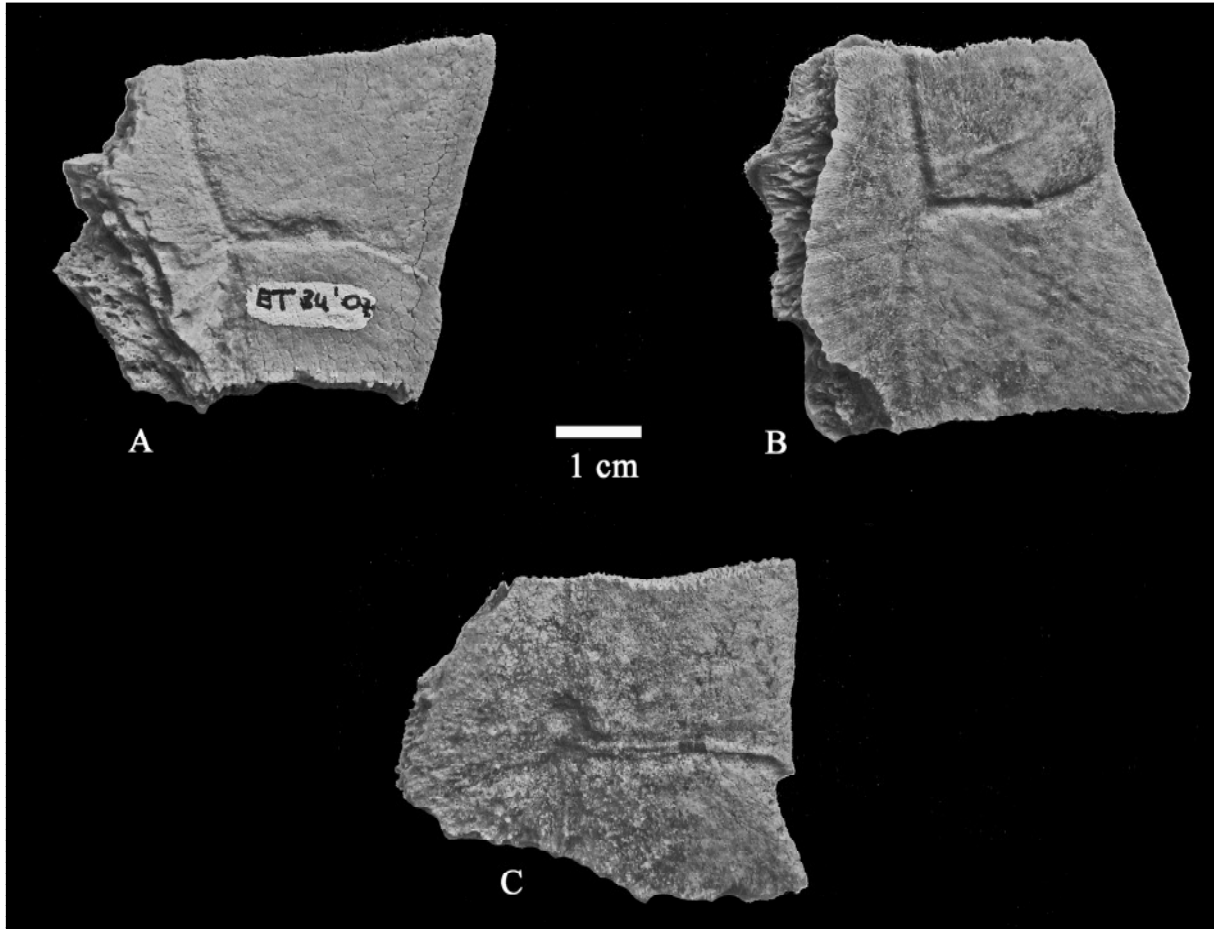


Figure 15: ET 34'07, *Pelusios* scutes from the Etosha Pan Clay Member, south of Oshigambo Peninsula, Etosha, Namibia.

Crocodylia (MP)

Crocodyles are common in the EPCM, being represented by cranial fragments, vertebrae and appendicular elements and by abundant scutes, some of large dimensions. Teeth are relatively rare.

Phoenicopteridae (CM-C)

Order Phoenicopteriformes

Family Phoenicopteridae

Phoenicopterus ruber Linnaeus, 1758

Material

ET 42'07 Right tibiotarsus, distal part, female size

ET 42'07 Left tarsometatarsus, proximal part and fragment of shaft, female size

ET 26'07 Right tibiotarsus, distal part, male size

ET 26'07 Right tarsometatarsus, fragment of

shaft, female size

Description and comparisons -

Comparison with recent forms

The Etosha fossils (Fig. 16 B-D) display the morphological characteristics of the genus *Phoenicopterus*, the Greater Flamingo, and differ from the genus *Phoeniconaias*, the Lesser Flamingo. In *Phoeniconaias*, on the distal part of the tibiotarsus, on the caudal side, the trochlea cartilaginis tibialis (Baumel and Witmer, 1993) is not very projecting caudally and not very developed in the proximo-distal direction. In distal view, the two cristae trochleae are almost symmetrical and are separated by a sulcus directed proximo-distally and situated in a median position. In *Phoenicopterus* the trochlea cartilaginis tibialis is strongly projecting caudally and more developed proximo-distally. The crista trochleae later-

alis (external condyle in Howard, 1929) is more projecting caudally than the crista trochleae medialis (internal condyle in Howard, 1929). These two cristae are separated by a proximo-distally directed groove which is closer to the medial side and the crista trochleae medialis has the shape of a cutting edge. On the tarsometatarsus, in *Phoeniconaias*, the eminentia intercotylaris in proximal view makes a medio-laterally elongated ridge, while in *Phoenicopterus* it makes a tubercle more rounded in the dorso-plantar direction and more projecting in the proximal direction. In *Phoenicopterus* there is a conspicuous narrowing between the proximal articular surface and the hypotarsus, while in *Phoeniconaias* this narrowing is barely perceptible.

Both tibiotarsi from Etosha are characterized by the strong projection of the trochlea cartilaginis tibialis in the caudal direction. However this characteristic is subject to a certain amount of variation in the extant forms of *Phoenicopterus ruber*. This characteristic can be expressed by the ratio Distal Depth : Distal Width (Table 3). Inside the same subspecies, in *P. ruber ruber*, the Caribbean Flamingo, which lives in the Caribbean and the Galapagos, as well as in *P. ruber roseus*, the Rosy Flamingo, which lives in Eurasia and Africa, the females have a larger D/W ratio than the males, which corresponds to a trochlea cartilaginis tibialis proportionally more projecting than that of the males. In addition, in the subspecies *P. ruber ruber*, both sexes have a D/W ratio greater than both sexes of *P. ruber roseus*, thus a trochlea cartilaginis tibialis proportionally more projecting. This last characteristic had already been reported by L. Miller (1944). For the two tibiotarsi from Etosha, ET 26'07, male size, and ET 42'07, female size, the D/W ratios are included in the variation range of both extant subspecies of *Phoenicopterus ruber*.

The other characteristics of the Etosha form are the wide distal opening of the canalis extensorius, which is almost circular on the tibiotarsus ET 26'07, male size. This characteristic is also variable in the extant

forms: some individuals have an elliptical opening, medio-laterally elongate and proximo-distally narrow, and some others have an almost circular opening. The shape of the trochlea cartilaginis tibialis is also variable, the extant small-sized individuals often have a proximo-distal sulcus situated closer to the medial side, and a crista trochleae medialis with the shape of a cutting edge, as in both specimens from Etosha.

The dimensions of the tibiotarsi and tarsometatarsi from Etosha are included in the variation range of both extant subspecies of *Phoenicopterus ruber* and are larger than those to the extant species *Phoeniconaias minor*.

Comparison with fossil forms

An extinct genus and species of flamingo, *Leakeyornis aethiopicus*, was described from the early and middle Miocene of Kenya (Dyke and Walker, 2008; Harrison and Walker, 1976; Pickford, 1986; Rich and Walker, 1983). In *Leakeyornis aethiopicus*, on the tibiotarsus, the prominence on the distal end of the pons supratendineus is lower and less pronounced than in the extant flamingos, the proximal opening of the canalis extensorius is narrow, the sulcus extensorius running proximal to it is deep and well defined, the distal opening of the canalis extensorius is directed antero-distally, not anteriorly. Still in *Leakeyornis*, on the tarsometatarsus, the shelf between the articular surfaces and the hypotarsus does not slope off posteriorly at such a high angle as in the extant flamingos (Rich and Walker, 1983). The characteristics of the Etosha flamingo remains correspond to the genus *Phoenicopterus* and differ from the genus *Leakeyornis*, and they are larger than *L. aethiopicus*.

Phoenicopterus floridanus was described on the basis of a distal part of tibiotarsus from the Pliocene of the Bone Valley Fm., in Florida (Brodkorb, 1953). The measurements of seven distal parts of tibiotarsus of *P. floridanus*, from the same locality, are given by Olson and Rasmussen (2001). One of the main specific characteristics given by P. Brodkorb, i.e. the low value of the ratio D/

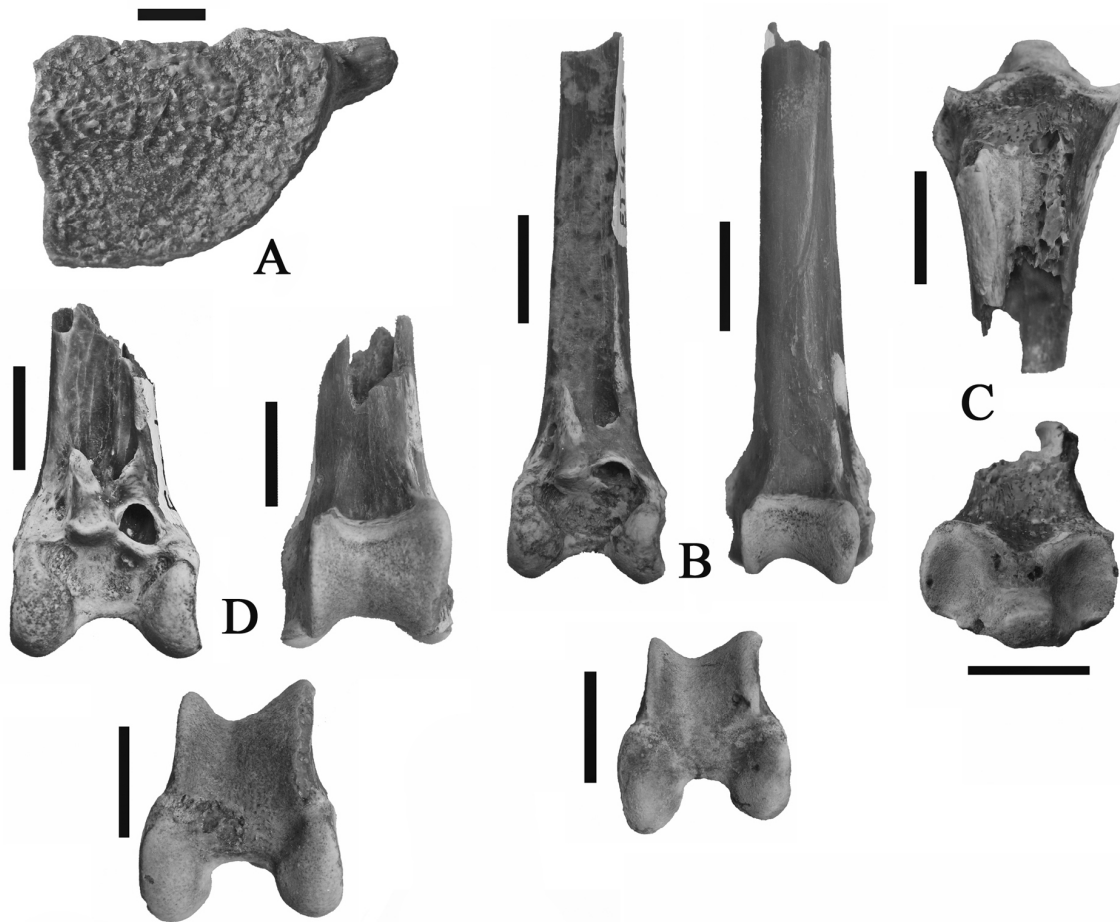


Figure 16: Vertebrates from the Etosha Pan Clay Member, northern rim of Etosha Pan, Namibia (scale bars : 1 cm). A) ET 33'07, Cyclanorbidae scute ; B) *Phoenicopterus ruber*, ET 42'07, right tibiotarsus, distal part, female size, cranial, caudal, and distal views ; C) *Phoenicopterus ruber*, ET 42'07, left tarsometatarsus, proximal part, female size, dorsal and proximal views ; D) *Phoenicopterus ruber*, ET 26'07, right tibiotarsus, distal part, male size, cranial, caudal, and distal views.

W (Distal width: 16.5; Distal of lateral condyle: ca. 17.6; D/W: 1.067), is not confirmed when a larger sample is available (Mean of distal depth: 18.3; mean of distal width: 15.3, D/W: 1,196). The dimensions of *P. floridanus* are almost entirely included in the range of variation of the extant *P. ruber*. Another specific characteristic of *P. floridanus* is the small width of the trochlea cartilaginosa tibialis in relation to the distal width. This characteristic is not present in the Etosha forms where the width of this trochlea is comparable to that of the extant forms.

Phoenicopterus stocki was described in the Rincón Pliocene of Chihuahua, Mexico, the holotype of which is a distal part of tibiotarsus (L. Miller, 1944). It is very small and the distal width is comparable to that of

Phoeniconaias minor, but ratio D/W (1.255) is larger than in *P. minor* and comparable to the values found in *Phoenicopterus ruber*.

Another genus, *Phoeniconotius*, and another species of *Phoenicopterus*, *P. novae-hollandiae*, were described in the late Oligocene or the early Miocene of Australia (A. H. Miller, 1963). They are only represented by distal parts of tarsometatarsi and they are much older than the Etosha specimens.

In conclusion, the fossil flamingos from Etosha can be ascribed to the extant species, *Phoenicopterus ruber*. The other data from the literature show that a form very close to the extant species is already present in the Pliocene (Olson and Rasmussen, 2001).

Tibiotarsus	Distal width	Distal depth	Ratio D/W
ET 26'07	18.0	22.3	1.239
ET 42'07	14.3	17.3	1.210
<i>Phoenicopterus ruber ruber</i>			
males, extremes	15.8-17.3	18.9-21.2	1.16-1.28
mean (n)	16.66 (9)	20.01 (9)	1.207 (9)
females, extremes	14.3-17.3	16.5-20.0	1.10-1.30
mean (n)	15.30 (10)	18.36 (10)	1.198 (10)
<i>Phoenicopterus ruber roseus</i>			
males, extremes	16.7-19.0	19.4-20.6	1.07-1.19
mean	17.98 (4)	20.15 (4)	1.123 (4)
females, extremes	14.4-17.0	17.9-18.5	1.09-1.24
mean	15.93 (3)	18.23 (3)	1.146 (3)
<i>Leakeyornis aethiopicus</i>			
extremes	11.2-11.8	13.8-14.3	-
n	3	3	
Tarsometatarsus and Phalanx 1 post. digit III	Tarsometatarsus Proximal width (1)	Tarsometatarsus Depth of prox. art. surf. (2)	Total length of phal. 1 post. digit III
ET 42'07	17.5	9.6	-
GPS 69	-	-	44.9
<i>Phoenicopterus ruber ruber</i>			
males, extremes	19.0-21.0	10.7-12.3	44.1-49.5
mean (n)	19.93 (10)	11.48 (10)	46.99 (9)
females, extremes	17.2-19.9	9.5-10.6	39.7-45.7
mean (n)	18.09 (10)	10.14 (10)	43.23 (8)
<i>Phoenicopterus ruber roseus</i>			
males, extremes	18.6-20.5	12.0-12.7	47.7-50.0
mean (n)	19.64 (5)	12.26 (5)	48.48 (4)
females, extremes	17.4-18.2	9.9-11.0	42.1-43.2
mean (n)	17.90 (3)	10.50 (3)	42.60 (3)
<i>Leakeyornis aethiopicus</i>			
extremes (n)	9.4-15.0 (10)	-	-

Table 3: Measurements (in mm) of the fossil material of *Phoenicopterus ruber* from Etosha Pan and Ekuma River, compared to modern individuals of *P. ruber* and fossil *Leakeyornis aethiopicus*, after Rich and Walker (1983).

- (1) For the tarsometatarsus the proximal width is measured including a small tubercle which is situated on the lateral side, just distally to the lateral cotyle.
- (2) The depth of the proximal articular surface is measured from the eminentia intercotylaris to the plantar border of the articular cotyles, i. e. without the hypotarsus.

Biostratigraphic distribution

Phoenicopteridae are present in a certain number of localities from the early and middle Miocene of Kenya, with *Leakeyornis aethiopicus* (Rich and Walker, 1983), or undetermined Phoenicopteridae (Pickford, 1986). According to Rich and Walker all these localities are early Miocene in age, but the locality of Maboko which has yielded a femur of *L. aethiopicus* is of middle Miocene age (Pickford, 1986). But later on the Phoenicopteridae are unknown in the African localities. They are absent from the middle Miocene Kenyan localities of the Nyakach Fm., and Fort Ternan (Pickford, 1986), from the late Miocene localities of Ethiopia and Chad (Louchart *et al.*, 2008), of Kenya (Lothagam, Harris and Leakey, 2003), of Tanzania (Laetoli, Harrison and Msuya, 2005), of Tunisia (Fm. Beglia, Rich, 1972) and of Libya (Sahabi, Ballmann, 1987; Louchart 2005b). They are still absent from the Pliocene localities of Chad (Louchart *et al.*, 2004, 2005a), of Ethiopia (Hadar and Omo, Brodkorb and Mourer-Chauviré, 1982; Louchart *et al.* 2005a), and from the Pliocene of Langebaanweg, South Africa (Rich, 1980). This is all the more surprising since all these avifaunas, with the exception of Langebaanweg, are almost uniquely composed of aquatic forms, such as Podicipedidae, Pelecanidae, Phalacrocoracidae, Anhingidae, Ardeidae, Ciconiidae, Balaenicipitidae, Anatidae, Gruidae, Rallidae and Heliornithidae. The

Phoenicopteridae occur again only in Olduvai, Bed I, Tanzania, dating from the latest Pliocene, where they are plentiful and correspond to the recent species *Phoenicopterus ruber* (Mourer-Chauviré, unpublished results; Harrison, 1980). Their absence from most of the sites is probably linked to ecological factors.

Paleoecology

The flamingos of the recent genus *Phoenicopterus* only live in saline or alkaline waters, such as saline lagoons, salt pans, and highly alkaline or saline inland lakes (del Hoyo *et al.*, 1992).

Felidae (JM)

A distal radius of a large felid, ET 29'07 (Fig. 17) was collected from the EPCM south of the Oshigambo Peninsula. The specimen accords in morphology and dimensions to that of extant lions, *Panthera leo* Linnaeus.

The fragment is a left distal radius, comprising about a third of the bone. The epiphysis is slightly eroded medially and laterally, but the articular surface is well preserved. The bone has the characteristic morphology of Pantherines, medio-laterally broad and narrow dorso-palmarly (Fig. 17). The articular surface for the scaphoid is concave, but moderately deep, except at the dorsal and palmar borders. The dimensions of the specimen are provided in Table 4.

Maximal medio-lateral diameter	57.2 mm
Medio lateral diameter of the articular surface	39.9 mm
Maximal dorso palmar diameter	31.7 mm
Dorso palmar diameter of the articular surface	25.0 mm

Table 4: Dimensions of the radius of *Panthera cf leo* from the EPCM, Namibia

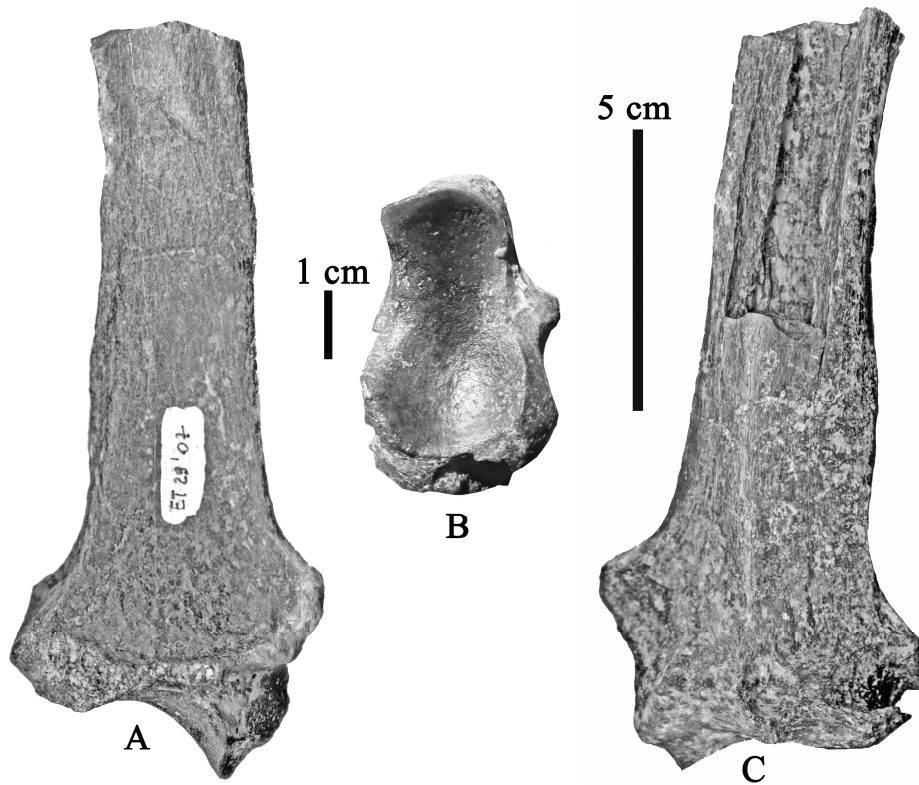


Figure 17: ET 29'07, distal left radius attributed to *Panthera cf leo*, from the Etosha Pan Clay Member. A) palmar, B) distal, and C) dorsal views.

The morphology of this radius is similar to that observed in *Panthera leo* and *Panthera pardus*. It differs from radii of more primitive machairodontines such as *Machairodus aphanistus* and *Paramachairodus ogygia* from the Late Miocene locality of Bataillon, Spain, which show a tendency to broaden the facet for articulation with the scaphoid, while maintaining overall proportions close to those of pantherines. However, in these machairodonts the scaphoid articulation is notably deeper, in consequence of the greater height of the dorsal border. These two primitive machairodontines are similar in morphology to each other despite the major difference in size of the two species, which indicates the validity of the character which is not related to size. More derived machairodontines such as *Homotherium* or *Smilodon*, have a shorter and broader articular surface than those of pantherines and primitive machairodontines (Ballesio, 1963; Merriam & Stock, 1932).

Proboscidea (MP)

The loxodont teeth from the EPCM of the Andoni Formation are incomplete, but they reveal potentially useful data. Enamel thickness in one specimen (Fig. 18 A) about 30% up from the base of the crown ranges between 3.7 to 5.6 mm ($n = 9$), unworn crown height is 77.4 and 80 mm in two fragments, the greatest breadth is low down (the pretrite half consists of a single cusp that diminishes in medio-lateral breadth from 30 mm at ca 30% crown height to 22 mm at 50% crown height to 9.5 mm near its occlusal apex (measured from the contact with the sinus)). The loxodont sinus is large, increasing in dimensions rootwards.

A complete molar loph (Fig. 18 B) is 65.8 mm broad at the base, narrowing occlusally to 33.5 mm at the broadest part of the apex. Pre-trite and post-trite halves comprise 5 columns each at the base, but these crowd each other apically so that only 4 tubercles reach the apex. The loxodont sinus, which is the innermost column on both the pre-trite and post-trite sides, is well devel-

oped apically where they twist away from the other cusps and come to lie mesially and distally respectively of the loph axis. The loxodont sinus in this specimen fades out towards cervix. In radicular view, the squared off margin of the tooth is evident on one side, as in primitive species of *Loxodonta*.

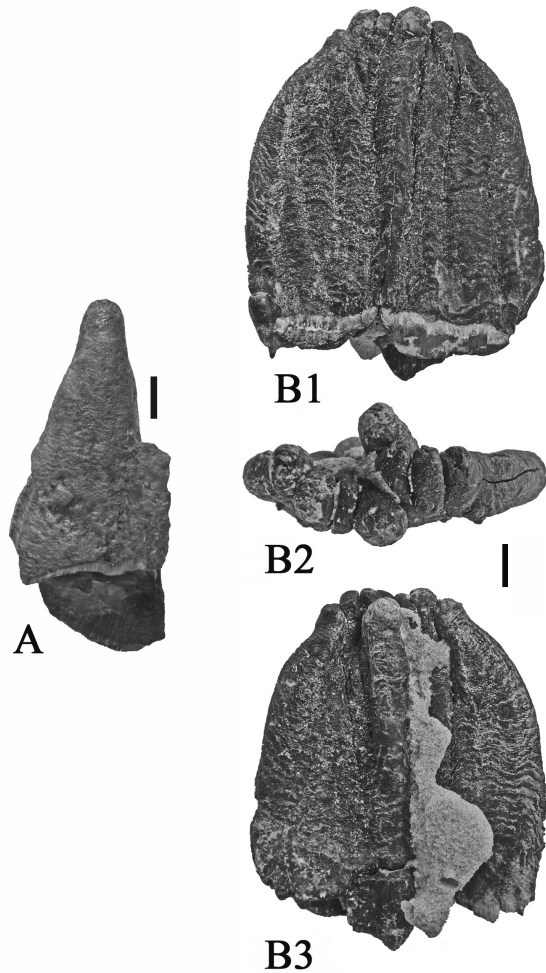


Figure 18: Fossil Proboscidea from the Etosha Pan Clay Member, northern rim of Etosha Pan, Namibia (scale bar : 1 cm). A) ET 10'07, *Loxodonta* cf *cookei*, half molar plate anterior view ; B) ET 53'07, *Loxodonta* cf *cookei* complete molar plate, B1) anterior, B2) occlusal and B3) posterior views.

The overall pattern of the proboscidean teeth from the EPCM is compatible with the species *Loxodonta cookei* from Langebaanweg, South Africa, and various late Miocene and early Pliocene sites in East Africa (Lukeino, Mabaget, Nkondo) (Sanders, 2007).

Suidae (MP)

The suid from the EPCM of the Andoni Formation is a very large one (Fig. 19) (patellar dimensions of EK 30'07 are 65 x 41 mm (proximo-distal x medio-lateral)) with an antero-posterior height of 48 mm (measured from the central articular ridge to the outermost extremity of the patella). Although the genus and species to which this patella belongs cannot be determined, it is larger than that of any extant suid (in *Potamochoerus porcus larvatus* (Fig. 19) the proximo-distal dimension is 36.7 mm) and its dimensions are compatible with large species of *Nyanzachoerus*, *Notochoerus* and *Metridiochoerus*. Extant *Potamochoerus* range in weight from 45-120 kg. The fossil patella from Etosha has almost twice the linear dimensions of a patella of *Potamochoerus porcus larvatus* from Madagascar, with which it was compared (Fig. 19). This would imply that the Etosha suid weighed between 360 and 960 kg (ie 8 x the weight of *P. porcus*).

Bovidae (JM & MP)

Two bovid horn cores and several unidentifiable bovid post-cranial bones have been found in the EPCM belonging to 2-3 size groups.

Tribe Alcelaphini

Genus *Damalacra* Gentry, 1980

Damalacra acalla Gentry, 1980

ET 21'07, a right horn-core lacking the apex, whose total length is ca. 180 mm, preserves part of the frontal with about 25 mm of the interfrontal suture, which indicates that the horns were close together at their bases (Fig. 20 A). The horns diverge outwards, and curve slightly towards the exterior. The pedicle has a strongly developed sinus, which penetrates as far as the base of the horn-core. The transverse section at the base of the horn-core is rounded (54 x 45 mm) (Fig. 21). The medial surface of the horn-core is clearly convex and the lateral side flattened. The margin between the two

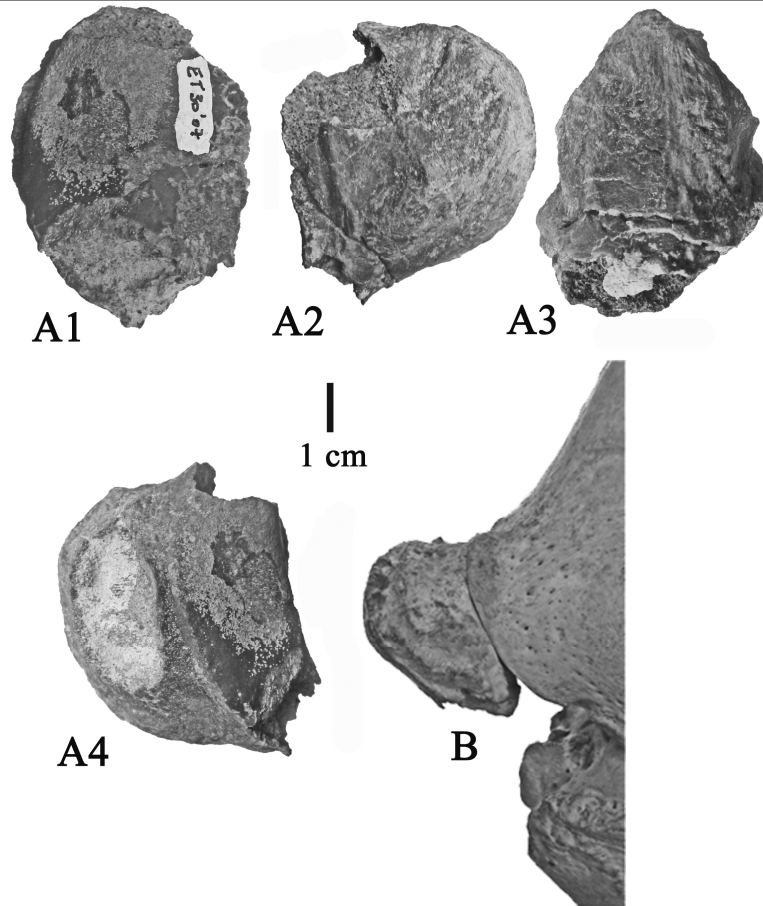


Figure 19: ET 30'07, suid right patella from the Etosha Pan Clay Member (A) ; A1) articular surface, A2) lateral surface, A3) distal view, A4) medial view, (B) medial view of right knee joint of *Potamochoerus porcus larvatus* from Madagascar.

surfaces is lightly keeled, visible in anterior view, whereas posteriorly the keel is stronger and is accompanied by a deep groove. The base of the lateral surface possesses many strong grooves, which are weaker medially. However, the medial surface is more ornamented up to the apex than the lateral side is.

ET 54'07 (GPS 108) a right horn core preserving part of the pedicle, is almost straight, with a slight curve which increases apically and outwards (Fig. 20 B). There is a strong sinus in the pedicle (enlarged by breakage of the internal base of the horn-core). The section is quasicircular (45 x ca. 35.5 mm). The anterior surface is convex and quite narrow. The medial side is convex and the lateral side flattened. The posterior surface is narrow and has strongly developed vertical grooves, especially towards the apex.

Discussion

The dimensions and morphology of the two Etosha horn-cores reveal that they are close to species of the genus *Damalacra* Gentry, 1980. Among other features, we should cite the narrow extent of the frontal between the horns which insert close together. They also have a strongly developed pedicular sinus. The horn-cores are conical in aspect, with slight compression and are almost straight, without obvious signs of curvature or torsion. The basal dimensions of the horn-cores are similar to those of *Damalacra acalla* (Fig. 21), and somewhat more compressed than those of *Damalacra neanica*. In particular, the horn-cores from Etosha are morphologically and metrically closer to specimens L1836 (Gentry, 1980, fig.32) and L46075 from Langebaanweg than they are to the holotype of the species (L40001, Gentry, 1980, fig. 31).

Damalacra is a primitive member of the Alcelaphini, a bovid tribe which is today widespread in open country in Africa. The genus has been reported from the Mio-Pliocene of Lothagam, Kenya, and the basal Pliocene of Wadi Natrun, Egypt (the latter record requires confirmation, as the sole specimen known from the site is fragmentary). All the Lothagam fossils (Harris,

2003) are smaller than the Etosha specimens (Fig. 21). The Wadi Natrun horn-core is broken (Vrba 1997), but its dimensions fall within the range of metric variation of *Damalacra neanica* from Langebaanweg.

Although the early stages of the evolution of alcelaphines are still relatively obscure, it would seem that the tribe originated in southern Africa and spread northwards as

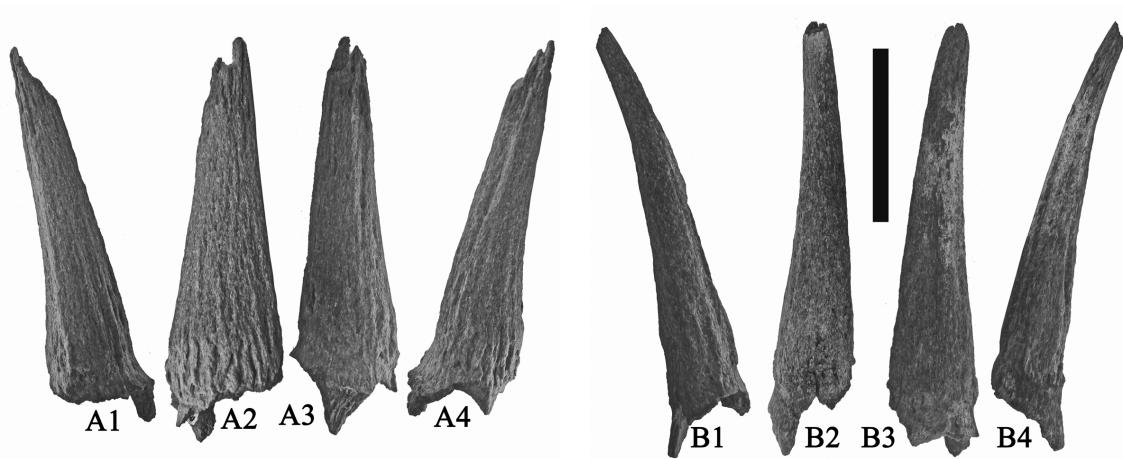


Figure 20: *Damalacra acalla*, A) ET 21'07, right horn-core, B) ET 54'07, right horn-core, 1) anterior, 2) lat-

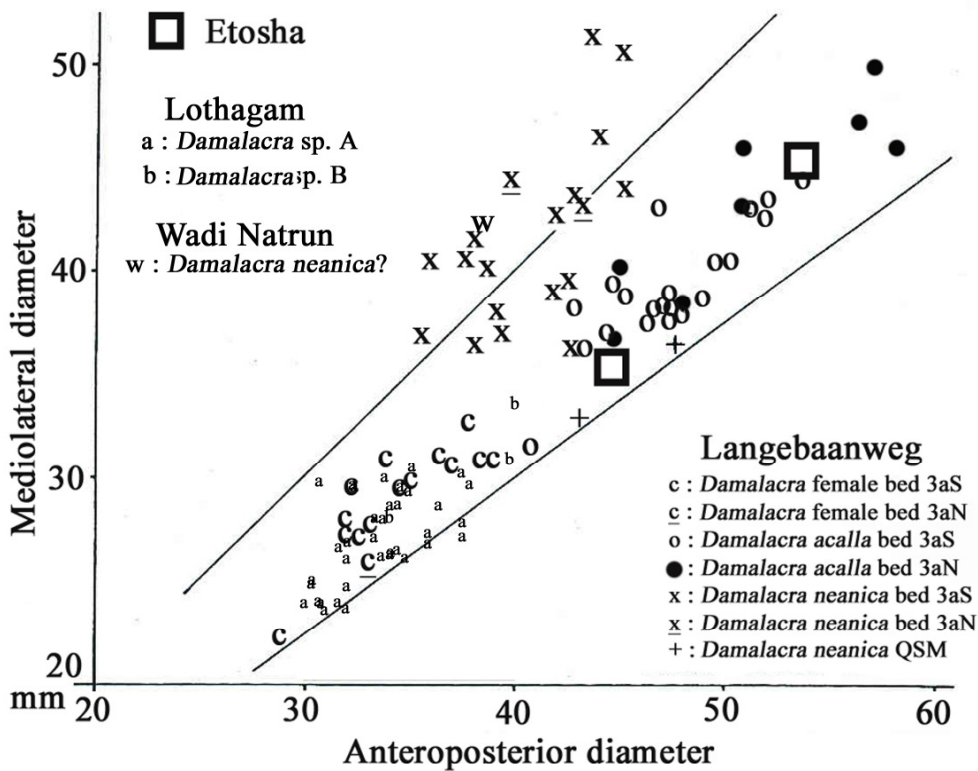


Figure 21: Bivariate plot of anteroposterior and mediolateral diameter of the base of the horn cores of *Damalacra* spp. The two specimens from the Etosha Pan Clay Member (large open squares) fall within the range of variation of *Damalacra acalla*.

open country habitats developed there. The Etosha horn-cores are sufficiently close morphometrically to those from Langebaanweg, that we may postulate similar habitats in the two areas and similar biochronology.

Although the diversity of vertebrates from the Etosha Pan Clay Member of the Andoni Formation is not very great, the overall aspect of the fauna suggests links to the Mio-Pliocene occurrences at Langebaanweg, South Africa, indicating an age between 5 and 6 Ma for the Namibian sites.

Flora and fauna from the Ekuma Delta Member of the Andoni Formation

Plant remains are common in the Ekuma Delta Member of the Andoni Formation, in particular casts of root systems and tree trunks. By their nature these fossils are difficult to identify (Fig. 22 B), but in one case the cast of a tree trunk surrounded by a swarm of narrow roots is sufficiently informative to reveal that it belongs to a palm tree (Fig. 22 A).

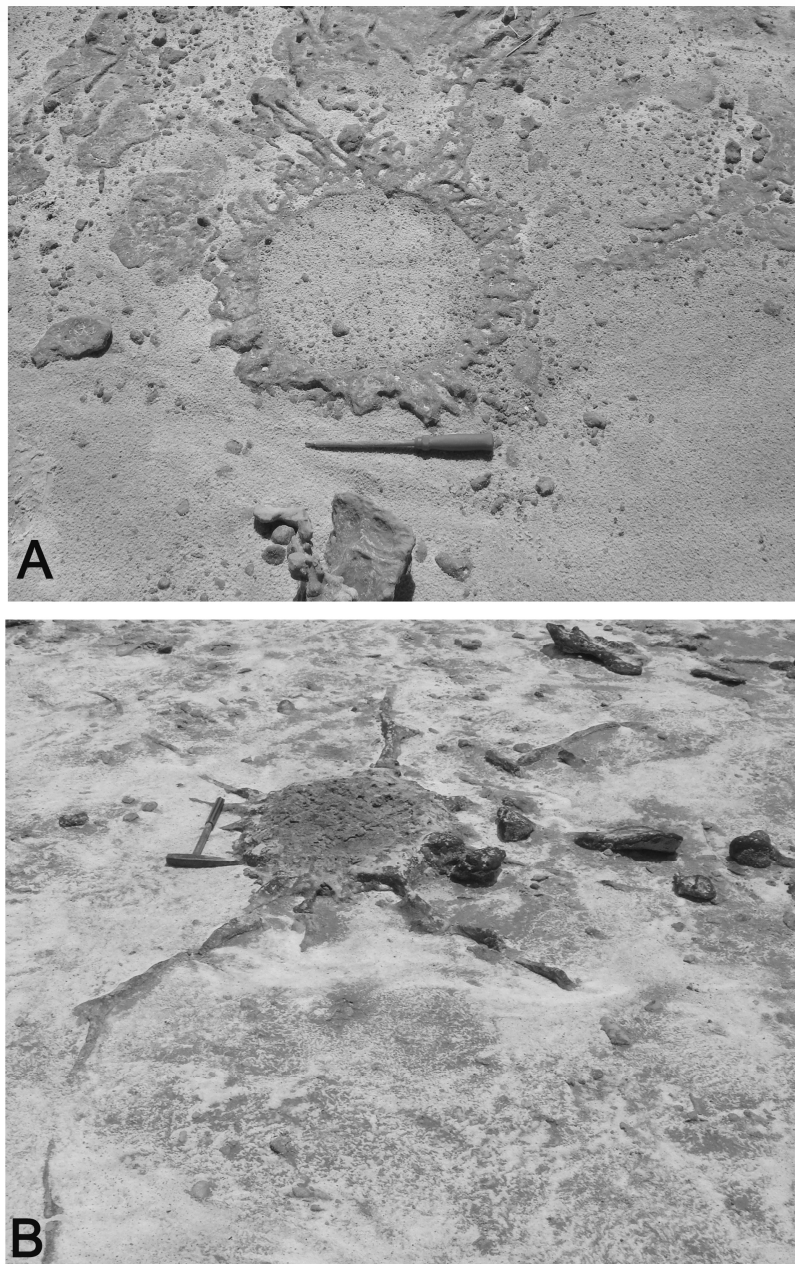


Figure 22: Tree boles and roots in quartzite of the Ekuma Delta Member, Ekuma River Valley, Etosha, Namibia. A) palm tree cast surrounded by dense root system, B) dicotyledon tree bole and root network (screw driver and geological hammer for scale)

Invertebrates occur in the quartzites of the EDM, the richest deposits consisting of shell banks containing abundant *Bellamyia unicolor* (Fig. 23 A) and bivalves (probably *Mutela*) (Fig. 23 B) both of which indicate freshwater deposition and well oxygenated water.

Apart from numerous fish remains which often occur as complete skulls and sometimes even as articulated skeletons (Fig. 25), the vertebrates in the EDM tend to be fragmentary and disarticulated (Fig. 24 D-H). Preliminary identifications of these fos-

sils indicate an age of about 4 Ma for the deposits.

Gastropoda (MP)

Abundant shells and internal molds of freshwater gastropods occur in quartzites of the EDM, sometimes in large concentrations (Fig. 21 A ; 24 A). The shape of the whorls, the finely pointed protoconch and the dimensions serve to identify these snails as *Bellamyia unicolor*, a freshwater mollusc common throughout Africa.

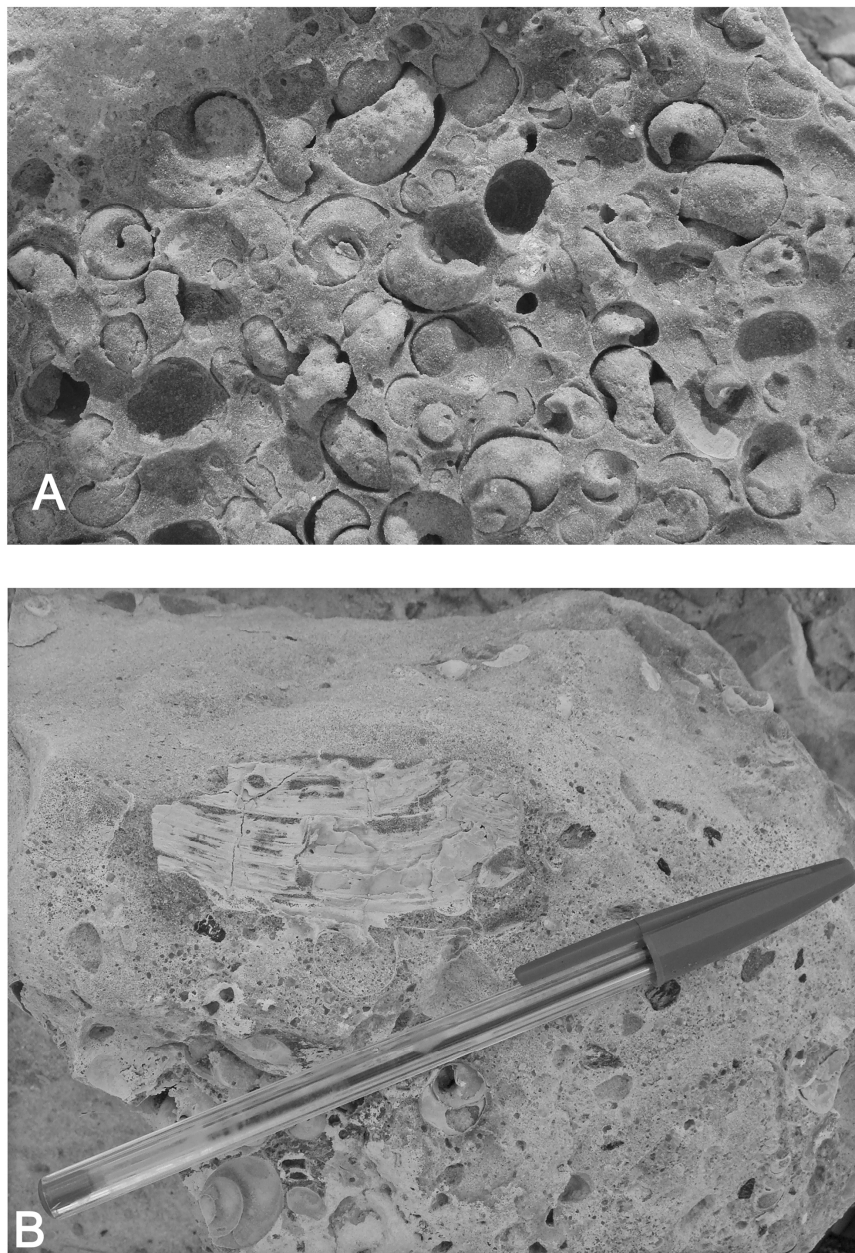


Figure 23: Mollusca in quartzite of the Ekuma Delta Member, Etosha, Namibia. A) a rich concentration of *Bellamyia unicolor*, B) a shell of *Mutela* sp. accompanied by *Bellamyia unicolor*.

Bivalvia (MP)

Internal molds and steinkern of mutelid bivalves are common in the EDM. The shell is usually absent, but in some individuals the characteristic concentric growth lines of mutelids can be observed (Fig. 23 B ; 24 B). Given the generally poor preservation of the samples, we prefer to identify the shells only to the genus level as *Mutela* sp. There are however, indications of a second species of bivalve at Ekuma, resembling the freshwater Donacidae *Egeria* (Van Damme, pers. comm.). Whatever the genera however, these bivalve specimens indicate the availability of well-oxygenated, fresh water at the time that the EDM was being deposited.

Pisces (HJ)

The fish remains from the EDM are similar to those from the EPCM, and we accordingly identify them as *Clarias* sp. (Fig. 24 D-H).

Cyclanorbidae

Patterned scutes characteristic of Cyclanorbidae have been found in the EDM (Fig. 24 K).

Pelusios

The scutes of *Pelusios* are common in the EDM (Fig. 24 I-J).

Crocodylia (MP)

Crocodile teeth, scutes, vertebrae and limb bones are frequently encountered in the EDM (Fig. 24 L, 24 M).

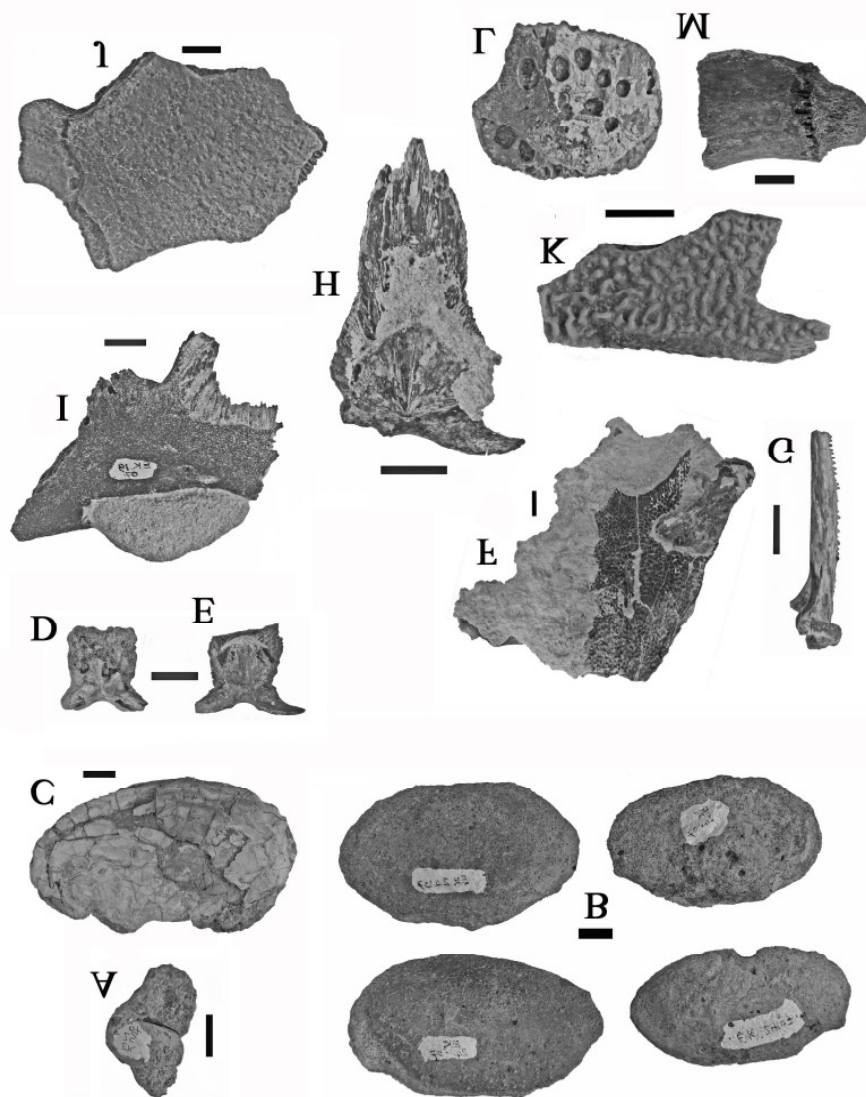


Figure 24: Invertebrates and vertebrates from the Ekuma Delta Member (ca 4 Ma) Ekuma River, Namibia (scale bars : 1 cm except N : 5 cm). A) EK 25'07, *Bellamyia unicolor*, shell ; B) EK 24'07, four specimens of *Mutela* sp., internal molds ; C) *Mutela* steinkern ; D-E) *Clarias*, two vomers, ventral view ; F) *Clarias*, skull, dorsal view ; G) *Clarias*, pectoral spine ; H) *Clarias*, vomer, ventral view ; I-J) EK 19'07, *Pelusios* sp., scute, dorsal view ; K) Cyclanorbidae, scute, dorsal view ; L) *Crocodylus* sp., scute, dorsal view ; M) Crocodile vertebra.



Figure 25: EK 52'07, *Clarias* sp., articulated skeleton in quartzite of the Ekuma Delta Member, Namibia.

Aves (Fig. 26, 27, 28, 29)

Two bird bones were collected in the EDM of the Ekuma River valley. GPS 69 Phalanx 1 of posterior digit III (Fig. 28). The size of this phalanx is included in the variation range of the extant species *Phoenicopterus ruber* (Table 1).

EK 21'07 right humerus, fragment of proximal part. This cannot belong to an Anseriform because there is a fossa on the cranial side, at the level of the impressio coracbrachialis.

Bird footprints are locally common in the Ekuma Delta Quartzites (Fig. 29).

Struthio daberasensis (LS, MP & BS).

Two fragments of ostrich egg shell were found on the northern margin of the Stinkwater Peninsula (Fig. 26, 27). The specimens preserve the characteristic pore structure and shell thickness of the species *Struthio daberasensis* (Senut and Pickford, 1995).

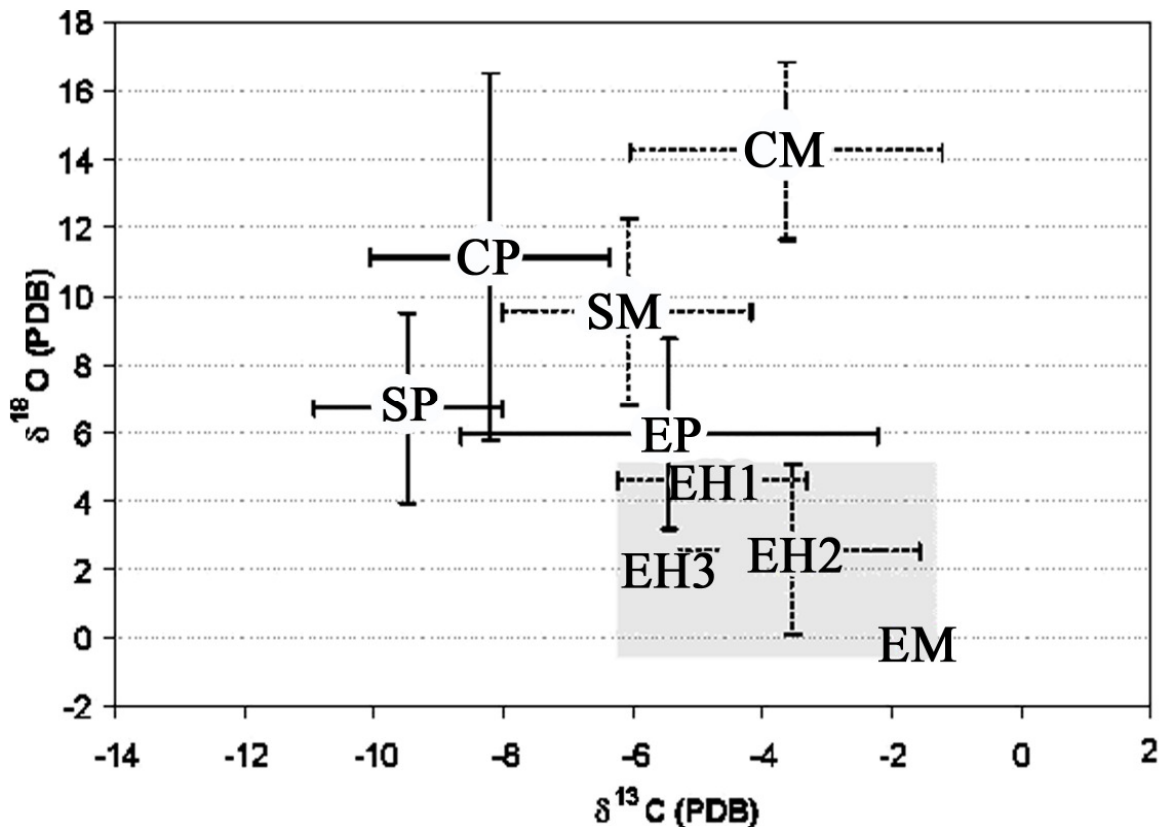
Preliminary results of isotope analyses of extant and Holocene eggshells of *Struthio*

camelus from Etosha (Fig. 26 ; Table 5) indicate that they have similar $d^{13}C$ isotope signatures (-6 to -1.8‰) as those from the Central Namib Desert. Both samples inhabit regions of summer rainfall, and the values reflect the presence of C4 plants in their diets. The main difference concerns the values of $d^{18}O$, which at Etosha, range between 0 and 4‰ whereas in the Central Namib they range from 12 to 16‰. This difference shows that the Namib ostriches consumed water that was more evaporated and lived in an arid environment whereas those from Etosha indicate a more humid environment. The variation observed at Etosha between the extant and Holocene samples is linked to climatic change during the Quaternary, but estimates of the ages of the localities are necessary to interpret the differences in a reliable chronological framework.

The shells of *Struthio daberasensis* from the Namib Desert are discriminating from the point of view of isotope composition. The differences noted reflect the presence of C3 and C4 plants in the central re-

gion and C3 and CAM plants in the south (Ségalen *et al.*, 2006, 2007). Furthermore, the central Namib is more arid than the southern part where the localities, being closer to the Atlantic Ocean, are more humid. For the egg shells from Etosha attributed to *Struthio daberassensis*, it is interesting to note that the $\delta^{18}\text{O}$ is similar to that of egg shells from the Southern Namib (ranging between 3 and 9‰). In contrast the $\delta^{13}\text{C}$ is

much more enriched ($\delta^{13}\text{C}_{\text{mean}} \sim -5.4\text{‰}$ n=3 ; versus $\sim -9.5\text{‰}$ n=19), the large range of variation is due to the small quantity of egg shells analysed but suggests the presence of C4 plants. This proportion would otherwise be greater than in the Central Namib for this period. Nevertheless the preliminary interpretations need to be confirmed by isotopic analyses of larger samples of egg shells.



Struthio camelus

Struthio daberassensis

CM - Central Namib Modern
 SM - Southern Namib Modern
 EM - Etosha Modern

CP - Central Namib Pliocene
 SP - Southern Namib Pliocene
 EP - Etosha Pliocene

EH1 - Etosha Holocene (GPS 112)
 EH2 - Etosha Holocene (GPS 117)
 EH3 - Etosha Holocene (161107)

Figure 26: $\delta^{13}\text{C}$ et $\delta^{18}\text{O}$ of extant and fossil ratites of Namibia (GPS 112, 18°37'43.3''S : 16°12'01.7''E ; GPS 117, 18°41.770'S : 16°04.012'E).

Sample	$\delta^{13}\text{C}$	<i>Struthio camelus</i> (modern)	<i>Struthio camelus</i> (Holocene)	<i>Struthio daberansensis</i> (Pliocene)
		$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{18}\text{O}$
ETO GPS 75	-8.1			7.6
ETO GPS 78 1	-6.3			2.7
ETO GPS 78 2	-1.9			7.5
ETO GPS 102 1	-7.1		5.3	
ETO GPS 102 2	-4.4		4.9	
ETO GPS 102 3	-3.6		4.6	
ETO GPS 102 4	-5.2		4.4	
ETO GPS 102 5	-3.6		4.1	
ETO GPS 117 1	-6.3		3.8	
ETO GPS 117 2	-2.7		1.7	
ETO GPS 117 3	-3.2		5.2	
ETO GPS 117 4	-1.5		-0.5	
ETO 161107 1	-1.6	-0.2		
ETO 161107 2	-5.5		1.9	
ETO Modern	-1.5	-0.3		
Central Namib (n = 11)	-3.6	14.2		
Central Namib (n = 16)	-8.2	14.2		11.1
Southern Namib (n = 21)	-6.1	9.6		
Southern Namib (n = 19)	-9.5			6.7

Table 5: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of fossil and extant ratite egg shells from Etosha and the Namib Desert, Namibia.

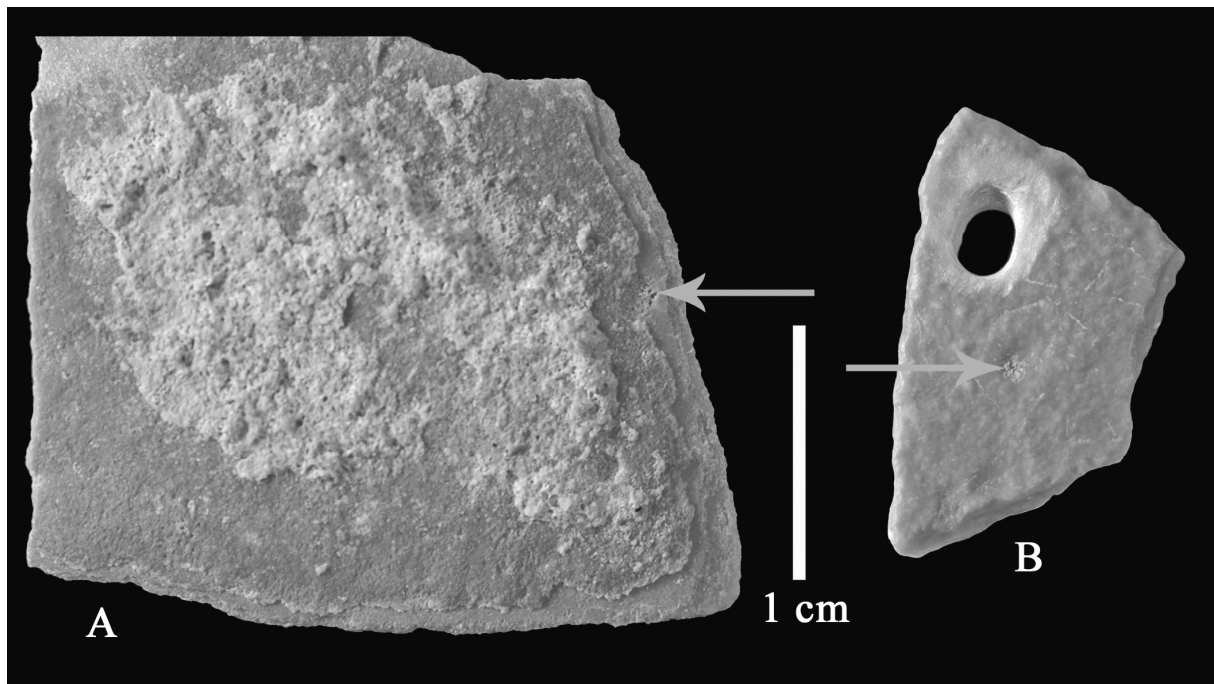


Figure 27: *Struthio daberansensis* fossil egg shells from the Andoni Formation at Stinkwater Peninsula, Etosha Pan, Namibia A) GPS 75 (18°36'58.0''S : 16°45'08.7E'') and B) GPS 78 (18°36'13.2''S : 16°41'51.9''E) (arrows point to pores, the dimensions and scattering are characteristic of this species).

Pedetidae (PM)

A molar of a pedetid from the Ekuma Delta Member is curved from occlusal surface to root, and is very hypsodont. EK18'07 (Fig. 30 A) is interpreted as a P4/ due to the strong anterior curvature of its basal part. The posterior lobe is higher than the anterior one (the opposite is the case in m/3). The tooth is almost unworn and preserves both grooves : a small hypostria 1.3 mm tall, and

a mesostria, 7.4 mm tall, which terminates almost at the base of the crown. The occlusal length of the tooth is 3.14 mm and its basal length is slightly greater at 3.27 mm. The occlusal breadth of the anterior lobe is 2.96 mm and its basal breadth is 3.40 mm. The occlusal breadth of the posterior lobe is 2.94 mm and at its base it is 4.20 mm. The height of the tooth is 10.7 mm, but its base is damaged. The buccal closure of the base of the



Figure 28: EK 68'07, Pedal phalanx of a wading bird, Phoenicopteridae, from the Ekuma Delta Member, Ekuma River valley near the Horse Camp, Namibia (dorsal, lateral, plantar, proximal and distal views).

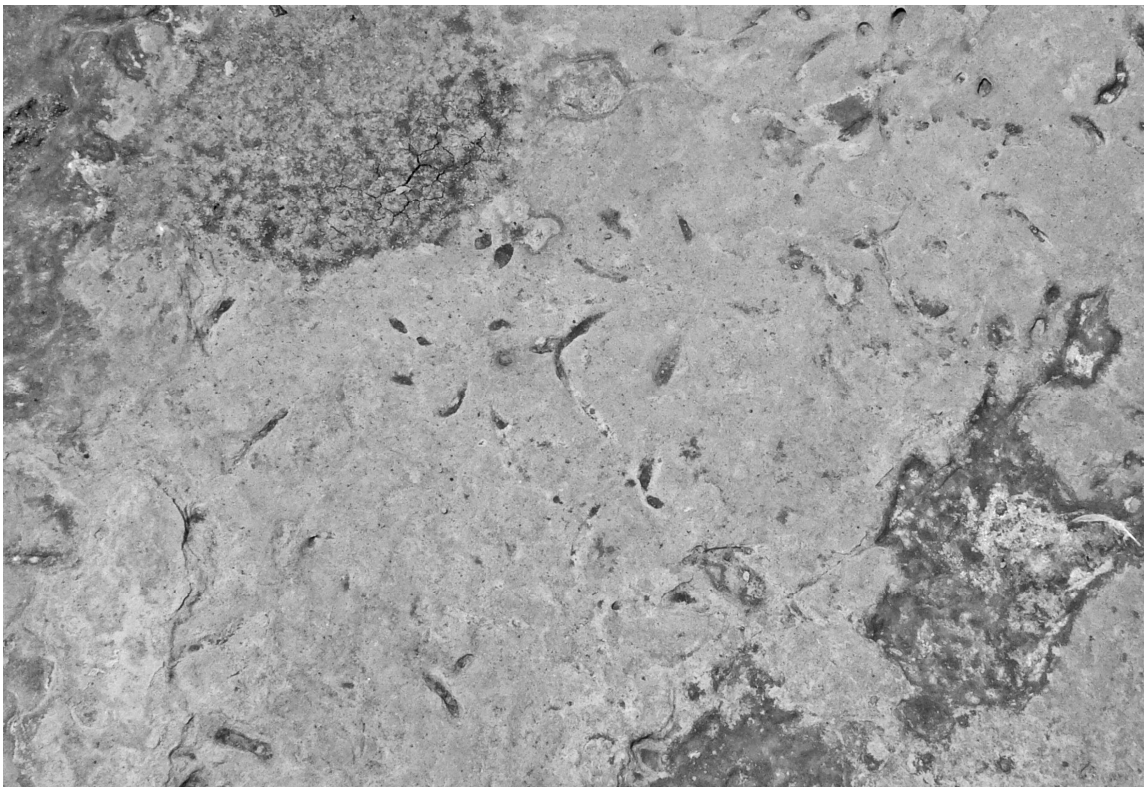


Figure 29: Bird foot prints and other traces in quartzite of the Ekuma Delta Member, Ekuma River Valley, Etosha, Namibia. The dimensions of the foot prints accord with those of ducks and flamingos.

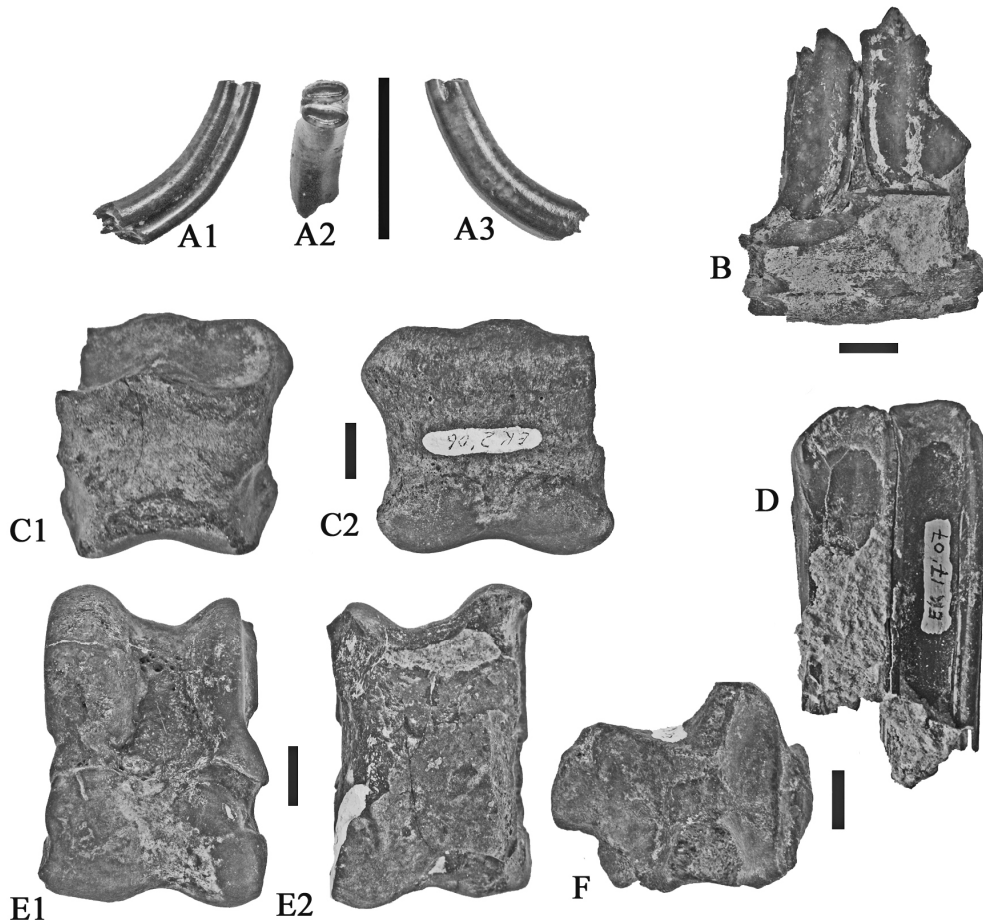


Figure 30: Mammals from the Ekuma Delta Member, Etosha, Namibia. A) EK 18'07, *Propedetes* sp. P4/, A1) lingual, A2) occlusal and A3) buccal views ; B) EK 1'06, *Redunca darti*, juvenile mandible fragment containing damaged teeth, buccal view ; C) EK 2'06, *Hipparion* sp. second phalanx, C1) dorsal and C2) plantar views ; D) EK 17'07, *Hipparion* sp. ectoloph of upper cheek tooth ; E) EK 9'06, Bovidae, left talus, E1) anterior and E2) posterior views ; F) EK 8'06, Bovidae distal tibia, distal view.

mesostria, as well as the absence of cementum indicates that this specimen belongs to a new genus of pedetid being described from the Sperrgebiet, Namibia. Its hypsodonty exceeds all the other known teeth of this genus, and it is therefore most likely the youngest.

Comparable teeth, belonging to *Propedetes*, have been found in various localities in Namibia (Tree Pan, Awasib) but no P4/ is known from these localities. Such a degree of hypsodonty is however less than that expressed in *Pedetes*. At Taung, South Africa, *Pedetes gracilis*, which we were able to study, has a longer and more curved P4/ and its height is 19 mm. In addition the mesostria does not close, the tooth is rootless, and there are traces of cementum.

In conclusion, The Ekuma pedetid likely represents a new species of *Propedetes*, probably older than the Laetoli (Davies, 1987) and Taung species (Broom, 1937) but younger than the species from the *Diamantornis laini* level (ca 10-8 Ma) (Senut and Pickford, 1995).

Proboscidea (MP)

Loxodont enamel fragments are common in the EDM, and there is a partial skeleton eroding out on the banks of the Ekuma River. However, none of the tooth fragments is complete enough for confident identification, but enamel is as thick as in material from the Etosha Pan Clay Member and the crown is relatively low. We attribute these specimens to *Loxodonta cf cookei*.

Specimen	Total height	Height of mesostria
Rooilepel RL 16'94, P4/	10.7	7.4
Ekuma EK 18'07, P4/	13.0	13.1
Taung 4194c, P4/	19.0	19.0

Table 6: Measurements (in mm) of the P4/ of pedetids from Namibia and South Africa.

Rhinocerotidae (CG)

Material

A left talus Ekuma EK 064 (Fig. 31 A), two first central phalanges, one abaxial second phalanx, a distal metapodial, a fragment of left magnum, and a fragment of left

pyramidal, all numbered EK 063, were found close together, and thus probably represent a single individual. Only the talus, the two incomplete carpals and a first phalanx are well enough preserved for study.

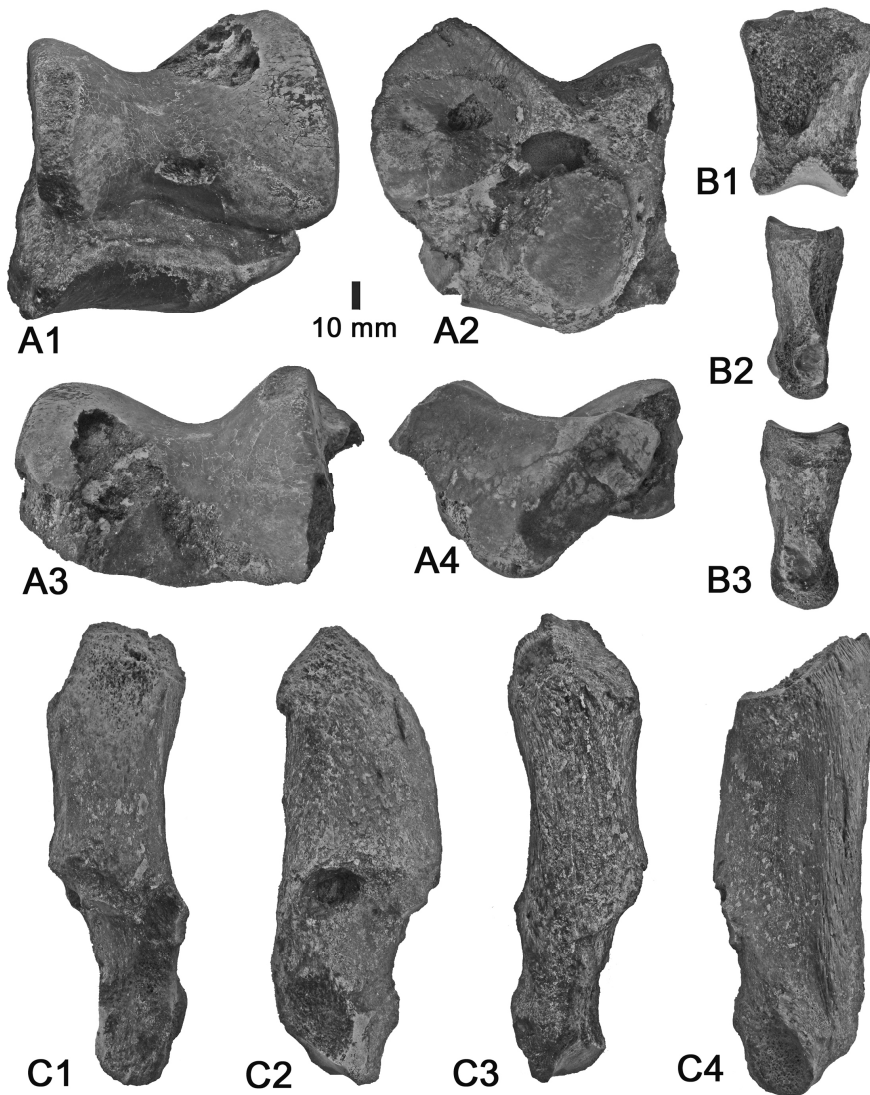


Figure 31: (A) EK 66'07, *Ceratotherium praecox* and (B, C) EK 67'07, *Hippopotamus* sp. from the Ekuma Delta Member (ca 4 Ma). A1) dorsal, A2) plantar, A3) cranial and A4) caudal views of left talus ; B1) dorsal, B2) lateral and B3) medial views of central 1st phalanx ; C1) cranial, C2) medial) C3) caudal and C4) lateral views of left calcaneum.

Magnum :

The bone which lacks the posterior apophysis and a small part of the lateral margin of the anterior surface, resemble that of extant *Ceratotherium simum* but are taller and narrower. The anterior surface has a rounded pentagonal contour which is asymmetric distally. The medial transverse extension is pointed but not very strong, but is better developed than in extant *C. simum*. The proximal articulation is wide. The articular height is at least 66 mm. For 11 specimens of *Ceratotherium praecox* from Laetoli (Tanzania) Hadar (Ethiopia) and Nkondo (Uganda), this dimension ranges from 60 to 70 mm (mean 65.05, standard deviation 3.037). It reaches 78.5 mm in *C. germanoaffricanum* from Olduvai, Tanzania and 56 mm in fossil *Diceros bicornis* from Olduvai.

Pyramidal :

This specimen lacks the antero-external surface. It resembles that of extant *C. simum* but differs in its proportions : it is taller and slightly narrower. The antero-external surface is slightly broader than tall. The breadth is at least 58 mm. In 15 specimens of *Ceratotherium praecox* from Laetoli and Nkondo it ranges in dimensions from 57 to 69 mm (mean 61.7 mm, standard deviation 3.453). It ranges from 72.5 to 74 mm (mean 73.5 mm) in three fossil specimens of *C. simum* from the Afar (Ethiopia) and Olduvai, and from 56 to 57.5 mm (mean 56.83 mm) for three fossils of *D. bicornis* from Laetoli and Olduvai.

Talus :

This bone is relatively well preserved, save for the postero-distal quarter of the medial surface. The morphological characters are very close to those of extant *C. simum*. The articular pulley is broad and deep (Fig. 28 A1, A2, A3). The distal tubercle of the medial surface is positioned well above the distal margin. The distal articulation has a weakly concave anterior margin, without an encoche between the facets for the navicular and cuboid ; these facets are not offset (Fig.

28 A4). All these characters are typical of the genus *Ceratotherium*. The dimensions are provided in Table 7. They are close to the upper limit of a sample of 10 to 16 *Ceratotherium praecox* from Hadar, Laetoli and Kanam W (Kenya), and the mean values of a sample of 6-9 *C. germanoaffricanum* from East Turkana (Kenya), Omo-Shungura (Ethiopia), Olduvai and Hadar. They exceed most of the maximal values obtained from a sample of 11 to 12 extant *C. simum*, and also those of 2 fossil *C. simum* from Omo-Shungura and Olduvai. They are much larger than a sample of 23 to 27 extant *D. bicornis* and 4 fossil *D. bicornis* from East Turkana and Omo.

Axial first phalanx :

This phalanx is 54.5 mm long, and its greatest proximal breadth is 60 mm.

Identification:

Morphologically, the rhino from Ekuma belongs to the genus *Ceratotherium*. The dimensions and proportions of the talus are compatible with those of a large *C. praecox* or a medium-sized *C. germanoaffricanum*, but the height of the magnum and the breadth of the pyramidal support the former identification. The Ekuma rhinoceros is thus identified as *Ceratotherium praecox* Hooijer & Patterson, 1972.

Biostratigraphic and palaeoenvironmental implications:

The species *C. praecox* is frequently reported from the Neogene of Africa (Hooijer & Patterson, 1972; Guérin, 1979, 1980, 1985, 1987, 1994). It was originally defined at Kanapoi (Kenya ; 4.5 Ma). In the same country it is also present at Lothagam-1 Members B and C (7.2 to 5.5 Ma), Ekora (4 to 3.5 Ma), in the Aterir Beds (4 Ma), in the Chemeron Formation loc. JM 507, at Koobi Fora (Kubi Algi, 4 to 2.5 Ma), at Lukeino (6 to 5.7 Ma), and at Mpesida (6.5 to 6 Ma). *C. praecox* is also known from Ethiopia at Omo (Mursi and base of the Shungura Formations, more than 4 to 3 Ma), from Hadar (Sidi Hakoma, 3.4 to 3.1 Ma). It

Talus		EK 064					
Maximum length				106			
Height				ca 102			
DAP int.				ca 69			
DT artic.dist.				ca 87.5			
DAP artic.dist.				62			
Dist. 2 lips				84			
DT dist.				ca 91			
<i>Ceratotherium praecox</i>							
		N	mean	min.	max.	std dev	coef. var.
Maximum length		16	100.1	92.5	112.5	5.4	5.4
Height		15	91.9	82.5	103	5.4	5.9
DAP int.		10	61.7	57	67	3.7	6.0
DT artic.dist.		14	81.5	70	92	5.7	7.0
DAP artic.dist.		11	49.0	39	60	5.9	12.1
Dist. 2 lips		15	70.5	67	79.5	3.9	5.5
DT dist.		15	89.3	83.5	101	4.6	5.2
<i>Ceratotherium germanoaffricanum</i>							
		N	mean	min.	max.	std dev	coef. var.
Maximum length		9	109.4	104	116	4.9	4.5
Height		9	101.9	94	112	7.3	7.2
DAP int.		7	68.5	65	74.5	3.8	5.5
DT artic.dist.		9	91.8	81.5	102.5	6.2	6.7
DAP artic.dist.		6	56.0	50.5	66	5.7	10.1
Dist. 2 lips		8	76.4	68	84	5.4	7.0
DT dist.		9	97.7	90.5	106	4.9	5.0
<i>Ceratotherium simum extant</i>							
		N	mean	min.	max.	std dev	coef. var.
Maximum length		12	95.1	88	111	6.3	6.7
Height		12	84.5	80	92	3.9	4.6
DAP int.		12	58.5	53.5	65	3.6	6.1
DT artic.dist.		11	80.0	74	86	4.6	5.7
DAP artic.dist.		11	48.0	44	52	2.7	5.6
Dist. 2 lips		11	64.9	60	71	3.2	5.0
DT dist.		12	86.5	81	93	3.8	4.4
<i>Ceratotherium simum fossils</i>							
		N	mean	min.	max.		
Maximum length		2	98.5	95	102		
Height		2	87.0	84	90		
DAP int.		2	62.2	60.5	64		
DT artic.dist.		2	78.0	77	79		
DAP artic.dist.		1	50.0	50	50		
Dist. 2 lips		2	65.5	62	69		
DT dist.		2	87.5	86	89		

Table 7: Measurements in mm of the Ekuma rhino talus and comparisons with extant and fossil *Ceratotherium* and *Diceros* species.

<i>Diceros bicornis</i> extant						
	N	mean	min.	max.	std dev	coef. var.
Maximum length	25	84.8	78	96	4.4	5.2
Height	23	77.9	73	88	4.2	5.4
DAP int.	27	56.0	50.5	61	2.5	4.5
DT artic.dist.	23	68.7	60	79	4.4	6.4
DAP artic.dist.	23	43.9	40	49.5	2.7	6.2
Dist. 2 lips	25	62.6	55.5	73	4.3	6.9
DT dist.	26	75.3	68.5	85.5	4.4	5.8
<i>Diceros bicornis</i> fossils						
	N	mean	min.	max.	std dev	
Maximum length	4	79.5	70.5	94	10.3	
Height	4	78.2	73	90	8.1	
DAP int.	4	54.5	50.5	63.5	6.1	
DT artic.dist.	4	67.2	59.5	82	10.2	
DAP artic.dist.	4	42.2	37.5	50.5	5.8	
Dist. 2 lips	4	52.9	47	61.5	6.2	
DT dist.	4	73.2	63.5	91.5	12.5	

Table 7: (continued)

has also been reported from Laetoli (3.8 to 3.5 Ma) in Tanzania and in the Nkondo (5 Ma), Warwire (4.5 Ma) and Hohwa Formations (2.3 Ma) in Uganda. The species is also present in South Africa at Langebaanweg-E quarry (5 to 4 Ma), Limeworks Cave-Makapansgat (3.4 to 3 Ma) and at Swartlintjes Farm, Hondeklipbaai (Namaqualand, Cape Province). Finally, Likies (2002) identified it in the Pliocene of Tchad at Kollé (5 to 4 Ma) and Koro Toro (3.5 to 3 Ma). *C. praecox* is thus known from deposits in eastern, central and southern Africa ranging in age between 7 and 2.5 Ma. It is likely the ancestor of *C. mauritanicum*, *C. germanoaffricanum* and *C. simum* of the Quaternary, which continued the same evolutionary tendencies: hypsodonty, extension towards the rear of the lingual extremity of the protoloph of the upper cheek teeth lowering of the head, and passage towards a graviportal locomotion. *C. praecox* was a denizen of the savannah, grazing mainly on grass.

Equidae (V. Eisenmann, pers. comm.)

The equid *Hipparion* is represented in the EDM by a characteristic axial phalanx (Fig. 30 C), showing the distal narrowing that is not as well developed in *Equus*. An unworn upper cheek tooth ectoloph (Fig. 30 D) shows the medium degree of hypsodonty

(66 mm tall x 33 mesio-distal length near apex, 29 mm mesio-distal length near cervix) characteristic of Pliocene examples of this genus.

Hippopotamidae (M. Faure, pers. comm.)

The Ekuma deposits yielded two bones of *Hippopotamus*, EK 064, left calcaneum (Fig. 31 C C); first central phalanx (Fig. 31 B), and diverse fragments including a badly damaged navicular and some sesamoids.

Calcaneum: The bone is poorly preserved, the sustentaculum tali is broken and the two extremities are incomplete. It is however, possible to compare two of its dimensions with those of a sample of extant *Hippopotamus amphibius* (Faure, 1985). The height is greater than 180 mm. For 16 specimens of extant *Hippopotamus amphibius* this dimension ranges from 159 to 204 mm (mean 177.8 mm, standard deviation 13.558). The transverse diameter of the diaphysis above the sustentaculum is 43 mm. For 16 specimens of extant *Hippopotamus amphibius* this dimension ranges from 31 to 41 mm (mean 34.7 mm, standard deviation 3.177).

Phalanx I central: It is broken along its anterior surface and at the distal extremity. It is 72 mm long, its proximal breadth attains 50.5 mm and the transverse diameter of the

diaphysis is 38.5 mm. The homologous measurements for a posterior phalanx I central of extant *Hippopotamus amphibius* in the Musée d'Histoire naturelle de Lyon (n° OST 361) are respectively 68.5, 42 and 30.5 mm.

Identification: The calcaneum and the central first phalanx from Ekuma undoubtedly belong to a hippopotamus, but the preservation is too poor for species identification. Nevertheless these two bones are the same length as those of a medium sized extant *Hippopotamus amphibius* and their breadth is greater. More than 15 species of the genus *Hexaprotodon* (in the broad sense) and *Hippopotamus* are known in the Pliocene and Pleistocene of Africa. (Gèze, 1980, 1985 ; Boisserie, 2005). Only three are more or less compatible in dimensions and age with the Ekuma specimens : *Hexaprotodon harvardi* Coryndon, 1977, *Hexaprotodon protamphibius* Arambourg, 1944 and *Hippopotamus kaisensis* Hopwood, 1926. The first two are somewhat smaller than *H. amphibius* and their extremities are more slender ; the last is the same size as *H. amphibius* but its extremities are more elongated. It is therefore necessary to obtain better material before the Ekuma hippo can be identified.

Bovidae (JM & MP)

Bovid remains are quite common in the Ekuma Delta Member, but most of them are damaged. There are however two horn cores and a frontlet with both horns and partial dentition. Bovid dental postcranial remains from the same area (Fig. 30 B, E, F) suggest that there are two or three additional species of bovid in the deposits, but they are not identifiable at the species level.

Tribe Reduncini

Genus *Redunca* Smith, 1827

Redunca aff. *darti* Wells & Cooke 1956

ETO 19'06, a left horn-core with almost circular section, (49.4 mm x 53.5 mm) without keels. The thickening of the frontal is transversal to a suture fades out at the posterior base of the horn (Fig. 32 B). It is difficult to discern how many surfaces there are due to

the almost round section and the very attenuated keels.

There is no hint of frontal sinuses. The frontal is thick (even though not well preserved), the pedicle is broad, especially anteromedially. There is a shallow but large post-cornual fossa.

The anterior zone of the base of the horn is inflated, clearly visible in lateral and medial views. In anterior view the horn is quite straight, with a slight inclination towards the exterior. In lateral and medial views, it is possible to observe that towards its apex the horn curves forwards.

The anterior surface is convex and the posterior one flattened which makes the section almost circular with the anteroposterior diameter slightly less than the mediolateral one. Because of this, the medial and lateral surfaces are difficult to delimit, medially the horn is slightly keeled, whereas the transition between the anterior and lateral surfaces is marked by deep, vertical grooves.

The ornamentation is strong, comprising vertical grooves, especially prominent postero-laterally, and anterolaterally there are at least three subhorizontal growth ridges arranged parallel to each other.

EK 1'07 (ETO 231) a right horn-core with a subrounded section, is smaller (37.9 mm x 44.1 mm) than the previous specimen (Fig. 32 A). Despite the poor preservation of the horn-core, it is possible to see a shallow but extensive post-cornual fossa. Overall, this fossil looks like a gracile version of the preceding one. The base of the horn is slightly inflated anteriorly, the anterior surface is convex, but up to the apex there are deep grooves which have a tendency to become keels. The posterior surface is flattened basally becoming convex towards the apex. The delimitation between the anterior and posterior surfaces is clearer than in the previous specimen, hinting at the presence of keels medially and laterally which fade out progressively towards the apex. In anterior and posterior views, the horn is straight, while in lateral and medial views it is possible to see that the horn is inclined backwards near the base and curves forwards near the apex.

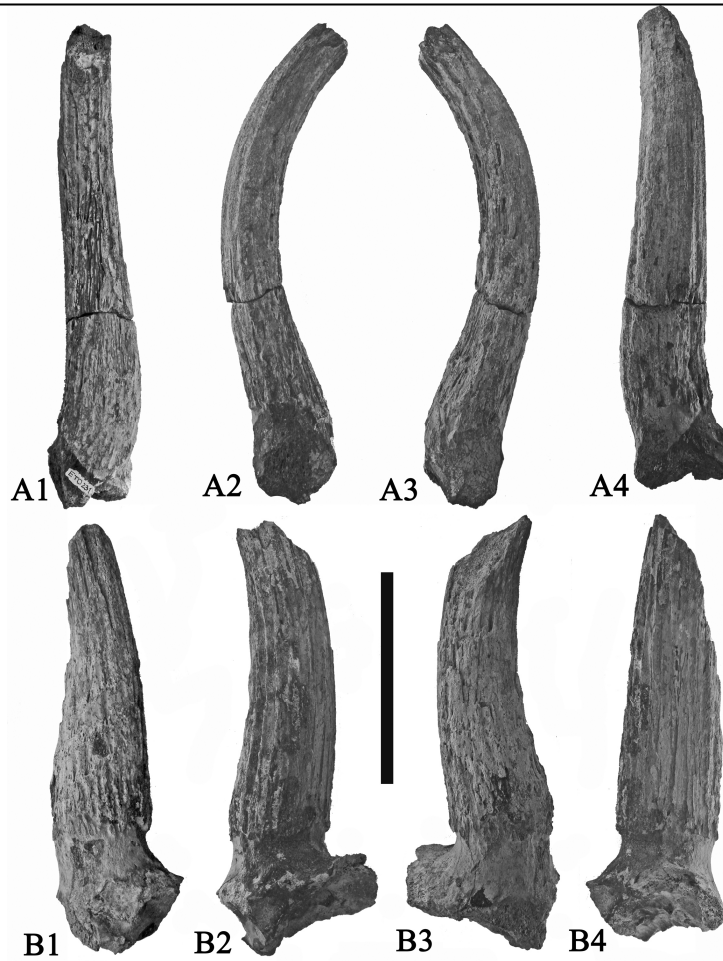


Figure 32. *Redunca* aff. *darti*, from the Ekuma Delta Member, Namibia, A) EK 1'07, right horn-core, B) ETO 19'06, left horn-core, 1) anterior, 2) lateral, 3) medial, 4) posterior views (scale : 10 cm).

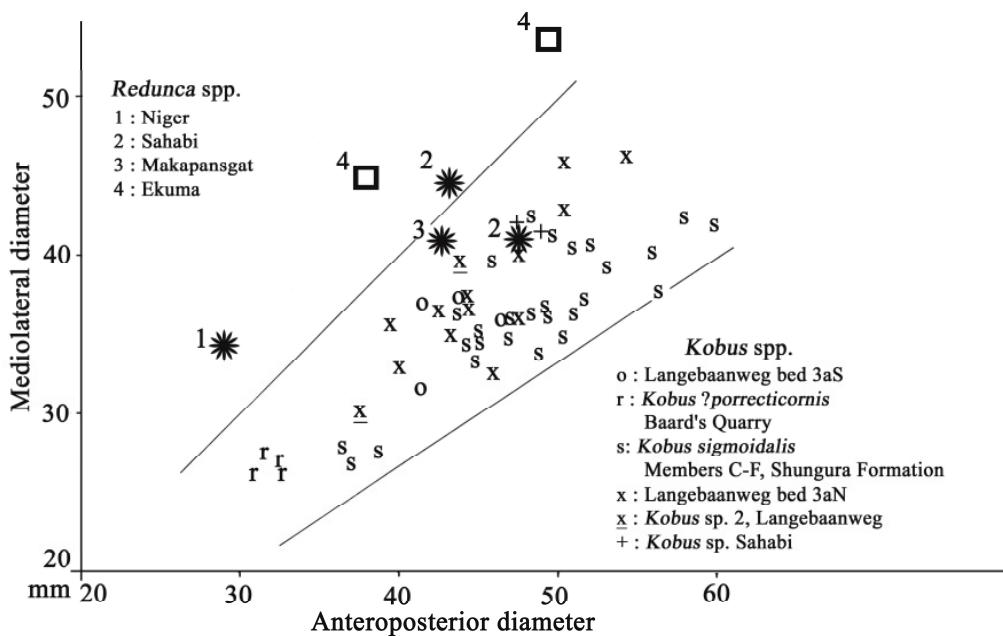


Figure 33. Bivariate plots of anteroposterior and mediolateral diameters of horn cores of *Redunca* spp. The two specimens from the Ekuma Delta Member are closest to *Redunca darti* from Makapansgat, South Africa and fossils attributed to this species from Sahabi, Libya.

Discussion

The morphological features of these two horn-cores are encountered in representatives of the tribe Reduncini. In general, they differ from those of species of *Kobus* by the transverse section of the horn-core, which is more circular, even though a few individuals have medio-lateral diameters greater than the anteroposterior one. Lehmann & Thomas (1987) employed this more circular morphology of the horn-core section to attribute to *Redunca* aff. *darti* Wells & Cooke (1956) two frontals and a horn-core from Sahabi, Libya, distancing them from *Kobus subdolosus* from Langebaanweg (Gentry, 1980) and from the ruminants from Mpesida and Lukeino (Thomas, 1980). The two best preserved horn-cores from Ekuma have almost circular transverse sections, in which the transverse diameter (mediolateral) is slightly greater than the anteroposterior one (Fig. 33). This is also the case in *Redunca* aff. *darti* from Niger (Pickford et al,

2008) and the frontals described from Sahabi by Lehmann & Thomas (1987), despite the fact that the second specimen from Sahabi has an anteroposterior diameter somewhat greater than the transverse one. As in *Redunca darti* from Makapansgat, South Africa (the type locality) and in the Sahabi form, those from Ekuma are inflated near the base of the horn-core, clearly visible in lateral and medial views, and the apex of the horn curves forwards. Apart from the localities cited above, *Redunca darti*, or a similar species, occurs at Langebaanweg, where two specimens (L10672 and L1748) present the characteristic features of *Redunca*, although the lateral compression is slightly stronger, as in one of the specimens from Sahabi. In the Natural History Museum, London, there is a horn-core (NHM M 15925) from Kanam Museum Cliff (Kenya) (Kent, 1942) which is comparable in morphology and dimensions to the Ekuma *Redunca*.

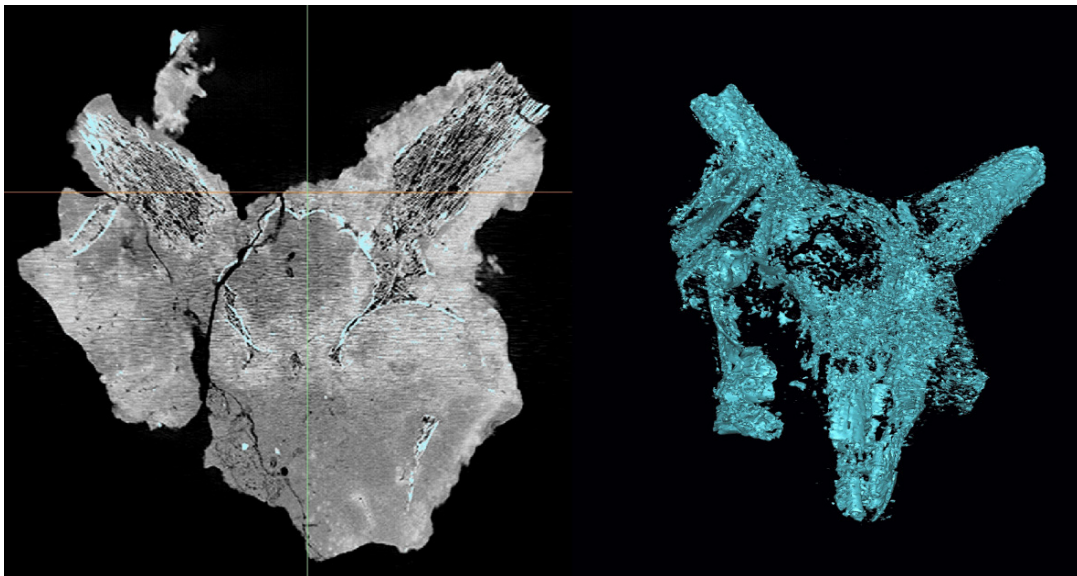


Figure 34: EK 5'07, fragmentary skull of a reduncine embedded in quartzite. Left image is a section through the block showing the quartzite and bone, right image is a 3D view after digital removal of matrix.

EK 05'07, a fragmentary reduncine skull embedded in quartzite preserves the posterior part of the palate and much of the frontals and the two horn-cores (Fig. 34). Interpretation is difficult due to the cover of matrix, but it seems that the two horn-cores are inserted far apart in the frontals, diverging strongly towards the exterior. The trans-

verse section of the right horn-core about 110 mm from the base is almost circular, without any signs of compression. Both M3/s are preserved (L= 24-26.7, W=15.3-16.1) and the roots or alveoli of the anterior molars are present. The molar series is about 65 mm long.

EK 1'06, an unerupted right lower pre-

molar row (p/2-p/4) is approximately 37 mm long, and could correspond to the same species as the skull. The p/4 has an open lingual wall and the mesiolingual conid is directed backwards.

Flora and Fauna from the Poacher's Point Carbonate Member of the Andoni Formation

The Poacher's Point Member of the Andoni Formation comprises a deposit of micro-oids cropping out extensively along the Oshigambo Peninsula, at Poacher's Point, the Stinkwater Peninsula and at Pelican Island where the ooids are larger, forming oolites up to 2 mm in diameter. In many places these deposits have yielded faunal remains comprising terrestrial snails (Fig. 10) similar to those that live in the Etosha Basin today, but thus far the only vertebrate remains found comprise eggshell fragments attributed to *Struthio camelus*. It is therefore difficult to estimate an age for the sediments, although it is evident that they post-date the Ekuma Delta Member, and are most likely to be Pleistocene, an estimate supported by the eggshell evidence (Senut & Pickford, 1995). The regional palaeoclimate at the time of deposition was probably sub-humid to semi-arid, as it is today.

Oncolites and stromatolites (AP and CP)

Oncolites occur abundantly on the west flank of Poacher's Point and round the shores and in cliffs along the Stinkwater Peninsula, and more rarely near Oshigambo in the floor of Etosha Pan (Fig. 35-38). These oncolites are polyphase structures, each interruption in growth representing a change from fresh water to evaporitic conditions. The nuclei of the oncolites are varied, ranging from indurated sediment to fragments of pre-existing stromatolites, or even to soft sediment which later developed septaria during desiccation.

Each growth phase represents a return to a more humid climate. Erosional phases can produce either rounded pebbles due to high energy conditions (waves for example)

or flatter pebbles produced during paroxysmal storms or in oncolites exposed in outcrops, due to thermal fracture resulting from many cycles of daily temperature changes.

The smectite sediment surrounding the oncolites (sodic smectite, analcime and sometimes halite) is not contemporary with their growth. The sediment originally associated with the growth of the oncolites is a lacustrine limestone containing ostracods, which have been incorporated into the inter-pillar spaces of the oncolites. In thin section abundant spherical globules (168.5 μm in diameter) are visible which probably represent the Chlorophyceae, *Chlorellopsis coloniata*, a thallophyte that is usually associated with lacustrine oncolites and cherts.

Succineidae (MP)

A shell of a succineid gastropod (h x b = 9.8 x 6 mm) (Fig. 39 A) has the same proportions and dimensions as extant *Succinea striata* from Namibia. Connolly (1939) recorded several species of the genus from Namibia, including *S. badia*, *S. arboricola*, and *S. exarata*, which differ from each other in size and shell proportions. The fossil from Poacher's Point is closer in size and shape to *S. striata* than to any of the other species.

Subulinidae (MP)

Subulinid shells are very common in the Poacher's Point Member (Fig. 39 B). They are all referable to a single species, *Xerocerastus burchelli* (h x b = 17 x 7 h/d 2.43; h x b = 16 x 6.6 h/d; 2.42, h x b = 15.7 x 5.7 h/d 2.75). At present there are several species of *Xerocerastus* in Namibia (Connolly, 1939). Van Bruggen (1970) recognised 5 species which differ from each other in dimensions and shell proportions; *X. damarensis* (h/d 2.21-2.61), *X. burchelli* (h/d 2.27-2.46), *X. subteres* (h/d 2.59-3.16), *X. nitens* (h/d 2.00-2.09), *X. hottentotus* (h/d 1.58-1.64) and *X. ovulum* (h/d 1.40-1.61). The material from Poacher's Point is similar in dimensions and shell proportions to two of these species *X. damarensis* and *X. burchelli*, but it appears to be morphologically closer to the latter than to the former.

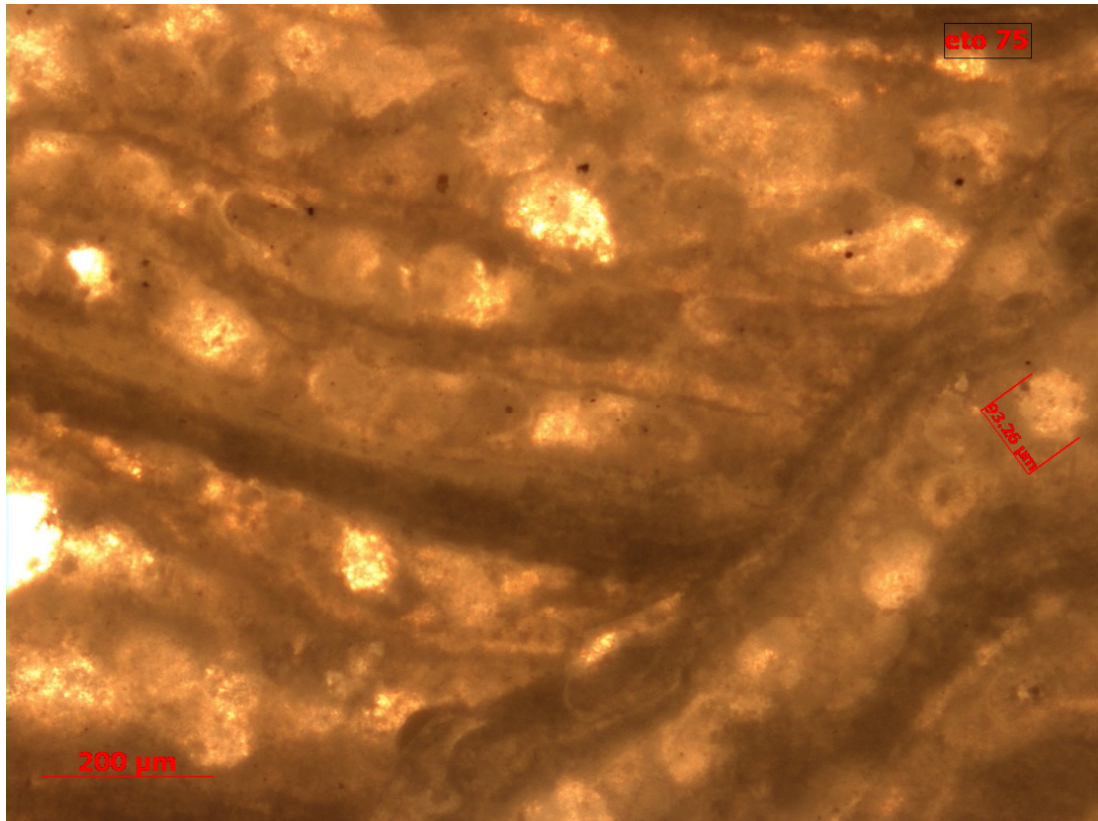


Figure 35: Microglobules (168.5 μm diameter) of organic origin are abundant in the interstices of stromatolites. These probably correspond to *Chlorellopsis coloniata*.

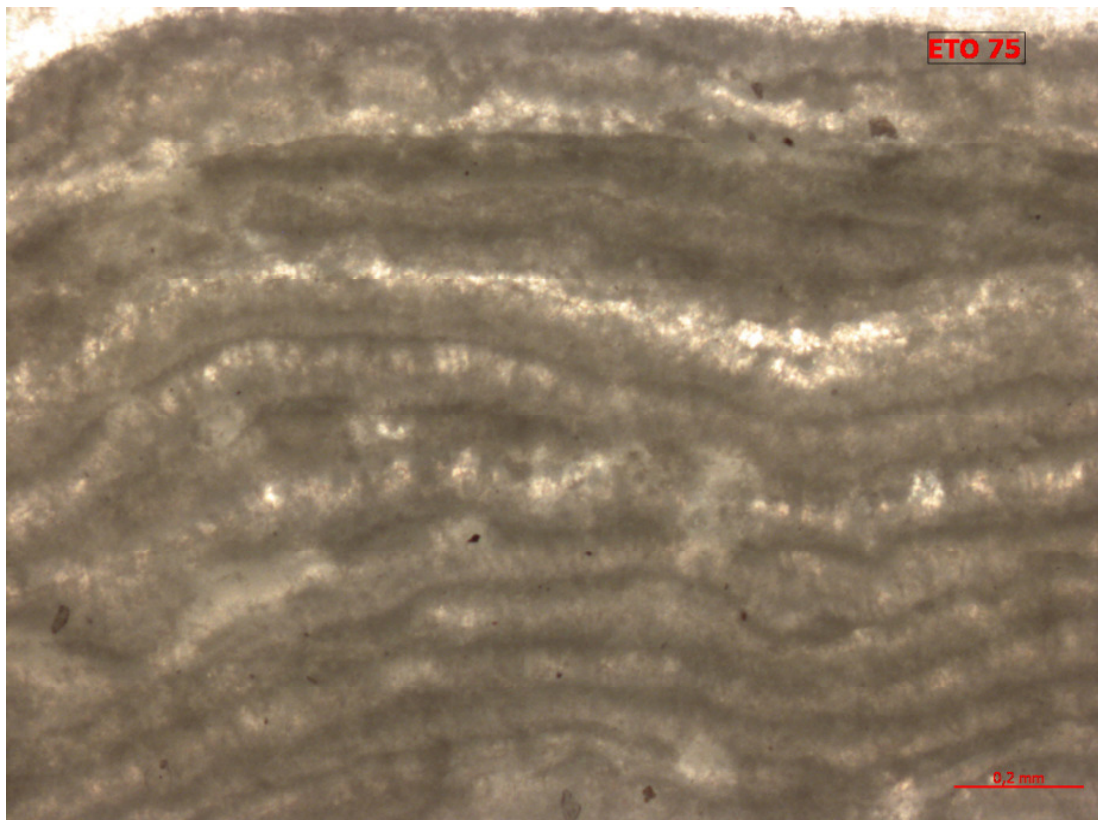


Figure 36: Microlaminations of Etosha oncolites are clearly visible in thin section.



Figure 37: Polished section of an oncolite from Poacher's Point, Etosha. Note the core comprised of sediment which includes phosphatic grains, possibly coprolites or rounded and polished fish bones. The polyphase growth of this individual is clearly demonstrated by a rupture which has removed part of the dark layer (to the left of the image) followed by a second growth phase (paler layers). Note the pillar-like growth pattern in parts of the oncolite, with open or sediment-filled gaps between the pillars.

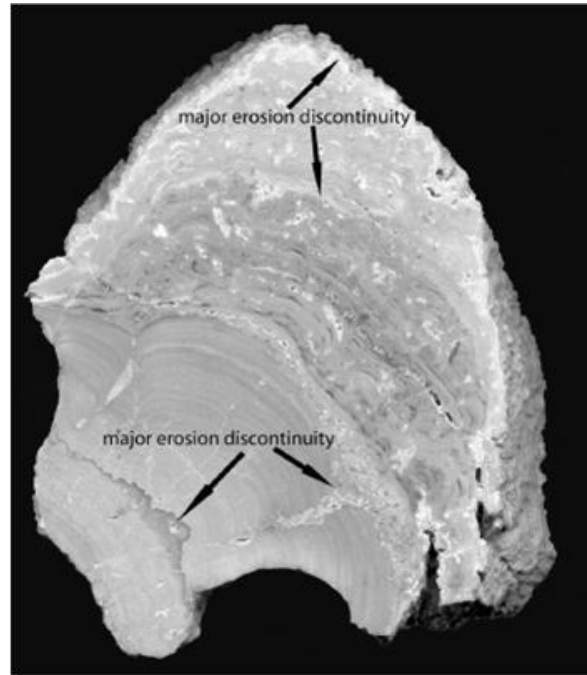


Figure 38: Polished surface of a stromatolite from Poacher's Point showing evidence of at least four periods of erosion and growth.



Figure 39: Landsnails from the Poacher's Point Carbonate Member, from the west flank of Poacher's Point. A) *Succinea striata*, B) *Xerocerastus burchelli*, C) *Achatina dammarensis* (apertural views). (scale bars : 10 mm).

Achatinidae (MP)

Achatinid shells are reasonably common at Poacher's Point, but few of them are fully adult or well preserved. An exception is a complete specimen (Fig. 39 C) attributed to *Achatina dammarensis* (h x b = 67 x 40; h/d 1.67). Connolly (1939) recorded several species of *Achatina* from Namibia, which differ from each other in dimensions and superficial shell sculpture such as the way the granulations are arranged on the surface of the shell. The Poacher's Point specimen is close in shape to *Achatina oedigyra* and *A. dammarensis*, but differs from *A. tracheia* and *A. passargei*, which are taller and narrower (Connolly, 1939). We attribute the specimen to *A. dammarensis* despite the somewhat greater dimensions than are usually encountered in this species.

Struthionidae (LS & MP)

The Poacher's Point micro-oid horizon yielded a single fragment of ostrich egg

shell, probably *Struthio camelus* judging from its thickness of 1.9 mm and the presence of pore complexes that are smaller than those of *Struthio daberasensis* (Senut and Pickford, 1995; Senut *et al.*, 1998).

Flora and fauna from the Etosha Limestone

The Etosha Limestone is a widespread calcrete horizon that formed by a variety of processes. In the south it is a groundwater calcrete, whereas in the north it is a pedogenic calcrete often containing abundant rhizoliths (Fig. 40).

The Etosha Limestone has been eroded from much of the surface of the Etosha Pan, and now occurs as discontinuous outcrops at the summit of islands and ridges within and close to the margins of the pan (Miller, 2007). In places such as Poacher's Point and Oshigambo Peninsula, the calcrete has yielded abundant fossils of terrestrial snails



Figure 40: Etosha Limestone in the banks of the Ekuma River Valley. This calcrete horizon is widespread in the Etosha Basin, frequently showing abundant rhizolith networks. Locally, at Ekuma River, this unit unconformably overlies an irregular surface incised into the Ekuma Delta Member, the Poacher's Point Carbonate Member, and an un-named rubble horizon containing black nodules (also present on Pelican Island).

(Fig. 41) but no vertebrates have been found. Lacustrine and paludal gastropods are rare in the calcrete and related deposits, but have been found at Homob waterhole on the southern margin of the pan in calcified marly silts that probably accumulated within the waterhole depression and in calcareous tufa depos-

its close to Namutoni. On stratigraphic and geomorphological grounds, the Etosha Limestone is likely to be Early to Middle Pleistocene in age, but there is no direct evidence for this estimate in the form of datable fossils.

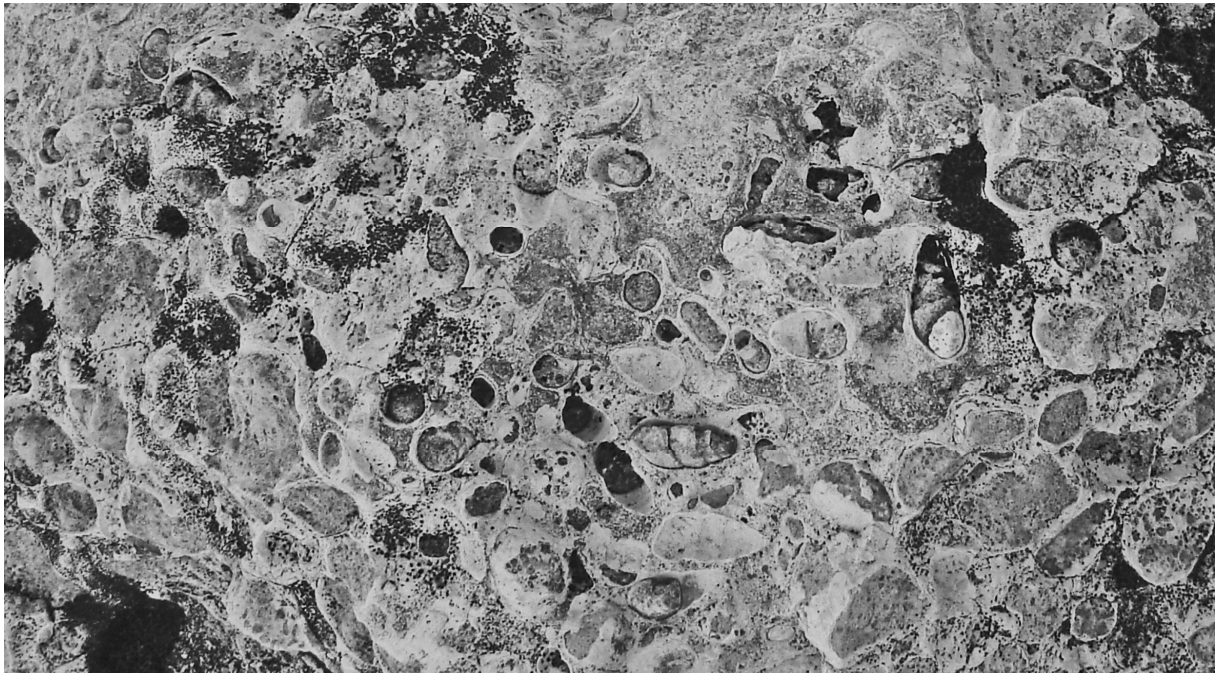


Figure 41: Abundant shells of *Xerocerastus burchelli* in calcrete (Etosha Limestone) atop the Oshigambo Peninsula on its northern flank, Etosha, Namibia (Some of these shells could be “inherited” from the Poacher’s Point Carbonate Member on top of which the Etosha Limestone formed).

Fauna from the Etosha raised beaches (1.5 - 2 m beaches)

Pale orange silt and sand, along with cobbles and reworked oncolites, which accumulated in beaches at an altitude of 1.5 to 2 metres above the present day floor of Etosha Pan, have yielded abundant fossils. In the Ekuma River Valley, these deposits have been incompletely indurated to the stage where pea-sized clumps of calcified sand have formed within the bed which is otherwise poorly consolidated. The commonest fossils from this deposit comprise shells of *Melanoides tuberculata*, which are accompanied by rarer shells of *Mutela* sp. and *Bellamyia unicolor*. No land snails have been found in these beach deposits.

The assemblage of molluscs in the raised beach deposits comprise freshwater

species. Although *Melanoides* is tolerant of slight alkaline or weakly saline water, *Mutela* sp. and *Bellamyia unicolor*, in contrast, are intolerant of such conditions, and attest to the presence of well-oxygenated, fresh water conditions. *Melanoides tuberculata* is widespread in Africa, but is absent from forested zones and desert areas (Brown, 1980). It does however occur as an isolated population at Namutoni Springs (Van Bruggen, 1963) well removed from its general distribution in Africa (Fig. 42).

Fauna from the Oshigambo Pan-loess

Late Pleistocene sands and silts exposed along the southern edge of the Oshigambo Peninsula, attributed to the Oshigambo Pan-loess, have yielded a rich variety of fossil vertebrates (Hipondoka, 2005) including aquatic bovids such as *sitatunga*

(*Tragelaphus spekei*) which have been interpreted to indicate the former presence of perennial lacustrine conditions in the area at the end of the Pleistocene (Hipondoka *et al.*, 2006). The inferred presence of a recent highstand of Palaeolake Etosha gains support from the occurrence at Pelican Island, of green silts that overlie an eroded and incised surface of Etosha Limestone and older rocks (Fig. 4). The Oshigambo faunal assemblage contains remains of terrestrial gastropods similar to those that occur in the region today (*Achatina dammarensis*, *Xerocerastus*

burchelli) as well as ostrich egg shells (*Struthio camelus*) (Fig. 43) and fungus gardens of termites, suggesting a sub-humid to semi-arid terrestrial environment nearby. Other mammals from the deposits comprise *Equus quagga* (quagga), *Damaliscus lunatus* (tsessebe), *Antidorcas marsupialis* (springbok), *Aepyceros melampus* (impala), *Tragelaphus spekei* (sitatunga), *Taurotragus oryx* (eland). The sediments also yield terrestrial snails (*Achatina dammarensis* and *Xerocerastus burchelli*) and there are also termite fungus gardens (*Hodotermes* sp.).

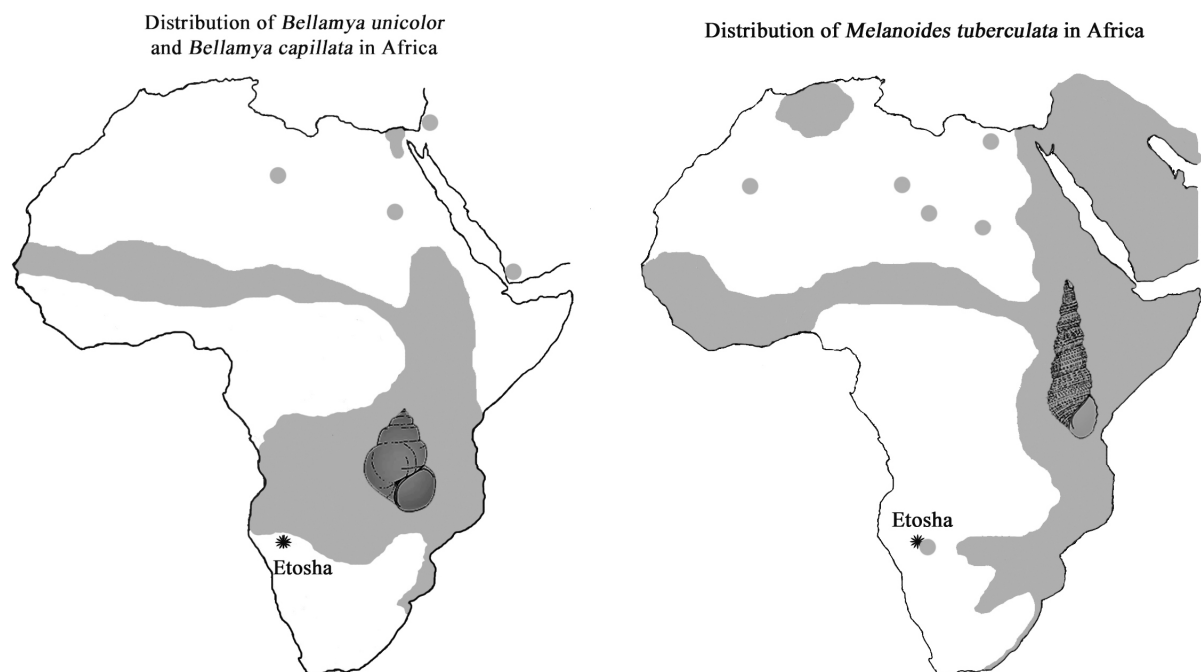


Figure 42: Distribution of *Melanoides* and *Bellamya* relative to Etosha Pan. *Melanoides* occurs today in the Namutoni Springs in the southeast corner of the Etosha Basin, but as an outlier of the main zone of distribution of the genus. The combined presence of these two genera in the raised beach deposits in the Ekuma River Valley implies a climate that was probably somewhat more humid at the time of deposition than it is today. The same is suggested by the presence of the bivalve *Mutela* sp.

Discussion

Biochronology of the Etosha Pan Clay Member and the Ekuma Delta Member of the Andoni Formation

Etosha Pan Clay Member

An age of ca 6 Ma is deduced for the Etosha Pan Clay Member on account of the presence of a primitive loxodont with low crowned molars and thick enamel. The

specimens, even though fragmentary, are close in morphology to material from Late Miocene deposits in South Africa (Langebaanweg) and East Africa (Nkondo, Lukeino) attributed to *Loxodonta cookei* by Sanders (2007). A similar age is indicated by the presence of a primitive alcelaphine, differing slightly in horn core shape from *Damalacra neanica* from Langebaanweg but close to *Damalacra acalla* from the same site (Gentry, 1970).

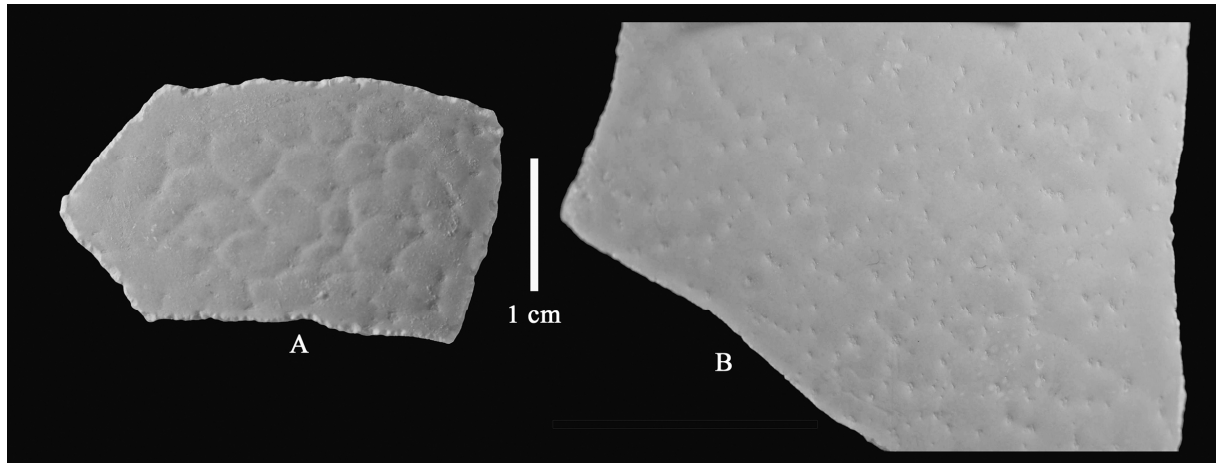


Figure 43: Egg shells of *Struthio camelus* from Etosha, Namibia, A) Holocene, GPS 102 (18°41'23.9''S : 16°09'22.8''E), and B) Modern, ETO 161107.

Ekuma Delta Member

Horn cores of *Redunca darti* from Ekuma resemble material from East African deposits aged about 4 Ma (Gentry, pers. comm.). The equid from Ekuma is *Hipparion* sp. (Eisenmann, pers. comm.). The pedetid tooth from Ekuma is older than material from Laetoli, Tanzania (3.7-4 Ma) (Davies, 1987) but younger than the *Diamantornis laini* levels at Rooilepel (8-10 Ma). The rhinocerotid from Ekuma is the large extinct species *Ceratotherium praecox* which ranges in age range from 7 to 4.5 Ma. The *Hippopotamus* from Ekuma is a large species, but the re-

mains are too fragmentary for species determination. On the basis of these faunal remains a Middle Pliocene age (ca 4 Ma) is estimated for the Ekuma Delta Member.

Radio-isotopic age determination of the Oshigambo Pan-loess fauna

New age determinations have been obtained from faunal elements from the Oshigambo Pan-loess deposits located at the western extremity of the Oshigambo Peninsula. The results are presented in Table 8, and indicate that the deposits date from the Late Pleisto-

nature	$\delta^{13}\text{C}_{\text{‰}}$	APGM	ASG	mg C	N°labo	Age AMS	Calibrated age (2s)
Bovid bone bioapatite	0,9	19	11	1,28	Pa650	10778±54 BP	12880-12720 cal bp
Bovid bone bioapatite	0,34	19	11,3	1,28	Pa651	11489±56 BP	13450-13230 cal bp
Bovid enamel bioapatite	0,14	28	17,6	1,95	Pa652	12091±59 BP	14090-13800 cal bp

Table 8: Radio-isotopic age determinations of faunal elements from the Oshigambo pan-loess.

These age determinations are considered to be more reliable than previous estimates obtained by analysing collagen from an equid bone from the site, because in this round of analyses the determinations were made on bioapatite, and not collagen, which is usually poorly preserved. We conclude that the site dates back to the very end of the Pleistocene after the hyper arid phase of the Last Glacial Maximum (18 ka).

Conclusions

Surveys of Etosha in 2006 and 2007 by the Namibia Palaeontology Expedition led to the discovery of fossil sites of Late Miocene and Mid-Pliocene age (Table 9). The flora is dominated by tree boles and root systems, whereas the fauna is rich in invertebrates and vertebrates (Table 9). These discoveries complement those of Hipondoka (2005, Hipondoka *et al.*, 2006) who found a rich and diverse fauna in the Late Pleistocene Oshi-

Formation/ Palaeontology	Etosha Pan Clay Member	Ekuma Delta Member	Poacher's Point Carbon- ate Member	Etosha Lime- stone	Oshigambo Pan-loess
Oncolites	X		X	X (reworked?)	
<i>Chlorellopsis coloniata</i>			X		
Palm		X			
Dicotyledon		X			
Ostracoda	X		X		
<i>Hodotermes</i> sp.				X	X
<i>Succinea striata</i>			X	X	
<i>Xerocerastus burchelli</i>			X	X	X
<i>Achatina dammarensis</i>			X	X	X
<i>Bellamyia unicolor</i>		X			
Planorbidae sp.				X	
<i>Mutela</i> sp.	X	X			
? <i>Egeria</i> sp.		?			
<i>Clarias</i> sp.	X	X			
Cyclanorbinae sp.	X	X			
<i>Pelusios</i> sp.	X	X			
<i>Crocodylus</i> sp.	X	X			
<i>Phoenicopterus ruber</i>	X	X			
<i>Struthio daberansensis</i>		X			
<i>Struthio camelus</i>			X	X	X
<i>Propedetes</i> sp.		X			
<i>Panthera cf leo</i>	X				
<i>Loxodonta</i> sp. cf <i>cookei</i>	X	X			
<i>Ceratotherium praecox</i>		X			
<i>Hipparion</i> sp.		X			
<i>Equus quagga</i>					X
<i>Hippopotamus</i> sp.		X			
Suidae (large sp.)	X				
<i>Damalacra acalla</i>	X				
<i>Redunca darti</i>		X			
<i>Damaliscus lunatus</i>					X
<i>Antidorcas marsupialis</i>					X
<i>Aepyceros melampus</i>					X
<i>Tragelaphus spekei</i>					X
<i>Taurotragus oryx</i>					X
Bovidae 2-3 spp.	X	X			

Table 9: Summary of the distribution of the palaeontological remains in the various stratigraphic units exposed in the floor and flanks of Etosha pan.

gambo Pan-loess, and Mid-Pliocene fossils in the Ekuma Delta, which belong to a wide variety of extant taxa, including aquaphilous antelopes. Palaeontology is proving to be crucial to the determination of the timing of geological events in the basin, and this impacts directly on the interpretation of the history of the basin.

It is clear that there was a complex history of alternating erosional and depositional episodes in the Etosha Basin, at least in the latter part of its history represented by the uppermost 20-30 metres of sedimentary deposits spanning the period 6 Ma to the Late Pleistocene. The three exposed members of the Andoni Formation attest to a shallowing upwards lacustrine system, with the Etosha Pan Clay Member recording fully lacustrine conditions, the overlying Ekuma Delta Member an increase in fluvial deposition, and the oolitic limestones of the Poacher's Point Carbonate Member, deposition in shallow water which towards the end became hyper-alkaline, to such an extent that Magadi-type chert plaquettes formed in abundance. The deposition of this carbonate unit was accompanied by the growth of abundant algal oncoliths. There followed a period of calcrete pedogenesis resulting in the formation of the widespread Etosha Limestone, which incorporated into it elements of the underlying deposits, such as oncoliths. In the south of the Etosha basin, calcrete formation was predominantly due to groundwater processes which produced dolomitic calcrete in huge, low-angle megadomes, while in the north, the Etosha Limestone is largely of pedogenic origin, with a rubbly, nodular structure and abundant rhizolith networks.

Unconformably on top of an eroded and incised surface of rocks of the Andoni Formation and Etosha Limestone, which left a widespread rubble horizon containing black nodules of sediment, there occur various Late Pleistocene deposits including fossiliferous raised beach deposits 1 – 1.5 metres above the present day floor of the pan, and the Pelican Island green silt which occurs up to 10 metres above the pan floor. The latter deposits attest to a Late Pleisto-

cene lacustrine high stand which filled Etosha Pan with water to a depth of at least 10 metres. A lake of this depth would cover an area of well over 5,000 km². Overlying the raised beach deposits there is an extremely widespread horizon 1 to 1.5 metres thick, of grey silt and clay comprising the Oshigambo Pan-loess. At the western extremity of the Oshigambo Peninsula, this unit has yielded a rich and diverse fauna. Some elements of the fauna, such as *sitatunga* indicate that there was a perennial lake in the basin some 12,000 to 14,000 years ago. The Pelican Island green silts and the raised beach deposits at Poacher's Point and in the Ekuma River valley, probably represent earlier manifestations of this palaeolake.

Finally, we emphasise that the Etosha Late Miocene and Ekuma Basal Pliocene fossil localities help to fill what used to be an enormous void in the palaeontological map of the African continent for the period between 8 and 4 million years. This is a period of interest to palaeoanthropologists who desire to throw light on hominid origins. The strata in the Etosha Basin are thus crucial not only for understanding the history of the basin, but are also because of their potential for the study of hominid origins and Late Miocene and Pliocene palaeoenvironments.

Acknowledgements

In Windhoek, we thank Dr Gabi Schneider, Director of the Geological Survey of Namibia, who provided essential help and encouragement, and Erica Ndalikokule of the Namibian National Heritage Council for arranging authorisation to carry out research in Namibia. The support of the University of Namibia is gratefully acknowledged. At Etosha we thank the Ministry of Environment and Tourism (Michael Sibatani, Rehabiam Erkie, Shane Kötting) and the Etosha Environmental Institute (Wilferd Versfeld and Nigel Berriman). We thank Manolo Salesa for making the CT scans of the Ekuma River bovid.

For financial, administrative and logistic support, we thank the French Embassy in

Namibia (His Excellency, Monsieur P. Boissière), the Cooperation Service of the French Embassy in Windhoek (M. Jouve, L. Ronis), the Collège de France (Prof. A. de Ricqlès), the Muséum National d'Histoire Naturelle, Paris, UMR 5143 of the CNRS, the University Pierre et Marie Curie, Paris, Université Claude Bernard, Lyon I, the Museo Nacional de Ciencias Naturales, Madrid, and the Naturhistorisches Museum Wien of Austria. A grant from the FWF-Lise Meitner program/M956-B17 attributed to Helene Jousse enabled isotopic dates to be made for the Oshigambo Late Pleistocene fauna. We are also anxious to thank Dr Roy Miller for his geological input to the understanding of Etosha. We thank Drs Alan Gentry for comments on the Etosha and Ekuma bovids, Vera Eisenmann for identifying the equid remains and Martine Faure for examining the hippopotamid remains.

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