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GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND SOUTHERN NAMIB

VOLUME 2: PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

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VOLUME 2: PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

by

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A new species of Crocodile from Early and Middle Miocene deposits of the lower Orange River Valley, Namibia, and the origins of the Nile Crocodile (*Crocodylus niloticus*)

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Fossil crocodiles are common in proto-Orange River deposits of Lower and Middle Miocene age. They are also known from the Middle Miocene of the Koa River Valley at Bosluis Pan, Namaqualand, South Africa. The skull of the species is similar in many respects to the extinct species *Crocodylus Iloydi*, known !Tom Early and Middle Miocene deposits of North Africa, and the Plio-Pleistocene of East Africa, but its mandible and neurocranium are closer to those of the extant species *Crocodylus niloticus*. It is possible that the Arrisdrift species rather than *C. lloydi*, gave rise to the Nile crocodiles in Africa considerably to the south of their present day distribution limits. The presence of crocodiles in southern Namibia and South Africa suggests that this part of the continent was tropical to subtropical during the Early and basal Middle Miocene, in strong contrast to its temperate nature today.

Fésume français

Les crocodiles fossiles sont abondants dans les dépôts sédimentaires du fleuve proto-Orange, Namibie, datés du Miocène inférieur a moyen. lis sont également connus dans Ie Miocène moyen à Bosluis Pan, dans la vallée de la rivière Koa, Namagualand, Afrique du Sud. Les fossiles sont proches de l'espèce éteinte Crocodylus lloydi, connue dans les couches du Miocène inférieur à moyen d'Afrique du Nord, et les niveaux plio-pléistocènes d'Afrique orientale, mais plusieurs caractères morphologiques se trouvént dans l'espèce actuelle, Crocodylus niloticus. Il est probable que le crocodile d'Arrisdrift plutôt que C. lloydi a donné naissance à C. niloticus. La limite méridionale de la répartition des crocodiles fossiles en Afrique se trouvé considérablement au sud des limites actuelles, ce qui suggère que l'Afrique australe était tropicale à sub-tropicale pendant le Miocène inférieur et moyen, tandis qu'àctuellement cette région est tempérée.

Introduction

The fluvial deposits which accumulated in a lateral channel of the Proto-Orange River at Auchas and Arrisdrift, southern Namibia, have yielded large quantities of crocodilian remains. Most of these are scutes and isolated teeth but in the collection there are two almost complete skulls, an anterior part of a skull and several lower jaw fragments which are complete enough to provide a reasonably confident identification of the species. Comparison of the Arrisdrift species with other crocodiles from Africa and Eurasia reveals that its skull has several characters in common with Crocodylus lloydi, Fourtau, 1918, first described from the Early Miocene of Wadi Moghara, Egypt, and later recorded from the Late Miocene and Plio-Pleistocene of East Africa. In a few features, in particular the proportions of its mandibular symphysis, it is closer to extant Crocodyus niloticus, and it, could well represent an ancestral stage of the Nile crocodile. At Arrisdrift, several of the mammalian skeletal remains show puncture marks of the sort made by crocodile teeth.

Geological setting and age of Arrisdrift

The Arrisdrift locality (Corvinus, 1978; Corvinus & Hendey; 1978; Hendey, 1978, 1983; Pickford, 1987, 1995) is a richly fossiliferous channel filling of basal Middle Miocene

age (Pickford *et al.*, 1996). Pickford (1995) concluded that the site is somewhat earlier than previously considered, being about 17.5 Ma, correlating with East African Faunal Set P ilia (Pickford, 1981) and European Mammal Zone MN04a (Mein, 1990). This was a period of high global sea-level and it is worth mentioning that the fossiliferous strata at Arrisdrift, which are now 41-42 metres above sea-level, contain serpulid worm tubes suggesting that, at the time of sediment accumulation, the Arrisdrift channel contained brackish water near sea-level. The basal Middle Miocene was also a period of massive faunal turnover in Europe, America and Africa. There is little doubt that Arrisdrift post-dates the classic sites of Elisabethfeld, Fiskus and Langental - usually referred to as Early Miocene - in the northern Spergebiet, which have not yet yielded crocodilian remains.

Over 10,000 individual fossils have been collected at Arrisdrift of which over 10% are crocodilian (for example, 18.2% of the fossils excavated in 1994, the fossils of which were individually catalogued, are crocodiles). Most of these are isolated teeth and scutes, with a scatter of vertebrae and limb bones, but there are a few more complete specimens in the collection, notably two almost complete skulls, a fragmented snout, and several jaw fragments with complete symphyses.

This material was identified as *Crocodylus* sp. by Corvinus (1978) and Corvinus & Hendey (1978) and was later identified as *?Crocodylus nilotieus* by Hendey (1978). Pickford (1996) considered it to be *Crocodylus lloydi* but recognised that it possessed a few features suggesting affinities to the extant Nile crocodile. The two skulls now known are relatively brevirostral suggesting affinities to *C. lloydi*, while the lower jaws are closer to those of *C. niloticus* (Pickford, 1996).

Geological setting and age of Auchas

Auchas is a diamond mine in the Orange River valley some. 50 km from Oranjemund (Pickford *et al.*, 1996b; Pickford & Senut, 2000). It is an abandoned loop or meander of the proto-Orange River containing sediments of Early and Middle Miocene age. From the deposit known as AM 02 (Auchas Main, 02) numerous silicified tree trunks and several vertebrate bones and skulls have been collected. Among the latter are at least three taxa of proboscideans including *Deinotherium hobleyi*, a gomphothere of small size and *Eozygo*-

Table 1: Summary of comparisons of cranial proportions comparing C. gariepensis sp. nov. to ranges of variations that occur in other crocodile species (Index numbers refer to the measurements defined in Table 2) (W = Width, L = Length).

Anatomy	Index	C.niloticus	C.lloydi	C.pigotti	C.checchiae	C.palustris
Orbital W/Snout L	5/10	Outside	Within	Outside	Overlap	Within
Premax W/ Premax L.	7/23	Outside	Within	Outside	Within	Within
Orbital W/Quad-jugal W	5/4	Outside	Within Outside Outside		Outside	Outside
Premax W/ Snout L	7/10	Outside	Within Outside		Within	Within
Maxillary W/Snout L	8/10	Overlap	Overlap Within		Within	Within
Orbital W/ Skull L	5/2	Outside	Within	Outside	Outside	Within
Quad-jugal W/ Skull L	4/1	Within	Outside	Outside	Outside	Within
Quad-jugal W/Snout L	4/10	Within	Outside	Outside	Outside	Close
Premax L/Cranial table W	23/15	Outside	Within	Outside	Outside	Within
Cranial table L/Cranial table W	14/15	Within	Outside	Outside	No data	Within

don morotoensis. The deposit has also yielded Diamantomys luederitzi, Myohyrax sp., Prohyrax hendeyi, rhinocerotids, Brachyodus, chelonians of large size and an isolated tooth and distal humerus of a crocodilian. The rodent and the small size of the Auchas gomphotheres indicate that the site is somewhat older than Arrisdrift where the proboscideans are appreciably larger and which so far has not yielded remains of Diamantomys. The vertebrate assemblage from Auchas, even though limited in diversity, is close in composition to that from the site of Elisabethfeld, Northern Sperrgebiet which is of Early Miocene age, suggesting that AM 02 is of comparable age or only slightly younger.

Systematic descriptions

Family Crocodylidae Cuvier, 1807 Genus *Crocodylus* Laurenti, 1768 Species *Crocodylus gariepensis* sp. nov.

Holotype: AD 774'99, partial skull lacking the left half of the snout (Pl. 1-4).

Type locality and Age: Arrisdrift, Namibia, ca 17.5 Ma.

Referred material: PQ AD 1856, almost complete skull (Pl. 5, Fig. 2); PQ AD 3300, left premaxilla and maxilla broken off behind anterior part of palatine fenestra; AD 70'94, left maxilla with three teeth; PQ AD 999, left mandible broken off behind the 9th tooth (symphysis is in good condition); PQ AD 1855, anterior left mandible broken off behind 10th tooth; PQ AD 2673, left mandible broken off behind the 14th (last) tooth (Pl. 5, Fig. 1,3); AD 115'94, left mandible broken behind the 14th (last) alveolus (Pl. 5, Fig. 4-5); AD 135'00, mandibular symphysis; AD 360'00, mandibular symphysis; AD 460'00, mandible with symphysis + many jaw fragments, isolated teeth, scutes, vertebrae and limb bones.

Diagnosis: A species of *Crocodylus* with relatively short snout as in *C. lloydi*, mandibular symphysis proportions as in the extant Nile Crocodile, 'canine' notch is comparable in depth to that of *C. niloticus*, anterior extremity of palatine opposite the 7th maxillary tooth as in the extant Nile crocodile, maxillo-premaxillary suture is V-shaped, with the point of the V opposite the 2^{nd} maxillary tooth, anterior end of the palatine is relatively far back, being opposite the 7th tooth (opposite the 6th tooth in *C. lloydi* and opposite the 7th in *C. niloticus*), anterior rims of the palatal fenestrae are opposite the 9th maxillary tooth, and their position is thus more similar to the Nile crocodile than to *C. lloydi*, angle made by the two branches of the mandible behind the symphysis is relatively narrow, and not widely divergent as in *C. lloydi*.

Etymology: The species name gariepensis refers to the Khoi name of the Orange River.

Description and measurements: The description and measurements (tables 2 and 3) are modelled on the work of Tchernov (1986) who analysed many of the fossil African crocodiles, including *Crocodylus lloydi*.

<u>Skull</u>

AD 774'99 (Pl. 1-4) is the skull of a young crocodile retaining 4 teeth in the right maxilla. It lacks the left half of the snout, part of the left orbit, and both pterygoids and ectopterygoids, but it is otherwise relatively complete and undistorted. The snout is appreciably narrower than that of PQ AD 1856 (Pl. 5, Fig. 2), but still falls within the range of variation of Crocodylus lloydi. The tips of the premaxillae are missing but the overall length of the specimen can be reasonably well estimated (Table 2). The premaxillae are longer than they are wide. The dorsal margins of the narial opening are not raised, and, in ventral view, the premaxillary-maxillary suture is at right angles to the sagittal suture but diverges anteriorly as it approaches the alveolar process. Its most distal point is opposite the first maxillary tooth. The 'canine' notch is comparable in depth to that of C. niloticus. The alveolar process is well developed and is separated from the main part of the palate by a groove which possesses a line of foramina on its alveolar wall. The palate is narrower than that of PQ AD 1856. The anterior end of the palatal fenestra lies opposite the 9th and 10th maxillary tooth. The palatine is broken away, but its anterior extremity was probably opposite the 7th maxillary tooth, as in the extant Nile 1

Table	2:	Measurements	(in	mm)	of	the	skulls	of	Crocodylus
garie	per	isis sp. nov. from	n A	rrisdri	ft, 1	Vami	ibia.		

Measurement/Fossil	AD 1856	AD 774'99
1. Skull length (occipital condyle to snout tip)	430+/-	305
2. Skull length (supraoccipital to snout tip)	416+	302
3. Skull height (pterygoid base to top supraoccipi-	0.77*	
4. Skull breadth (across quadrato-jugals)		151
5. Skull breadth (at anterior end of orbits)	186	123
6 Skull breadth (at postorbital bars)	206	127
7 Skull breadth (across premaxillaries)	104	61
8 Skull breadth (at 5th maxillary teeth)	145	88
9 Skull breadth (at anterior end of palatines)	134	86
10 Spout length (anterior orbit rim to snout tip)	282+/-	205
11 Orbit length	52	51
12 Orbit width	41.5	34
13 Interorbital constriction	45	26.7
14. Cranial table length	76	47
15. Cranial table width (maximal)	130	87
16. Cranial table width (at postorbital bars)	100.5	76
17 Nasal anerture external length	40	27
19. Nasal aperture external width	35+/-	28
10. Palating fenestra length		
20. Inter-palatine fenestral constriction		
21. Palatine fenestra width		
22. Distance between posterior processes of		
23 Premavillary length (along median suture)	80+/-	61+/-
24. Maxillary length (along median suture)	93	71+/-
25. Balatine length (along ventral median suture)		
26. Prepagoid length		
27 Maxillany length (along tooth row)	235	181
28. Distance between premaxilla-maxilla suture	115	112
20 Nacalia length		
30. Distance between 1st and last premaxillary	61+/-	42+/-
31 Snowt breadth (in front of 1st maxillary tooth)	82	50
32. Distance from front 1st to rear 3rd maxillary	34.5	29
33 Spout width behind 3rd maxillary tooth	127.3	72
34 Sport width behind 5th premaxillary tooth	142.6	88
35. Inter-supratemporal fenestrae constriction	14?	12.5
26 Currentemporal fonactra width	29.5	19.5

crocodile. There are 14 or perhaps 15 maxillary teeth. There are four teeth in the premaxilla posterior to the premaxillary pit as in *C. niloticus*.

PQ AD 1856 (Pl. 5, Fig. 2) is a relatively complete edentulous skull, unfortunately lacking the pterygoids, quadratojugals, most of the palatines and parts of the quadrates. The dorsal surface is almost complete, although the tips of the premaxillae are broken. The specimen is slightly crushed dorsoventrally which has undoubtedly led to an exaggeration of the width, a feature which enhances the brevirostral aspect of the snout. The snout is short and wide. Even though the tips of the premaxillae are missing, it is possible, by tracing the curve of the outer surface round towards the midline, to infer that they were much shorter than their width. The dorsal margins of the narial opening are not elevated and, in ventral view, the maxillo-premaxillary suture is V-shaped, with the point of the V opposite the 2^{nd} maxillary tooth. This is somewhat as in C. niloticus except that the V is more open, and thus more like the condition in C. lloydi. The 'canine' notch is intermediate in depth between those of C. niloticus and C. lloydi. The distal end of the premaxillary suture is opposite the 1st maxillary tooth, as in C. lloydi. The external edges of the maxillaries are reflected downwards, thereby forming a pronounced alveolar ridge separated from the palatal part of the maxillae by a row of foramina. The palate is wide and the anterior ends of the palatal fenestrae are wide apart. The anterior end of the palatine is relatively far back being opposite the 7th tooth (opposite the 6th tooth in C. lloydi and opposite the 7th in C. niloticus). The anterior rims of the palatal fenestrae are opposite the 9th maxillary tooth, and their position is thus more similar to the Nile crocodile than to C. lloydi. PQ AD 1856 thus shows an interesting melange of characters, some of which indicate affinities with C. lloydi while others suggest relationships with C. niloticus. In effect, this Arrisdrift specimen is brevirostral, but not to the exaggerated extent seen in Plio-Pleistocene C. lloydi from East Africa (Tchernov, 1986). The combination of characters (Figs. 1-10) indicates that the Arrisdrift crocodile represents a hitherto undescribed species. For this reason a new species Crocodylus gariepensis is erected for it.

Table 1 summarises the proportional analyses of the Arrisdrift fossil skulls versus those of other extinct and extant species (see Figs 2-10 for details). Where the Arrisdrift crocodile is similar to the Nile crocodile is in the proportions of the neurocranium to total skull length and in proportions of different parts of the neurocranium. In proportions which feature the snout length and breadth, it differs from the Nile crocodile, and is similar to or approaches the proportions of *C. lloydi*.

Mandible (Pl. 5, Fig. 1, 3, 4-5).

The symphyseal morphology and proportions of the lower jaws of the Arrisdrift crocodiles fall within the range of variation of the extant Nile Crocodile (Fig. 11). The angle made by the two branches of the mandible behind the symphysis is relatively narrow, and not widely divergent as in *C. lloydi* from North and East Africa. The gap for housing the upper 4th premaxillary tooth occurs between the 2nd and 3rd mandibular teeth but the gap is not very long. The mandibular diastema for the fifth maxillary tooth lies between the 8th and 9th mandibular teeth.

Teeth

Most of the cranial and mandibular specimens are edentulous. The exception is PQ AD 1855 which has the 4th and 5th, and 9th and 10th teeth *in situ*. On two specimens it is possible to estimate the total number of mandibular teeth, although the

Table 3: Measurements (in mm) of mandibles of Crocodylus gariepensis sp. nov. from Arrisdrift. Parameters are from Tchernov (1978)

Measurement/Fossil	AD 1855	AD 999	AD 135'00	AD 396'00	AD 460'00	
41. Symphysis length	83	77	69.5	46.4	67.5	
47. Mandible width at rear of symphysis	2 x 48 = 96	2 x 44 = 88	2 x 36.8 = 73.6	26.8 x 2 = 53.6	35.7 x 2 = 71.4	



Figure 1: Comparison of extant and fossil crocodilian skulls - index of width of skull across orbits over length of snout.

state of preservation leaves room for doubt. In mandibles PQ AD 2673 and AD 115'94 there were at least 14 teeth.

In the skull, PQ AD 1856, there are at least 13 and possibly 14 maxillary teeth, which is one more than in Plio-Pleistocene specimens of *C. lloydi*. AD 774'99 had at least 14 maxillary teeth. In PQ AD 1856 the pit which receives the 3rd mandibular tooth when the jaw is closed is located medial to the 5th premaxillary tooth, as in *C. lloydi* and in contrast to its position in *C. niloticus* where it is located in line with and between the 4th and 5th premaxillary teeth. In contrast, in AD 774'99, this pit conforms to the pattern in *C. niloticus*.

Material from Auchas, Namibia

The crocodilian remains known from Auchas consist of fragmentary limb bones and an isolated tooth. The latter was found in a block of sediment that contained a rhinocerotid atlas vertebra. The identification of such fragmentary remains is difficult, but it is noted that the fossils resemble those from Arrisdrift.

Discussion

In a previous paper Pickford (1996) considered that the Arrisdrift crocodilian was brevirostral and was thus related to



Figure 2: Comparison of extant and fossil crocodilian skulls - index of width of skull across premaxillaries over length of premaxillaries.



Figure 3: Comparison of extant and fossil crocodilian skulls - index of width of skull across anterior ends of orbits over width of skull across quadrato-jugals

Crocodylus lloydi, known from the Early Miocene deposits at Wadi Moghara (Egypt) (Fourtau, 1918 (1920)), early Middle Miocene strata at Gebel Zelten (Arambourg & Magnier, 1961) and from many Plio-Pleistocene sites in East Africa (Tchernov, 1976, 1986). However, as was pointed out by Pickford (1996) the lower jaws from Arrisdrift were intermediate between those of *C. lloydi* and *C. niloticus* and if the Arrisdrift croco-dile were known only by lower jaws, they might have been identified as *C. niloticus*. Newly collected mandibular material confirms that the lower jaws are not as brevirostral as those of *C. lloydi*, but fall within the range of variation of *C. niloticus*. The new skull AD 774'99, increases the known variation

in the Arrisdrift population, revealing that some individuals were close in some skull proportions to extant Nile crocodiles. Some of the skull index calculations (figs. 1-10) fall within the range of variation of *C. lloydi*, but some of them (width of skull across maxillaries/length of snout and others) are outside the range of *C. lloydi* but within the range of *C. niloticus*, while the mandibular index falls outside the range of variation of *C. lloydi* and within the range of *C. niloticus*. Taken as an assemblage, the Arrisdrift species shows affinities to both *C. lloydi* and extant Nile crocodiles, underlining the close relationship between these two species, as was already suggested by Tchernov (1986). The combination of characters indicates



Figure 4: Comparison of extant and fossil crocodilian skulls - index of width of skull across premaxillaries over length of snout.



Figure 5: Comparison of extant and fossil crocodilian skulls - index of width of skull across maxillaries over length of snout.

that the Arrisdrift crocodiles represent neither *C. lloydi* nor *C. niloticus*, but a new species *C. gariepensis*, which, however, is close to the former two species.

The Arrisdrift crocodile differs markedly from the Early Miocene East African species *Crocodylus pigotti* Tchernov & Van Couvering (1978) and the Late Miocene *C. checchiai* Maccagno (1947) from Libya. It differs greatly from *Crocodylus nkondoensis* Pickford (1994) from the Western Rift, Uganda, which is a relatively longirostral form related to *C. niloticus*.

The Arrisdrift crocodile is slightly more brevirostral than the extant Nile crocodile (Kälin 1955; Steel, 1973; Wermuth &

Mertens, 1961), yet it has some characters, such as symphyseal proportions, which fall within its range of variation. In many of its proportions, the Arrisdrift species is close to *Crocodylus palustris*. The question naturally arises whether the Namibian species should not in fact be identified as *C. palustris*. However, the detailed morphology of the anterior part of the snout, the reflected margin of the maxilla, the position of the pits in the premaxilla and maxilla for reception of mandibular teeth, and the unelevated dorsal margin of the narial opening indicate that it is more closely related to *C. lloydi* and *C. niloticus* than to any other known fossil or extant crocodiles.



Figure 6: Comparison of extant and fossil crocodilian skulls - index of width of skull at anterior end of orbits over length of skull.



Figure 7: Comparison of extant and fossil crocodilian skulls - index of width of skull across quadrato-jugals over length of skull

It should be kept in mind that Arrisdrift is well south of the modern range of crocodiles, and its location at what was presumably near the southern extremity of its distribution during the Middle Miocene, may have played a role in the development of crocodile populations sufficiently different from those at the centre of their range for speciation to occur.

Origins of the Nile Crocodile

Tchernov (1986) wrote that the earliest known *C. niloticus* occur in Pliocene deposits in the Omo beds and the Kanapoi region of the Turkana Basin. He concluded that the species began its history from an earlier Pliocene stock of *C. lloydi*, and that once it had evolved it could successfully have invaded dif-

ferent areas populated by *C. lloydi* and replaced it by a process of competitive exclusion. He envisaged that *C. niloticus* could represent a case of gradual phyletic evolution of an isolated population of *C. lloydi*.

The discovery at Arrisdrift of basal Middle Miocene crocodiles which share many features with Nile crocodiles as well as some with *C. lloydi* raises an alternative scenario. It is possible that *C. gariepensis* represents the ancestral group from which the Nile crocodile arose, in which case the latter species did not arise from *C. lloydi* by rostral elongation, but by relatively minor adjustments from a species that was already quite close in morphology to the Nile crocodile. If the latter scenario is valid, then the Nile crocodile could have evolved well before the early Pliocene, possibly from a southern African species



Figure 8: Comparison of extant and fossil crocodilian skulls - index of width of skull across quadrato-jugals over length of snout.



Figure 9: Comparison of extant and fossil crocodilian skulls - index of length of premaxillaries over width of cranial table.

such as *C. gariepensis*, which then spread northwards, reaching the equatorial regions during the Pliocene and from then onwards gradually replacing the widespread and hitherto very successful short snouted species *C. lloydi*.

Palaeoecological implications of the presence of crocodiles at Arrisdrift

There can be little doubt that Arrisdrift was appreciably more tropical during the early part of the Middle Miocene than it is now. The presence of large land tortoises and crocodiles provides strong evidence for this.

Crocodiles, in particular, are extremely sensitive to temperature, because seasonal activation of their reproductive organs (gametogenesis) is to a great extent regulated by body temperature, which is in turn controlled by ambient temperature, while the sex of hatchlings is determined by the temperature of the nesting environment (Levy, 1991). Although many crocodile species can control the temperature of their nests by using decaying vegetation as a heat source, such controls break down if the ambient temperature is such that it over-rides the efforts of the parent crocodile to maintain the optimal incubation tem-



Figure 10: Comparison of skulls of extant and fossil crocodilian skulls - index of length of cranial table over width of cranial table.



Figure 11: Comparison of mandibles of extant and fossil crocodilians - index of length of symphysis over width of mandible across posterior end of symphysis.

perature (31.5-32.5 C) which results in a balanced sex ratio of hatchlings. Temperatures slightly below this optimal range (28-31 C) during the first few weeks of incubation will result in a hatching of females only, while above it (33 C) the hatchlings will all be male, a situation that soon results in local extinction if it occurs over several years. If the temperatures are markedly different from optimum (<27 C or >34 C) eggs become addled. The discovery of a mandible of a hatchling crocodile at Arrisdrift (AD 136'95) reveals that crocodiles were indeed breeding near the fossil locality.

Taphonomy

An interesting aspect of the Arrisdrift fossil assemblage is that several of the medium to large mammal bones have series of puncture marks on their surfaces, best interpreted as tooth marks. Consideration of the number of puncture marks, their outlines, the gaps between them and their distribution in lines either side of the bones (distal humeri, femora and talus) suggests that the bones had been clamped between the jaws of crocodiles. Although the number of specimens affected is too few to provide an unequivocal idea of their distribution according to bodyparts, the most noticeable specimens affected are distal humeri, distal femora and the ankle joint. For example, a climacoceratid talus also shows crocodile tooth marks. It is possible that one of the modes of attack on large prey by the Arrisdrift crocodiles was to snap at the elbow or knee joint and then to drag the victim into the water to drown it. The relatively short snout would be suited for such a method of obtaining large mammal prey that came to the water side to drink or to browse on riparian vegetation (see discussion in Tchernov, 1986).

Conclusions

Abundant Middle Miocene crocodile remains from Arrisdrift in the lower Orange River Valley can all be assigned to a single species of *Crocodylus* which shares features with both the extant Nile crocodile and the extinct species *Crocodylus lloydi*. The new species *Crocodylus gariepensis* is erected, which differs from *C. lloydi* in the proportions of the mandibular symphysis and the cranial table, and from *C. niloticus* in the proportions of the snout, which is relatively brevirostral and broad. *C. gariepensis* could represent the ancestral group from which the extant Nile crocodile evolved. The presence of crocodiles in the Middle Miocene of southern Namibia attests to the presence of a tropical to sub-tropical climate at the time of deposition, in stark contrast to the present day temperate, desert, climate with winter rainfall.

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Note added at proof stage:

Storrs (2003) erected the genus *Rimasuchus* for *Crocodylus lloydi* which strengthens the arguments developed in this paper that the Arrisdrift crocodile is likely to be the ancestral group of the extant Nile Crocodile. He also described *Crocodylus niloticus* from Lothagam, Kenya, and thus the Nile crocodile occurred in East Africa somewhat earlier (ca 6 Ma) than previously estimated (4.2 Ma).

Reference

Storrs, G. 2003. Late Miocene - Early Pliocene crocodilian fauna of Lothagam, Southwest Turkana Basin, Kenya. *In*: M.Leakey and J. Harris (eds) *Lothagam : The Dawn of Humanity in Eastern Africa*. Pp. 137-159, New York, Columbia Univ. Press.



Plate 1: AD 774'99, Crocodylus gariepensis sp. nov. Holotype skull, dorsal view, Arrisdrift, Namibia. (Scale bar = 5 cm).



Plate 2: AD 774'99, Crocodylus gariepensis sp. nov. Holotype skull, palatal view, Arrisdrift, Namibia. (Scale bar = 5 cm).



Plate 3: AD 774'99, Crocodylus gariepensis sp. nov. Holotype skull, right lateral view, Arrisdrift, Namibia. (Scale bar = 5 cm).







Plate 5: Crocodylus gariepensis sp. nov. Arrisdrift, Namibia. (Scale bar = 5 cm).
1, 3. PQ AD 2673, left mandible broken off behind the 14th (last) tooth, lateral and occlusal views.
2. PQ AD 1856, almost complete skull, dorsal view.
4-5. AD 115'94, left mandible broken behind the 14th (last) alveolus, lateral and occlusal views.