Freshwater aquatic and aquaphile vertebrates from Black Crow (Ypresian/Lutetian, Namibia) and their palaeoenvironmental significance

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Abstract: The freshwater limestone deposits at Black Crow, Namibia, have yielded a low diversity of aquatic and aquaphile vertebrates comprising three species of fishes, one frog and a crocodile. As a fauna these vertebrates suggest that, at the time of deposition during the Late Ypresian or Early-Middle Lutetian, the area lay within a tropical to sub-tropical climatic regime, and that the water bodies were fresh, clear and well-oxygenated, contrasting with the hyper-arid conditions that prevail in the area today. One of the fishes, *Hydrocynus*, is exclusively African. Its Palaeogene distribution was wider than it's extant range, the five localities where it has been recorded occurring well outside its present-day range. The Black Crow occurrence of this genus is potentially the oldest known (if the deposits are Late Ypresian).

Key words: Ypresian/Lutetian; Namibia; Palaeobiogeography; Alestidae; *Hydrocynus*; *Alestes*; Cichlidae; Crocodylia; Pipidae.

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Introduction

Almost pure limestone at Black Crow contains the remains of land snails, freshwater vertebrates, and terrestrial squamates, birds and mammals. The mammals from the carbonates indicated a Mid-Lutetian correlation (Pickford *et al*. 2008a, 2008b; Pickford 2015b) which was challenged by Seiffert (2010) who thought that the fauna was considerably younger (Latest Eocene to Early Oligocene). This led to a reassessment of the age of the limestones in the Sperrgebiet, a procedure that led to the discovery of the limestone sites of Eocliff and Eoridge, both of which are extremely rich in fossils, mainly micromammals (rodents, macroscelidids, tenrecoids, potamogalids and chrysochlorids) but there are some large mammals such as *Rupestrohyrax* and *Bothriogenys* which indicate deposition during the Late Bartonian or Early Priabonian (Pickford 2015c, 2015d, 2015e, 2015f, 2015g; Seiffert 2010). However, additional discoveries of mammals at Black Crow indicate that the limestone there could be older than originally estimated (Pickford 2015a). Rodents from the Black Crow deposits comprise two species of Zegdoumyidae and a reithroparamyid, the latter record being the first record of the family from the continent, and suggesting an Ypresian or Early Lutetian correlation (Korth 1984; Escarguel 1999; Wood 1962). Thus it is concluded that instead of one phase of carbonate deposition in the Sperrgebiet during the Palaeogene as intially interpreted, there were in fact two phases of deposition, one during the Ypresian/Lutetian separated by several million years from a second phase during the Bartonian/Priabonian.

This paper focuses on the aquatic and aquaphile vertebrate remains from the Black Crow Limestone which include fishes, frogs and crocodiles. As an assemblages the aquaphiles indicate that the water body at Black Crow comprised fresh, well-oxygenated water, and that the palaeoclimatic conditions at the time of deposition were tropical to sub-tropical, in stark contrast to the present-day hyper-arid regime with winter rainfall. It complements the paper by Rage *et al*. (2013) on the amphibians and squamates from the Late Bartonian/ Early Priabonian limestones of the Sperrgebiet.

Material and Methods

100 kg of limestone from Black Crow was dissolved in 7% formic acid without buffer. The insoluble residue comprised a few sand grains and rock particles derived from the basement Gariep Group schist and dolomite, accompanied by many silicified pedotubules often comprising agglomerations of minute quartz crystals which model the shape of the pedotubules, and invertebrate and vertebrate fossils. There are also silicified algal mats and opalised nodules in the deposit, and these can also contain fossils. The fossils were consolidated by soaking them in a weak solution of glyptol dissolved in acetone, and some were reinforced with cyano-acrylate (super glue).

Images were taken with a Sony Cybershot Camera placed over the lenses of a stereoscopic microscope, and processed using Photoshop Elements3. Measurements were taken with sliding calipers.

Geological and faunal context

The geological context of the Black Crow Carbonate has been described in detail by Pickford *et al*. (2008a, 2008b) and Pickford (2015a). In brief, the fossiliferous deposit comprises a 16 metre thickness of limestone overlying Proterozoic Gariep Group dolomites and " Pomona " Quartzite, and in its turn is overlain by Neogene Blaubok Conglomerate and Namib-1 Calc-crust.

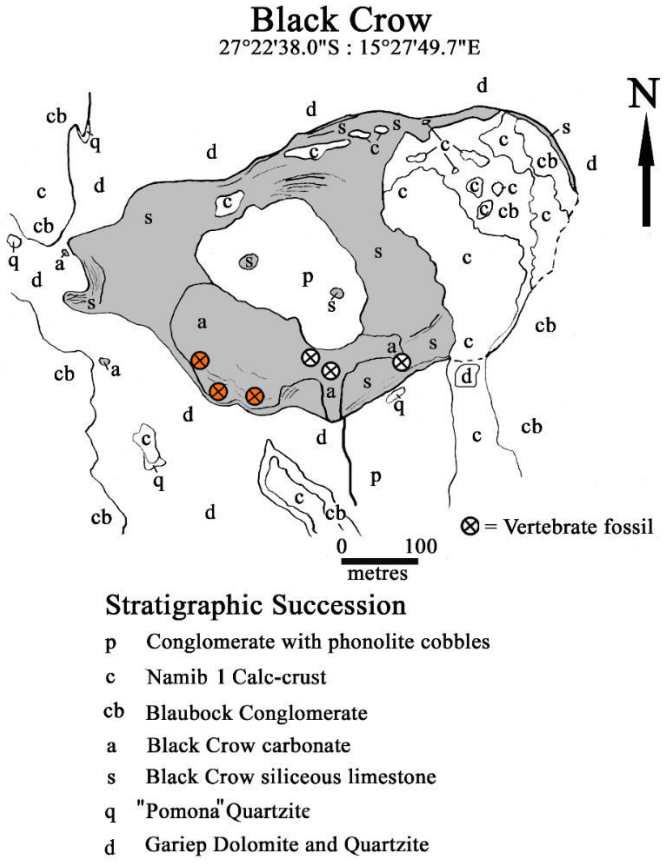

Figure 1. Geology of the Black Crow Carbonate occurrence, Sperrgebiet, Namibia. Red symbols indicate the sample locations which have yielded aquatic and aquaphile faunal elements in association with the Late Ypresian/Early Lutetian terrestrial fauna.

All the aquaphile vertebrate remains from Black Crow (Fig. 1) described in this paper came from the same outcrops in the southwest corner of the basin that yielded *Namahyrax corvus*, zegdoumyid and paramyid rodents and primitive chrysochlorids, all of which indicate a Late Ypresian to Early Lutetian age.

Systematic Palaeontology

Order Characiformes Regan 1911

Family Alestidae Hoedeman 1951 (*sensu* Géry 1977)

Genus *Hydrocynus* Cuvier 1816

Description and comments

The tooth from Black Crow attributed to *Hydrocynus* (GSN BC Pc 14'17, Fig. 2) is a tall, slender cone with mesio-distally narrow but sharp flanges on the mesial and distal sides of the cone. The tooth is slightly concave on the lingual side, and in labial view is gently curved from base to apex. The base of the tooth is missing. The enamel is smooth.

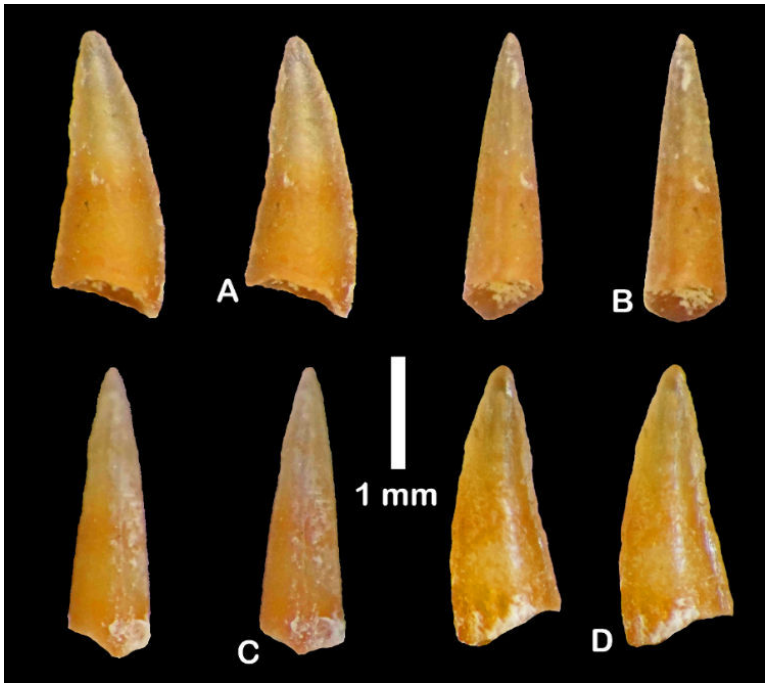

Figure 2. Stereo images of an isolated tooth of *Hydrocynus* from Black Crow, Ypresian/Lutetian, Black Crow, Namibia. A) side view, B) lingual view, C) labial view, D) side view (scale : 1 mm).

Five (Goodier *et al*. 2011) or six (Hammouda *et al*. 2016) extant species of *Hydrocynus*, the Tigerfish of Africa, are known, all of which inhabit well-oxygenated, freshwater rivers and lakes of tropical and sub-tropical Africa. It is a genus of carnivorous fish, preying on other fish species and small vertebrates and invertebrates. The taxa avoid shallow, poorly oxygenated backwaters, swamps and lagoons. At present the genus is not present in rivers at the northern and southern extremities of the continent (Fig. 3) seemingly being maladapted to areas which experience winter rainfall regimes and neighbouring Mediterranean type climatic regimes. It is also largely absent from desert areas.

Fossilised remains of *Hydrocynus* (mainly isolated teeth) are known from several Neogene and Palaeogene localities in Africa (Table 1). The Palaeogene localities, in particular, lie well outside the present day range of the genus, occurring in south-central Libya, western Algeria and southwestern Namibia. If the Palaeogene members of the genus had similar environmental adaptations to the extant

forms, then the palaeodistribution would indicate that virtually all of Africa would have been tropical to sub-tropical during the Lutetian and Bartonian.

Table 1. Summary of the distribution of fossil *Hydrocynus* in Africa, arranged in approximate chronological order (data from Greenwood 1972; Hammouda *et al*. 2016; Murray *et al*. 2010; Otero & Gayet 2001; Otero *et al*. 2009, 2010a, 2010b, 2011, 2015; Schwartz 1983; Stewart 1994, 1997, 2001, 2003a, 2003b, 2009; Stewart & Murray 2013; Van Neer 1994; Weiler 1926).

Locality	Country	Age
Omo	Ethiopia	Plio-Pleistocene
Turkana	Kenya	Plio-Pleistocene
Malema	Malawi	Plio-Pleistocene
Kaiso	Uganda	Plio-Pleistocene
Kollé	Chad	Plio-Pleistocene
Kossom-Bougoudi	Chad	Pliocene
Koro Toro	Chad	Pliocene
Wadi Natrun	Egypt	Latest Miocene
Toros-Menalla	Chad	Latest Miocene
Nkondo	Uganda	Late Miocene
Nawata	Kenya	Late Miocene
Manonga	Tanzania	Late Miocene
Lothagam	Kenya	Late Miocene
Ngorora	Kenya	Middle-Late Miocene
BQ-2 Fayum	Egypt	Late Eocene
Dur At-Talah	Libya	Late Eocene
Garet Dermchane	Algeria	Lutetian-Bartonian
Black Crow	Namibia	Ypresian-Lutetian
Méridja	Algeria	Late Thanetian-Early Ypresian

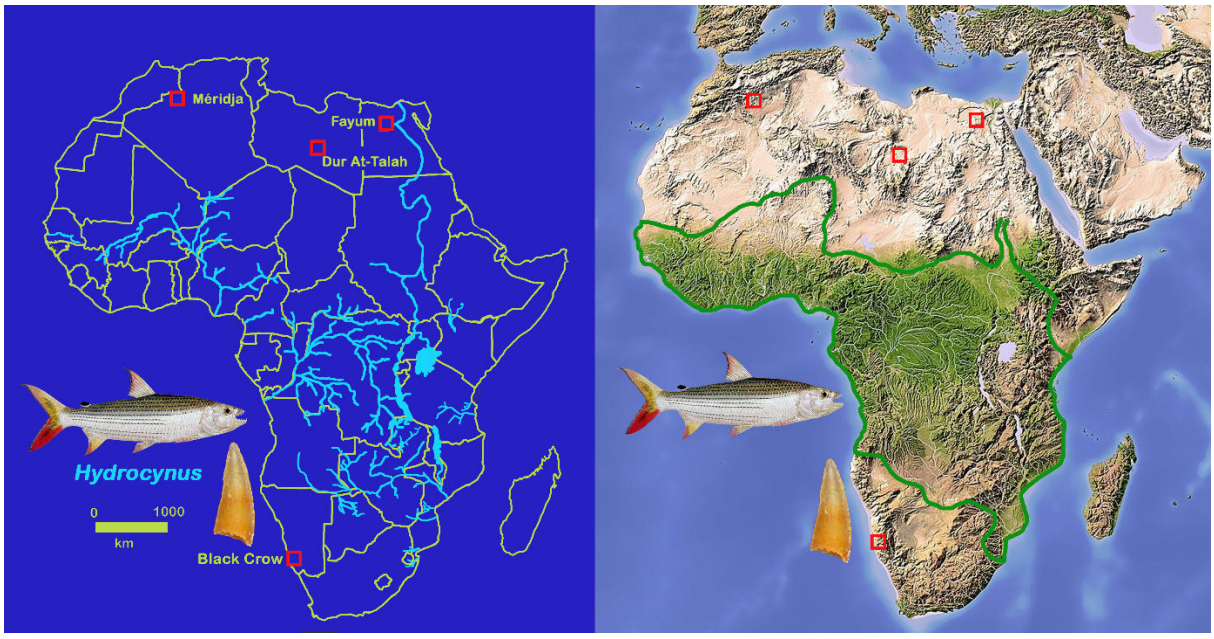

Figure 3. Distribution of the extant alestid fish *Hydrocynus* (the Tigerfish of Africa) (light blue lines in left frame) and Palaeogene fossils of the genus (red squares). For details of extant distribution of *Hydrocynus* species, see Goodier *et al*. (2011). Note that *Hydrocynus* is restricted to the equatorial and sub-equatorial parts of the continent (green tinges in the right hand map) and is absent from rivers and lakes in the northern and southern extemities of the continent that experience winter rainfall. The Eocene fossils all occur outside the present day limits of the genus, indicating overall warmer climate regimes in Africa probably without winter rainfall and neighbouring climatic regimes.

Genus cf *Alestes* Müller & Troschel 1846

Description and comments

An isolated tricuspid tooth from Black Crow probably represents the genus *Alestes* or a close relative such a *Brycinus* (Fig. 4) (Murray 2004; Zanatti & Vari 2005). The pulpal cavity is an elongated oval with thickened edges. The crown has a tall central cusp, accompanied by lower cusplets on either shoulder of the tooth, one somewhat lower than the other. The labial surface of the tooth is considerably taller than the lingual side suggesting that this tooth is from the labial part of the dentary. The labial and lingual surfaces of the crown meet at round-edged crests that run between the three cusps.

The « bunodont » aspect of the tooth suggests that its function was to grip and crush rather than to cut.

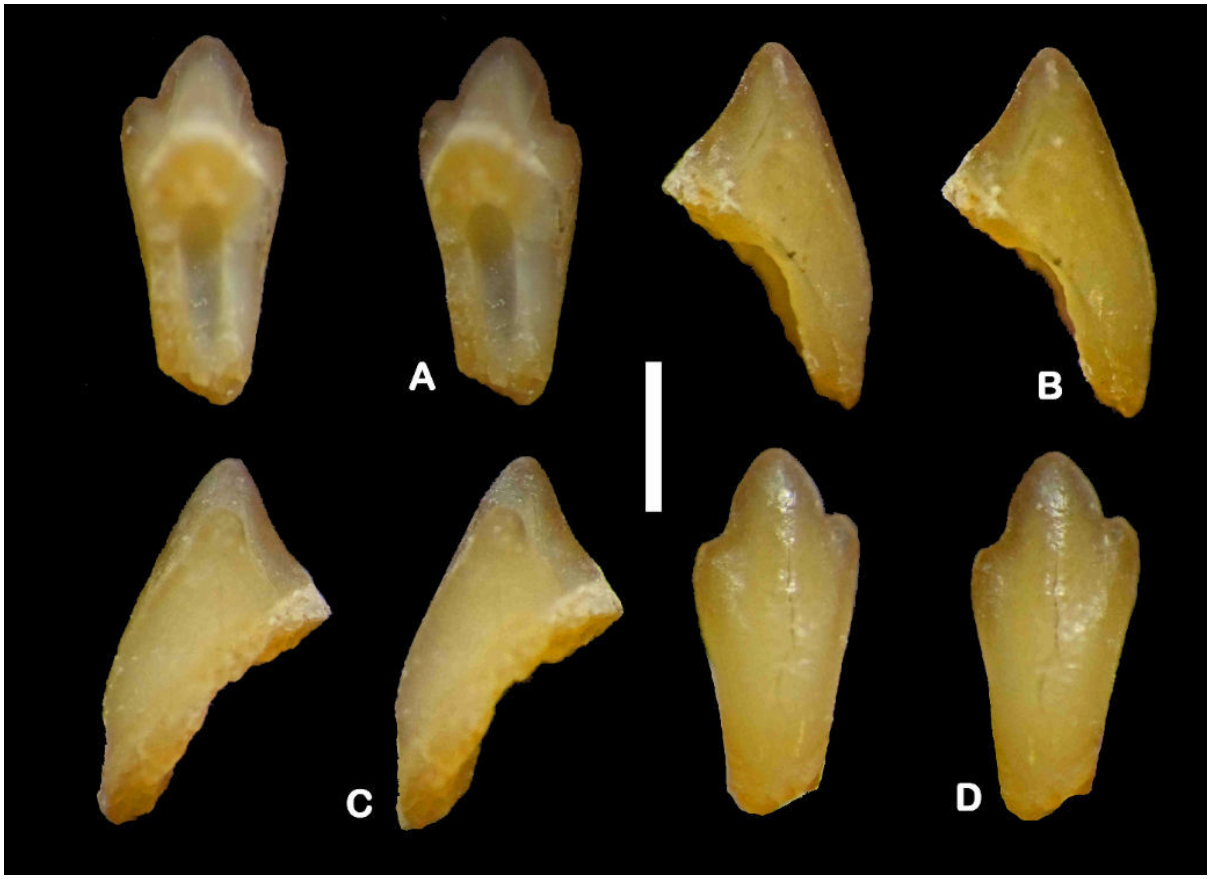

Figure 4. Stereo images of GSN BC Pc 11'17, isolated tricuspid tooth from Black Crow, Namibia, attributed to cf *Alestes* sp. A) radicular/lingual view, B) side view, C) side view, D) labial view (scale : 1 mm).

Genus indet. cf Cichlidae Gill 1872

Description and comments

Black Crow has yielded a quantity of flattish, « button-shaped » teeth which have varied outlines ranging from circular to ovoid and « heart-shaped », and are of diverse sizes (GSN BC Pc 1'17-10'17) (Fig. 5, 6). All the specimens have smooth relatively flat enamel on the occlusal surfaces without any hint of currugations or cusplets. The specimens resemble a collection of cichlid teeth attributed to *Tylochromis* Regan 1920, from the Jebel Qatrani Formation in the Fayum, Egypt (Murray 2004). But, such teeth could belong to a diversity of fish species, both freshwater and marine. They are illustrated in order to complete the reportage on the fishes from the locality. Their presence attests to the former presence at Black Crow of fishes with a crushing dentition. A more refined identification will require the discovery of the teeth *in situ* in dentaries.

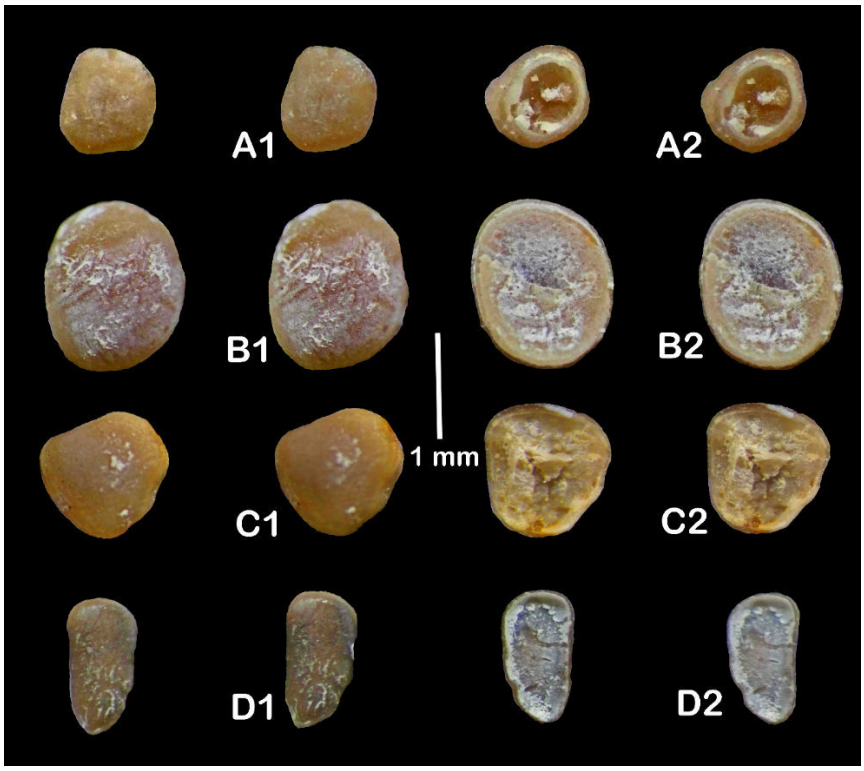

Figure 5. A-D) GSN BC Pc 1’17-4’17, isolated button-like teeth from Black Crow interpreted to be from Cichlidae (1- stereo occlusal views, 2 - stereo radicular views) (scale : 1 mm).

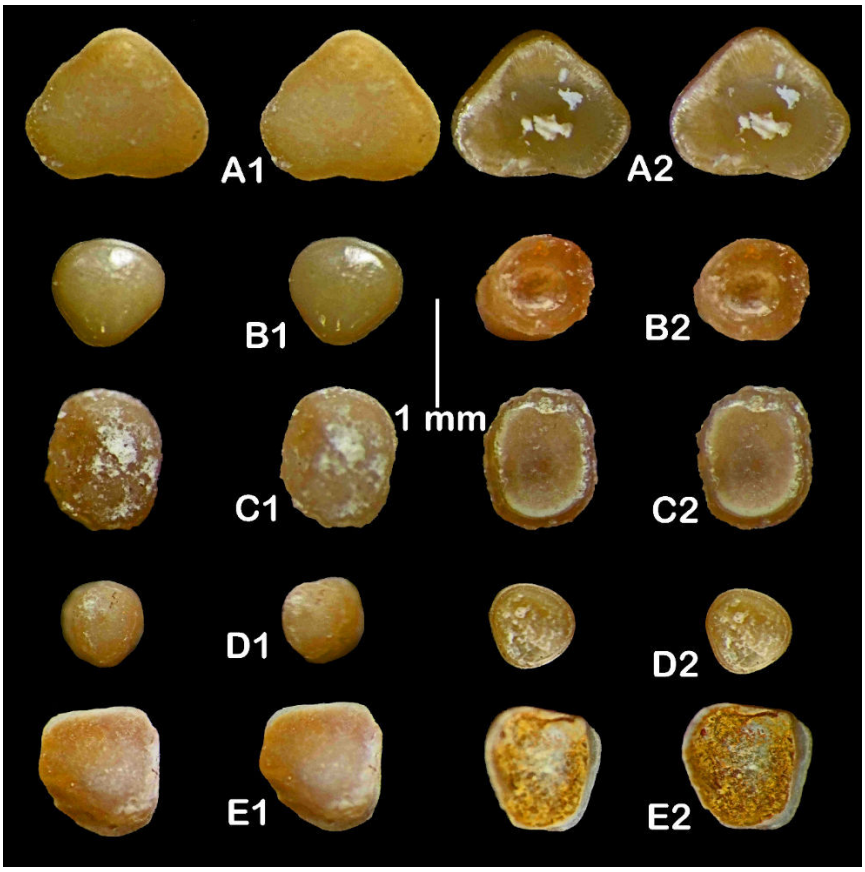

Figure 6. A-E) GSN BC Pc 6’17-10’17, isolated button-like teeth from Black Crow interpreted to be from Cichlidae (1- stereo occlusal views, 2 - stereo radicular views) (scale : 1 mm).

Order Amphibia Linnaeus 1758

Family Pipidae Gray 1825

Genus indet.

Description and comments

The Black Crow limestone yielded a few frog bones. The illustrated radio-ulna (Fig. 7) is close in morphology to those of pipids (Trueb & Hanken 1992; Trueb *et al*. 2000). Pipidae were already described from the Eocene of the Sperrgebiet at Silica North (Rage *et al*. 2013). The Black Crow record is thus the earliest from the southern half of the continent.

This family of frogs (colloquially known as « clawed-frogs ») is exclusively aquatic and today occurs only in Africa and South America.

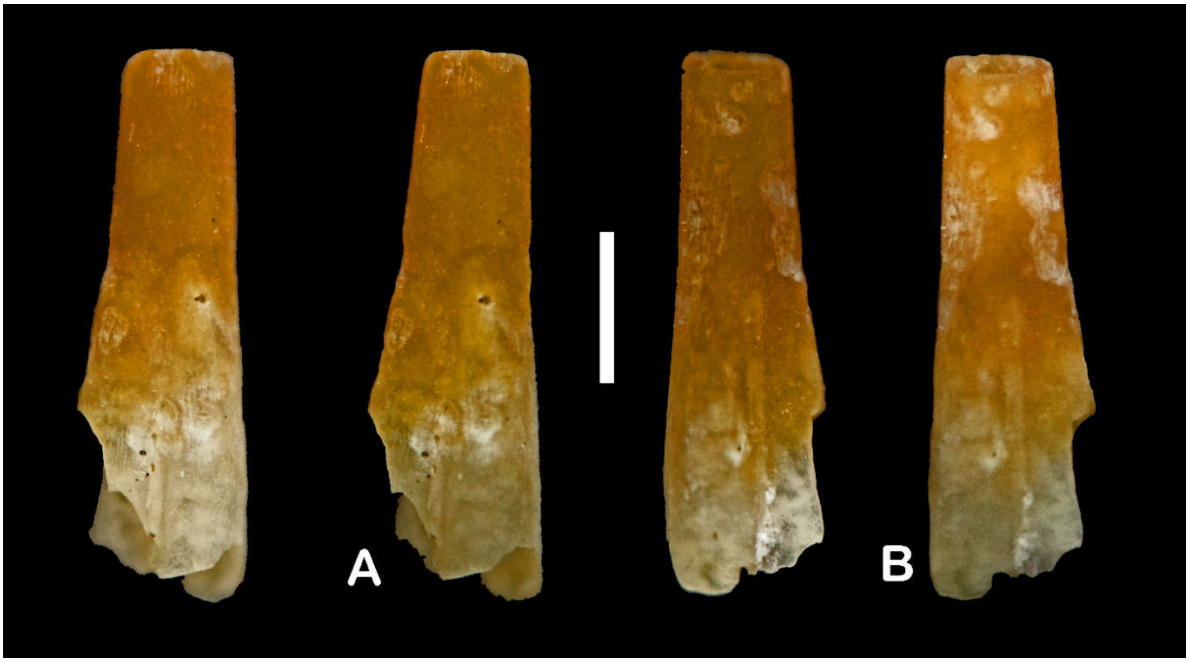

Figure 7. Stereo anterior (A) and posterior (B) views of GSN BC Pi 1'17, anuran radio-ulna, probably Pipidae (scale : 1 mm).

Order Reptilia Laurenti 1768

Family Crocodylidae Cuvier 1807

Genus indet.

Description and comments

Crocodile teeth are quite common at Black Crow, over 170 specimens having been found. One specimen is in a fragment of maxilla, and a vertebra and fragments of scutes were also found. There are four main crocodile dental morphotypes at the site, representing diverse tooth positions in the upper and lower jaws. Most of the teeth lack roots, but a few specimens have a root sheath preserved.

A maxillary specimen from Black Crow contains a wind-abraded « caniniform » tooth (Fig. 8). The palatal surface of the maxilla shows depressions for the acceptance of the lower teeth when the jaws are closed, which in this specimen would be lodged slightly inside the line of the upper teeth.

Figure 8. GSN BC Cr 142’17, left maxilla fragment containing a rooted « caniniform » tooth (morphotype 2) behind which is part of the alveolus of a second tooth. A) stereo occlusal view, B) stereo lingual view, C) stereo view of the wind-eroded lateral view. Note the nutritive foramina and the deep rounded depressions in the palatal surface of the maxilla in which the lower teeth would lodge when the jaws are closed (scale : 10 mm).

Morphotype 1 (Fig. 9A-E) consists of relatively low crowned teeth which, when viewed from the buccal or lingual aspect have a semi-circular crown profile, some with a slight point at the apex, others without. In occlusal view these teeth are somewhat bucco-lingually compressed, with a concave to almost straight lingual surface and a convex buccal one. The enamel is often adorned with vertical furrows and ridges.

Morphotype 2 (Fig. 9F-J) has slightly taller and more pointed crowns than morphotype 1, and some specimens retain a root structure, including a specimen *in situ* in a maxilla fragment. These teeth also possess a sharp flange on the mesial and distal edges of the crown.

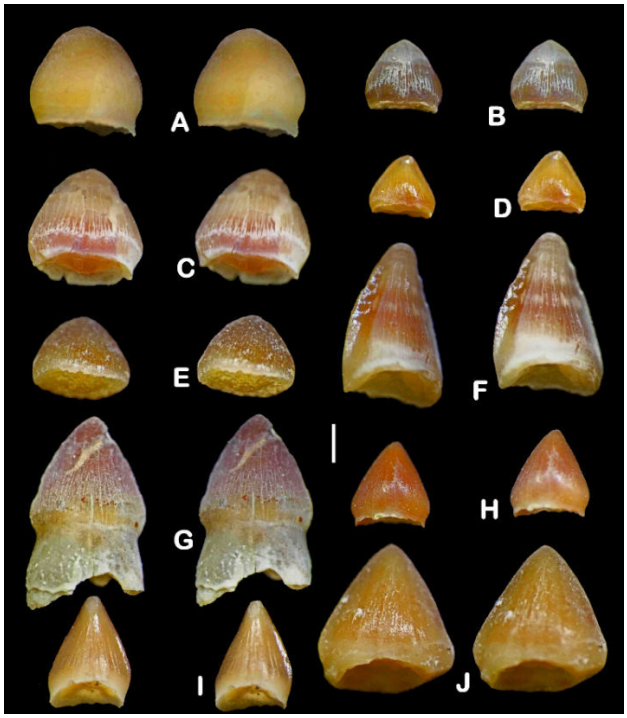

Figure 9. Crocodile teeth from Black Crow. A-E) dental morphotype 1, GSN BC Cr 1’17-5’17; F-J) dental morphotype 2, GSN BC Cr 13’17-18’17 (scale : 1 mm).

Morphotype 3 (Fig. 10) has taller crowns than morphotype 2 which are almost circular in occlusal view and with a pointed apex. Some specimens show a fluted enamel surface, other specimens have wear facets down one side (or two) presumably caused by abrasion against the antagonising tooth in the opposite jaw.

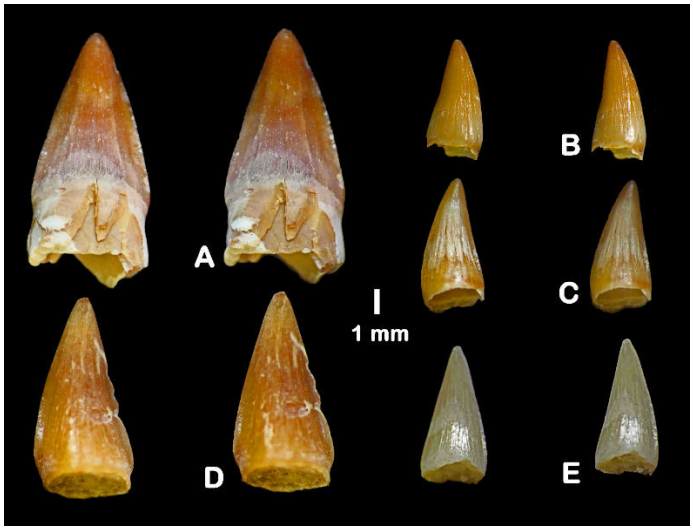

Figure 10. Isolated crocodile teeth from Black Crow. A-E) dental morphotype 3, GSN BC Cr 13'17-18'17 (scale : 1 mm).

Dental morphotype 4 resembles morphotype 3 save for the presence of a blunt apex rather than a pointed one (Fig. 11).

On the basis of the dimensions of the teeth, the Black Crow sample suggests that there is likely to be a single crocodile species of small body-size (1-2 metres head-tail length) at the site. With the available sample it is not possible to determine to which genus these teeth belong, but it is possible to discount appurtenance to *Euthecodon* and other crocodiles with tall, pointed teeth. The overall impression is that the teeth are not very different from those of *Crocodylus*, suggesting that the Black Crow crocodile was a dietary generalist rather than a specialist piscivore.

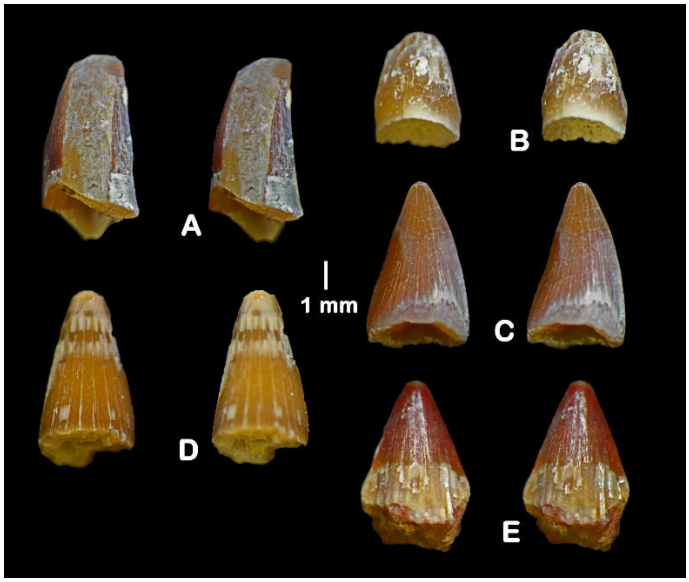

Figure 11. Isolated crocodile teeth from Black Crow. A-E) dental morphotype 4, GSN BC Cr 91'17-96'17 (scale : 1 mm).

Discussion

Freshwater aquatic and aquaphile vertebrates are reasonably common at Black Crow, a deposit of freshwater limestone of Late Ypresian/Mid-Lutetian age. The commonest fossils belong to a small species of crocodile, the teeth of which suggest that it was a dietary generalist. Next in abundance of specimens is a possible species of cichlid fish with button-like teeth lacking ornamentation on the occlusal surface. These button-shaped teeth show various outlines ranging from circular to ovoid, but the diversity of shapes does not necessarily indicate the presence of more than one taxon in the deposits, as extant cichlids, characids and other families of fish which possess button-like teeth show a range of tooth shapes depending on the position of the teeth within the mouth. Furthermore, the shape of the teeth can change as they are shed and replaced as the individual matures (Murray 2004). Much rarer at Black Crow are two taxa of characiforms, each represented by a single tooth, one a Tigerfish (*Hydrocynus*) with a tall, conical, pointed tooth sporting narrow, sharp-edged flanges, the other a more bunodont tricuspid tooth, possibly representing the genus *Alestes* or *Brycinus*. In addition to crocodiles and fishes, there are rare frog bones at the site, probably pipids.

The composition of the aquaphile vertebrates from Black Crow indicates that the water body in which the carbonates accumulated was probably fresh and well oygenated, and that it occurred within a region that enjoyed a tropical to sub-tropical climatic regime.

Conclusions

The Ypresian/Lutetian limestones at Black Crow have yielded a low diversity of freshwater aquatic and aquaphile vertebrates comprising, in descending order of their fossil representation, crocodiles (over 170 teeth), a possible cichlid with button-shaped teeth (10 teeth), a Tigerfish (*Hydrocynus* sp. one tooth) and a possible *Alestes* or *Brycinus* (one tooth). The carbonates have also yielded a few incompletely preserved frog bones, probably from pipids. The water body in which the carbonates accumulated was fresh and well-oxygenated and likely lay within a tropical to sub-tropical climatic regime.

Acknowledgements

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