Fossil Fruit Bat from the Ypresian/Lutetian of Black Crow, Namibia

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Abstract: The freshwater limestone at Black Crow of Ypresian/Lutetian age, has yielded a diverse fauna including aquatic and terrestrial forms but few aerial elements (indeterminate bird bones). The 2017 campaign of acid treatment of blocks of limestone from the site yielded a distal humerus of a megachiropteran, and an isolated tooth which possibly belongs to this suborder. These fossils are the oldest fruit bat fossils known, and as such they raise intriguing questions concerning the origin of the suborder and its relationships to microchiropterans (insectivorous bats) and Primates.

Key Words: Palaeogene; Namibia; Megachiroptera; Fruit Bat; Humerus; Molar; Radicular system.

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Introduction

Fossils from the Ypresian/Lutetian limestones at Black Crow are dominated by aquatic, aquaphile and terrestrial invertebrates and vertebrates, with only a few fragmentary bird bones representing the aerial fauna. It is therefore of interest to describe a fossil bat humerus from the site, and a lower molar which might belong to the same form.

Fruit Bats are rare in the African fossil record with a few specimens known from the Early Miocene of East Africa (*Propotto leakeyi* Simpson 1967) and Plio-Pleistocene to Recent deposits of Africa and Madagascar (*Eidolon* spp. and *Rousettus* spp.) (Gunnell 2010).

Geological context

Black Crow geology was discussed by Pickford *et al*. (2008a, 2008b). Overlying an eroded surface of Proterozoic Gariep Group dolomite (Kaiser & Beetz 1926) there is a thin layer of sandstone, overlain by well-bedded chalcedonic limestones which are overlain by the Middle Eocene freshwater Black Crow Limestone (Pickford 2015) (Fig. 1). Overlying an eroded surface of the limestone there is the Late Oligocene to Early Miocene Blaubok Conglomerate which in its turn is overlain by the Late Miocene Namib 1 Calc-crust, and Recent loose sand.

Age of Black Crow

The fauna from the Black Crow limestone, especially the arsinoithere *Namatherium blackcrowense* Pickford *et al*. (2008b) and the reithroparamyid rodent *Namaparamys inexpectatus* Mein & Pickford (2018) indicate a Late Ypresian or Early Lutetian age for the deposits. The limestones are likely to be older than 42.5 Ma on the basis of radio-isotopic dates obtained from phonolite cobbles reworked from lavas considered to have erupted later than the limestone deposition (Pickford *et al*. 2014). The carbonates could be as old as 47 +/- 1 Ma, i.e. Late Ypresian to Early Lutetian (Ogg *et al*. 2016).

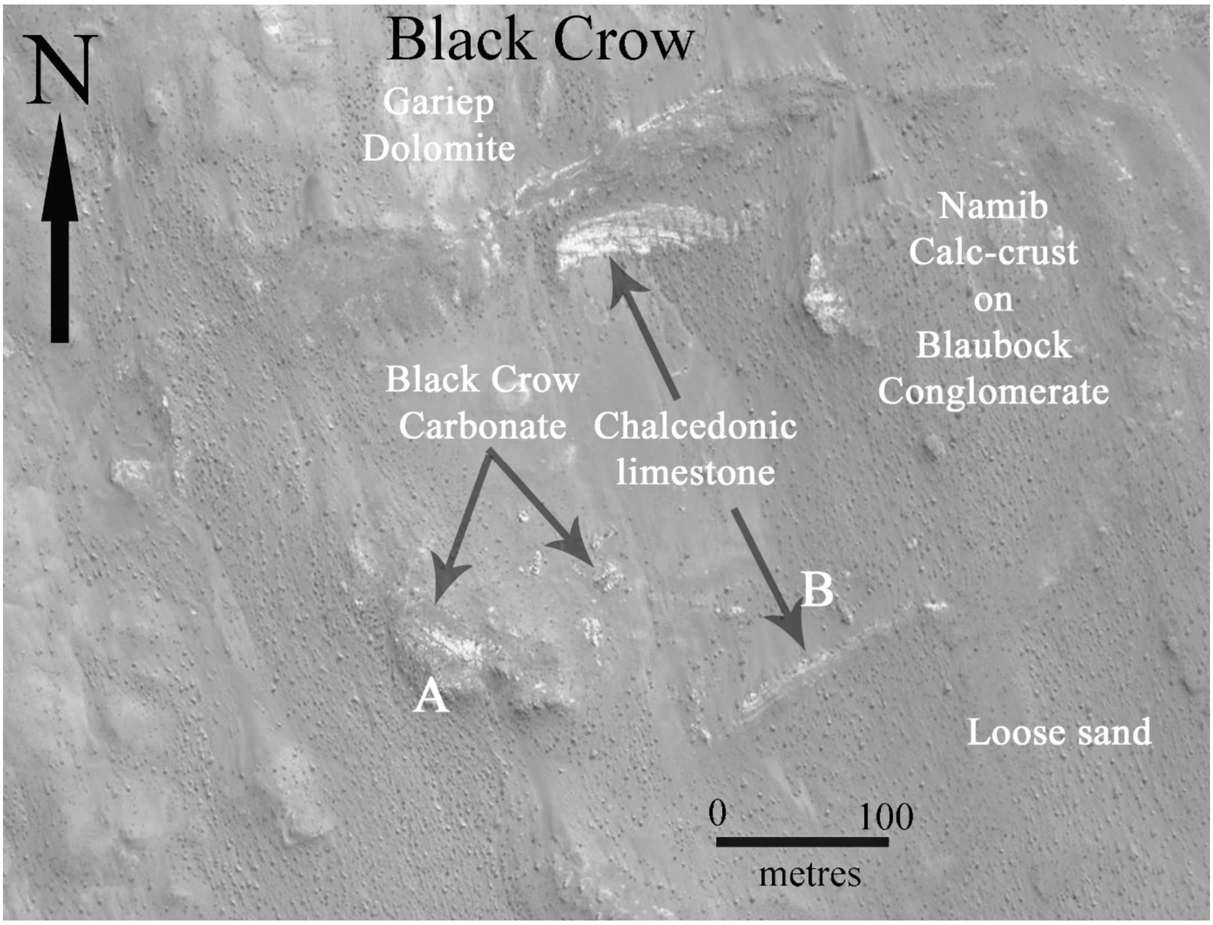

Figure 1. Satellite image of the Black Crow Carbonate Basin, Sperrgebiet, Namibia. The fossil fruit bat humerus and the lower molar described herein were collected at outcrop 'A'. Image modified from Google Earth.

Material, Methods and Nomenclature

GSN BC Ch 1'17 distal humerus.
Tentative attribution, *GSN BC Ch 2'17*, left lower molar.

Stereo images were captured by placing the objective of a Sony Cybershot digital camera over the eyepieces of a stereo microscope. Images were enhanced using Photoshop Elements3. Measurements were taken with sliding calipers.

Nomenclature of the distal humerus of bats follows the schema of Walton & Walton (1970) (Fig. 1).

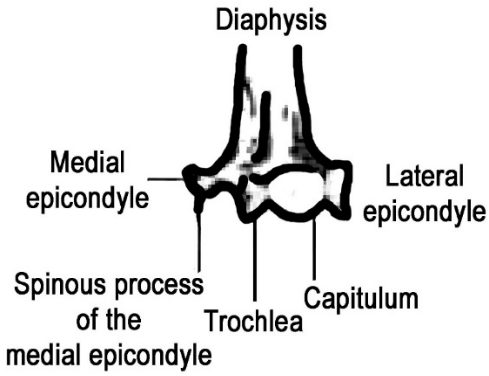

Figure 1. Nomenclature of the distal humerus of bats (modified from Walton & Walton 1970), anterior view (breadth of specimen : ca 1.5 mm).

Systematic Palaeontology

Suborder Megachiroptera Dobson 1875

Family Pteropodidae Gray 1821

Subfamily cf Propottininae Butler 1984

Genus and species indet.

Locality: Black Crow, Namibia.

Age: Ypresian/Lutetian.

Description and comments

In the distal humerus the epiphyseal part is offset laterally relative to the diaphysis, such that the capitulum is not in line with the axis of the diaphysis, but lies slightly lateral to it. The medial epicondyle is broad, comprising about 1/3rd of the distal breadth of the bone and there is a distinct step between its base and the trochlea which has a sharp, vertical margin. The valley between the trochlea and the capitulum extends onto the distal end of the shaft forming a shallow depression between the medial and lateral pillars of the bone which diverge from each other distally at an angle of some 60°. The surface of the capitulum is almost spherical on the anterior side, separated from the lateral epicondyle and the trochlea by shallow valleys with curved floors. The spinous process of the medial epicondyle is weak to absent as in Megachiroptera, not projecting distally as in Microchiroptera.

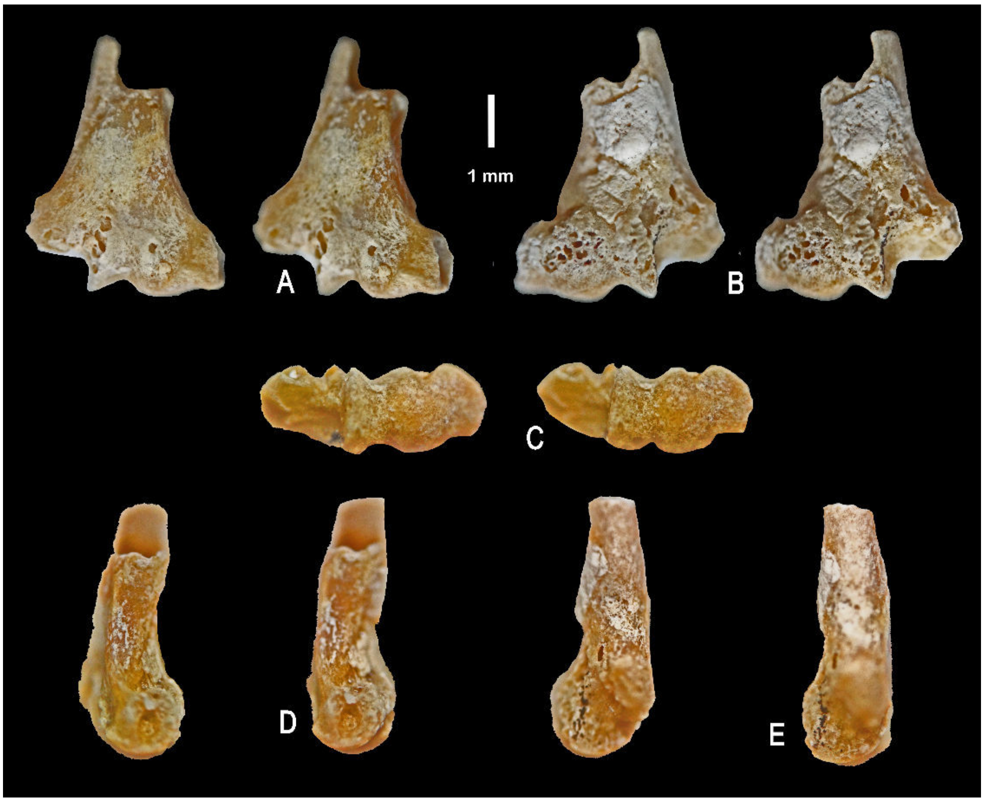

Figure 2. Stereo images of GSN BC Ch 1'17, distal end of right humerus attributed to Megachiroptera from the Ypresian/Lutetian limestone at Black Crow, Namibia. A) posterior view, B) anterior view, C) distal view, D) lateral view, E) medial view (scale : 1 mm).

The epiphysis of this humerus is slightly anteriorly rotated, such that the capitulum is slightly anterior to the long axis of the diaphysis. The preserved part of the diaphysis shows a dense cortical layer inside of which the bone is completely hollow, with no sign of spongy tissue. The lateral epicondyle has a deep fossa for attachment of the supinator (Hand *et al*. 2009).

Discussion

The bat humerus from Black Crow shows many of the classic morphological traits of the Order Chiroptera (Walton & Walton 1970; Butler 1984; Hand *et al*. 2009). Among the various subgroups of the order, it shows the closest resemblances to Megachiroptera. The small or absent distally directed spinous process of the medial epicondyle is like the situation in the family Pteropodidae, unlike the usually well-developed and elongated process that occurs in many Microchiroptera (Butler 1984).

The dimensions of the specimen (medio-lateral diameter of the distal epiphysis at the epicondyles: 3.9 mm) indicates that the species from which it came was quite small for the suborder. Nevertheless, the species was medium-to-large in the overall context of Chiroptera.

Specimen tentatively attributed to Megachiroptera

GSN BC Ch 2'17 is a lightly worn left lower molar, complete with two roots (Fig. 3). The crown measures 1.9 mm mesio-distal length x 1.4 mm bucco-lingual breadth anterior lophid x 1.5 mm bucco-lingual breadth posterior lophid.

The trigonid has a low, small paraconid in a midline position, projecting slightly mesially from the pre-protocristid and pre-metacristid which reach its base. The protoconid is slightly taller than the metaconid, but in occlusal view the two cuspids are subequal in area. There is a short, low cingular swelling along the base of the mesial part of the protoconid. The post-protocristid reaches lingually towards the midline of the crown, but is separated from the post-metacristid by a sulcus. This forms a v-shaped vertical wall at the rear of the trigonid basin (Fig. 3D).

The talonid is slightly lower than the trigonid and is comprised of three cusplets surrounding a central basin. The hypoconid is the largest cusp in the talonid and has a prominent pre-cristid leading obliquely towards the base of the trigonid in the midline of the tooth, thereby leaving room for a largish buccal sinusid. The post-hypocristid is short and descends lingually towards a centrally positioned hypoconulid which is mesio-distally compressed and which closes off the rear of the talonid basin. The entoconid is prominent and is well-separated from the hypoconid, the hypoconulid intervening between it and the hypoconid. The pre-metacristid runs directly anteriorly, reaching the base of the metaconid while the post-entocristid is short and extends buccally towards the hypoconulid. The talonid is marginally broader than the trigonid.

In lingual view, the cervix of the talonid is seen to be somewhat lower than that of the trigonid, bending downwards much as in the m/2 of *Propotto* Simpson (1967) from the Early Miocene of East Africa (Gunnell 2010).

The most interesting point about this tooth, apart from its generally primitive crown morphology, is its radicular system. There are two roots, one beneath the trigonid, the other supporting the talonid. The most striking aspect is the fact that the two roots are narrow and conical, being only half the breadth of the crown at their bases just beneath cervix, and tapering apically with a quasi-circular section throughout their height. They are both inclined slightly distally, indicating that the tooth is probably a first or second molar, rather than the third. The root height is sub-equal to the length of the crown.

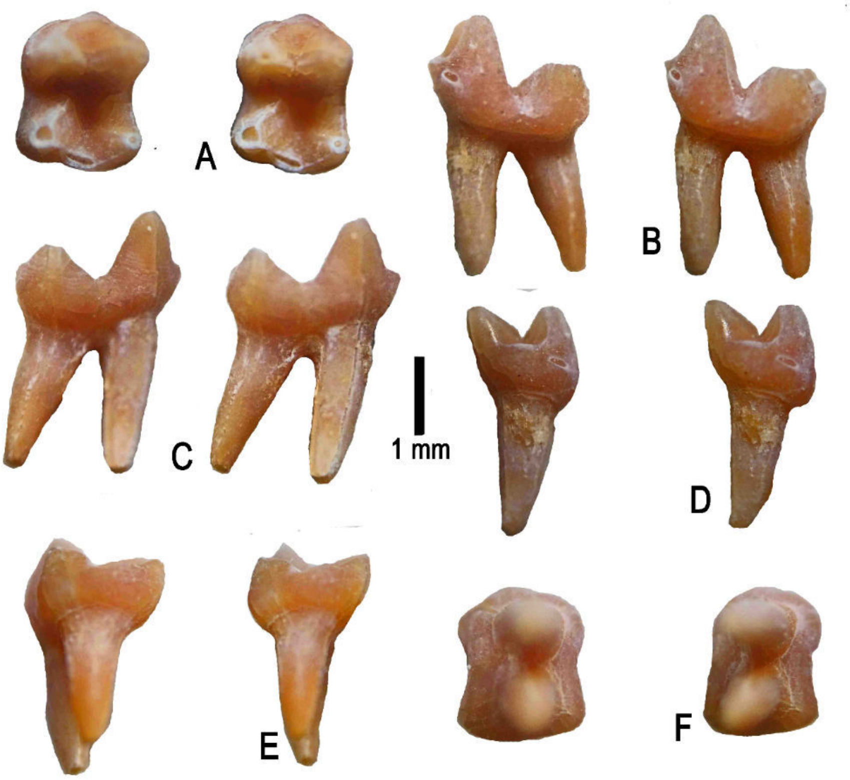

Figure 3. Stereo images of GSN BC Ch 2'17, left lower molar tentatively attributed to Megachiroptera from the Ypresian/Lutetian limestone at Black Crow, Namibia. A) occlusal, B) buccal, C) lingual, D) mesial, E) distal, and F) radicular views (scale : 1 mm).

Discussion

Simpson (1967) described the genus *Propotto* from the Early Miocene of Kenya, on the basis of a mandible fragment containing four cheek teeth (Fig. 4) which suggested to him that he was dealing with a small lorisiform primate close to extant *Perodicticus potto* Statius Müller (1766). Walker (1969) showed that the type specimen was in reality the lower jaw of a fruit bat, a reinterpretation that has found general acceptance among primatologists and chiropteran specialists (Butler 1984; Gunnell 2010). What this history reveals is that primitive fruit bats, put into the subfamily Propottininae by Butler (1984) have lower molar crowns that recall those of Primates. The presence of a well-formed trigonid, behind which there is a large talonid is like that found in pottos and some bushbabies (*Progalago* MacInnes 1943, and *Mioeuoticus* Leakey 1962, for example). The basic similarity in the dental morphology of primitive bats and primates has long been taken to indicate a relationship between these two orders, but the dichotomy between Chiroptera and Primates is generally considered to have occurred during the Late Cretaceous, with some lineages of bats retaining the basic molar grundplan for a considerable period of time, well into the Palaeogene and even into the basal Miocene.

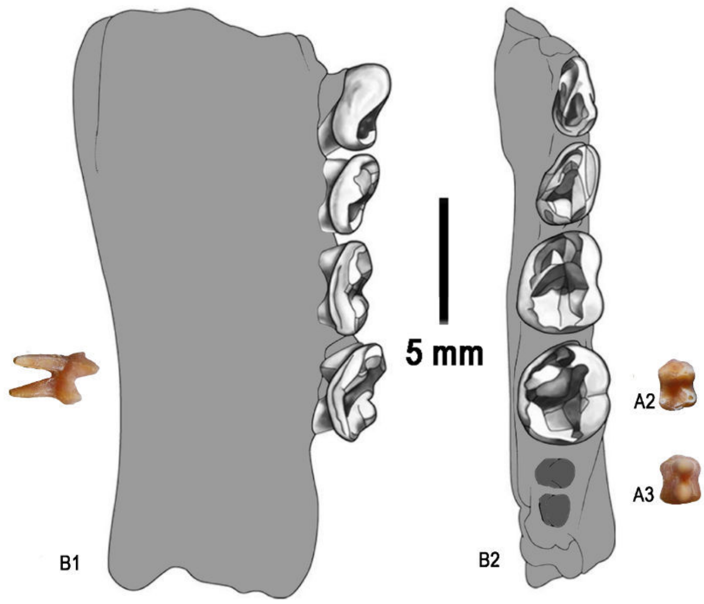

Figure 4. Comparison between A) GSN BC Ch 2'18, left lower molar (reversed) (Note the two relatively small conical roots in the lower molar from Black Crow which are much narrower than the base of the crown) and B) KNM SO 508, right mandible of *Propotto leakeyi*. A1) lingual view, A2) occlusal view, A3) radicular view, B1) lingual view, B2) occlusal view (image modified from Gunnell 2010). Note the sub-rounded alveoli for the m/3. (scale : 5 mm).

The Black Crow tooth recalls the genus *Purgatorius* Van Valen & Sloan (1965) often thought to be a primitive primate (McKenna & Bell 1997). However, there is one feature that suggests affinities of the Black Crow tooth with Megachiroptera (and Chiroptera in general) rather than Primates, and that is the form and strength of the roots. Primate lower molars usually possess stronger, more robust roots than bats do, and their roots are mesio-distally compressed and bucco-lingually broad (Harrison 2010; McCrossin 1992), unlike the molar roots of bats which tend to be small relative to tooth size, almost circular in section and relatively short. More derived primates of larger dimensions even develop four roots in the lower molars. It would be interesting to examine the root morphology of *Purgatorius* to determine whether it is like that of Primates or that of megabats. A lower molar doubtfully attributed to *Purgatorius* shows a small, conical root as in megabats (Van Valen & Sloan 1965, fig. 1c).

A particular similarity between the Black Crow tooth and the extinct fruit bat *Propotto*, is the downward bending talonid of the lower molar, especially evident in the m/2 of *Propotto* (Fig. 4). There are differences between these teeth, especially the presence of a buccal sinusid in the Black Crow specimen, and the overall taller trigonid and talonid, but the morphology in *Propotto* lower molars could be derived from a Black Crow starting point by relatively minor changes, such as rotation of the trigonid and talonid relative to each other, and reduction of the relief of the trigonid and talonid.

The reduced dimensions of the radicular system of the Black Crow molar indicates that the chewing forces employed by the Black Crow species, whatever it turns out to represent, were relatively modest as they are in pteropodids in general, which eat ripe fruits, nectar and other soft parts of plants. Not only that, but also the chewing forces were likely predominantly vertical, with little or no medial or lateral component of force. Primates, which develop greater masticatory forces while chewing, evolved bucco-lingually broad roots in the lower molars which not only anchor the crowns securely in the mandible, but also disperse the chewing forces through a greater surface area of the body of the mandible, with strong medial and lateral components of force reflected in the mesio-distally compressed and bucco-lingually expanded form of the roots.

The difference between primate and megachiropteran lower molar radicular systems means that fruit bats have molar roots that are less than half the mass of those of primate molars of equivalent crown dimensions. In a flying animal, where total body weight is a crucial factor, reduction of the volume of tooth roots is probably an important way to lessen the mass of the individual, even if it represents only a few grams.

Conclusions

This paper records the presence of fruit bats in the Palaeogene of Namibia, the earliest record of Megachiroptera in Africa, and indeed, the world (Gunnell 2010; Gunnell & Simmons 2005) the next oldest megabat being from the Eo-Oligocene of Thailand (Ducrocq *et al*. 1993). From a palaeo-ecological perspective, the presence of this suborder of bats in the Ypresian/Lutetian of Namibia, suggests that the climate was probably tropical to sub-tropical, with year-round availability of flowers or soft fruit within flying distance of Black Crow. This scenario accords with other evidence from the fauna, including the land snails and the aquatic vertebrates which indicate a region enjoying a summer rainfall climatic regime. An isolated lower molar from the same site is tentatively attributed to Megachiroptera on the basis of its radicular morphology and some features of the crown shape. If the taxonomic attribution is confirmed by future discoveries, then the Black Crow fossils will be of great importance for throwing light on the origins of the Megachiroptera, and on their relationships to the Microchiroptera. As it is, the Black Crow lower molar shows some primate-like features, as well as others indicating a possible relationship to the fruit bats.

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