Additional material of *Namahyrax corvus* from the Ypresian/Lutetian of Black Crow, Namibia

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Abstract: Three teeth of a small hyracoid were found during the 2017 campaign of acid digestion of blocks of limestone from Black Crow, Namibia. The specimens, a left D1/, half an upper premolar and a right p/1 can be attributed with confidence to *Namahyrax corvus*, up to now the only hyracoid known from the site. The D1/ is more complete than the broken P1/ in the holotype and yields additional information about the crown morphology of the anterior cheek teeth. The p/1 was not previously known for the species. The three teeth underscore the primitive brachyodont morphology of the teeth. The teeth are somewhat more primitive than the corresponding teeth in *Dimaitherium patnaiki* from the Fayum, Egypt. Direct comparisons cannot be made with *Seggeurius amourensis* and *Bunohyrax matsumotoi* because these tooth positions are unknown in these species, but the shape of the p/1 of *Namahyrax* corresponds with what would be expected from the p/2 morphology in them. Comparisons with *Microhyrax lavocati* are difficult to make because not even the p/2 is known in that species, but the simplicity of its p/3 (lack of crescentic cusps) suggests a ground plan for the p/1 that could correspond to that observed in the Black Crow specimen. The new specimens of *Namahyrax* resolve the uncertainty concerning its familial status, indicating that it belongs to the family Geniohyidae.

Key words: Hyracoidea; Geniohyidae; Fossil; Palaeogene; Namibia; Dental morphology.

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Introduction

A primitive hyracoid from the Palaeogene of Namibia was described by Pickford *et al*. (2008b) who erected a new genus and species, *Namahyrax corvus* for it. It was subsequently compared by Barrow *et al*. (2010) with a brachyodont hyracoid from the Late Eocene of the Fayum, Egypt (*Dimaitherium patnaiki*). Three new teeth have been found at Black Crow, which yield additional information concerning the anterior upper and lower cheek teeth of the species, which highlight the primitive nature of the taxon, allying it with Ypresian-Lutetian hyracoids such as *Seggeurius* Crochet 1986, "*Bunohyrax*" *matsumotoi* Tabuce *et al*. 2000 (similar primitive p/1 morphology is also evident in Early Oligocene *Geniohyus* Andrews 1904) rather than with more selenodont and hypsodont taxa commonly occurring in the Eo-Oligocene faunas of North Africa.

Geological and faunal contexts

The locality of Black Crow lies a few km north-east of Bogenfels Ghost Town, in the central part of the Tsau//Khaeb National Park (old name – Sperrgebiet) Namibia. The Black Crow Carbonate is a freshwater limestone mass that accumulated in a small basin eroded into Proterozoic Gariep Group dolomites. The fossiliferous limestone locally overlies a metre thick well-bedded, indurated sandstone and three to four metres of flaggy chalcedonic limestone (silicified carbonatite tuffs and reworked tuffs for the most part). It is overlain by Late Oligocene/Early Miocene Blaubok Conglomerate which, in its turn, is overlain by the Namib-1 Calc-crust of Late Miocene age (Pickford *et al*. 2008a, 2008b; Pickford 2015a).

There has been debate about the age of the Black Crow fauna. Originally correlated to the Middle Lutetian (Pickford *et al*. 2008a, 2008b) some authors considered it be to be younger (Seiffert 2010) while others accepted a Lutetian age (Coster *et al*. 2012). Part of the disagreement resulted from the fact that Pickford *et al*. (2008a) initially thought that all

the carbonates in the region resulted from a single phase of deposition, but it is now known that there were at least two phases of carbonate accumulation in the region, the first of Ypresian/Lutetian age (Black Crow), the other considerably younger, correlating to the Bartonian/Priabonian (Silica North, Silica South, Eocliff, Eoridge).

The mammal faunas from the two sets of limestone are radically different, those from Black Crow comprising elements indicative of relatively humid tropical to sub-tropical environments (adapids, two zegdoumyids, a reithroparamyine, brachyodont hyracoids, a relatively brachyodont arsinoithere, characiform fishes that lived in fresh, well-ogygenated water bodies, crocodiles) whereas those from the younger deposits at Eocliff and related sites comprise a high proportion of hypsodont rodents, macroscelidids, and relatively hypsodont hyracoids (*Rupestrohyrax palustris*) (Pickford 2015b, 2015c, 2015d, 2015e, 2015g) and open country bird species (Mourer-Chauviré *et al*. 2011, 2014). The prevalence of hypsodont taxa at Eocliff and Eoridge indicate that grass was an important element of the ecosystem at the time of deposition, in contrast to the situation at Black Crow where an woodland ecosystem appears to have comprised the main category of vegetation.

Material and methods

Blocks of limestone from the south-western outcrops at Black Crow were dissolved in 7% formic acid. The teeth and bones released by this method were consolidated in a solution of glyptol dissolved in acetone, or were reinforced by cyano-acrylate (super glue).

Images were obtained by placing the lens of a Sony Cybershot Camera over the eye pieces of a stereoscopic microscope. The resulting images were treated using Photoshop Elements3 in order to enhance the contrast and to remove unwanted background.

Measurements were taken with sliding calipers.

Dental nomenclature

In Early Palaeogene hyracoids the anterior premolars are extremely simplified, but unworn specimens show some of the basic structures that are clearly distinguished in Late Palaeogene and subsequent hyracoids (Fig. 1).

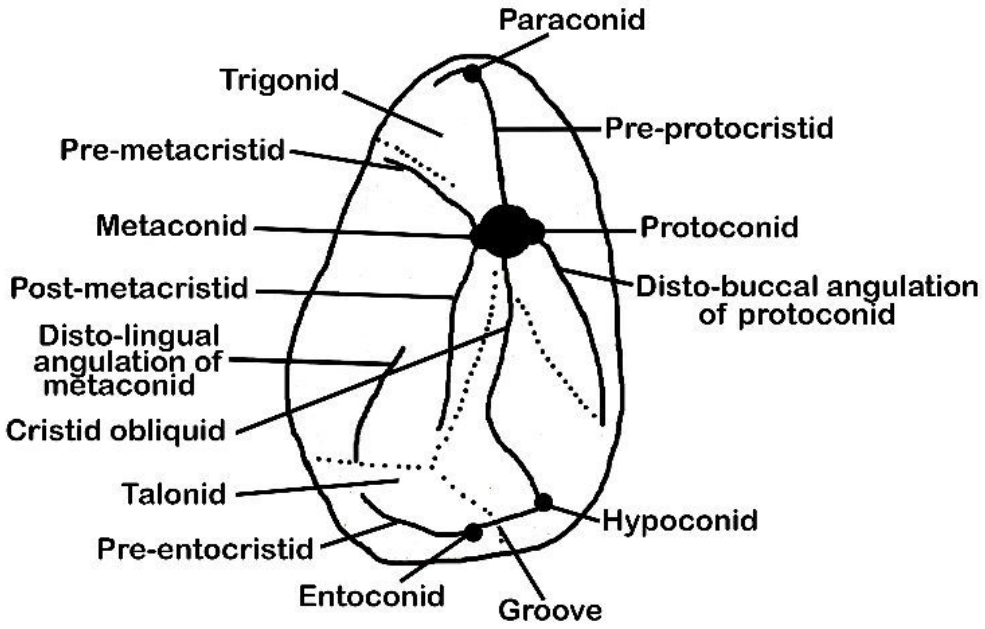

Figure 1. Nomenclature of right anterior lower premolar of Geniohyidae. Note that the protoconid and metaconid are so closely applied to each other that there is no post-protocristid between them. In these small hyracoids the cingulum is also rudimentary (dotted lines represent grooves and valleys).

Systematic Palaeontology

Order Hyracoidea Huxley 1869

Genus *Namahyrax* Pickford *et al*. 2008b

Species *Namahyrax corvus* Pickford *et al*. 2008b

Description

The left D1/ from Black Crow (GSN BC Nc 1'17) is heavily worn, but enough remains of the occlusal surface to indicate that the ectoloph was comprised of a paracone and metacone which are close together linked to a prominent but low parastyle which is well-separated from the paracone. The metastyle is feebly developed. The lingual half of the crown is comprised of a large protocone and a diminutive hypocone. There is a strong mesial cingulum behind which a remnant of the mesial fossette is preserved (between the paracone and protocone). The enamel is thin and the roots appear to be in the process of being resorbed, features which indicate that the tooth is a dediduous molar. The crown shape, with anteriorly projecting parastyle, suggests that it is an anterior cheek tooth, most likely the D1/. There is also an accessory rootlet in the midline of the tooth at the distal end, unlike permanent premolars which are quadriradicular.

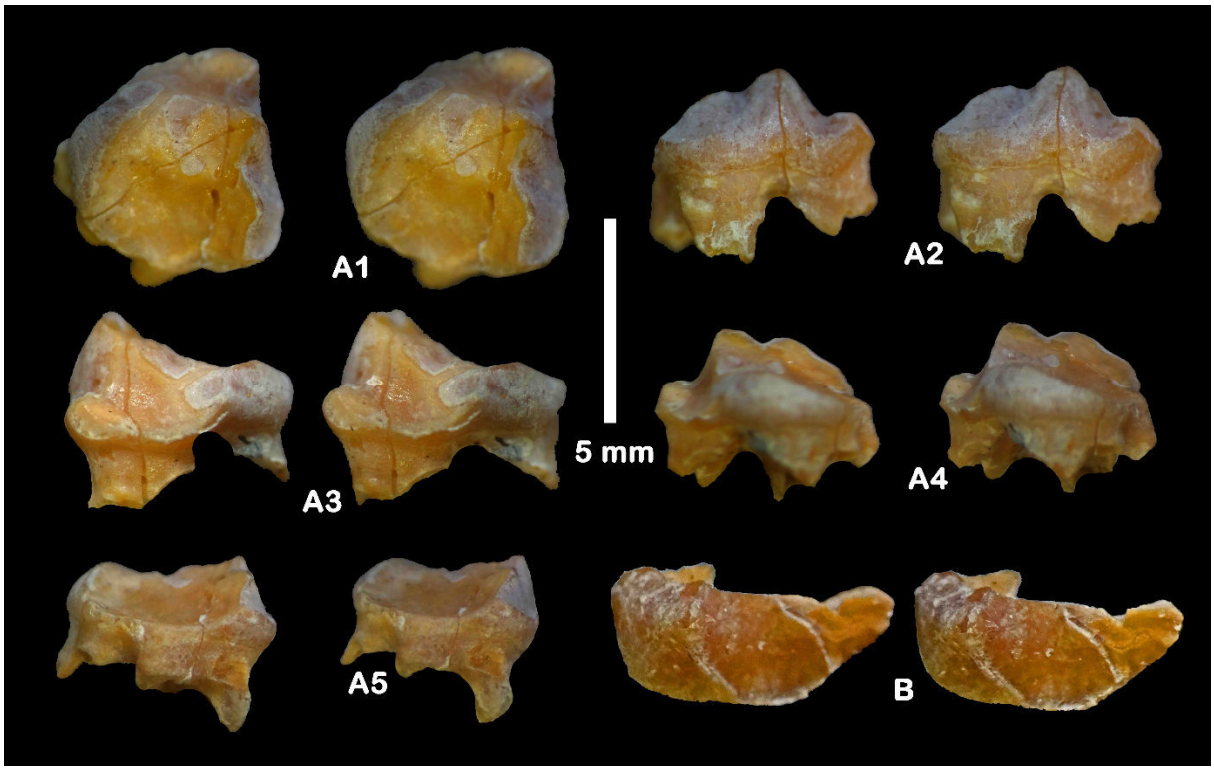

Figure 2. Stereo images of upper teeth of *Namahyrax corvus* from Black Crow, Namibia. A) GSN BC Nc 1'17, left D1/ (A1 - occlusal, A2 - buccal, A3 - mesial, A4 - lingual, A5 - distal view) ; B) GSN BC Nc 3'17, distal loph of left upper premolar (probably P2/) (occlusal view) (scale : 5 mm).

GSN BC Nc 3'17 is the rear half of an unworn upper premolar. The transverse diameter of the fragment indicates that it is likely to be a P2/. The hypocone has prominent pre- and post-cristae which are directed obliquely across the crown towards the buccal side of the tooth. The metacone is broken but retains a clear post-crista which joins the post-crista of the hypocone thereby walling off the rear of the distal fossette, which is shallow.

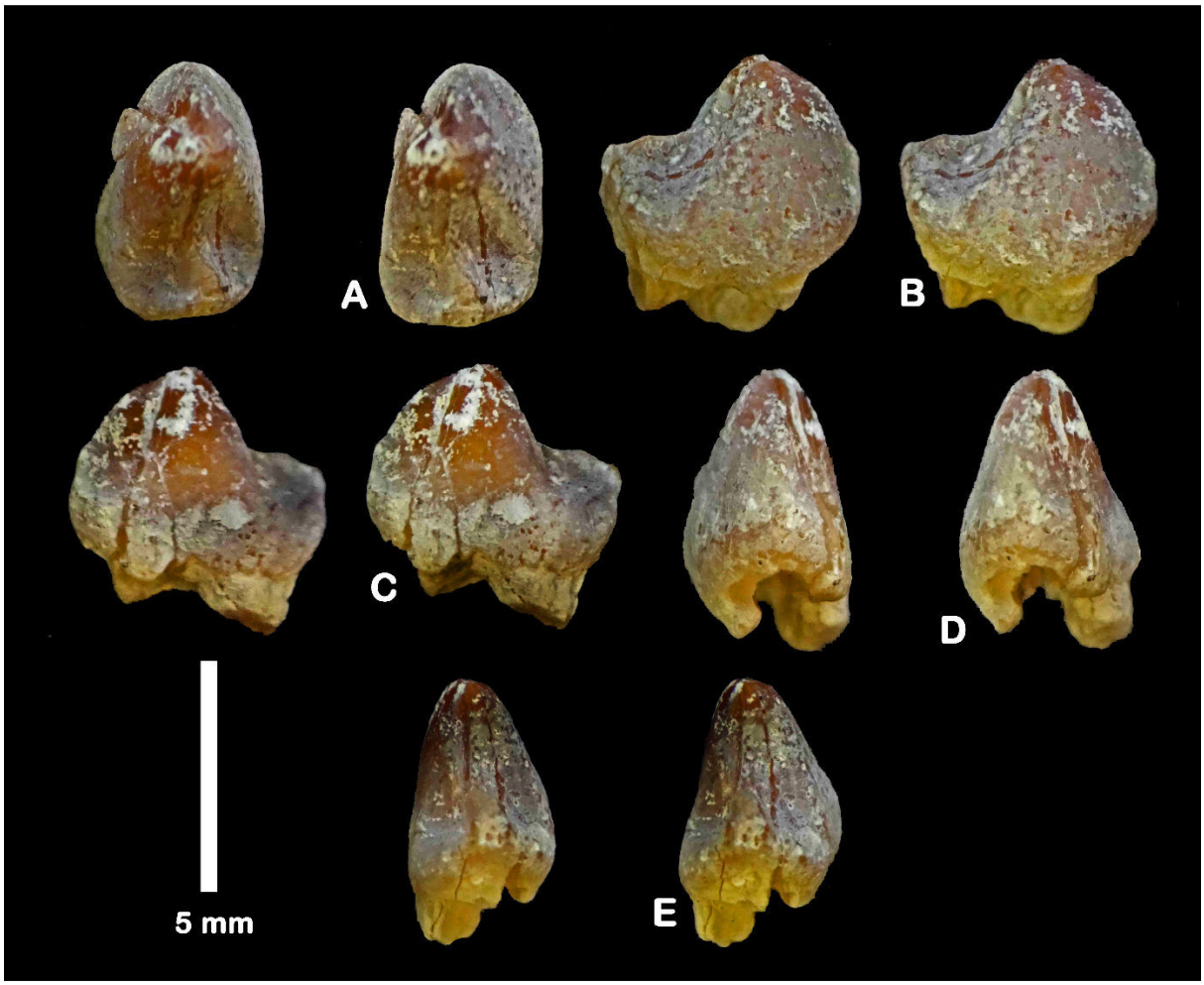

Figure 3. Stereo images of a lower premolar (GSN BC Nc 2'17, right p/1) of *Namahyrax corvus* from Black Crow, Namibia. A) occlusal, B) buccal, C) lingual, D) mesial, and E) distal views) (scale : 5 mm).

GSN BC Nc 2'17 is an unworn right p/1 lacking the roots. There is a prominent main cusp, the protoconid, which has a steep pre-cristid oriented in line with the long axis of the tooth. In lateral view the pre-cristid has a convex profile, and it terminates basally in an indistinct stylid, interpreted to be a diminutive paraconid. Apically the metaconid is so close to the protoconid that it is difficult to make it out, yet the post-metacristid is developed and forms a sharp, almost vertical cristid separated from the cristid obliquid by a narrow but quite deep, vertical groove (Fig. 1, 3). The disto-lateral edge of the protoconid is strongly angulated and forms a wall of the bucco-distal basin. The disto-lingual edge of the metaconid is also angulated. The hypoconid is slightly to the buccal side of the centre-line of the tooth and it gives rise to a short post-hypocristid which ends in a small, low entoconid. The talonid basin is on the mesio-lingual side of the hypoconid-entoconid, and is less capacious than the bucco-distal basin.

Table 1. Dimensions (in mm) of three teeth of *Namahyrax corvus* from Black Crow, Namibia.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
GSN Nc 1'17	D1/ left	5.6	5.3
GSN Nc 3'17	P2/ left	--	7.0
GSN Nc 2'17	p/1 right	5.6	3.4

Discussion

The p/1 from Black Crow (GSN BC Nc 2'17) is an extremely primitive tooth within a hyracoid context, with the metaconid and protoconid almost entirely coalescent, the paraconid diminutive, and the hypoconid and entoconid very small and poorly developed. Thus the double crescent morphology which characterises the cheek teeth of many taxa of hyracoids is, in *Namahyrax*, in a very nascent stage of evolution. Comparable simplicity of premolar crown structure occurs in the anterior cheek teeth of other Early Palaeogene hyracoids of the family Geniohyidae such as *Seggeurius* and even *Microhyrax* (Benoit *et al*. 2016; Crochet 1986; Sudre 1979; Tabuce *et al*. 2000, 2001) and later Palaeogene forms such as *Geniohyus* (Schlosser 1911; Dechaseaux 1958; Gheerbrant *et al*. 2005). In their previous paper, Pickford *et al*. (2008b) could not decide to which family *Namahyrax* belonged, but the new teeth clarify its relationships to Geniohyidae.

Conclusions

Newly discovered hyracoid teeth from Ypresian/Lutetian limestone at Black Crow, even though limited to three isolated teeth, support the view that the genus to which they belong is an extremely primitive member of the order Hyracoidea. The morphology of the anterior premolars indicates that *Namahyrax* is likely to belong to the family Geniohyidae, rather than to the more selenodont taxa comprising Titanohyracidae, Saghatheriidae, Pliohyracidae and Procaviidae.

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