

New *Namalestes* remains from the Ypresian/Lutetian of Black Crow, Namibia

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Abstract: Continued acid digestion of blocks of limestone from the Ypresian/Lutetian deposits at Black Crow, a fossiliferous locality in the Sperrgebiet, Namibia, has resulted in a crop of mammalian, reptilian and fish remains, among which there is a maxilla with four teeth of the poorly known Todralestidae, *Namalestes gheerbranti*. This is the first known upper dentition of the genus, and it permits detailed comparison to other todralestids from North Africa.

Key Words: Palaeogene; Namibia; Biochronology; Fossil; Carbonates; Teeth.

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Introduction

The fossiliferous Ypresian/Lutetian carbonate deposits at Black Crow, Namibia, which were discovered in 2008, yielded a restricted diversity of mammals, including a hyracoid (*Namahyrax corvus*) an arsinoithere (*Namatherium blackcrowense*) creodonts (*Pterdon*, Proviverrine) a primate (*Notnamaia bogenfelsi*) a zegdomyid rodent (*Glibia namibiensis*) a possible xenarthran (previously thought to be a pangolin) and a possible erinaceomorph (Pickford *et al.* 2008a).

Additional fossils have been recovered from the site by acid digestion of limestone. Among the new taxa there are a chrysochlorid (*Diamantochloris inconcessus*) (Pickford 2015b) a tiny zalambdodont, a medium-sized tenrecoid and an adapid primate. There are also remains of previously identified taxa, including several teeth and a mandible of a second zegdomyid rodent representing an undescribed genus. A maxilla and other dentognathic remains of *Namalestes* were also recovered which are described and interpreted herein.

Geological context

The geology of the Black Crow basin has been described in detail by Pickford *et al.* (2008a, 2008b) and Pickford (2015a) (Fig. 1, 2). It is one of a series of small outcrops of freshwater limestone that occur in the Sperrgebiet, Namibia. Most of the occurrences are of Late Bartonian/Early Priabonian age, but the Black Crow occurrence yields a distinct fauna with a decidedly older aspect than those from the other basins such as Silica North, Silica South, Eocliff and Eoridge. It is concluded that there were two phases of

carbonate deposition in the Sperrgebiet during the Palaeogene, the earlier one represented by Black Crow being Late Ypresian/Early Lutetian, and the later one comprising the Silica sites, Eocliff and Eoridge, being Bartonian/Priabonian. Both phases of carbonate deposition in the region could have been related to carbonatite volcanic activity at Ystervark and other volcanoes in the region (Pickford 2015a) which periodically injected vast quantities of carbonate into the sub-aerial terrestrial ecosystem.

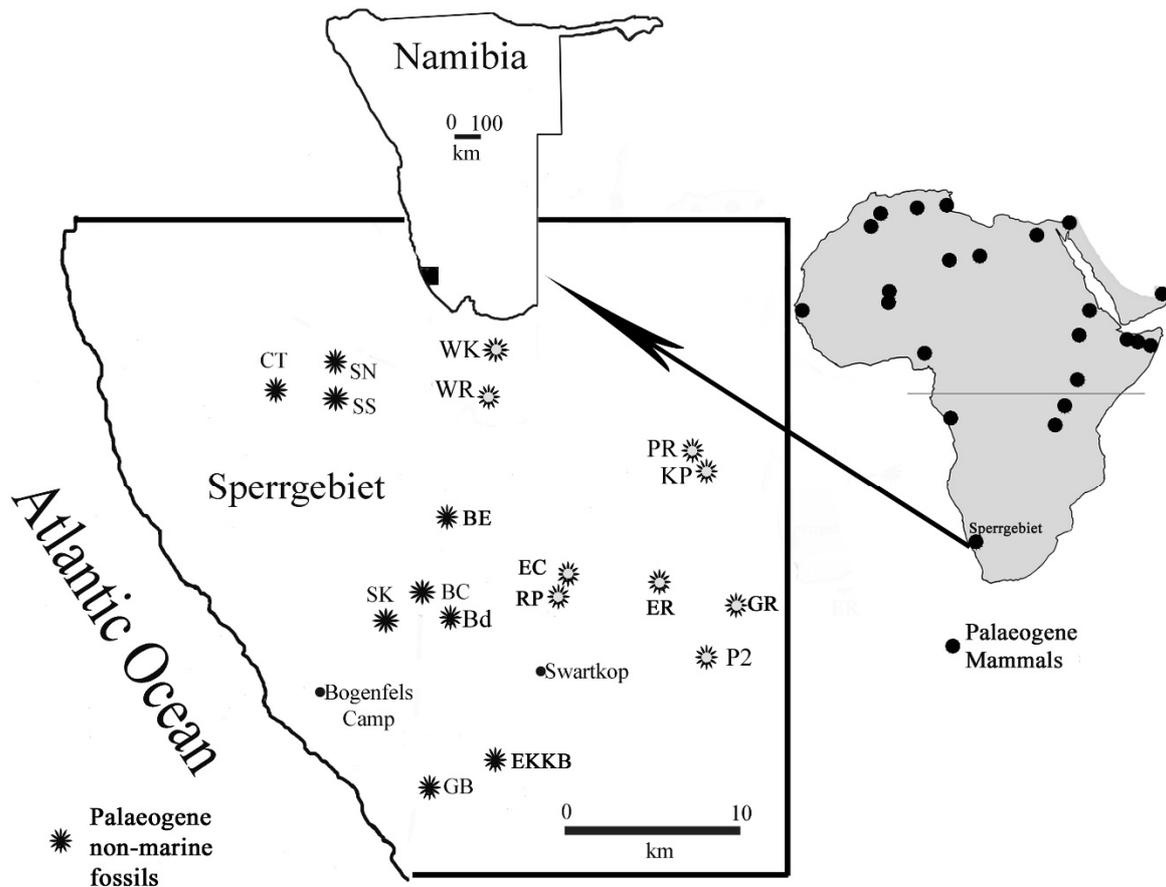


Figure 1. Small Eocene continental basins in the Sperrgebiet, Namibia, infilled with limestone (and chalcedonic limestone) derived directly or indirectly from volcanic activity at the Ystervark Carbonatite Centre (near Phytoherm Ridge). BC - **Black Crow** ; Bd - Bedded limestone ; BE - Bull's Eye ; CT - **Chalcedon Tafelberg** ; EC - **Eocliff** ; EKKB - **Eisenkieselklippenbake** ; ER - **Eoridge** ; GB - **Gamachab** ; GR - Graben ; KP - Klinghart's Pan ; PR - **Phytoherm Ridge** ; P2 - Pietab 2 Limestone ; RP - **Reuning's Pan**, SK - **Steffenkop** ; SN - **Silica North** ; SS - **Silica South**, WK - Werf Kopje ; WR - White Ring. (Localities in **Bold Roman** have yielded mammals, those in **Bold italics** have yielded invertebrates and/or plants, the remainder being unfossiliferous ; solid stars are located in the Trough Namib, hollow stars are in the Plain Namib).

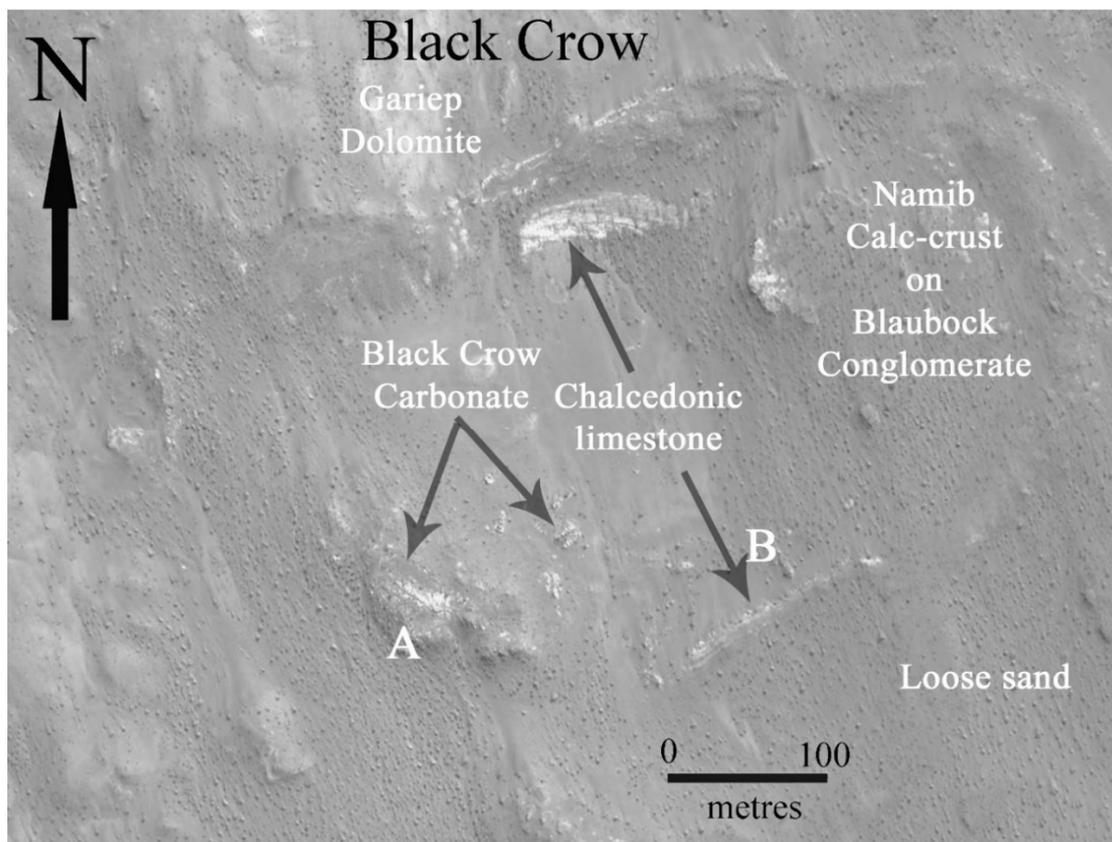


Figure 2. Satellite image of the Black Crow Carbonate Basin, Sperrgebiet, Namibia. The *Namalestes* maxilla described herein was collected at the western flank of outcrop A. Image modified from Google Earth.

Age of Black Crow

The fossiliferous carbonate deposits in the Sperrgebiet were originally interpreted to result from a short-lived but regionally widespread depositional phase related to carbonatite activity at the Klinghardt Volcanic Complex (Pickford *et al.* 2008a, 2008b). Mammals from Black Crow indicated an age considerably earlier than any of the deposits at the Fayum in Egypt, and radio-isotopic dates from phonolite lava cobbles indicated an age greater than 42.5 Ma (Pickford *et al.* 2014). On these bases, the Black Crow and other deposits were correlated to the Lutetian (Pickford 2015a).

However, recent discoveries at Eocliff and Eoridge, which are carbonate deposits close to the Klinghardt Mountains, have resulted in the assembling of an exceptionally diverse mammalian fauna which indicates that these particular carbonates are younger than Black Crow, being closer in age to the Fayum strata. The relatively poor faunas from Silica North and Silica South correlate well with those from Eocliff (Pickford 2015b, 2015c, 2015d, 2015e,

2015f, 2015g). Our estimate of the age of the Eocliff carbonate (Pickford 2015a) places it close to the Bartonian/Priabonian boundary : the Eocliff rodents in particular, appear to be more primitive than any from the Fayum, the oldest of which are from Quarry BQ 2, correlated to the Priabonian by Sallam *et al.* (2010, 2011, 2012).

Coster *et al.* (2012) placed the Sperrgebiet sites between early Lutetian (ca 48.5 Ma) and Late Lutetian (ca 40.5 Ma). The earlier date corresponds to Black Crow, the younger to Eocliff, Silica North and Silica South. The discovery of a reithroparmyine rodent at Black Crow suggests correlation to the Late Ypresian/Early Lutetian (the only other rodents found there are primitive zegdoumyids) but, in marked contrast, following extensive new collections we consider that the Eocliff and Eoridge assemblages are somewhat younger than the Lutetian/Bartonian boundary zone, and place them within the Bartonian (Pickford 2015b). This revision takes into account the presence of the anthracothere *Bothriogenys* at

Eoridge, which was unknown at the time of the first papers on the biostratigraphy of the deposits (Pickford *et al.* 2008a). The presence of the large titanohyracid *Rupestrohyrax* at Eoridge also accords with this correlation (Pickford 2015g). Nevertheless, considering the uncertainties inherent in the correlation of Egyptian site BQ2, then it could be argued that Eocliff is Priabonian rather than Bartonian, but the fauna from Eocliff, especially the abundant rodents and other micromammals, makes it difficult to propose a convincing scenario that it is as young as Oligocene.

The rodents from Eocliff and Eoridge are more primitive than any of the species from

BQ2 (P. Mein, pers. comm. 2016), the oldest locality in the Fayum, Egypt succession (Seiffert *et al.* 2008). BQ2 is positioned at the Bartonian/Priabonian boundary by these authors. If the positioning of BQ2 is correct, then the Eocliff occurrence is likely to be Bartonian, i.e. older than 37 Ma according to the time scale employed by Seiffert *et al.* 2008 (see also Seiffert 2010, who placed BQ2 at 37.2 Ma and Walker *et al.* 2012, who placed the Bartonian/Priabonian boundary at 37.8 Ma). The more recent Geological Time Scale of Ogg *et al.* (2016) places the Bartonian/Priabonian boundary at 38 Ma, but this does not represent a radical change of dating.

Methods

The teeth were measured with a "Nikon Meuroscope 10 5x microscope with an

incorporated micrometer of an accuracy of 0.025 mm"

Systematic Palaeontology

Family Todralestidae Gheerbrant 1991

Genus and species *Namalestes gheerbranti* Pickford *et al.* 2008b

Locality: Black Crow, Namibia.

Material: GSN BC Ng 1'16, right maxilla with P4-M3.

Description

The P4/ is similar in size to the M1/ (Fig. 3, 4). The paracone is voluminous and tall, and occupies almost the entire buccal surface of the tooth. The parastyle is short and tall. The metastyle is short and closely united to the posterior crista of the paracone. The protocone

is very broad and tall, and is joined to the paracone via a broad isthmus. The postcrista is well-developed and joined to a high cingulum at the posterior base of the metastyle. The buccal cingulum is weak.



Figure 3. Stereo images of right maxilla containing P4/-M3/ of *Namalestes gheerbranti* from Black Crow, Tsau//Khaeb National Park (Sperrgebiet) Namibia. A) buccal, B) occlusal, C) oblique lingual views (scale : 10 mm).

M1/ has a lightly worn, conical paracone. The metacone which is also conical is slightly bucco-lingually compressed. Both cusps are located in a rather central position, thereby forming an ample styler platform which is bordered by a robust and tall cingulum. The parastyle is short, but well-developed. The metastyle is well-developed, and extends to the post-crista of the metacone, without an obvious interruption. The paraconule and metaconule are small and form a “V”. The protocone is V-shaped, and is quite worn. There is a well-developed hypocone. The trigon basin is deep. The anterior cingulum is moderately developed on the anterior surface of the crown.

The M2/ is morphologically similar to the M1/, but is larger and differs by the greater development of the ectoflexus. Minor wear of the molar indicates that the paracone is slightly lower than the metacone. In addition, the post-crista of the metacone is not differentiated from the metastyle and is quite sectorial, without a notch between them. The paraconule and metaconule are dune-shaped and well developed. The mesial cingulum is better developed than that of the M1/. In spite of damage to the postero-lingual margin of the tooth, it is possible to discern a quite well-developed hypocone.

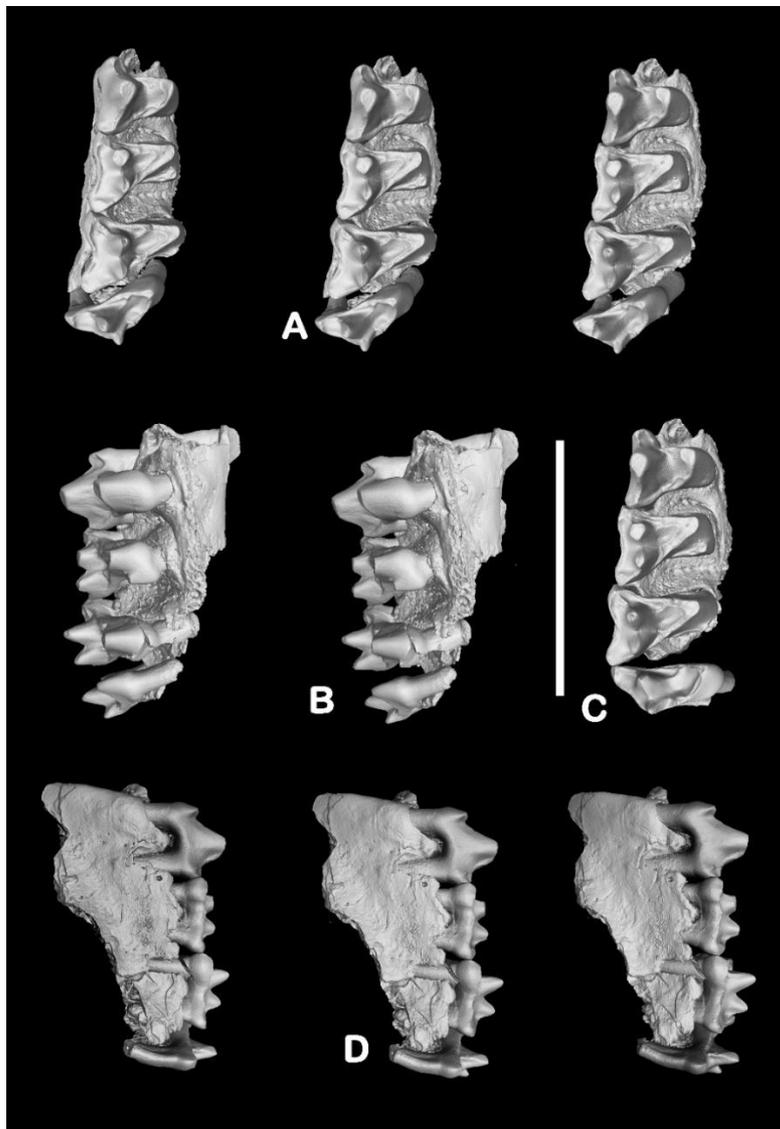


Figure 4. Micro-CT scanned images of GSN BC Ng 1'16, right maxilla with P4/-M3/ of *Namalestes gheerbranti* from Black Crow, Tsau//Khaeb National Park (Sperrgebiet) Namibia. A) stereo triplet occlusal view, B) stereo lingual view, C) occlusal view with the M3/ positioned approximately in its life position, D) stereo triplet buccal view (scale : 10 mm).

The M3/ is appreciably smaller than the anterior molars. It has been displaced due to post-mortem damage to the maxilla. Its original position relative to the M2/ would have been divergent, with the lingual part well-separated from the M2/, whereas there would have been contact between the postero-buccal part of the metastyle of the M2/ and the antero-buccal end of the parastyle of the M3/ (Fig. 4C). It has a tall, voluminous, paracone which occupies most of the buccal surface of the crown. The stylar

area is greatly reduced, except for the anterior part, where the parastyle is strongly developed and projects buccally. It would appear that the anterior crista of the parastyle joins the lingually positioned paraconule. The metacone is comparatively small and projects posteriorly. The paraconule is well developed, and extends to the posterior crista of the protocone. There is no hypocone, although a small bulge indicates its position.

Table 1. Measurements (in mm) of the upper teeth of *Namalestes gheerbranti* from Black Crow.

Tooth	Antero-posterior length	Metastyle-Parastyle length	Breadth
P4/	2.85	--	3.38
M1/	3.16	--	3.73
M2/	3.12	--	3.64
M3/	1.62	2.31	3.92

Discussion

The new maxilla from Black Crow is here attributed to the species *Namalestes gheerbranti* Pickford *et al.* (2008b) previously described from the same locality. There is close correspondence in dimensions and morphology with the lower molar (holotype of the species) and the upper molars here described, using *Todralestes variabilis* from the Palaeocene of Morocco (Gheerbrant 1991) as a model, a species in which the lower molar shows significant affinities to the fossil from Black Crow (Pickford *et al.* 2008b), and the same applies to the upper dentition.

The maxilla fragment from Black Crow contains the complete upper molar row as well as the P4/ and the posterior alveolus of the P3/, similar to the holotype maxilla of *Todralestes variabilis*, which facilitates comparison between the two forms. The similarities between the two species is clear, even though the Namibian one is almost three times larger than the Moroccan one; large and voluminous P4/, molars with very strong buccal cingulum, paracone and metacone separated basally, with a taller paracone. Ectoflexus quite moderate in the M1/-M2/, and both with a hypocone and well-developed mesial cingulum. Nevertheless, there are differences between these forms, the P4/ of the Black Crow species has almost no trace of a buccal cingulum and the isthmus which links the protocone to the buccal part of the tooth is broad and its crests are almost parallel. In the M1/-M2/ the protocone is

positioned anteriorly, with a straight anterior crista, whereas the posterior crista is aligned with the metastyle, in such a way that the trigon comprises a right-angled triangle, in which the shortest side corresponds to the buccal surface. This morphology, allied to the moderate development of the metastyle imparts a certain secodont aspect to the tooth, resembling some primitive creodonts, although there are several other characters which distance them from each other, such as the presence of the hypocone in the molars.

Differences between *Namalestes* and *Chambilestes foussanensis* Gheerbrant & Hartenberger (1999) are the same as those already pointed out above with respect to *Todralestes*. However, in addition, the molars of *Chambilestes* are above all broader than those of *Namalestes*, with better developed parastyles which project anteriorly into a parastylar hook, as in the molars of *Widanelfarasia* (Seiffert *et al.* 2007). The hypocone of the M1/ of *Chambilestes* seems to be better developed than in *Namalestes* and *Todralestes*, and its P4/ has a rudimentary hypocone in the posterior cingulum of the protocone. Finally, the M3/ of *Chambilestes* is relatively bigger than that of *Namalestes*.

In conclusion, *Namalestes* appears to be closer to *Todralestes* than to *Chambilestes*. The latter differs from the two former genera by the strong development of the parastyle and the parastylar area of the molars and the P4/, the

greater development of the hypocone in the M1/-M2/ and P4/, the greater breadth relative to the length of the molars and the relatively larger M3/. As a precaution it is pointed out that many of these features also occur in much older forms, such as for example, *Maelestes gobiensis* of the upper Cretaceous of Mongolia (Wible *et al.* 2007, 2009). However, it is possible to consider that *Todralestes* and *Namalestes* could be derived from a form close to *Chambilestes foussanensis*.

Todralestes and *Chambilestes* were considered by Seiffert (2010) as Palaeogene “Insectivores” for geographic reasons, without exploring the possibility of a relationship with the Afrosoricida. *Widanelfarasia bowni* Seiffert & Simons (2000) was included in the former group. *Widanelfarasia* has a strong tendency to broaden the upper molars (M1/-M2/) combined with the reduction of the M3/, as well as to shift the protocone to a more anterior position with

respect to the paracone, in which features it approaches *Namalestes* and to a lesser extent *Todralestes*. But the other resemblances are less significant than the observable differences. The most important differences occur in the molars, as was pointed out by Seiffert *et al.* (2007). In *Widanelfarasia* the M1/ and M2/ show a marked shift of the paracone and metacone to more lingual positions prefiguring a dilambdodont dental pattern. The stylar platform is broad with a deep ectoflexus and the development in the anterior part of a well-marked crest (stylocone or ectocone) and terminating in a parastylar hook. Additionally, the absence in *Widanelfarasia* of cingula on the lingual and buccal surfaces of the molars represents a major difference from *Namalestes*, *Todralestes* and *Chambilestes*, even though the last one shares with *Widanelfarasia* a well-developed parastylar area ending in a parastylar hook.

Conclusions

Namalestes and *Todralestes* show many similarities to each other, despite the differences indicated above. The inclusion of *Namalestes* in the family Todralestidae is, in the present state of our knowledge, a plausible hypothesis. *Chambilestes*, which was classified in its own family Chambilestidae (Gheerbrant & Hartenberger 1999), has a dental morphological pattern close to Todralestidae, but the morphological differences between the two families pointed out above suggest that it

has a more basal phylogenetic position. *Widanelfarasia* is more derived than the species of these two families, possessing a clear dilambdodont morphological pattern of the molars, but the retention of a well-developed metacone in the molars excludes the genus from the basal Tenrecoidea (Seiffert 2010). Other “Palaeogene” African insectivores (Seiffert 2010) are either very poorly known, or comparisons are difficult to make because there is no homologous material.

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