

# New Titanohyracidae (Hyracoidea: Afrotheria) from the Late Eocene of Namibia

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**Abstract:** The Bartonian freshwater limestone deposits at Eocliff and Eoridge, immediately west of the Klinghardt Mountains in the Sperrgebiet, southwestern Namibia, have yielded an impressive quantity of well preserved micromammals and gastropods (land and freshwater snails). Large mammal remains are rare, but during 2014 the partial skull of a large hyracoid was found, and during the 2015 field survey, a maxilla of the anthracothere *Bothriogenys* was recovered. The microfaunas, especially the rodents, of which there are at least 8 genera, indicate that the limestones accumulated slightly earlier than the oldest mammalian levels of the Fayum, Egypt (Priabonian) meaning that the deposits are likely to be Bartonian. A new genus and species of hyracoid is described from Eoridge, which is attributed to the family Titanohyracidae.

**Key Words:** Sperrgebiet, Namibia, Eocene, Hyracoidea, Titanohyracidae

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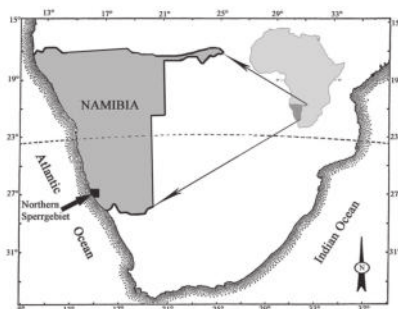
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## Introduction

Fossiliferous freshwater limestones were first recognised in the western margin of the Klinghardt Mountains in the Northern Sperrgebiet (Fig. 1) during the 2013 NPE (Namibia Palaeontology Expedition) field survey of the region. Outcrops of calcareous spring tufas at Eocliff and swamp travertines at Eoridge crop out as positive relief features and contain immense quantities of fossils, both terrestrial (at Eocliff) and freshwater (at Eoridge) (Fig. 2, 3). The geology of the region was described by Pickford *et al.* (2008a) and Pickford (2015) who interpreted the limestones as a late phase of Ystervark Volcanic Activity (Ystervark Formation) during which a hard water spring built up a tufa dome at Eocliff, the

runoff flowing 1.5 km east to pond in a swampy depression where the Eoridge limestones accumulated.

The Eocliff limestone yields immense quantities of well-preserved micromammals, associated with abundant plant root systems which traverse the limestone. The Eocliff tufa evidently accumulated as a subaerial positive topographic feature around a hard water spring, upon which trees and other vegetation were growing. Owls roosting in the trees regurgitated pellets containing skeletons of micromammals and birds, which fell to the ground and were rapidly buried by ongoing tufa deposition. The Eocliff limestone is notable for the absence of any aquatic faunal elements and the rarity of medium to large mammals.



**Figure 1.** Location of the Northern part of the Sperrgebiet, Namibia, in which Late Eocene (Bartonian) limestones occur at Eoridge and Eocliff.

At Eoridge, in contrast, the limestone accumulated in a paludal situation, with freshwater pools flooded by algal mats traversed by sedge stems. In these pools lived snails (*Lymnaea*, planorbids) of which hundreds of specimens may be collected. The vegetal matter has been silicified, which has perfectly preserved aspects of the microstructure of the algal mats while the morphology of the outer surfaces of the sedge stems is clearly visible. The Eoridge limestone contains not only abundant chelonian remains, but also some rare mammalian fossils, both micromammals and large mammals. The micromammals from Eoridge (rodents, tenrecoids) represent the same taxa as those at

### Geological context

The presence of “freshwater limestones” in the zone immediately west of the Klinghardt Phonolite Cluster has been known since the 1960’s, but their age has been a matter of uncertainty, with most geologists correlating them to the Cretaceous (Bennett, 1976; Clarke, 1962; Fowler, 1970; Fowler & Liddle, 1970; Kalbskopf, 1976a, 1976b, 1977; Liddle, 1970a; 1970b, 1970c, 1971; Stocken, 1978; Sullivan, 1961, 1962; Van Greunen,

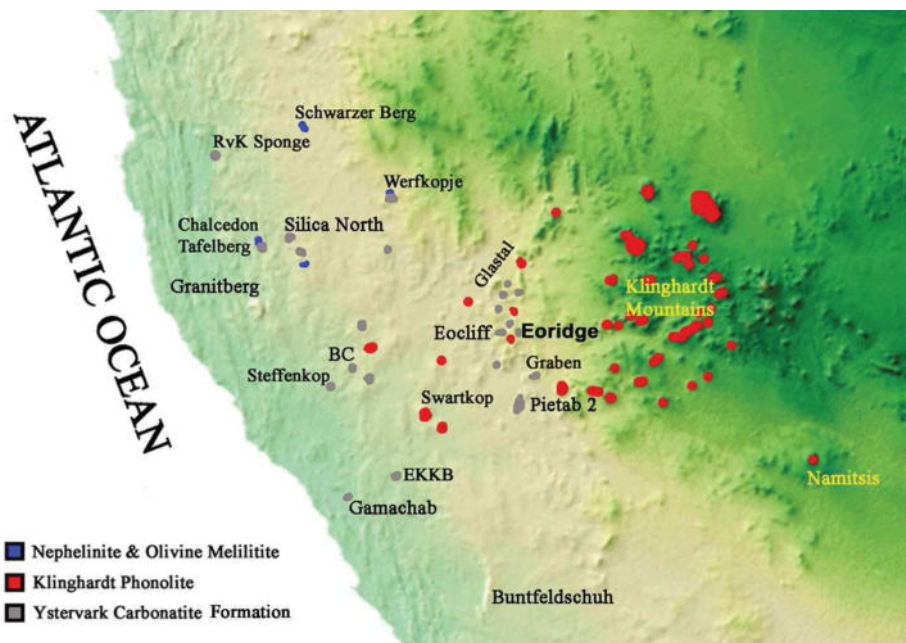
Eocliff, indicating that the two deposits accumulated at the same time.

Eoridge also yields terrestrial gastropods such as *Dorcasia*.

Among the large mammals found at Eoridge are a hyracoid skull, first spotted by Megan Runds (Namdeb, Oranjemund), a hyracoid mandible (found by the author) and an anthracothere maxilla (found by Brigitte Senut) along with various post-cranial elements or mammals the size of arsinotheres or proboscideans.

The aim of this paper is to describe and interpret the hyracoid skull and mandible from Eoridge.

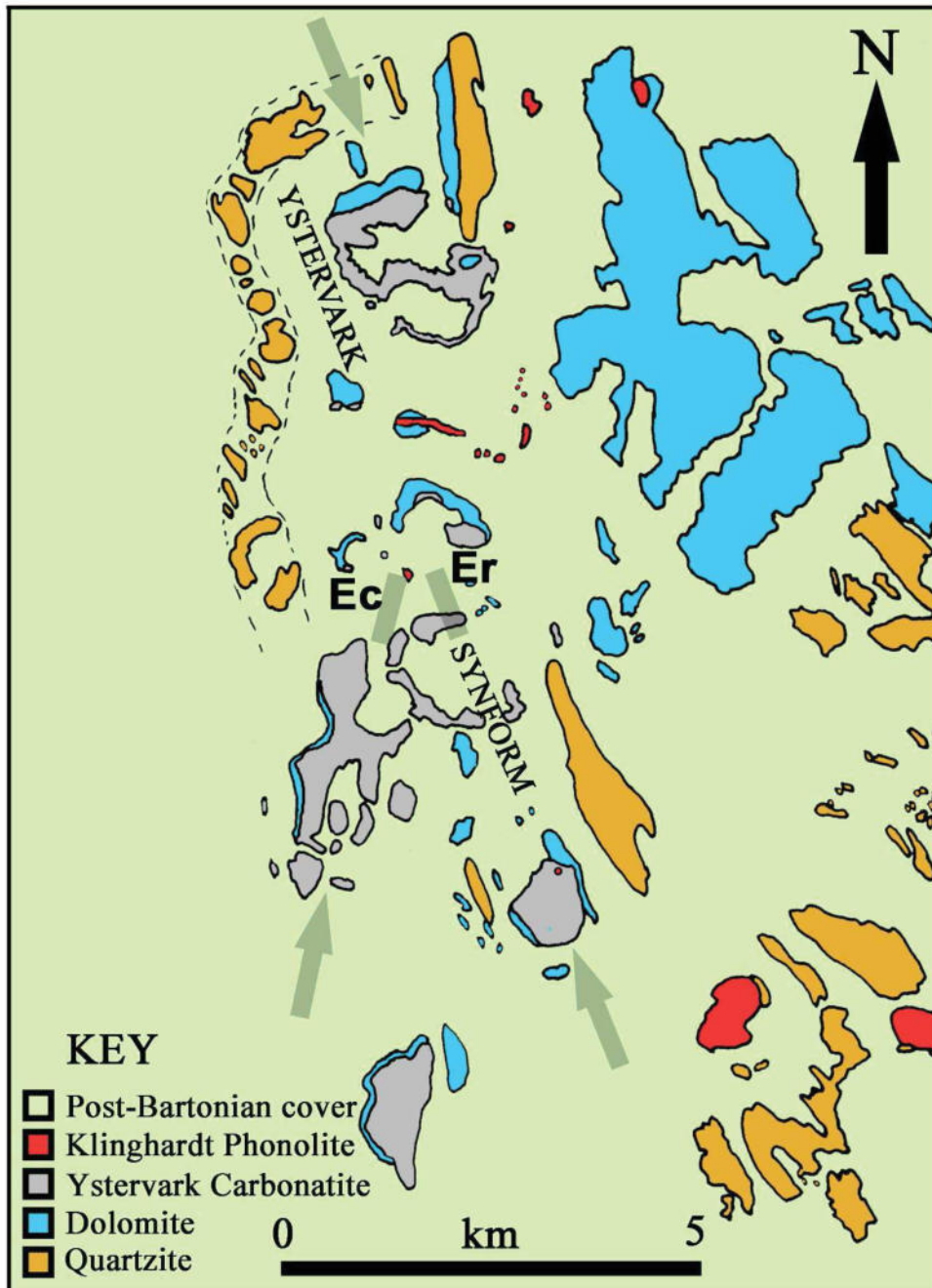
undated). The origin of the calcareous deposits has also been controversial and for a long time they were thought to represent limestone infillings of volcanic craters of parakimberlitic affinities (Fowler, 1970; Fowler & Liddle, 1970; Kalbskopf, 1976a, 1976b, 1977). However, detailed mapping by the NPE reveals that most of the well-bedded limestones in the region are subaerial carbonatitic ashes and agglomerates which erupted from a small centre at Ystervark (Pickford, 2015) (Fig. 2).



**Figure 2.** Digital Elevation Map of the Northern Sperrgebiet showing Phonolite outcrops of the the Klinghardt Mountains (red), outcrops of Nephelinite and Olivine Melilitite lavas (blue) and the distribution of the Ystervark Carbonatite Formation and derivatives from it (grey). Eoridge is highlighted, 1.5 km east of Eocliff, two immensely rich palaeontological sites of Bartonian age.

Unconformably overlying the Ystervark carbonatitic ashes and agglomerates are various lime-rich deposits such as phytoherms, tufa domes and palustral marls and limestones. The carbonate in the latter suite of deposits was evidently derived ultimately from the carbonatitic activity, partly by erosion of clastic material followed by transportation and deposition in localised depressions and partly by dissolution of carbonate from the tuffs by

groundwater followed by precipitation in swamps in the same basins (Fig. 3). During the waning phases of the Ystervark volcanic activity, hot springs and hard water springs were active. Phytoherms accumulated near the hot springs (associated with rare tree branches) and tufa domes grew around the hard water springs.



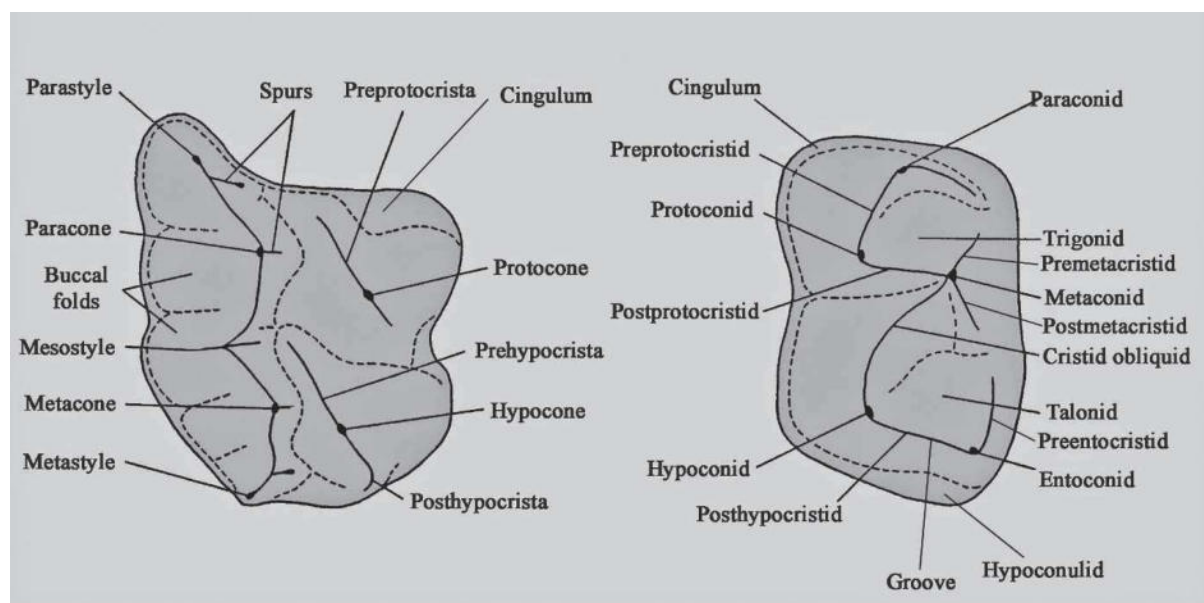
**Figure 3.** Geological setting of the Eocliff and Eoridge Limestones (grey) in the western margin of the Klinghardt Mountains. Ec – Eocliff, Er – Eoridge. The Dolomite and Quartzite are Late Proterozoic in age (Gariiep Group).

## Materials and Methods

The fossils described herein are curated at the Museum of the Geological Survey of Namibia (GSN). The specimens were extracted from *in situ* limestone at Eoridge by means of rock cutters and drills (with the help of Morne van Jaarsveld and Stephan Steenkamp, Namdeb, Oranjemund). The blocks were transported to Paris where they were treated in 7% solution of Formic Acid buffered with Calcium Triphosphate

powder. Once exposed, the fossil bones and teeth were consolidated with acrylic.

Dental nomenclature (Fig. 4) is based on the scheme of Rasmussen & Simons, 1988. Upper teeth are designated with a capital letter (C, P, M – canine, premolar, molar) with a forward slash after the meristic position (which denotes the occlusal plane (eg P1/ first upper premolar). Lower teeth are in lower case (c, p, m) and the forward slash is before the meristic position (eg p/1 first lower premolar).



**Figure 4.** Nomenclature of the teeth of hyracoids (modified from Rasmussen & Simons, 1988) (left image – right upper molar, right image – left lower molar).

## Taphonomy

The Eoridge limestone crops out as a windswept cliff upon which rare plants grow. The roots of the plants penetrate deeply into the limestone producing cylindrical holes. Close examination of the hyracoid skull and mandible before they were extracted, reveals that plant roots had grown towards the teeth, preferentially dissolving them and leaving the surrounding limestone relatively intact. The resultant hollows in the limestone preserve the original shape of the tooth but in a poor and somewhat enlarged state. In order to preserve evidence of the now absent teeth, the hollows were filled with super glue and fine sand, which produced casts of the hollows which were resistant to acid treatment. Although far from perfect replicas of the original teeth, these

casts are nonetheless instructive in terms of tooth position and gross morphology.

The Eoridge hyracoid skull was found within a limestone layer overlying a silicified mass of algal mat, into which the teeth and the right zygomatic arch had been impressed. During preparation, the right zygomatic arch was left inside the algal mat to which it was securely stuck, but the teeth were easily detached. The upper part of the skull was broken into many fragments but the ventral parts were more or less in their correct anatomical relationships to each other, but are slightly distorted.

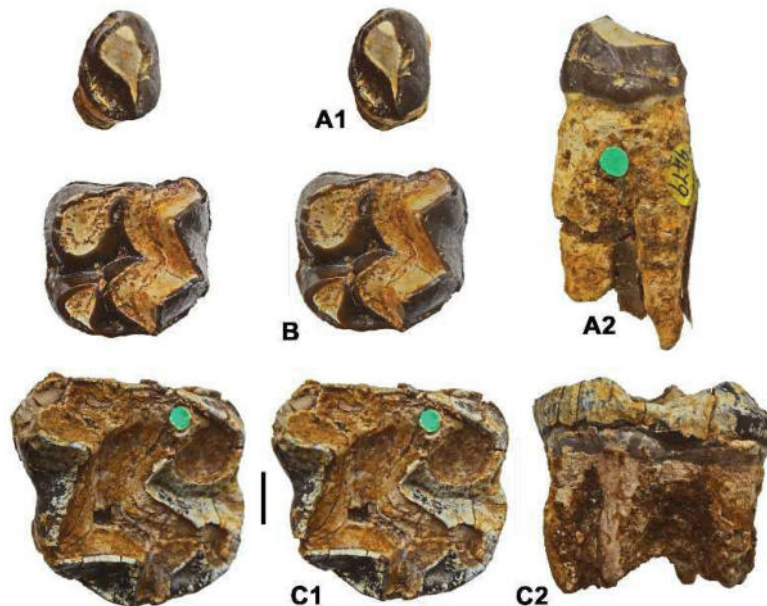
### Taxa mentioned in this paper

Taxon	Author and Year
<i>Afrohyrax</i>	Pickford, 2004
<i>Antilohyrax</i>	Rasmussen & Simons, 2000
<i>Bunohyrax</i>	Schlosser, 1910
<i>Dimatherium</i>	Barrow, Seifert & Simons, 2010
<i>Geniohyus</i>	Andrews, 1904
<i>Megalohyrax</i>	Andrews, 1903
<i>Microhyrax</i>	Sudre, 1979
<i>Namahyrax</i>	Pickford <i>et al.</i> 2008b
<i>Pachyhyrax</i>	Schlosser, 1910
<i>Saghattherium</i>	Andrews & Beadnell, 1902
<i>Seggeurius</i>	Crochet, 1986
<i>Selenohyrax</i>	Rasmussen & Simons, 1988
<i>Thyrohyrax</i>	Meyer, 1973
<i>Titanohyrax</i>	Matsumoto, 1921

#### Note on the holotype of *Titanohyrax ultimus*

Ever since its first description, the holotype specimen of *Titanohyrax ultimus* from the Fayum, Egypt, has been interpreted as a second upper molar (Matsumoto, 1921, text-fig. 2; Rasmussen & Gutierrez, 2010). Comparison with *Rupestrohyrax*, in which the upper molar row is complete in the maxilla, reveals that the Fayum specimen is likely to be an upper third molar on the grounds that it possesses a doubled root supporting the hypocone (Fig. 5) as in *Rupestrohyrax*, an

inference supported by the fact that, given the heavy occlusal wear that it shows, the tooth shows no sign of a distal interstitial facet, which would likely be the case if it were indeed an M2/. A third piece of evidence is that the rear loph of the tooth is long and narrow, unlike the broader, shorter loph that characterises the M2/ of hyracoids in general. This means that the species *Titanohyrax ultimus* would have had somewhat smaller body dimensions than previously thought when the type specimen was considered to be an M2/.



**Figure 5.** *Titanohyrax ultimus* from the Fayum, Egypt. A) NHMUK M 9479, left C1/, stereo occlusal view (A1) and lingual view (A2), B) NHMUK M 12054, left P4/ or M1/, stereo occlusal view, C) NHMUK M 12057, holotype right M3/, stereo occlusal view (C1) and lingual view (C2) to show doubled root supporting the hypocone (scale: 10 mm).

## Systematic Palaeontology

### Order Hyracoidea Huxley, 1869

#### Family Titanohyracidae Matsumoto, 1926

#### Genus *Rupestrohyrax* nov.

#### Type species.- *Rupestrohyrax palustris* nov.

**Diagnosis.-** Large hyracoid with posterior choanae opening up opposite the front of M3/; rear of maxillary process of the zygomatic arch opposite the front of M3/; prehypocrista of upper molars directed towards the metacone; paraconule swelling weak; buccal ribs weak; ectoloph steep; parastyle, mesostyle and metastyle pinched apically, fading out cervically; spurs absent or weakly developed; weak but sharp, discontinuous buccal cingulum in upper cheek teeth, no cingulum on protocone of molars; upper canine two rooted; M3/ with two roots supporting the hypocone; buccal surfaces of upper and lower premolar enamel lightly wrinkled; C1/, P1/ and P2/ with clear buccal groove on ectoloph; lower premolars with anteriorly directed preprotocristid, weak paraconid with low preparacristid; cristid obliquid terminating forwards between the protoconid and metaconid; entoconid weak and low; no buccal cingulum.

**Differential diagnosis.-** *Rupestrohyrax* differs from *Titanohyrax* by the more upright ectoloph in the upper molars, by the more complete fading out of the styles cervically, by the sharper cingula buccally and lingually, by the weaker ribs on the ectolophs of the upper molars, by the lightly wrinkled buccal enamel on the upper and lower premolars, and by the more molarised C1/. *Rupestrohyrax* differs from *Antilohyrax* by its greater dimensions, by the pinched in styles in the upper molars (not strong and swollen as in *Antilohyrax*) by the presence of swollen premetacristid and postmetacristid in the lower premolars, and by the abbreviated mesial lophid of the lower premolars (ie the trigonid basin is small and short, unlike the elongated, capacious basin in *Antilohyrax*). *Rupestrohyrax* differs from *Afrohyrax* by its less hook-shaped preprotocristid and weaker paraconid in the lower premolars, by its weaker anterior cingulum, by the more central anterior termination of the cristid obliquid, by the wrinkled enamel on the

buccal surfaces of the lower premolars, by the weaker, lower entoconid which is more centrally positioned than in *Afrohyrax*, and in the upper molars by the orientation of the prehypocrista which is directed towards the metacone as opposed to its more anterior orientation in *Afrohyrax* in which it impinges on the median transverse valley, and by the absence of a cingulum on the protocone of the upper molars (strong in *Afrohyrax*) and by the presence of two roots which support the hypocone of M3/ (single root in *Afrohyrax*).

**Derivatio nominis.-** The genus name combines the Latin word for «belonging to a rocky place» (from *rupes* (neuter) cliff, rock) and the genus name *Hyrax* (from the Greek «hurax» – shrewmouse) often used for hyracoid genera.

#### Species *Rupestrohyrax palustris* nov.

**Holotype.-** GSN ER 1'14, damaged skull with parts of both tooth rows, anterior fragment with left C1/-P3/, posterior fragment with left M2/-M3 (damaged buccally) and right M1/-M3/ and cast of P4/.

**Paratype.-** GSN ER 3'15, mandible fragment containing p/2-p/4 and a cast of m/1.

**Diagnosis.-** Species of *Rupestrohyrax* in which the upper molar row measures ca 64 mm, slightly larger than *Afrohyrax championi*.

**Derivatio nominis.-** The species name *palustris* refers to the fact that the holotype and paratype were found in palustral limestones (from the Latin *palustris* (adjective) marshy).

**Type locality.-** Eoridge (27°20'47.6"S : 15°36'42.8"E) Western Margin of the Klinghardt Mountains, Sperrgebiet, Namibia.

**Age.-** Late Eocene, Bartonian, ca 39-40 Ma.

#### Description

GSN ER 1'14 is a partial skull with cheek dentition of a large hyracoid. The individual was adult when it died, the M3/ being fully erupted and in light wear. The M1/ in contrast, is deeply worn.

The skull of *Rupestrohyrax palustris* is damaged dorsally, but the ventral parts are better preserved, even though somewhat

distorted, with fragments of the palate and basi-cranium displaced relative to each other (Fig. 6-9). The posterior choanae invade the palate as far forwards as the front loph of the M3/. The palatine bones are distinct as far forwards as the M1/, being unfused in this adult individual. The suture between the palatine and the maxilla is close to the alveolar process, as in recent hyraxes such as *Procavia*. The rear of the maxillary process of the zygomatic process lies opposite the middle of the M3/, and above it there is a well developed and flat maxillary recess. The zygomatic arch is robust with well marked muscle insertions ventrally. The anterior root of the zygomatic process of the maxilla fades out anteriorly at the level of M1/. The glenoid cavity is stopped behind by a swollen post-glenoid process (out of position on the left side but correctly positioned on the right side), and immediately to the rear of this process is the external auditory meatus which is almost horizontally oriented. The vertical paroccipital process is immediately behind the meatic tube. There is an isolated occipital condyle which was floating in the limestone matrix just behind the paroccipital process but there is no contact to show its true position. As is usual in hyracoids, the basioccipital is not fused to its neighbours, and the bones are lying slightly out of position but in the correct relationship to each other.

The upper canine, which possesses two roots, has a prominent buccally positioned cusp (paracone) with a preparacrista terminating low anteriorly in a small low cusplet, the parastyle. Distally it shows a postparacrista which ends low down near the cervix. The buccal surface of the tooth has a vertical groove behind the main cusp (ie the paracone and metacone are distinct, even if very reduced in topography), and its enamel is lightly wrinkled. The lingual part of the crown shows three sloping depressions, an anterior one closed basally by a low cingulum which covers about one quarter of the tooth's surface, a larger depression behind also closed basally by a rounded cingulum, separated from the distal fovea by a low crista.

The P1/ is broader than the canine, with better expressed morphology on the lingual part of the crown. The ectoloph shows

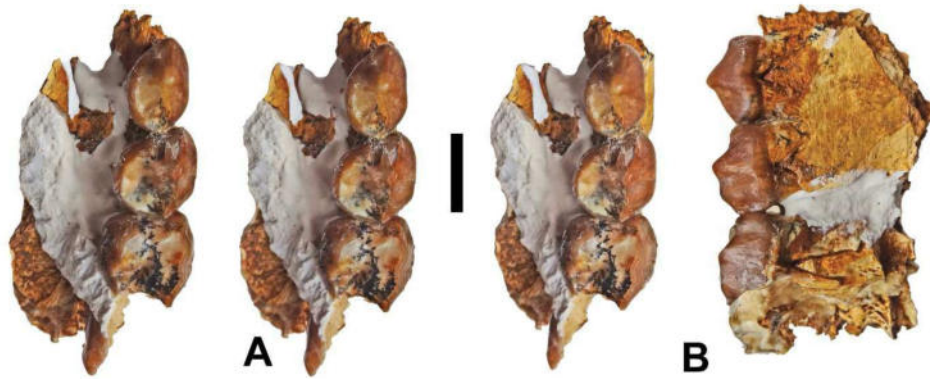
two cusps, the paracone anteriorly and the metacone posteriorly separated from each other buccally by a vertical groove. The buccal enamel is lightly wrinkled. The preparacrista ends anteriorly at a low cusplet, the parastyle, and the postmetacrista descends cervically, ending at a low metastyle. Like the upper canine, there are three sloping basins on the lingual side of the crown, but they are better expressed and more voluminous. They are bounded lingually by a low rounded cingulum which shows two swellings corresponding to the protocone and the hypocone. The anterior fovea is strongly separated from the distal basins by a tall crista that descends from the apex of the paracone towards the protocone. The crista descending from the metacone towards the hypocone is incomplete and does not reach the base of the hypocone, leaving the two distal basins confluent with each other.

The P2/ is a more molarised version of the P1/ with a better expressed parastyle, and a larger more distinct protocone (Fig. 6). The rear of the tooth is broken off, but shows that the central basin on the lingual part of the crown is confluent with the distal one, but is separated from the mesial fovea by a ridge. The groove on the buccal surface of the ectoloph, between the paracone and metacone, is weaker than in the P1/.

The P3/ is represented only by a tiny fragment of the lingual surface which shows the presence of a cingulum between the protocone and hypocone.

The P4/ is represented by a natural cast where the crown was eroded by plant roots. As such, most of the surface morphology has been eradicated, but it is possible to determine that the rear part of the crown resembled that of the M1/ behind it.

The M1/ is partly preserved on the right side, the paracone of the tooth having been eroded by plant roots. The crown is deeply worn with only a small remnant of the distal basin preserved lingually. The buccal cingulum is sharp on the metacone, and there is a lingual cingulum at the end of the median transverse valley, but which does not extend onto the base of the protocone, nor onto the base of the hypocone. The mesial cingulum is partly preserved in front of the protocone.



**Figure 6.** GSN ER 1'14, left maxilla, part of the holotype of *Rupestrohyrax palustris* nov. gen. nov. sp., containing C1/-P2/ and the lingual part of P3/, stereo triplet of the occlusal view, buccal view (scale: 10 mm).

The M2/ is worn to the stage where it is difficult to interpret the crista and other minor structures (Fig. 7). However, it is clear that the preprotocrista ended anteriorly in a small paraconule which was not confluent with the mesial cingulum. The ectoloph is « w-shaped » with strong parastyle, mesostyle and metastyle, and prominent paracone and metacone, the ensemble being quite steep. The styles are pinched in apically, gradually rounding out and fading out cervically. There is a sharp cingulum that runs along the ectoloph from the parastyle to the mesostyle, thence to the metastyle. The hypocone is smaller than the protocone and shows a

prehypocrista that is directed towards the metacone where it terminates in a low swelling at the lingual base of the metacone. There is a low endohypocrista which trends towards the metacone, which it joins via a low swelling at the base of the metacone, thereby forming a small fovea in the midline of the tooth, in front of the distal basin, and behind the median transverse valley. The posthypocrista is directed distally where it merges into the distal cingulum. The protocone is heavily worn, but shows remains of the preprotocrista and postprotocrista where the enamel / dentine junction has small, sharp extensions mesially and distally.

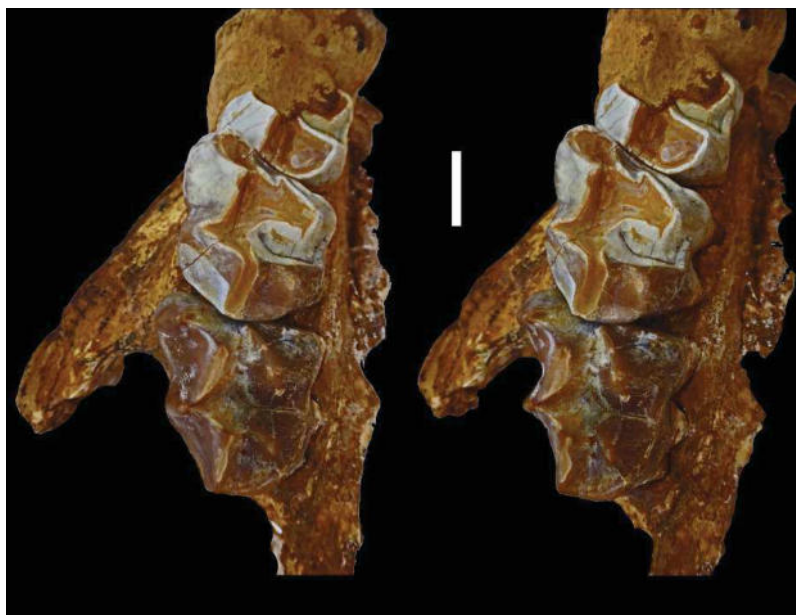


**Figure 7.** GSN ER 1'14, the rear part of the holotype skull of *Rupestrohyrax palustris*, nov. gen. nov. sp., stereo occlusal view (scale: 10 cm).



The M3/ is lightly worn, so all the structures can be made out. The protocone has a low postprotocrista which is directed distally as a low swelling (Fig. 8). Internally there is a tiny endoprotocrista which reaches across to the base of the paracone, subdividing the anterior part of the longitudinal valley into two basins, one in front extending as far as the paraconule, the other behind confluent with the median transverse valley. The preprotocrista leads anterocentrally, ending in a diminutive paraconule which is clearly not confluent with the anterior cingulum. The hypocone is smaller than the protocone, the prehypocrista is orient-

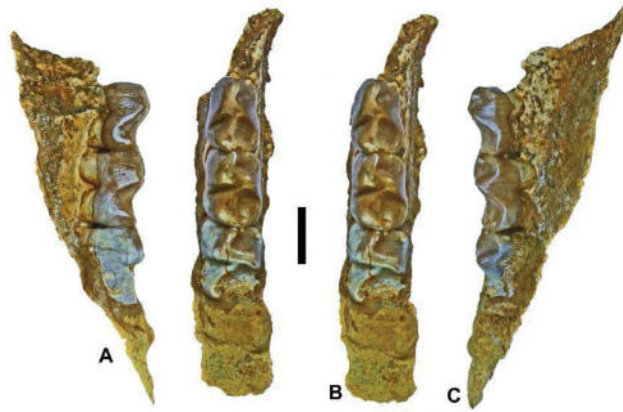
ed directly towards the base of the metacone, which it joins via a low crest (spur) descending from the apex of the metacone. The endohypocrista is low, and barely separates the central fovea from the distal basin. The M3/ has a more elongated occlusal outline than the M2/, its distal basin is prolonged antero-posteriorly and bordered distally by a more prominent distal cingulum. The bases of the protocone and hypocone show no signs of cingula. The M3/ differs from the other cheek teeth by the presence of two roots supporting the hypocone (Fig. 9) the other molars having only four roots.



**Figure 8.** GSN ER 1'14, right maxillary dentition of the holotype skull of *Rupestrohyrax palustris*, nov. gen. nov. sp., stereo occlusal view (scale: 10 mm).



**Figure 9.** GSN ER 1'14, right maxilla of *Rupestrohyrax palustris* showing the three molars in lingual view. Note the doubled root supporting the hypocone of the M3/, and the single roots under this cusp in M2/ and M1/ (scale: 5 cm).



**Figure 10.** GSN ER 3'15, left mandible fragment containing p/2-p/4 and cast of m/1, paratype of *Rupestrohyrax palustris* nov. gen. nov. sp. (scale: 10 mm).

**Table 1.** Measurements (in mm) of the teeth of *Rupestrohyrax palustris* nov. gen. nov. sp. from Eoridge, Sperrgebiet, Namibia (e – estimated measurement).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
GSN ER 1'14	C1/ left	13.1	9.2
	P1/ left	13.6	12.7
	P2/ left	14.0	15.1
	M3/ left	24.0	--
	M1/ right	19.0	23.5
	M2/ right	22.4	24.7
	M3/ right	24.0	25.2
GSN 3'15	p/2 left	13.1	9.8
	p/3 left	14.0	11.0
	p/4 left	15.5 <sup>e</sup>	12.4 <sup>e</sup>

The lower premolars of *Rupestrohyrax* (GSN ER 3'15) are weakly molarised, with the transverse crests poorly formed except in the p/4 (Fig. 10). The preprotocristid is short and centrally positioned ending in a weak paraconid. As a result, the trigonid basin is small, antero-posteriorly short and shallow. The metaconid is almost confluent with the protoconid in the p/2 but it becomes more distinct in the posterior premolars, in the p/4

being well offset from the protoconid. The postmetacristid is swollen apically, fading out cervically. The prehypocristid terminates anteriorly midway between the protoconid and metaconid and delimits a talonid basin which increases in dimensions and definition from p/2 to p/4. The postprotocristid is strongly developed in all the premolars, forming a sloping anterior wall for the hypoflexid.

## Discussion

### Affinities of *Rupestrohyrax*

Among Titanohyracidae, *Rupestrohyrax* is closest in dental morphology to *Titanohyrax* Matsumoto, 1921, but it shows sufficient differences to warrant the erection of a new genus. Like *Titanohyrax*, the M3/ shows a doubled root supporting the hypocone. Also like this genus, *Rupestrohyrax* shows a more upright ectoloph in the upper molars and the prehypocrista extends towards the lingual base of the metacone rather than more anteriorly towards the median transverse valley, the latter

morphology found in *Afrohyrax*, for example. Also like *Titanohyrax*, the upper canine is two rooted (Fig. 5A), but the crown shape in the two genera is markedly different, more complex in *Rupestrohyrax* with clear, even if weak, paracone and metacone, and diminutive protocone and hypocone bordering three lingual basins, in contrast to a simple single cusped crown in *Titanohyrax* in which there is a single small distal lingual basin. Other differences from *Titanohyrax* concern the steepness of the molar ectolophs, which are more inclined lingually in *Titanohyrax*, even though in the latter genus they are steeper than

in most other genera of hyracoids such as *Bunohyrax*, *Geniohyus* and *Saghatherium* as well as *Namahyrax* from the Sperrgebiet, Namibia (Pickford *et al.* 2008b) and *Dimatherium* from the Fayum, Egypt (Barrow *et al.* 2010).

There are many differences between the teeth of *Rupestrohyrax* and *Afrohyrax*, including the less hook-shaped preprotocristid in the premolars with a weaker paraconid and anterior cingulid, the more centrally directed prehypocristid, which in *Afrohyrax* trends much further towards the lingual side of the crown. Furthermore the buccal cusps of the premolars are wrinkled in *Rupestrohyrax*, unlike the smooth enamel in *Afrohyrax*. In the upper molars, the most striking difference between these two genera is the orientation of the prehypocrista: directly towards the

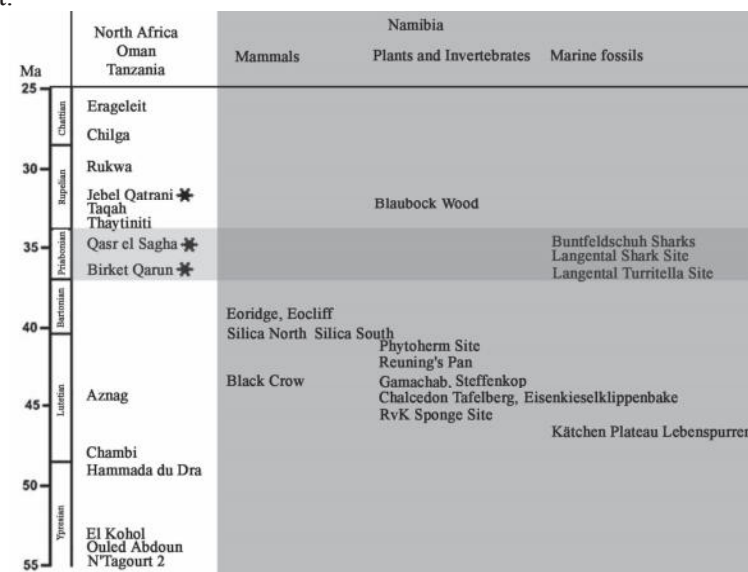
metacone in *Rupestrohyrax* - obliquely forwards in *Afrohyrax*, terminating in the median transverse valley. In addition, *Afrohyrax* has a strongly developed and sharp cingulum on the protocone, which is not present in *Rupestrohyrax*. Finally, the hypocone of the M3/ of *Afrohyrax* is supported by a single root, unlike the doubled root in *Rupestrohyrax*.

There are also major dental differences between *Rupestrohyrax* and *Antilohyrax*, including the strongly swollen styler bases in the upper molars of *Antilohyrax* (obsolete in *Rupestrohyrax*), and the lower degree of hypsodonty (greater in *Rupestrohyrax*). But perhaps the greatest differences concern the anterior lophids in the lower premolars – shortened in *Rupestrohyrax* and elongated in *Antilohyrax* (De Blieux & Simons, 2002).

#### Diversity, Biostratigraphy and Biogeography of Titanohyracidae

The description of *Rupestrohyrax* brings to four the diversity of genera in the family Titanohyracidae, the others being *Titanohyrax*, *Antilohyrax* and *Afrohyrax*. The family experienced its acme during the Eocene and Oligocene from which seven species have been described, but it persisted until the Early Miocene in East Africa and Namibia, as well as the Arabian Peninsula (Pickford, 2009) but during the Middle Miocene, ca 15 Ma, the family went extinct.

Titanohyracidae are known from the base of the Middle Eocene at Chambi, Tunisia, which yielded *Titanohyrax tantalus* (Court & Hartenberger, 1992) and at Glib Zegdou, Algeria (Fig. 11) from which *Titanohyrax mongereaui* was described (Sudre, 1979), although there are some doubts about the affinities of the latter species (Rasmussen & Guttierrez, 2010) based as it is on a partial upper molar which is more brachyodont than other species of *Titanohyrax*.



**Figure 11.** Biostratigraphy of African Palaeogene mammalian sites, showing the positions of hyracoid localities at Black Crow in the Lutetian and at Eoridge and Silica North in the Bartonian.

The discovery of *Rupestrohyrax palustris* in the Late Eocene of Namibia enlarges the known distribution of Titanohyracidae over 6000 km to the south of its previous records in North Africa (Middle Eocene to basal Oligocene), East Africa (Late Oligocene to Early Miocene) (Rasmussen &

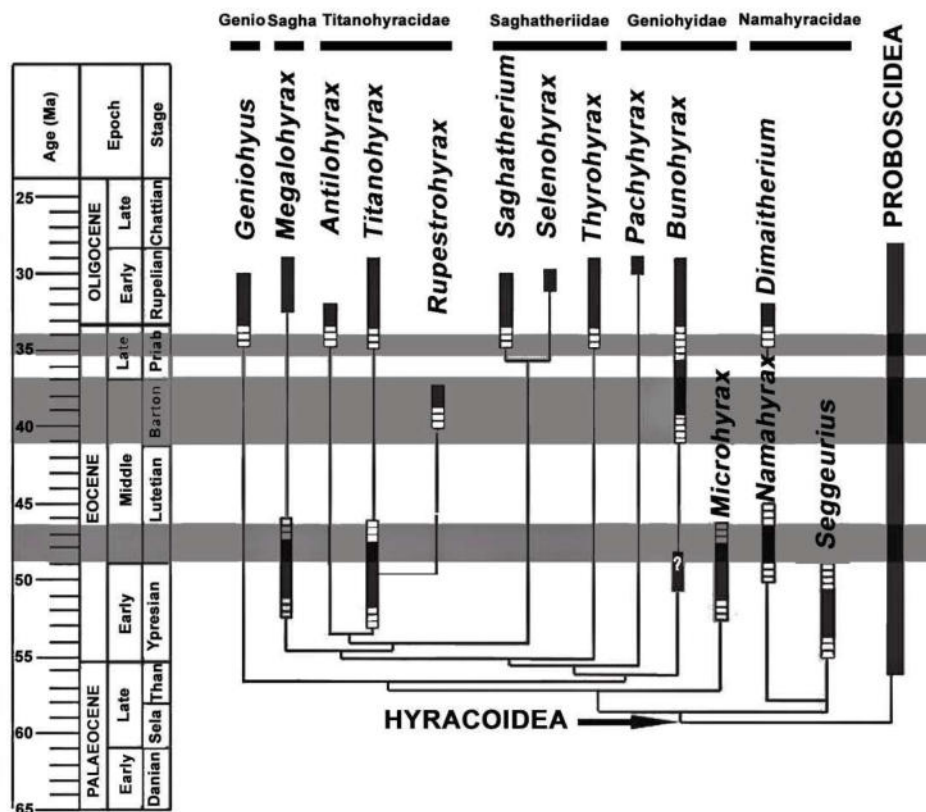
Gutierrez, 2010) and the Arabian Peninsula (Early Miocene) (Pickford, 2009). The presence of giant hyracoids in the Late Eocene of Namibia is not unexpected, because equally large hyracoids are known from the Middle Eocene of Algeria (Sudre, 1979).

#### Other Namibian Eocene Hyracoidea

The Middle Eocene Namibian species *Namahyrax corvus*, from Black Crow, Sperrgebiet (Pickford *et al.* 2008b) belongs to a different family (Namahyracidae, new family) from the Titanohyracidae. In addition to the type genus from Namibia, Namahyracidae contains *Seggeurius* Crochet, 1986, and *Dimatherium* Barrow *et al.* 2010, from North Africa (from El Khol, Algeria, and the Fayum, Egypt, respectively). The distinguishing features of the new family are

the greatly enlarged and swollen styles in the upper molars and the marked brachyodonty of the molars.

Among the Hyracoidea, the new family Namahyracidae is most closely related to Geniohyidae Andrews, 1906, which contains the genera *Geniohyus*, Andrews, 1904, *Bunohyrax* Schlosser, 1910, *Pachyhyrax* Schlosser, 1910, all from the Late Eocene to basal Oligocene of the Fayum, Egypt (Schlosser, 1911), and *Brachyhyrax* Pickford, 2004, from the Early Miocene of East Africa (Fig. 12).



**Figure 12.** Phylogeny of Palaeogene Hyracoidea based partly on Tabuce *et al.* 2001, with the addition of *Namahyrax*, *Dimatherium* and *Rupestrohyrax*, and the new family Namahyracidae (Genio – Geniohyidae, Sagha – Saghattheriidae).

#### Conclusions

A new genus and species of large hyracoid are described from the Late Eocene

(Bartonian) Eoridge Limestone deposit of the Sperrgebiet, Namibia. The affinities of the new taxon lie with Titanohyracidae, but its dental morphology is significantly divergent from that of other taxa of the family to warrant the

creation of the new genus *Rupestrohyrax*, of which the type species is *R. palustris*.

This new genus extends the range of the family 6000 km south of its previously known Eocene-Oligocene distribution.

This new taxon augments the Palaeogene representation of Hyracoidea in Namibia

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to two genera in two families, Titanohyracidae from the Bartonian Eoridge locality, and Namahyracidae, a new family from the Lutetian Black Crow site, defined herein. Two North African genera (*Seggeurius* Crochet, 1986 and *Dimatherium* Barrow *et al.* 2010) join *Namahyrax* in the new family.

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