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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

Dr Martin Pickford[1,2] and Dr Brigitte Senut[2]

[1]Collège de France, and [2]Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris

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Hyracoidea from the Early Miocene of the Northern Sperrgebiet, Namibia

Martin Pickford
Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS,
Case postale 38, 57, rue Cuvier, 75005, Paris
e-mail : pickford@mnhn.fr

Hyracoid fossils are rare in the Early Miocene fluvio-paludal deposits of the Northern Sperrgebiet. The commonest species is *Prohyrax tertiarius*, represented by 19 specimens, whilst the new species *Afrohyrax namibensis* (140% the size of *A. championi* from East Africa) is known by two fossils.

Newly collected material attributed to *Prohyrax tertiarius* from Langental, Grillental and Elisabethfeld, reveals interesting information about the deciduous dentition of the species as well as adding to the known morphometric variation of the permanent teeth. It appears that the family Pliohyracidae (*sensu stricto*) originated in Southern Africa and then spread northwards during the late Middle Miocene, first into tropical and northern Africa, and then into Eurasia, where it eventually colonised the mid-latitudes of the continents from Spain in the west to China in the east.

Introduction

Hyracoids have been found at three localities in the Northern Sperrgebiet, Langental (the type locality of *Prohyrax tertiarius*), Grillental and Elisabethfeld. The NPE recovered several new specimens which throw a great deal of light on the dental, mandibular and maxillary morphology including that of the deciduous dentition of the commonest species represented at the sites, *Prohyrax tertiarius*. As usual, post-cranial bones of hyracoids are rare, only a single phalanx and a distal humerus having been discovered. A fragmented skull with partial dentition of a large hyracoid found at Grillental 6 is identified as a species larger than *Afrohyrax championi* of East African Early Miocene and basal Middle Miocene localities.

Stromer (1923) created the genus and species *Prohyrax tertiarius* on the basis of a fragment of maxilla with four and a half teeth (P3/ to half M3/ as was realised by Stromer (1923) and not the P4/ to M3/ as reported by Stromer, 1926, plate 41) and an isolated upper incisor. Pickford (1994) mentioned a specimen from Langental housed in the South African Museum, Cape Town, and Pickford *et al*., (1997) described new, more complete, material found at Langental and Elisabethfeld in 1996. Since then several more specimens have been collected, including some partial mixed dentitions.

Systematic descriptions

Order Hyracoidea Huxley, 1869

Family Titanohyracidae Matsumoto, 1926

Genus *Afrohyrax* Pickford, 2004

Type species : *Afrohyrax championi* (Arambourg, 1933)

Diagnosis : Medium sized titanohyracids in which the upper molars possess reduced to absent buccal ribs on the paracone and metacone, lacking lingual spurs on the paracone and metacone, ectoloph relatively upright, buccal wall of metacone oriented at ca 60° to the axis of the tooth row, metastyle weak and low, parastyle and mesostyle strong with pinched in apices and swollen bases, hypocone much smaller than protocone, well developed buccal and lingual cingula, posterior premolars molarised with prominent parastyle and mesostyle, anterior crest (prehypocrista) of hypocone short. Large facial fossa above the anterior cheek teeth positioned anterior to and above the infra-orbital foramen. Mandible with prominent lingual foramen below the posterior molars (at least in some individuals : perhaps a sexually dimorphic character) which enters a voluminous mandibular chamber. Talus with head offset from trochlea.

Species *Afrohyrax namibensis* nov.

Holotype : GT 30'04, fragmentary skull with parts of left and right maxillary cheek teeth (Plates 1, 2).

Locality : Grillental, locality GT 6.

Age : Earl Miocene.

***Derivatio nominis* :** The species name means "from the Namib".

Referred material : Unnumbered mandibular symphysis stored in the South African Museum, collected by L. Greenman at Grillental (GT 6?).

Diagnosis : Species of *Afrohyrax* with approximately 140% greater dimensions than the mean of *A. championi*.

Description :

Note on dental nomenclature in hyracoids : There is general agreement about dental terminology in hyracoid teeth (Meyer, 1978), even if various authors have used different names for cusps, crests, ribs, fos-

settes, and cingula. The disto-lingual cusp in upper molars and premolars is usually called the hypocone (Whitworth, 1954; Rasmussen and Simons, 1988), but some authors prefer to call it the metaconule (Sudre, 1979). The preprotocrista (Meyer, 1978) is called the protoloph by Sudre (1979) and the paraconule by Tabuce *et al*., (2001) and the prehypocrista of Meyer is called the metaloph by Sudre. I here use the terminology proposed by Rasmussen and Simons (1988).

Cranio-dental remains : The skull from Grillental 6 is extremely fragmentary, having largely eroded from the sediments and suffered from extensive sand blasting and salt crystallisation. The two maxillae were still *in situ* in the sediments but were in the friable surface layer rich in salt, and the teeth in particular had already broken into many pieces, even though most of the fragments were in their correct positions relative to each other. The posterior edge of the infraorbital foramen is preserved 20.8 mm above the distal root of the anteriormost tooth in the specimen. The dorso-ventral extent of the margin of the foramen

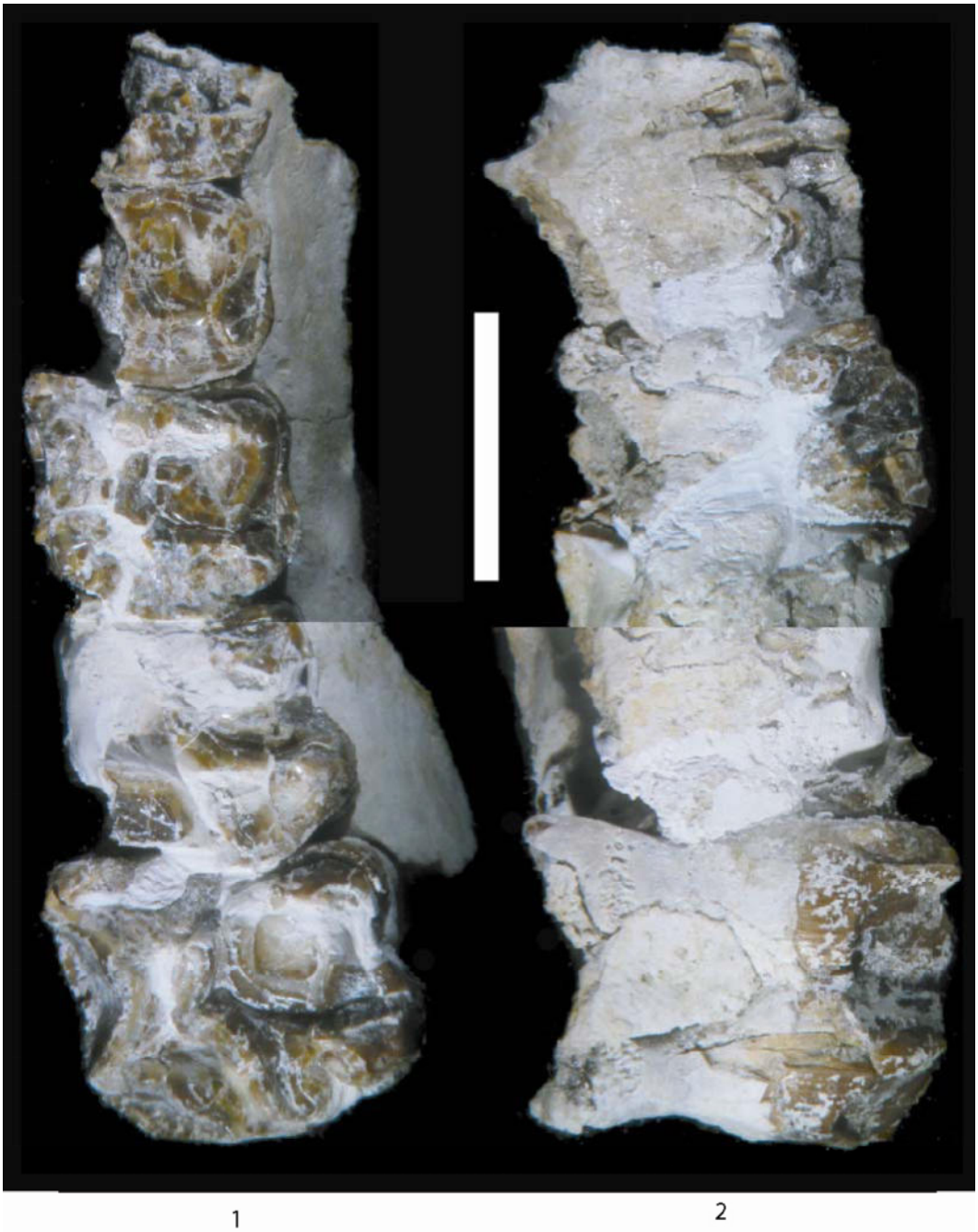

Plate 1. GT 30'04, *Afrohyrax namibensis* sp. nov. from Grillental. (Scale bar : 20 mm).
1. Occlusal view of right P1/-M1/.
2. Buccal view of right maxilla with P1/ to M1/. Note posterior margin of infraorbital fossa above the P1/.

(which is missing its dorsal part due to breakage) is large and suggests that there was a correspondingly large facial fossa, as in *A. championi* and *Megalohyrax niloticus* (Matsumoto, 1926) (Whitworth, 1954). In *Afrohyrax championi* and *Megalohyrax pygmaeus* this fossa lies above the C/-P1/, and on this basis the teeth present in the right maxilla of the Grillental specimen are considered to be P1/ to M1/ (Pl. 1, Fig. 2).

The occipital condyles of the skull were found about 50 cm from the maxillae. Little can be said about the osteology of the specimen, except for the occipital condyles which are of the usual mammalian type, being slightly compressed hemi-cylinders externally for articulation with the atlas, and excavated internally.

Most of the teeth are in poor condition but enough is preserved to reveal the generic affinities of the species. The premolars are in advanced wear, leaving little in the way of structures that can be interpreted, except for the lingual side which shows the presence of a strong cingulum. Occlusally there is a groove separating the two lingual cusps from each other, and a valley separates the lingual cusps from the buccal ones. The position and size of these grooves indicate that the teeth were quadricuspidate, with an undulating w-shaped ectoloph, a large protocone with an anterior extension which reaches the mesial edge of the crown, and a smaller hypocone, also endowed with a short anterior ridge, the prehypocrista. The P3/ has most of the ectoloph preserved, but damaged (Pl. 2, Fig. 2), and one can make out the remnants of a parastyle and mesostyle where the enamel has flaked off. The buccal surface of the paracone is sub-parallel to the long axis of the tooth row. There is a prominent buccal cingulum, and the metacone is angled at about 30° to the long axis of the tooth row. There is a well defined cingulum on the mesial and lingual sides of the protocone which extends distally as far as the hypocone, thereby closing off the lingual end of the median transverse valley.

What remains of the P4/ is similar to the P3/ save for the more oblique orientation of the buccal surface of the metacone relative to the tooth row A reduced metastyle is preserved in the P4/. Like the premolars in front of it, it has four roots.

The M1/ is less worn than the premolars and is relatively well preserved, lacking minor parts of the protocone and paracone and small flakes of enamel on the protocone and hypocone (Pl. 2, Fig. 1). The ectoloph is markedly w-shaped with strongly developed but apically pinched parastyle and mesostyle and a weakly developed metastyle which is located almost in the centre line of the tooth. There are no signs of spurs on the lingual sides of the paracone and metacone. There is a well developed buccal cingulum which passes round to the distal surface of the tooth. This cingulum rises apically at the parastyle, mesostyle and metastyle. The paracone is positioned near the buccal margin of the crown, its buccal surface being almost vertical and sub-parallel to the toothrow. It has no sign of a 'rib' (buccal fold) running rootwards from its apex such as characterise chalicothere teeth and many other hyracoid teeth. In contrast the apex of the metacone is lingually positioned, being almost in the midline of the tooth, and as a consequence its buccal surface is oriented at almost 60° to the axis of the toothrow (ie it faces almost distally). The protocone is voluminous and positioned more distally than the paracone and is bordered mesially by a prominent cingulum. It has a low, rounded crest directed distally into the median transverse valley but the preprotocone crista is poorly developed. The hypocone is appreciably smaller than the protocone and has a concave anterior outline due to the presence of an anterior crest (prehypocone crista) that runs towards the base of the metacone, but stops short at the junction of the antero-posterior and median transverse valleys. This crest forms a positive relief feature in the antero-posterior valley, such that, with wear, the distal part of the valley becomes separated from the anterior part, thereby forming a posterior fossette in the centre line of the tooth. This fossette is not homologous to the fossette formed at the distal base of the metacone where the distal metacone spur curves backwards to join the distal cingulum. In the latter case there are two distal fossettes, side by side. The median transverse valley is curved and is blocked at its lingual end by a cingulum, and buccally it forms a re-entrant angle between the paracone and metacone, opposite the mesostyle. The antero-posterior valley which separates the buccal cusps from the lingual ones is deep and has a re-entrant angle which partly separates the paracone from the metacone. There are four roots which develop several small irregular apophyses at their apices. On the M1/ there is a prominent distal interstitial wear facet caused by abrasion against the M2/. The M2/ is dam-

Table 1. Measurements (in mm) of the teeth of *Afrohyrax namibensis* from Grillental 6. (e - approximate measurement).

Tooth	Length	Breadth
Right P1/	12.8e	14.6e
Right P2/	16.0	17.2e
Right P3/	17.9	21.0
Right P4/	19.3	21.0e
Right M1/	24.8	25.6
Left P3/ roots	15.5e	15.0e
Left P4/	18.4	22.0e
Left M1/	--	24.4e
Right P1/-P4/	65	--

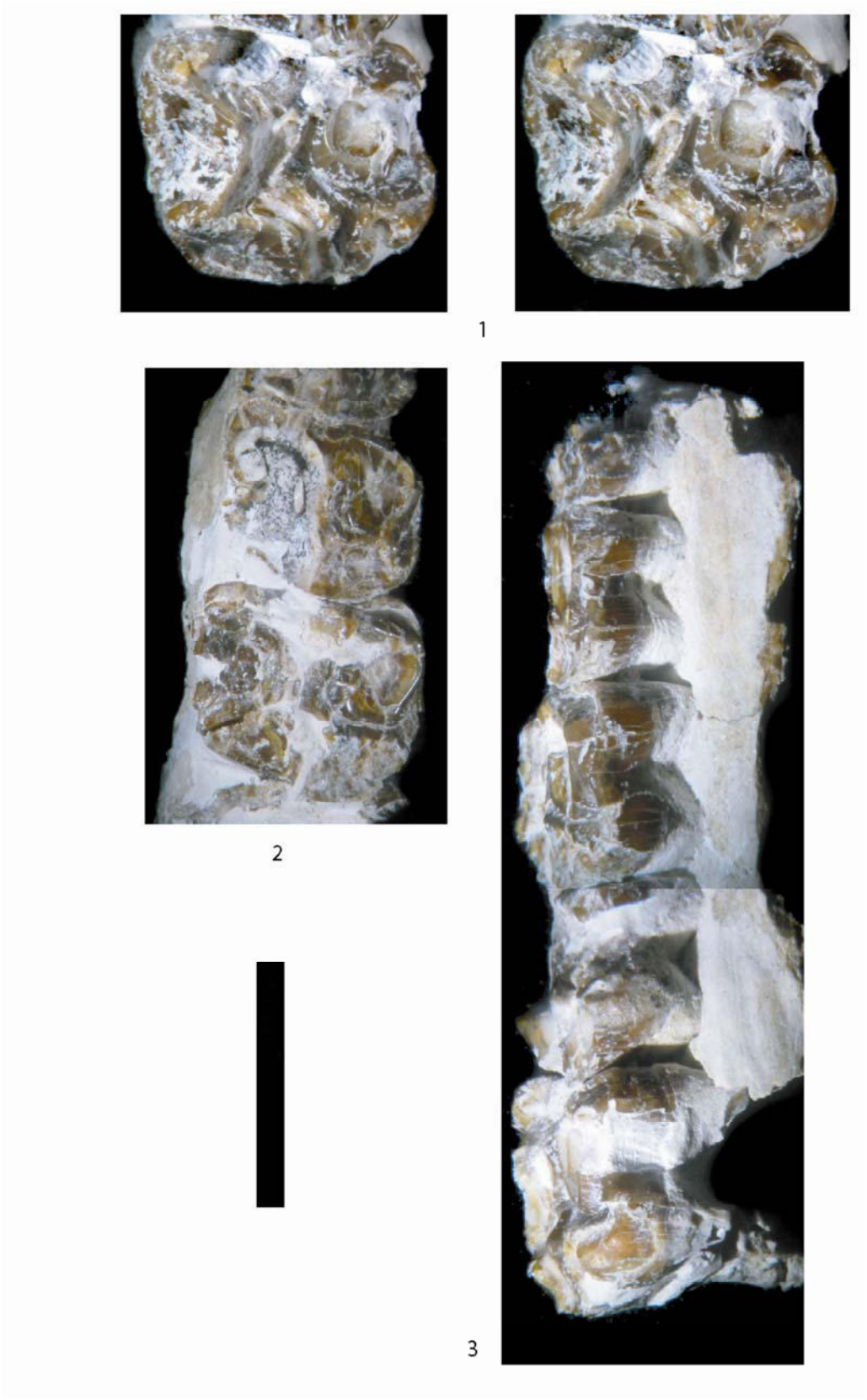

Plate 2. GT 30'04, *Afrohyrax namibensis* sp. nov. from Grillental. (Scale bar : 20 mm).
1. Right M1/, stereo occlusal view.
2. Right P2/ to P3/, occlusal view.
3. Lingual view of right maxilla with P1/ to M1/.

aged, but parts of the paracone and protocone are preserved which show that it was larger than the M1/.

The mandibular symphysis is severely wind-eroded and has only the roots of the anterior teeth and part of the left ramus preserved. The symphysis is anteroposteriorly elongated (ca 34-35 mm) and robust (9.6 mm labio-lingual thickness). Little can be said about this specimen save for the fact that it is appreciably larger than specimens of *Prohyrax tertiarius*. As such it is referred to *Afrohyrax namibensis*, despite its drawbacks as a specimen.

Discussion : The specimen GT 30'04, represents a medium-sized titanohyracid, of which the closest morphological affinities are with the species *Afrohyrax championi* from various sites in Kenya (Whitworth, 1954). Particular resemblances occur in the dentition and in the presence of an enlarged infraorbital foramen indicating the probable occurrence of a large facial fossa above the anterior cheek teeth. The buccal and lingual cingula are more strongly developed in the Namibian specimens, but apart from that the two species are morphologically close, the main difference being one of dimensions.

The Grillental specimen is approximately 140% of the size of the mean of material from Kenya attributed to *A. championi* as shown in tables 3 and 4 based on data published by Whitworth (1954) and the author's own measurements, and for this reason it is referred to a new species of *Afrohyrax*. The specimen does not belong to *Bunohyrax* or *Geniohyus* which have more inflated styles in the upper cheek teeth and ribs on the paracone and metacone. It differs from *Titanohyrax* which has the outer surface of the metacone of the molars sub-parallel to the axis of the toothrow, unlike the strongly angled condition in the Grillental fossil. Furthermore, the mesostyle of the premolars is not as well developed as it is in *Titanohyrax* (Matsumoto, 1926). It differs from *Saghatherium* species by its considerably larger dimensions as well as by its dental morphology (lack of spurs on the paracone and metacone, among other features).

This is the first record of the family Titanohyracidae from southern Africa, but the genus *Afrohyrax* is known as far north as the Arabian Peninsula where *A. championi* has been recorded from Al-Sarrar (As-Sarrar) (Thomas *et al*., 1982).

Matsumoto (1926) extended the pioneer work on *Megalohyrax* from the Fayum by Andrews (1903, 1906) and Schlosser (1911), recognising 5 species. The length of P1/-P4/ in the type specimen of *A. namibensis* is 65 mm which is close to the species *Megalohyrax minor* from the Fayum, Egypt (Matsumoto, 1926), smaller than *M. eocaenus* and larger than *M. niloticus*, *M. suillus* and *M. pygmaeus* (Table 3).

Taxonomic status of East African and Namibian *Afrohyrax*

Comparison of the Kenyan and Namibian fossils attributed to *Afrohyrax* indicate that they do not belong to *Megalohyrax* as thought by Whitworth (1954), nor do they fit into *Pachyhyrax* as concluded by Meyer (1978).

Meyer (1978) argued that the Fayum, Egypt, mandibles attributed to *Megalohyrax* were wrongly classified, and should be identified as *Pachyhyrax*. There are major differences in the slope of the ectoloph in the upper molars in *Megalohyrax* and *Afrohyrax* (more inclined in the Fayum species, more

Table 2. Ranges of metric variation (in mm) of the upper cheek teeth of *Afrohyrax championi*, based on data in Whitworth (1954).

Tooth	Length (range)	Breadth (range)
P1/	9.5 - 10.7	9.3 - 9.8
P2/	11.1 - 11.4	11.0 - 12.3
P3/	11.0 - 11.8	12.5 - 14.3
P4/	13.1 - 15.5	14.0 - 16.0
M1/	15.2 - 18.6	16.9 - 19.0
M2/	17.3 - 19.5	18.7 - 20.8

Table 3. Length of P1/-P4/ (in mm) in various species of *Megalohyrax* (from Matsumoto, 1926 and own measurements).

Species	Length P1/-P4/
Megalohyrax eocaenus	75
Megalohyrax minor	63
Megalohyrax niloticus	54
Megalohyrax suillus	44 (p/1-p/4)
Megalohyrax pygmaeus§	35.5
*Afrohyrax championi**	45.8, 47.2
Afrohyrax namibensis°	65

§ This species was classified in *Pachyhyrax* by Meyer (1978)
* own measurements of two specimens in the Natural History Museum, London (M 21294, M 21295)
° own measurement

Table 4. Comparison of length of ectoloph of M1/ and length of upper premolar row (in mm) of M1/ in *Afrohyrax championi* and *Afrohyrax namibensis*.

Specimen	Length of ectoloph M1/	% *A. championi* mean	Length P1/-P4/	% *A. championi* mean
M 21294	17.5	104%	45.8	98%
M 21295	16.1	96%	47.2	102%
GT 30'04	24.8	147%	65	140%

upright in the Kenyan and Namibian ones), and the rear loph of the premolars of *Megalohyrax eocaenus* is reduced in mesio-distal length relative to the anterior loph, whereas in *A. championi* the premolars are more molarised.

There are major dental differences between the Kenyan and Namibian hyracoids on the one hand and *Pachyhyrax* on the other, as was shown by Meyer (1978), including the lack of lingual spurs on the protocone and metacone in the former, the more upright ectoloph, the relatively reduced hypocone and other features listed in the diagnosis above.

In their classifications, Whitworth (1954) and Meyer (1978) appear to have been heavily influenced by the presence of a large lingual foramen in the mandible leading into a mandibular chamber. Whilst this is an important feature, it is only one character (probably sexually dimorphic) among many that reveal that the Palaeogene genera on the one hand and those from the Neogene of East and Southern Africa on the other, are quite divergent. The mandibular foramen and chamber indicate that the various genera could well belong to the same suprageneric grouping, and it may be necessary when more evidence is available, to erect a subfamily within Titanohyracidae.

Family Pliohyracidae Osborn, 1899
Genus *Prohyrax* Stromer, 1923
Species *Prohyrax tertiarius* Stromer, 1923

Holotype : Upper jaw with P3/ to half M3/ (Stromer, 1926, figs 33a,b)

Hypodigm : From Langental - SAM PQN 116, right maxilla with dM2/-dM4, M1/ stored in the South African Museum, Cape Town (Pickford, 1994); LT 393'96, left mandible with abraded teeth; LT 147'98, symphysis with part of right ramus, edentulous; LT 242'99, left M3/; LT 244'99, right mandible with m/1-m/3 (Pl. 3, Fig. 7); LT 35'03, right mandible and symphysis with m/2 (Pl. 3, Fig. 10); LT 245'99, right upper premolar; LT 34'00, left I1/ (Pl. 3, Fig. 6); LT 36'03, left maxilla with P1/-P2/ (Pl. 3, Fig. 5); LT 52'03 and LT 157'03, fragmented left maxilla with mixed dentition; LT 53'03, right maxilla with dM2/ to dM4/ (Pl. 3, Fig. 1); LT 104'04, left maxilla with P2/-M1/ and front half of M2/; LT 130'04, left mandible with p/4, m/1 and front half of m/2 in crypt; LT 65'06, right maxilla fragment with P4/.
From Elisabethfeld - EF 42'93, second phalanx and parts of upper and lower deciduous dentition; EF 43'93 series of cheek teeth (Pl. 3, Figs 2-5, 8-9, 11-13); EF 17'94, right maxilla with M2/-M3/; EF 103'94, right mandible with p/2-m/3.
From Grillental - GT 87'96, distal humerus from Grillental 1.

Morphological descriptions
Maxilla. The maxilla of *Prohyrax tetiarius* is poorly represented in the available sample. The most remarkable aspect of the bone is the presence of a horizontal groove immediately above the roots of the deciduous molars and permanent premolars. In LT 36'03 it is clearly preserved above the P1/-P2/, the apices of the roots even showing through the bone as a result of alveolar dehiscence (Pl. 3, Fig. 5). In LT 53'03, the groove is well developed and courses above the dM2/-dM3/ entering the maxilla in a large foramen above the anterior end of the dM4/ (Pl. 3, Fig. 1). In LT 391'96 it runs forwards from its foramen above the anterior end of P4/ and fades out before reaching the level of the P1/. In LT 104'04 it courses above the premolars as far back as P3/ and then enters the infraorbital foramen. The morphology and position of this groove is similar to that in the larger species *Prohyrax hendeyi* from Arrisdrift. In the latter species there is a second, larger foramen located above the one described herein, and separated from it by a low, rounded, horizontal ridge of bone. None of the specimens of *P. tertiarius* preserves this part of the maxilla.

Above the molars, the maxilla possesses well developed sinuses, as seen in LT 391'96.

Upper dentition.
Deciduous upper teeth. Maxilla LT 53'03 possesses three milk teeth. Judging from the position of the facial groove and from their size, the teeth present are the dM2/-dM4/. All these teeth have strong styles on the ectoloph, thereby differing from permanent premolars which usually have weak styles, and in this the milk teeth more closely resemble permanent molars. The dM4/ in particular could be mistaken for a permanent molar. The dM2/ and dM3/ are like small versions of permanent molars except for the presence of an additional, enlarged style at the anterior end of the ectoloph which is placed slightly forwards of the antero-buccal cusp. This style is particularly large in the dM2/. All these teeth have sharp but low buccal cingula.

LT 157'03 is a fragmented maxilla with mixed dentition. The deciduous teeth preserved are the dM1/-dM4/, while the permanent teeth represented are the P2/ and the M1/. The dM1/ and dM2/ are deeply worn so little can be said about their morphology, but the dM3/ and dM4/ are well preserved and are similar to those in LT 53'03.

EF 43'93 is a collection of deciduous upper and lower teeth found together, possibly representing a single individual (Pl. 3). The dM2/ has weaker styles than those developed in LT 53'03, and the anterior one is prolonged mesially, imparting a trapezoidal occlusal outline to the tooth. The dM3/ and dM4/ are close in morphology to those in LT 53'03.

Permanent upper dentition. LT 34'00 is a left upper central incisor. It has a flat wear facet lingually that extends about 9 mm from base to tip. The section of the crown is triangular with a rounded anterior edge. There is enamel only on the mesial and distal sur-

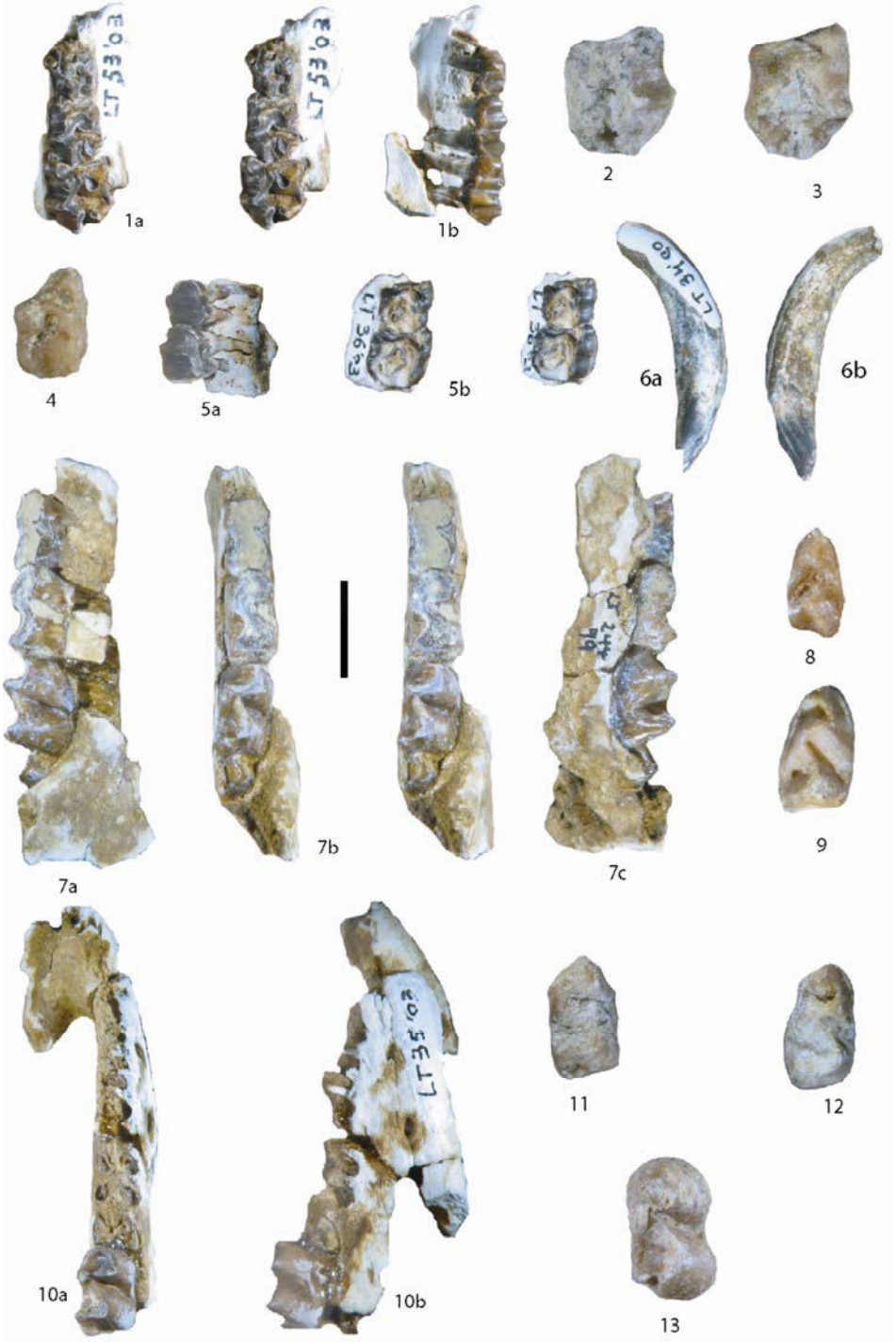

Plate 3. *Prohyrax tertiarius* from the Northern Sperrgebiet (scale 1 cm).

1. LT 53'03, right maxilla with P4/-M2/, a) stereo occlusal, b) buccal views.
2. EF 43'93, left dM3/, occlusal view.
3. EF 43'93, left dM4/, occlusal view.
4. EF 43'93, left dM2/, occlusal view.
5. LT 36'03, left maxilla with P3/-P4/, a) buccal, b) stereo occlusal views.
6. LT 34'00, upper central incisor, a) distal and b) mesial views.
7. LT 244'99, right mandible with m/1-m/3, a) buccal, b) stereo occlusal, c) lingual views.
8. EF 43'93, right dm/1, occlusal view.
9. EF 43'93, right dm/2, occlusal view.
10. LT 35'03, right mandible and symphysis, with m/2, a) occlusal, b) buccal views.
11. EF 43'93, right dm/3, occlusal view.
12. EF 43'93, right dm/4, occlusal view.
13. EF 43'93, right p/4 or m/1, occlusal view.

faces, the lingual side being devoid of enamel, either due to wear or to non-deposition. The mesial surface is flatter than the distal one. The root is 18 mm high and curves evenly, tapering gradually towards its tip, the pulp canal being open at the time of death.

Descriptions of the upper cheek teeth of *P. tertiarius* found up to 1996 are given in Pickford *et al,*, 1997. LT 242'99 is an unworn third upper molar lacking the anterolingual cusp. The lingual side of the tooth is brachyodont (4.3 mm from cervix to the apex of the distolingual cusp) whereas the buccal cusps are considerably more hypsodont (9.6 mm from cervix to antero-buccal cusp apex) and curved. There is a third lobe distally which is bifurcate, forming a small third, distal fossette on the buccal side of the crown. In other specimens, such as LT 391'96, this bifurcation is weaker, and the distal fossette is reduced in size and depth.

LT 104'04, a left maxilla with three premolars, M1/ and the mesial half of M2/ has a prominent facial groove above the premolar row as in other specimens, with the infraorbital foramen emerging from the maxilla above the rear of P3/. The only remarkable point about the cheek teeth which are in medium wear, is the greater than usual development of the buccal cingulum on all the teeth.

Mandible. None of the mandibles of *P. tertiarius* is complete, but there are two specimens with symphyses and one with much of the ventral border of the jaw. There are no signs of buccal or lingual fossae in any of the specimens. Mental foramina occur below the p/3 and p/4 in the lower third of the mandible. The symphysis is solidly fused in the available specimens.

Lower dentition.

Deciduous lower teeth. Deciduous lower teeth of *P. tertiarius* are preserved in EF 43'93, associated with some upper milk teeth (Pl. 3). The teeth present are here interpreted to be the dm/1-dm/4 and the p/4 or m/1. Like permanent premolars the crescentids have a sharp angulation buccally which differs from the more evenly curved crescentids of the permanent molars. Unlike premolars, the deciduous molars are more elongated with the anterior cristid and hypoconulid being separated further from the main cusps than they are in permanent teeth. They possess buccal cingula, as do the premolars.

Permanent lower teeth. Descriptions of the lower dentition of *P. tertiarius* found up to 1996 are provided by Pickford *et al*., (1997). Since then some additional pieces have been recovered including a mandible with three molars. LT 244'99 is a right mandible fragment with m/1-m/3 (Pl. 3, Fig. 7). The m/1 is deeply worn but still shows the two crescent shaped lophs and a buccal cingulum restricted to the median valley. The m/2 is half worn. The m/3 is only lightly worn, with talonid completely untouched by wear as it is still in the process of erupting from its alveolus. The first two lophs consist of crescents which are concave lingually. The anterior branch of the first crescent terminates in the midline of the tooth from which a low, sharp cingulum descends rootwards both buccally and lingually. The posterior arm of the anterior crescent ends on the lingual side of the crown where it meets the anterior branch of the second crescent, which is however, positioned slightly buccally to the termination and a bit lower than it. The rear branch of the second crescent ends near the lingual edge of the tooth. The hypoconulid forms a third crescent, but it is buccolingually narrower and is appreciably lower than the two anterior crescents. Its anterior branch terminates in the midline of the tooth, whilst its posterior branch ends lingually.

Table 5. Measurements (in mm) of the upper teeth of *Prohyrax tertiarius* from the Northern Sperrgebiet.

Catalogue Number	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 52'03	dM1/	4.5	3.7
	dM2/	5.8	5.3
	dM3/	7.4	6.4
	dM4/	8.0	6.3
	P2/	5.7	5.3
	M1/	9	8
LT 53'02	dM2/	5.1	4.5
	dM3/	6.1	5.1
	dM4/	7.5	6.3
SAM PQN 116	dM2/	6.0	5.4
	dM3/	6.8	6.3
	dM4/	8.1	7.5
	M1/	9.7	8.8
EF 42'93	dM2/	5.5	4.2
	dM3/	6.1	5.3
	dM4/	7.5	6.1
LT 34'00	I1/	4.1	5.6
LT 36'03	P1/	4.7	4.9
	P2/	5.4	5.8
LT 245'99	P1/	5.1	--
LT 391'96	C1/	4.7	3.7
	P1/	4.8	5.0
	P2/	5.2	5.6
	P3/	6.3	6.5
	P4/	7.6	8.2
	M1/	9.5	8.9
	M2/	10.7	10.0
	M3/	13.4	11.3
LT 392'96	C1/	4.2	4.2
	P1/	5.3	5.0
	P2/	5.5	5.7
	P3/	6.6	--
LT 395'96	P4/	7.7	8.4
	M1/	9.0	8.7
	M2/	10.3	9.8
	M3/	--	11.3
EF 17'94	M1/	9.2	8.3
	M2/	9.9	10.0
LT 242'99	M3/	16.0	10.1
LT 104'04	P2/	5.4	5.9
	P3/	6.8	7.3
	P4/	6.6	7.7
	M1/	9.1	9.4
	M2/	--	11.5
LT 65'06	P4/	6.8	7.4

LT 130'04 is a fragment of left mandible with lightly worn p/4 and m/1 in occlusion and the anterior loph of m/2 in its crypt. The most notable point about the specimen is the well developed hypoconulid in m/1, which is usually worn away in other specimens.

The Elisabethfeld mandible described by Pickford *et al*., (1997) shows a similar wear gradient to the specimen from Langental. Thus *Prohyrax* has a marked differential wear gradient in the lower cheek teeth, with the first molar wearing almost flat before the third molar has completed its eruption.

Table 6. Measurements (in mm) of the lower teeth of *Prohyrax tertiarius* from the Northern Sperrgebiet.

Catalogue number	Tooth	Mesio-distal length	Bucco-lingual breadth
EF 42'93	dm/1	5.5	2.7
	dm/2	5.2	2.8
	dm/3	6.3	3.7
	dm/4	6.7	3.9
	p/4 or m/1	7.0	4.2
EF 103'94	p/2	5.3	3.6
	p/3	6.0	4.5
	p/4	6.4	5.1
	m/1	8.0	5.5
	m/2	9.3	5.7
	m/3	14.7	6.1
LT 393'96	p/4	5.8	--
	m/1	7.9	5.4
LT 244'99	m/1	7.8	5.0
	m/2	9.4	5.7
	m/3	14.6	5.6
LT 35'03	m/2	9.4	5.4
LT 130'04	p/4	6.6	4.2
	m/1	7.7	5.0
	m/2	--	5.0e

Post-cranial skeleton.

As is usual at most localities where hyracoids have been recorded, in the Sperrgebiet their post-cranial bones are rare, the only specimens found being a distal humerus and a second phalanx.

Humerus. The distal humerus, GT 87'96 from Grillental 1, is badly sand blasted but what remains is similar morphologically to material from Arrisdrift where this bone is well represented, but the specimen is smaller, the distal width being 13.5 mm compared with those of *P. hendeyi* which range in breadth from a minimum of 18.2 to a maximum of 25.7 mm, with a mean of ca 21 mm.

Phalanx. EF 42'93, is a second phalanx similar to those of other hyracoids. The articular surfaces are simple cylinders. The distal end is only slightly narrower than the proximal end but is appreciably deeper from dorsal to volar than the distal end of the diaphysis.

Discussion : The new remains of *Prohyrax tertiarius* from the type locality (Langental) and other sites (Elisabethfeld, Grillental) in the Sperrgebiet provide useful information about this hitherto poorly known species. Stromer (1923, 1926) had only an upper incisor and a fragment of maxilla with four and a half teeth in it, which, in 1926, he interpreted as P4/-M3/, but which in fact contains the P3/-M3/, the last tooth lacking its distal half. Pickford (1994) described and provided measurements of a juvenile maxilla from Langental stored in the South African Museum (SAM PQN 116). Pickford *et al*., (1997) described several more complete maxillary and mandibular fragments which not only resolved the issue of what teeth were present in the holotype, but also showed the close relationship of this species to *Prohyrax hendeyi*, a larger and much better preserved species from Arrisdrift, Namibia, represented by almost all parts of the skull, mandible and skeleton.

The collections made since 1997 contain elements of the deciduous dentition which were poorly or not known previously, and these confirm the close relationship between the Langental and Arrisdrift species. The only significant differences between them are metric, their morphological features being virtually identical. In the Pliohyracidae, to which *Prohyrax* belongs, there was a gradual increase in body size with time, from the Early Miocene to the Pliocene and Pleistocene. *Prohyrax tertiarius* is the earliest and smallest known Neogene member of this family.

Churcher (1956) considered that the extant genus *Procavia* was derived directly from *Prohyrax*, most probably because both are small. The newly available material of *P. tertiarius* suggests that this is unlikely, since unlike *Procavia*, which has a reduced dental formula and not very hypsodont buccal cusps in the upper molars, *Prohyrax* has a complete eutherian dental formula, and the buccal cusps in its upper molars are extremely hypsodont. Furthermore, the M3/ of *Prohyrax* has a third lobe which is bifid distally, whereas *Procavia* has a short M3/ with no third lobe. If there is a relationship between *Prohyrax* and *Procavia*, then it is not a direct ancestor-descendant one, but most probably had some unknown intermediate forms (Hopwood, 1929).

Pickford (2004) described new dental remains of

Table 7. Measurements (in mm) of the second phalanx attributed to *Prohyrax tertiarius*.

Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
EF 42'93	5.2	2.9	2.2	2.3	1.6

Meroehyrax from Uganda, including the first recognised upper teeth of the genus. These specimens reveal that the upper molars of *Meroehyrax* are close morphologically to those of *Saghatherium* on the one hand, and those of Procaviidae on the other. A rather direct evolutionary lineage can be envisaged between *Saghatherium* from the Fayum, Egypt, via *Meroehyrax* from East Africa, to extant procaviids.

Meyer (1978, figure 14.10) attributed a maxilla with two teeth from Loperot, Kenya, (ca 17 Ma) to *Prohyrax* sp. He identified the teeth in the specimen as the first and second molars, but the large difference in size between the teeth suggest that they are in fact the P4/ and M1/. Morphologically the teeth in this specimen do not resemble those of *Prohyrax tertiarius* but are close to those of *Meroehyrax bateae*. The molar in particular is close to specimens from Moroto II, Uganda described by Pickford (2004).

The earliest Procaviidae known are from the Late Miocene of Berg Aukas, Namibia (ca 10 Ma) and Nakali, Kenya (ca 9.5 Ma) and in appearance they are similar to modern hyracoids (Rasmussen *et al*., 1996; Fischer, 1986).

Biogeography and the origins of the Pliohyracidae

The Early Miocene hyracoids of East Africa belong to the families Titanohyracidae, Saghatheriidae and Geniohyidae, with Pliohyracidae in the strict sense of the term being unknown in the tropics until about 12.5 Ma. Thus the family Pliohyracidae seems to have evolved in southern Africa from an unknown precursor, probably a Sagatheriinae, where it survived for more than 10 million years before spreading northwards into tropical and northern Africa at the end of the Middle Miocene (Ngorora, Kenya; Beni Mellal, Morocco; Kairouan, Tunisia). The family subsequently spread into Eurasia where it colonised much of the mid-latitude extent of the continent from Spain in the west to China in the east (Pickford and Fischer, 1987; Pickford *et al*., 1997). All the Eurasian forms are large, some genera such as *Postschizotherium* attaining the size of a rhinoceros. Thus the family Pliohyracidae joins the list of vertebrate lineages that originated in southern Africa and subsequently spread northwards into the rest of the Old World.

Conclusions

A medium-sized titanohyracid from Grillental is the first member of this family discovered in southern Africa. It represents a new species (*Afrohyrax namibensis*) which is about 140% the dimensions of *Afrohyrax championi* from East Africa and the Arabian Peninsula. Previously these Early Miocene titanohyracids were variously classified in the genera *Pliohyrax*, *Megalohyrax* or *Pachyhyrax*, but detailed examination of the cheek tooth morphology reveals that they belong to none of these genera, nor to any other of the known Palaeogene and Neogene hyracoids. The genus *Afrohyrax* was created for them (Pickford, 2004), with the type species *A. championi* (Arambourg, 1933).

The small hyracoid from the Northern Sperrgebiet, *Prohyrax tertiarius*, belongs to a family, Pliohyracidae, that originated in southern Africa, and lived there for several million years before spreading northwards into the rest of Africa, and eventually into Europe and Asia. The pliohyracids grew larger and larger with the passage of geological time, *Prohyrax tertiarius*, the earliest known and smallest species being barely the size of extant *Procavia capensis* (about the size of a rabbit) whereas *Postschizotherium* from the Late Pliocene of China was almost the size of a rhinoceros.

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