Afrohyrax namibensis (Hyracoidea, Mammalia) from the Early Miocene of Elisabethfeld and Fiskus, Sperrgebiet, Namibia

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Abstract: An almost complete skull of *Afrohyrax namibensis* from the Early Miocene green sands at Elisabethfeld, Namibia, and a maxilla from Fiskus, clarify the systematic position of this species of titanohyracid, previously known from a palate and a mandibular symphysis from Grillental. Osteological features of the skull and the dental anatomy accord with the species *Afrohyrax championi* from East Africa and the Arabian Peninsula, but the Namibian fossils are appreciably larger. A summary of world hyracoid distribution is provided and reveals that southern Africa played an important role in the evolution of the order, during both the Palaeogene and Neogene.

Key words: Miocene; Titanohyracidae; Skull; Dentition; Sexual dimorphism; Biogeography.

Introduction

Afrohyrax is a medium-sized genus of titanohyracid hyracoid (dassies, hyraxes) which has been found in Early Miocene deposits of East Africa (Arambourg 1933; Whitworth 1954; Pickford 2004a; Rasmussen & Guttiérez 2010), the Arabian Peninsula (Thomas *et al*. 1982; Pickford 2009) and Namibia (Pickford 2008a) (Fig. 1). The previously available sample of *Afrohyrax namibensis* comprised a palate with parts of the left and right cheek tooth rows (Pickford 2008a). New specimens have been found at two additional sites in the northern part of the Sperrgebiet, Namibia : 1) a skull from Elisabethfeld which is particularly informative, and confirms the generic identity of the species, and 2) a maxilla from Fiskus which is very large, confirming the presence in Namibia of a species distinct from East African *Afrohyrax championi*.

This paper describes and interprets the new large hyracoid specimens from the Early Miocene of Namibia. It complements recent papers on hyracoids from the Sperrgebiet, which in terms of numbers of specimens are dominated by a small species of Pliohyracidae, *Prohyrax tertiarius* Stromer (1922 1926) (Pickford 1994, 2003, 2008a; Pickford *et al*. 2008a) a species which is associated with *Afrohyrax namibensis* in the green sands at Elisabethfeld. The basal Middle Miocene hyracoids of Namibia comprise a large species, *Prohyrax hendeyi*, known from abundant fossils from Arrisdrift and Auchas on the Orange River (Pickford 2003) while some isolated teeth from late Middle Miocene karst infillings at Berg Aukas, in the Otavi Mountainland, represent either a large species of *Prohyrax* or a small species of *Parapliohyrax* (Pickford 1996). Basal Late Miocene breccias at the same site yielded the earliest known procaviid hyraxes, *Heterohyrax auricampensis* (Rasmussen *et al*., 1996).
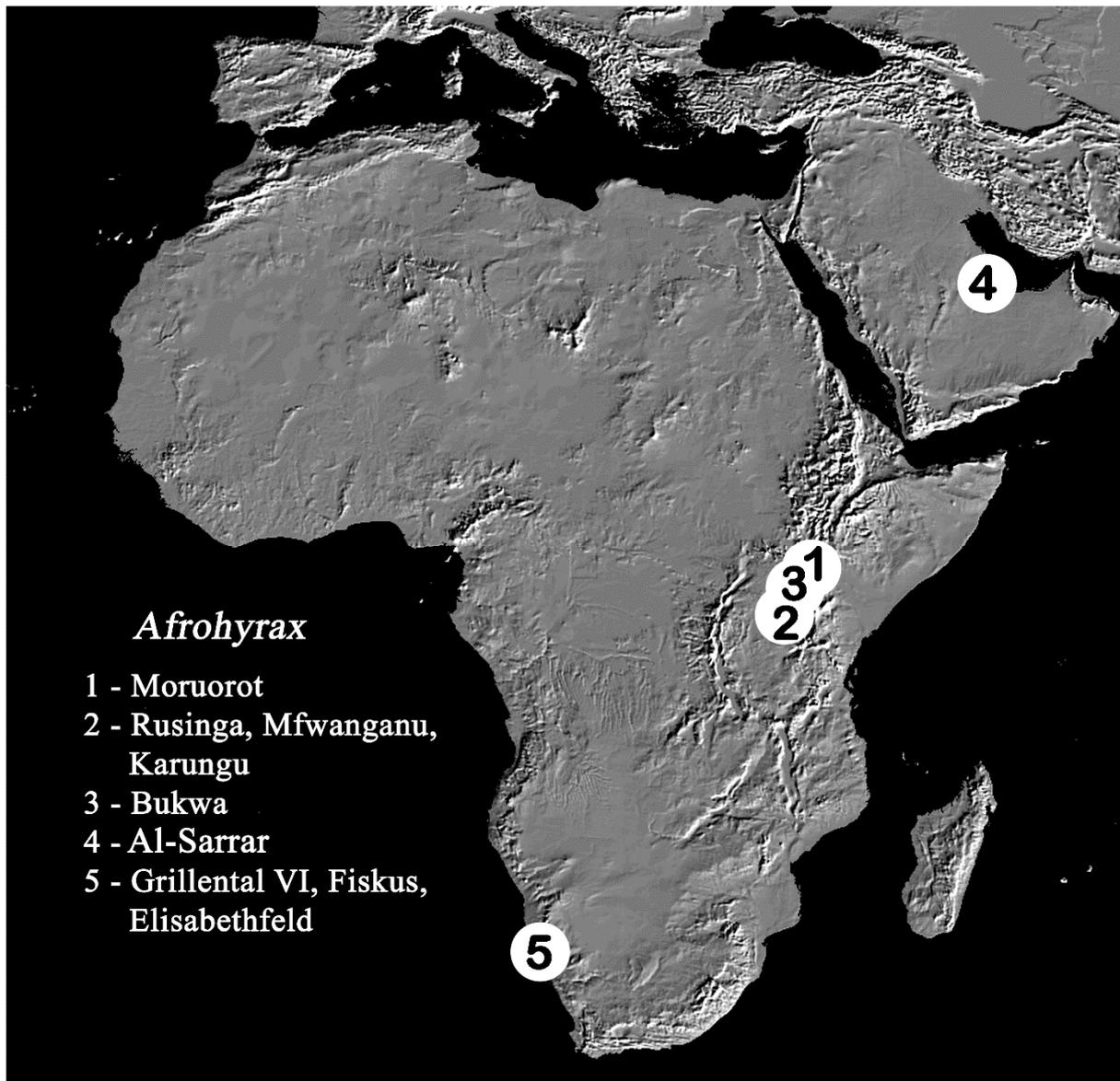
Figure 1. Distribution of *Afrohyrax championi* in East Africa and the Arabian Peninsula, and *Afrohyrax namibensis* in Namibia. Ad Dabtiyah is south of Al-Sarrar.

Institution and locality abbreviations

EF - Elisabethfeld
FS - Fiskus
GT - Grillental
GSN - Geological Survey of Namibia Museum, Windhoek

NHMUK - Natural History Museum, London (register numbers begin with the letter 'M')
SAM - South African Museum, Cape Town (now known as the Iziko Museum)

Cranial and dental nomenclature

Nomenclature of the skull bones follows the system defined by Thewissen & Simons (2001) and Pickford (2003) while cheek tooth nomenclature follows the system defined by Rasmussen & Simons 1988 (Fig. 2).
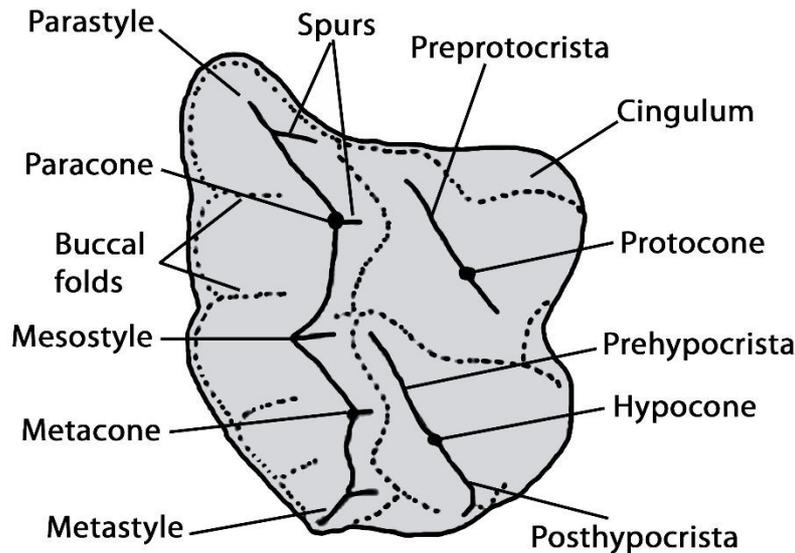
Figure 2. Nomenclature of right upper molar of Hyracoidea.

Systematic Palaeontology

Order Hyracoidea Huxley 1869

Family Titanohyracidae Matsumoto 1926

Genus *Afrohyrax* Pickford 2004a

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

Species *Afrohyrax namibensis* Pickford 2008a

Holotype: GSN GT 30'04, fragment of snout
with incomplete left and right cheek tooth rows.

Type locality: Grillental 6, Sperrgebiet, Namibia.

Age: Early Miocene.

Referred material: SAM unnumbered mandibular symphysis, possibly from Grillental; GSN FS 1'08, right maxilla with damaged C1/-M3/ from Fiskus, Sperrgebiet; GSN EF 10'17, skull, lacking the rear part of the neurocranium, the right I3/, M2/ and M3/, from green sands at Elisabethfeld, Sperrgebiet.

Diagnosis: A large species of *Afrohyrax*, ca 140% larger than *Afrohyrax championi* (from Pickford 2008a).

Description
Cranial osteology
GSN EF 10'17 is a skull without the mandible of a large hyracoid (Fig. 3-6). The specimen is slightly crushed and much of the nuchal area and basicranium are missing. The right premaxilla and the bone between the incisive fissures were displaced in the sediment such that the incisor was close to the right canine, and the rear of the premaxilla close to

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the left central incisor. The displaced parts were relatively easily replaced in their proper position, although there is some residual distortion evident in the reconstruction. The nasals are poorly preserved, but sediment infilling the nasal cavity has preserved part of the profile of the snout.

The better preserved left side of the skull shows the following features. The orbit is positioned far back, the anterior margin being above the mesial loph of the M3/, the rear of the orbit being a few mm behind the rear of the M3/. In front of the orbit there is a long, shallow antorbital fossa, bordered beneath by a strong, straight ridge with a rounded profile (the facial ridge) which is an anterior elongation of the root of the zygomatic arch. Beneath this ridge the maxilla descends steeply towards the alveolar process. Immediately beneath the anterior end of the facial ridge there is a small foramen (infra-orbital foramen) positioned above the P2/. The lateral surface of the premaxilla is deeply concave, forming a large naso-maxillary fossa (or facial fossa) (Whitworth 1954) which is associated with a naso-maxillary foramen (poorly preserved).

Figure 3. Stereo left lateral view of GSN EF 10'17, skull of *Afrohyrax namibensis* from Elisabethfeld green sands (scale : 10 cm).

The ventral margin of the orbit is strongly developed and overhangs to a small degree the malar tubercle of the zygomatic arch. The contribution of the jugal bone to the base of the orbit is exceptionally strong, much more so than in *Procavia*. Indeed it forms a curved platform about 12 mm broad medio-laterally, separated from the more ventrally positioned maxillary floor of the orbit by a distinct step and it extends from the suture with the lacrimal anteriorly as far back as the post-orbital process of the jugal. The rear of the orbit is open, and the post-orbital process of the parietal descends towards the post-orbital process of the jugal bone, but without reaching it.

There are diastemata between the I1/ and I3/, as well as between the I3/ and C1/. The diastemata have raised, beaded edges. The lacrimal is poorly preserved, but part of it

preserved on the left side shows that it was large.

In ventral view, the two central incisors are well separated from each other (ca 16 mm apart). The incisive fissures are mesio-distally elongated (ca 15 mm) and are separated from each other by a robust process of the premaxilla which rises ventrally and anteriorly to form a low, sharp-edged boss between the anterior parts of the two fissures. There is a notch between the anterior ends of the maxillae between the upper central incisors.

Figure 4. Stereo palatal view of GSN EF 10'17, skull of *Afrohyrax namibensis* from Elisabethfeld green sand (scale : 10 cm).

The lingual margins of the two cheek tooth rows diverge at a slight angle from one other from mesial to distal. The alveolar process is tall and the palatine foramen enters the palate opposite the middle of the M1/. The posterior choanae lie slightly behind the rear of the M3/. There is no sign of a palatal fossa or pocket. The temporo-mandibular articular surface (glenoid cavity) is composite, as in *Procavia*, part of it being on the jugal and part on the squamosal. The maxillary recess lies immediately behind the rear of the M3/ and the lower part of the temporal fossa is quite small, increasing in size postero-dorsally (somewhat crushed).

The snout is broadest at the malar tubercle of the zygomatic arch (i.e. immediately beneath the centre of the orbit) and it narrows gently anteriorly and posteriorly. About half way between the lacrimal and the post-orbital process of the jugal, the jugal sends a small crest ventrally (malar tubercle) which walls off a shallow, ventrally facing fossa in the maxilla. This is much as in *Procavia*, but is more exaggerated in *Afrohyrax namibensis*. This

fossa has a smooth floor and lies entirely anterior to the muscle scars where the masseter inserted into the zygomatic process of the maxilla. The masseter insertion scar extends from the rear of the malar fossa backwards almost to the glenoid surface of the temporo-mandibular articulation, narrowing distally as it goes.

Figure 5. Stereo dorsal view of GSN EF 10'17, skull of *Afrohyrax namibensis* from Elisabethfeld green sand (scale : 10 cm).

In dorsal view, the frontal bones are observed to be somewhat concave between the orbits and between the nasals anteriorly and the parietals posteriorly. The parietal ridges converge towards each other distally and meet about 45 mm behind the rear of the orbit. The upper edge of the orbit is sharp and the anterior part is closer to the sagittal plane than the posterior part. Most of the neurocranium is broken, but the upper parts of the parietals are preserved, but yield little information about the morphology and extent of the brain case. Most of the nasal bones are missing, but it is evident that the dorsal profile of the snout rises in front of the frontal table, as in fossils of *Afrohyrax championi* from Kenya (Whitworth 1954).

Being an aged individual, most of the sutures in GSN EF 10'17 are so heavily fused that they cannot be discerned, the only readily observed ones being the inter-premaxillary suture between the incisive fissures and the jugo-maxillary suture in the floor of the orbit.

Dentition

The I1/ is a spatulate tooth with a relatively low crown. The mesial surface of the crown is at right angles to the lingual surface, and the labial surface is convex. The root is elongated and curves upwards and distally, its jugum forming the anterior and superior borders of the facial fossa. There is a prominent wear

facet lingually which was caused mostly by abrasion against the lower i/2.

There is no sign of an I2/ in this specimen. The I3/ is well behind the I1/ and consists of a small ovoid crown posed on a slender root. This tooth is closer to the upper canine than it is to the I1/, and is for this reason interpreted to be the I3/ rather than a distally positioned I2/ (see Whitworth 1954 for discussion about the teeth between the I1/ and the C1/).

The cheektooth row comprises the canine to M3/ with no gaps between the teeth.

The upper canine is in contact with the P1/, and its crown is premolariform (imperfectly so). The deep wear of the occlusal surface prevents details of the crown morphology from being accessed, but there is a lingual cingulum and the rear of the tooth is bucco-lingually broader than its mesial part. The parastyle is clearly formed and is joined to the paracone by a crista. The crown is rotated somewhat with respect to the long axis of the cheektooth row, its buccal surface converging anteriorly towards the diastemal ridge.

Figure 6. Stereo palatal view of GSN EF 10'17, skull of *Afrohyrax namibensis* from Elisabethfeld green sand (scale : 10 cm).

The upper premolars are molariform, but with relatively small hypocones and styles compared to the molars. The P1/ has a tiny hypocone, a large metacone, and subequal protocone and paracone. The lingual sinus has a sharp cingulum extending onto the lingual aspect of the protocone. The parastyle is weak and the mesostyle and metastyle are obsolete, but the crown is deeply worn and these structures could have been present in the unworn condition. In the posterior premolars the styles are prominent occlusally and fade out

towards cervix, and the same may have been the case in the P1/.

The P2/-P4/ are heavily worn, but it is possible to see that the hypocone was slightly smaller than the protocone, and the parastyle and mesostyle were strong and pinched in, whereas the metastyle is weak to absent. The lingual cingulum extends slightly onto the lingual surface of the protocone in all the premolars, and there is a low but sharp buccal cingulum which undulates along the ectoloph, rising occlusally at the styles, and descending

rootwards opposite the main cusps (paracone, metacone).

The M1/ and M2/ are deeply worn but it is possible to observe that the hypocone was smaller than the protocone while the parastyle and mesostyle were strong and inflated, and the metastyle low and sharp. There is a strong but sharp buccal cingulum at the base of the ectoloph, as in the premolars. The M3/ is in medium wear, and thus provides useful morphological information. The parastyle and mesostyle are prominent and inflated, imparting a w-shaped buccal outline to the ectoloph. The paracone and metacone are lingually positioned relative to the styles and are devoid of spurs. The protocone is obliquely oriented and sends a precrista towards the centre line of the tooth, the end of the crista overlapping the lingual part of the paracone. The post-protocrista is directed posteriorly but is rounded and does not encroach on the lingual sulcus (median transverse valley). There is a low but sharp cingulum all along the lingual and mesial side of the protocone. The hypocone is smaller than the protocone and has a precrista that reaches towards the base of the metacone, but does not join it. The post-hypocrista reaches distally where it joins a posterior cingulum which itself extends across the rear of the tooth towards the low metastyle, with a small bulge in the centre, thereby closing off the posterior fovea. The buccal cingulum is thin but sharp.

Table 1. Measurements (in mm) of the upper tooth rows of *Afrohyrax championi* from Rusinga Island (Kenya, 'M' catalogue numbers) and *Afrohyrax namibensis* from Grillental, Elisabethfeld and Fiskus (Namibia) (lb – lingual breadth; ll – labio-lingual diameter; mdl – mesio-distal length) (* I1/-I3/ and I3/-C1/).

Anatomy	M 21294	M 21295	M 21307	M 21296	M 21297	GSN GT 30'04	GSN EF 10'17	GSN FS 1'08
M1/-M3/	49.5	50.0					65.7	76.4
P1/-P4/	45.8	47.0	47 ca			65.0	52.0	66.8
C1/-M3/	104.3	105 ca					120.9	152.0
Diastema I1/-I2/	19.3						33.0*	
Diastema I2/-C1/	26.0						9.0*	
I1/-C1/	45.3						47.6	
I1/ mdl	8.0			9.5	6.7		11.0	
I1/ ll	5.5			6.0	6.3		11.0	
I1/ lb	6.4			6.6	6.6		7.7	

Table 2. Measurements (in mm) of the upper teeth of *Afrohyrax namibensis* from Grillental, Elisabethfeld and Fiskus (Namibia) (blb – bucco-lingual diameter; mdl – mesio-distal length).

GSN GT 30'04 right maxilla	mdl	blb
P1/	12.8	14.6
P2/	16.0	17.2
P3/	17.9	21.0
P4/	19.3	21.0
M1/	--	24.4

GSN FS 1'08 right maxilla	mdl	blb
Upper canine	8.8	8.0
P1/	13.3	13.6
P2/	16.2	16.5
P3/	17.0	19.6
P4/	20.3	23.0
M1/	23.0	--
M2/	24.4	--
M3/	29 .0	--

GSN EF 10'17 snout	mdl	blb
I3/ lt	4.0	3.2
Upper canine (lt : rt)	8.9 : 9.3	7.0 : 7.0
P1/ (lt : rt)	9.9 : 10.7	11.2 : 11.4
P2/ (lt : rt)	12.7 : 12.1	14.0 : 13.6
P3/ (lt : rt)	13.0 : 14.0	15.6 : 16.0
P4/ (lt : rt)	14.5 : 14.6	18.7 : 19.0
M1/ (lt : rt)	19.3 : 20.6	21.6 : 21.7
M2/ (lt)	20.7	23.9
M3/ (lt)	25.0	27.6

GSN FS 1'08 is a right maxilla of a large hyracoid containing damaged C1/-M3/ (Fig. 7). The occlusal surfaces of most of the cheek teeth are badly damaged, only the ectoloph remaining intact. What is preserved of the cheek teeth corresponds closely to the specimen from Grillental 6, both in dimensions and morphology. The specimen is similar in dental morphology to the Elisabethfeld specimen but is larger than it.
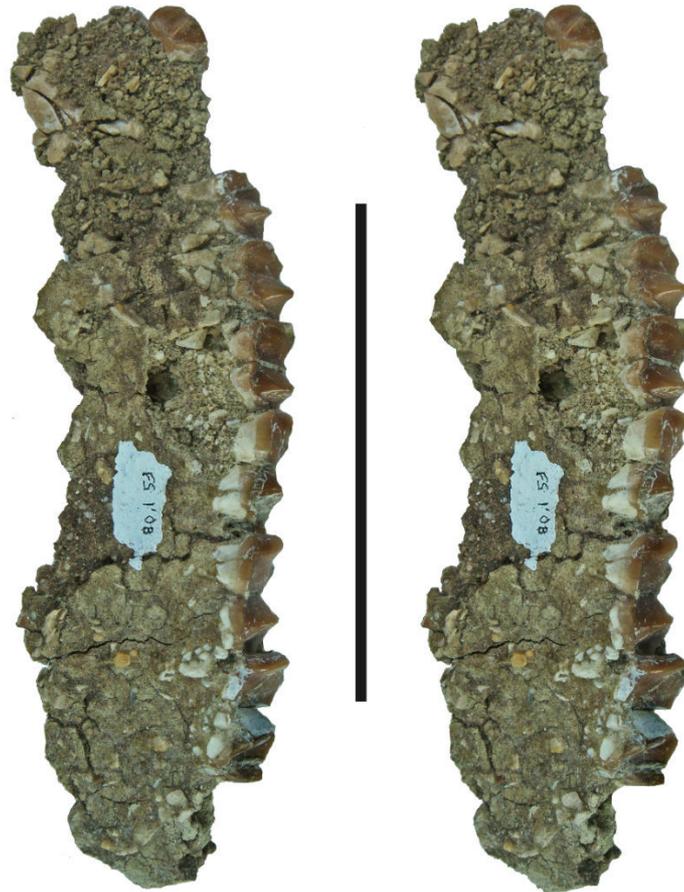

Figure 7. GSN FS 1'08, right maxilla of *Afrohyrax namibensis* containing C1/-M3/ from Fiskus, Sperrgebiet, Namibia, stereo lateral view (scale : 10 cm).

Figure 8. SAM un-numbered mandibular symphysis and part of left ramus of *Afrohyrax namibensis* from Grillental, Sperrgebiet, Namibia, containing the roots of the left and right i/2, right i/3 and c/1, and left premolar roots (damaged) A) lingual view, B) occlusal view (scale : 5 cm).

The wind-eroded mandibular symphysis from Grillental housed in the Iziko Museum, Cape Town, has some coarse sand matrix adhering to it, typical of the grits of Grillental which overlie the green clays (Fig. 8). Little can be said about the morphology of the specimen, but the symphysis is long (ca 40 mm superiorly) and proclive. The root of the tusk-like i/2 reveal that this tooth was large and laterally positioned, with the i/3 distally positioned and separated from the i/2 by a short diastema. There is a short diastema between the i/3 and the small canine.

Discussion

Pickford (2004a) erected the genus *Afrohyrax* for the East African Early Miocene hyracoid variously named in the literature as *Pliohyrax championi*, *Megalohyrax championi* and *Pachyhyrax championi* (Arambourg 1933; Whitworth 1954; Meyer 1978; Rasmussen & Gutiérrez 2010). Subsequently, a fossil similar in morphology to *Afrohyrax championi*, but much larger than it, was found at Grillental 6, Namibia, and was named *Afrohyrax namibensis* by Pickford (2008a). Continued field surveys in the Sperrgebiet have resulted in the collection of additional specimens of this large hyracoid, including a maxilla with cheek teeth at Fiskus, and a snout with most of the dentition from Elisabethfeld. The latter two specimens are described herein.

The Fiskus specimen is as large as the holotype from Grillental 6, whereas the Elisabethfeld specimen is smaller, but is still appreciably larger than any of the East African fossils attributed to *Afrohyrax championi*.

Whitworth (1954) described three skulls of *Afrohyrax championi* from Rusinga, Kenya, along with several mandibles and isolated teeth (Fig. 9-11). He suggested that the morphological variation observed in the shape of the roof of the skull and the form of the upper central incisors represented sexual dimorphism comparable in degree to the differences present in males and females of extant Procaviidae (dassies, hyraxes).
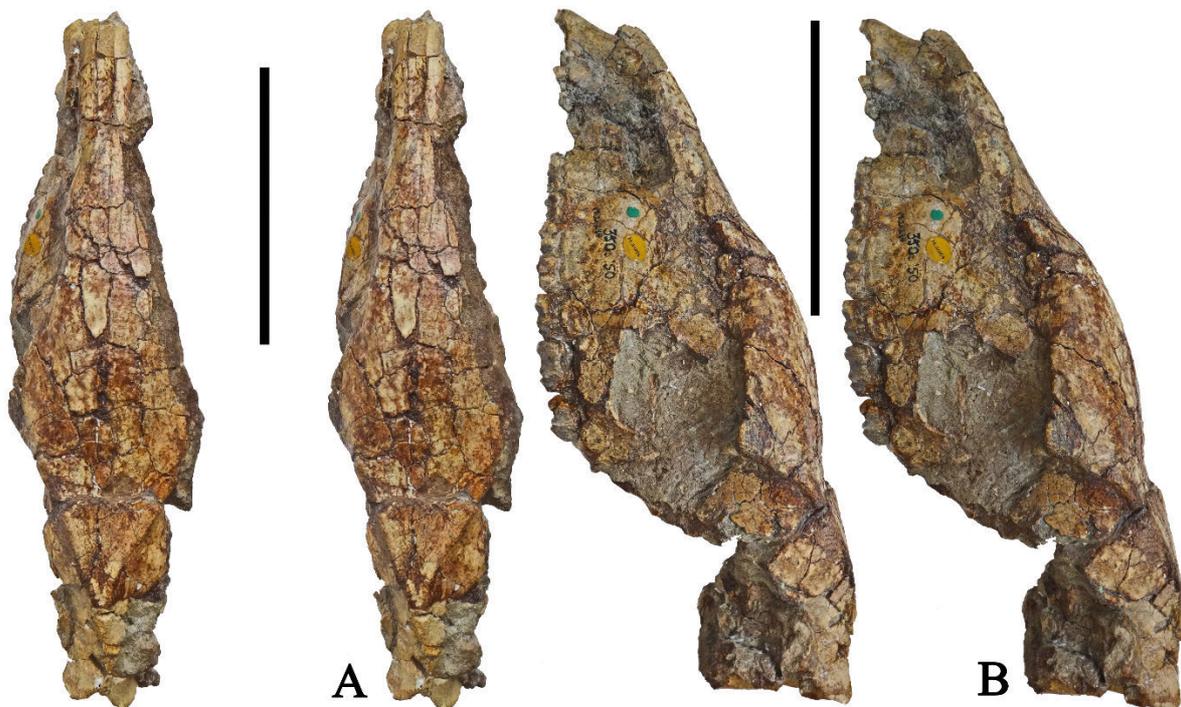

Figure 9. NHMUK M 21294, skull of female individual of *Afrohyrax championi* from Rusinga Island, Kenya, A) stereo dorsal view, B) stereo left lateral view. Note the presence of two fossae, one in front of the orbit, the other deeply impressed into the premaxilla (scales : 10 cm).
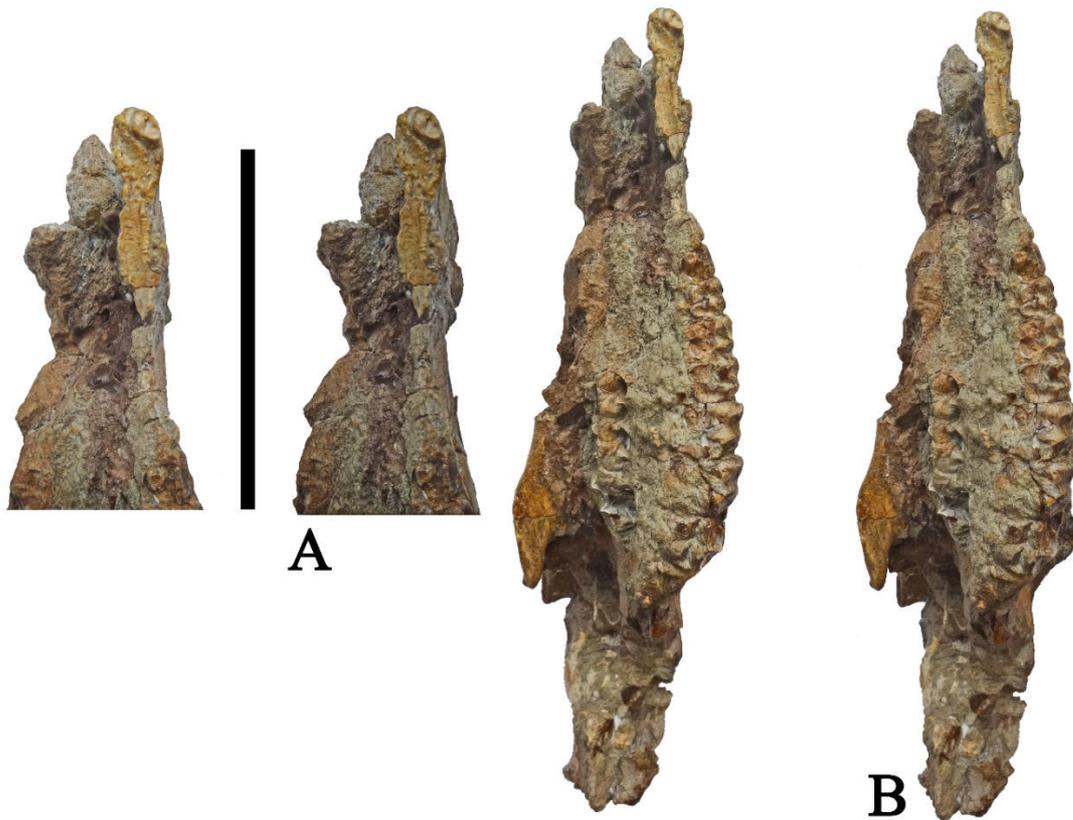
Figure 10. NHMUK M 21294, female skull of *Afrohyrax championi* from Rusinga Island, Kenya, stereo palatal views A) details of left central incisor and diastema to C1/, B) palatal view (scale : 5 cm for A, 10 cm for B).

Overall, the Rusinga fossils show similar facial morphology to that present in the Elisabethfeld specimen, notably a large shallow fossa in front of the orbit and a deeper fossa associated with the premaxilla. The facial ridge is stronger in GSN EF 10'17 than it is in any of the Rusinga fossils (Whitworth 1954). The anterior extremity of the root of the zygomatic arch lies above the front of M2/ in both species but the orbit is slightly further distally positioned in the Elisabethfeld fossil. The Rusinga fossils have a convex profile of the nasals anterior to the orbits, like the Elisabethfeld fossil (damaged but still visible). The slight differences in osteology of the two species do not support a generic separation between them.

Figure 11. NHMUK M 21295, stereo views of partial skull of *Afrohyrax championi* from Rusinga Island, Kenya, A) right lateral view, B) palatal view (scale : 10 cm).

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Sexual dimorphism

Using the dental criteria defined by Whitworth (1954) (male upper central incisor tusk-like, recurved and sharply pointed : female upper central incisor large, pro-odont with shovel-like tip) the spatulate morphology of the upper central incisors of the Elisabethfeld specimen indicate that it is likely to represent a female of the species. In contrast, according to the osteological criteria listed by Whitworth (1954) (males with strong development of temporal and sagittal crests : females with weaker crests) the concave morphology of the cranial table would suggest that the Elisabethfeld specimen is a male.

However, the strength of the temporal and sagittal crests probably varies individually and ontogenetically, and as such, the dorsal

profile of the cranium is not as reliable a criterion for determining the sex of an individual as the form of the upper central incisor is. The Elisabethfeld specimen possesses deeply worn cheek teeth, and would thus be expected to possess more strongly developed temporal and sagittal crests than younger individuals of the species would. Thus, despite the supposedly masculine aspect of the cranial table, the specimen most likely represents a female on the basis of its upper central incisor morphology. The sex of the other two specimens from the Sperrgebiet cannot be determined because they lack the parts that can be used to determine the sex, but on the basis of their greater dimensions it is possible that both represent males

Taxonomy and the representation of fossil dassies at Elisabethfeld

Even though the Elisabethfeld specimen is appreciably smaller than the material from Fiskus and Grillental 6, it is significantly bigger than any of the East African fossils attributed to *Afrohyrax championi*. In some tooth positions (P4/, C1/) the differences between the Elisabethfeld fossil and *Afrohyrax championi* are not very great, but the differences are appreciable in other teeth (P2/, M3/) and the overall size of the snout. In conclusion, then, there can be little doubt that the new skull from Elisabethfeld belongs to *Afrohyrax namibensis* rather than to *Afrohyrax championi*.

The Early Miocene green sands at Elisabethfeld have also yielded specimens of

the small hyracoid *Prohyrax tertiarius* (Pickford 2004a) proving that this taxon was a contemporary of *Afrohyrax namibensis*. By the onset of the Middle Miocene, however, *Afrohyrax* seems to have disappeared from southern Africa, although it persisted in East Africa for a while (until ca 16 Ma). In both areas, the genus *Parapliohyrax* became dominant during the Middle Miocene of Southern and Eastern Africa (Pickford & Fischer 1987; Pickford 2009) and it even spread to Northern Africa (Lavocat 1961) from where the subfamily eventually dispersed to Europe and Asia (Pickford *et al*. 1997).

Biogeography and evolutionary trends

Hyracoidea were confined to Africa for most of their history (Fig. 12), but one genus (*Geniohyus* from Bugti, Pakistan) managed to cross the Tethys during the Palaeogene (Pickford 1986) and two genera crossed during the Neogene (*Prohyrax* to Crete (Kuss 1976; Van der Made 1996) and *Pliohyrax* known from several sites in Europe (Osborn 1899; Fischer & Heizmann 1992) and the Middle East (Pickford 2009)). The genus *Pliohyrax* probably originated in Africa (Beglia, Tunisia) (Pickford 2009) likely descending from *Parapliohyrax*, and it crossed the Mediterranean northwards where it spread from Spain in the west (Alcala

et al. 1986) to France (Viret 1949; Viret & Mazenot 1948), Greece (Gaudry 1862), Turkey (Baudry 1994), Iran (Pickford 2009), Transbaikalian Russia (Nakaya *et al*. 2009; Kalmykov 2013) and possibly even to China in the East (Yungsheng & Wanpo 1974). Having arrived in Eurasia, *Pliohyrax* has been interpreted to have given rise to several genera of dentally and cranially specialised giant hyracoids : *Postschizotherium* in China and Russia (Von Koenigswald 1966; Qiu *et al*. 2002; Kalmykov 2013; Nakaya *et al*. 2009) and possibly at Montpellier in France (Viret & Thenius 1952), *Kvabebihyrax* in Georgia

(Gabunia & Vekua 1966 1974; Vekua 1972) and *Hengduanshanhyrax* in Tibet (Chen 2003). *Sogdohyrax* in Kazakhstan (Dubrovo 1978) is likely to be a synonym of *Pliohyrax* (Pickford 2009). Finally, the extant genus *Procavia* occurs in the Arabian Peninsula (Pickford, 2005).
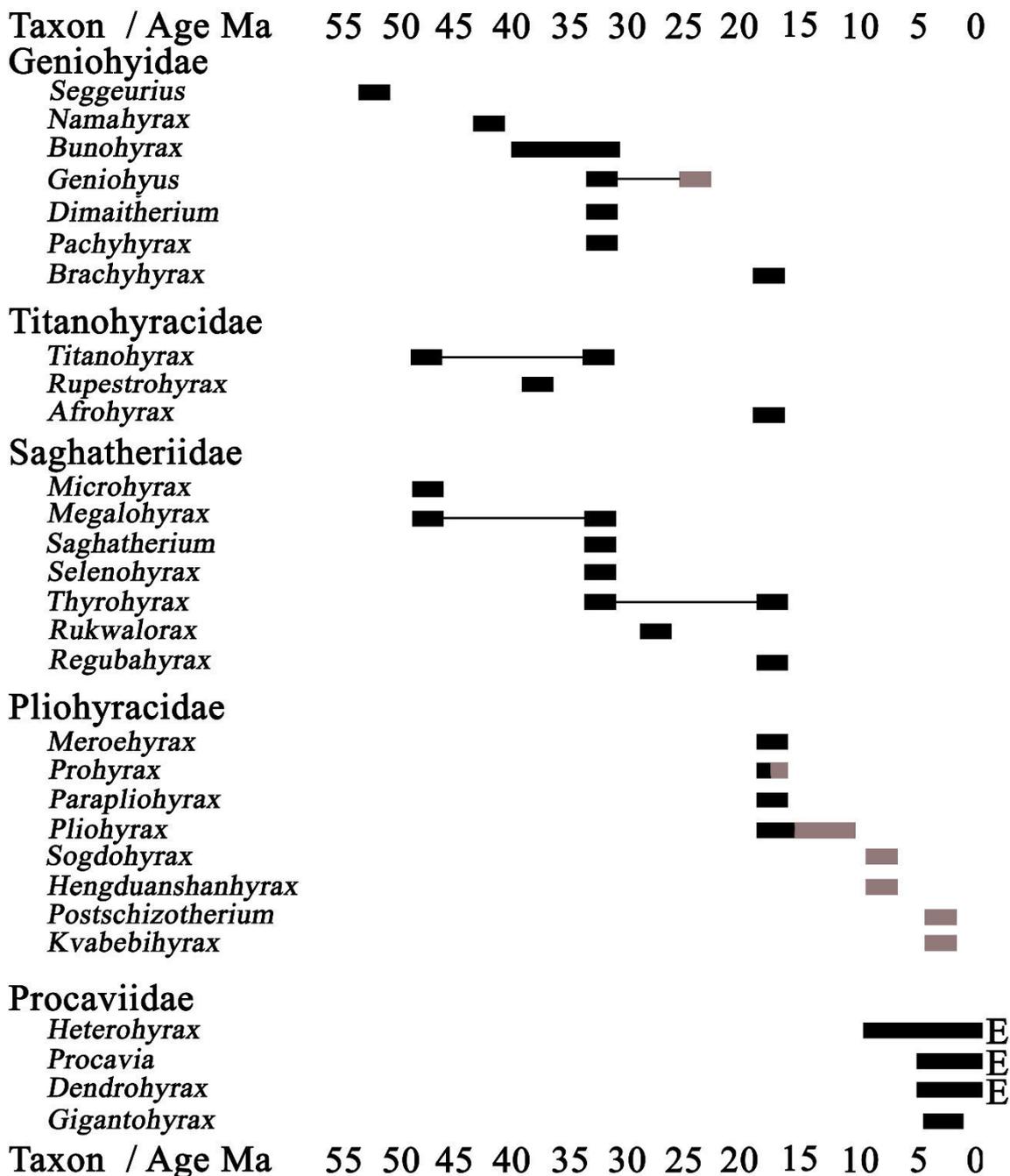

Figure 12. The distribution of genera of Hyracoidea through geological time, arranged by family (*Helioseus* is omitted, even though some authors consider it to be a hyracoid (Marivaux *et al*. 2015)). Black bars – African occurrences; Grey bars – Eurasian occurrences; E – extant occurrences. *Afrohyrax* and *Procavia* occur in the Arabian Peninsula. N.B. the supposed late Oligocene record of *Meroehyrax* from Kenya (Rasmussen & Gutiérrez 2009) is in fact of Early Miocene age (Reynoso 2014).

The fossil record of Hyracoidea in Africa has been enriched by recent discoveries of Eocene taxa in Namibia : *Namahyrax corvus* from Black Crow (Ypresian/Lutetian, Pickford *et al*. 2008a) and *Rupestrohyrax palustris* from Eoridge (Bartonian: Pickford 2015). The former is a species of Geniohyidae, and the latter is a Titanohyracidae, as is the Early Miocene

Afrohyrax namibensis. The family Sagha-theriidae has not yet been reported from southern Africa, the most southerly known record of the family being *Rukwalorax* from Rukwa, Tanzania (Stevens *et al.* 2009), but the Pliohyracidae are represented in the Neogene of Namibia by two species of *Prohyrax* (Early Miocene and base of the Middle Miocene) and possibly one of *Parapliohyrax* (late Middle Miocene). Finally the extant family Procaviidae is represented by fossils of *Heterohyrax* and *Procavia* (Pickford 2005; Pickford & Hlusko 2007; Rasmussen *et al.* 1996).

Table 3. Summary of the fossil record of Hyracoidea in the Southern African Subregion. Data from Adams (2012); Broom (1934, 1936, 1937, 1948); Churcher (1954, 1956); Hendey (1978); Kitching (1965); McMahon & Thackeray (1994); Pickford (1994, 1996, 2003, 2005, 2008a, 2015); Pickford *et al.* (1990, 2008a, 2008b); Pickford & Mein (1988); Plug & Keyser (1994); Rasmussen *et al.* (1996); Schwartz (1996, 1997); Schwartz *et al.* (1995); Shaw (1937); Stromer (1922, 1923, 1926); Wells (1939); Zeally (1916).

Taxon	Localities	Age
Namahyrax corvus	Namibia (Black Crow, Silica North)	Ypresian/Lutetian, Bartonian
Rupestrohyrax palustris	Namibia (Eoridge)	Bartonian
Afrohyrax namibensis	Namibia (Grillental 6, Elisabethfeld, Fiskus)	Early Miocene
Prohyrax tertiarius	Namibia (Langental, Elisabethfeld)	Early Miocene
Prohyrax hendeyi	Namibia (Arrisdrift, Auchas)	Basal Middle Miocene
Parapliohyrax or *Prohyrax* sp.	Namibia (Berg Aukas)	Late Middle Miocene
Heterohyrax auricampensis	Namibia (Berg Aukas)	Late Miocene (Vallesian)
Procavia pliocenica	South Africa (Langebaanweg)	Mio-Pliocene
Procavia transvaalensis	South Africa (Gauteng Karst sites)	Plio-Pleistocene
Procavia antiqua	South Africa (Taung, Gauteng Karst sites)	Late Pliocene
Procavia sp.	Namibia Otavi Mountains (Rietfontein, Asis Ost, Kombat) Namibia Kaokoland (Ondera, Rocky II) Angola (Cangalongue, Malola) Botswana (Gcwihaba, Koanaka)	Plio-Pleistocene
Gigantohyrax maguirei	South Africa (Makapansgat) Angola (Malola)	Late Pliocene
Genus indeterminate	Zimbabwe (Bulawayo)	Pleistocene

Even though the fossil record of Hyracoidea in the Southern African Subregion is less complete than that of northern Africa, notably that of the Fayum deposits, Egypt (Barrow *et al.* 2010; Coster *et al.* 2015), it is evident that Southern Africa played an important role in the evolution of the order. The oldest known Pliohyracidae (*Prohyrax*) and Procaviidae (*Heterohyrax*) are known from Namibia, in agreement with the hypothesis that the region was a centre of evolution of plants and animals due to the installation of arid ecosystems in the subcontinent long before they developed elsewhere in the continent (Pickford 2004b, 2008b). In contrast, the palaeo-environment in Eastern Africa was more humid through the Miocene and did not become arid until the Plio-Pleistocene, while the Sahara was humid into the earlier part of the Late Miocene (ca 8 Ma : Pickford *et al.* 2006, 2008b; Wanas *et al.* 2009).

Conclusions

The discovery of an almost complete skull of *Afrohyrax namibensis* in the green sands of Elisabethfeld, Sperrgebiet, Namibia, greatly enhances our information about this species, hitherto known from a single maxilla which is considerably larger than the type species of the genus, *Afrohyrax championi*, originally defined on the basis of a fossil from Moruorot, Kenya (Arambourg 1933) but represented by abundant material from Rusinga Island, Mfwanganu, Karungu and other sites in Kenya (Whitworth 1954; Pickford 2004a) a few isolated teeth from Bukwa, Uganda (Walker 1969; Pickford 2009, 2017) and some cranio-dental and post-cranial fossils from Al-Sarrar and Ad Dabtiyah, Saudi Arabia (Thomas *et al.* 1982; Pickford 2009). A maxilla from Fiskus is also of large dimensions, and is attributed to *Afrohyrax namibensis*.

Afrohyrax namibensis, the large extinct dassie from the Sperrgebiet, is associated with a smaller one, *Prohyrax tertiarius* at the same stratigraphic level at Elisabethfeld (green sands). By the base of the Middle Miocene the genus *Afrohyrax* seems to have gone extinct in southern Africa, the only hyracoid known from

this period being *Prohyrax hendeyi* from Arrisdrift, Namibia, and nearby sites in South Africa (Pickford 1994). *Afrohyrax* persisted into the Middle Miocene in Kenya, but went extinct well before the end of the period, being replaced by the large hyracoid *Parapliohyrax ngororaensis* Pickford & Fischer 1987.

Afrohyrax is the last known representative of the family Titanohyracidae, ceding way to the Pliohyracidae in the Middle Miocene, and it wasn't until the Late Miocene that the extant family of dassies, Procaviidae evolved and diversified (Rasmussen & Guttiérez 2010).

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Annex 1. List of African Hyracoidea arranged chronologically in 5 million year time slices. The circles indicate genera represented in Namibia and South Africa. N.B. *Parapliohyrax ngororaensis* was defined at Ngorora, Kenya (Pickford & Fischer 1987), but may also be present at Berg Aukas, Namibia (Pickford 1996).

Taxon / Age Ma	55-50	50-45	45-40	40-35	35-30	30-25	25-20	20-15	15-10	10-5	5-0	Extant
Seggeurius amourensis	x											
Microhyrax lavocati		x										
Megalohyrax gevini		x										
Titanohyrax tantalus		x										
Titanohyrax mongereaui		x										
Namahyrax corvus			o									
Bunohyrax matsumotoi				x								
Rupestrohyrax palustris				o								
Thyrohyrax libycus					x							
Dimaitherium patnaiki					x							
Geniohyus mirus					x							
Geniohyus magnus					x							
Geniohyus diphycus					x							
Bunohyrax fajumensis					x							
Bunohyrax major					x							
Pachyhyrax crassidentatus					x							
Saghatherium bowni					x							
Saghatherium antiquum					x							
Saghatherium humarum					x							
Selenotherium chatrathi					x							
Thyrohyrax meyeri					x							
Thyrohyrax domorictus					x							
Thyrohyrax litholagus					x							
Thyrohyrax pygmaeus					x							
Megalohyrax eocaenus					x							
Titanohyrax andrewsi					x							
Titanohyrax angustidens					x							
Titanohyrax ultimus					x							
Antilohyrax pectidens					x							
Rukwalorax jinokitana						x						
Brachyhyrax aequatorialis								x				
Brachyhyrax oligocenus								x				
Regubahyrax selleyi								x				
Thyrohyrax kenyaensis								x				
Thyrohyrax microdon								x				
Afrohyrax championi								x				
Afrohyrax namibensis								o				
Prohyrax tertiarius								o				
Prohyrax hendeyi								o				
Prohyrax bukwaensis								x				
Meroehyrax bateae								x				
Meroehyrax kyongoi								x				
Parapliohyrax mirabilis									x			
Parapliohyrax ngororaensis									o			
Heterohyrax auricampensis										o		
Dendrohyrax samueli										x		
Procavia pliocenica										o		
Procavia antiqua											o	
Procavia transvaalensis											o	
Gigantohyrax maguirei											o	
Dendrohyrax arborealis												o
Heterohyrax brucei												o
Procavia capensis												o

Annex 2. Chronological distribution of Hyracoidea in Eurasia and the Arabian Peninsula, arranged in 5 million year time slices. The record of extant *Procavia* is from the Middle East. *Sogdohyrax soricus* is close to, or identical to, *Pliohyrax graecus* (Qiu *et al*. 2002).

Taxon / Age Ma	30-25	25-20	20-15	15-10	10-5	5-0	Extant
Bunohyrax adiposum		x					
Afrohyrax championi			x				
Prohyrax cf *hendeyi*			x				
Pliohyrax rossignoli				x	x		
Pliohyrax graecus					x		
Pliohyrax kruppi					x		
Sogdohyrax soricus					x		
Hengduanshanhyrax tibetensis					x		
Postschizotherium chardini						x	
Postschizotherium intermedium						x	
Pliohyrax orientalis						x	
Kvabebihyrax kachethicus						x	
Postschizotherium occidentalis						x	
Procavia capensis							x