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Orangemeryx hendeyi

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Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia

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The commonest mammalian remains from Arrisdrift belong to a species of hyracoid, *Prohyrax hendeyi* Pickford, 1994. The same species has been found at Auchas, but it is extremely rare there. It has also been found in the Baken Diamond Mine on the South African bank of the Orange River. *P. hendeyi* is similar in morphology to *Prohyrax tertiarius* Stromer, 1922, but is appreciably larger (Pickford *et al.*, 1997).

Version française abrégée

L'hyracoïde (procaviidé) *Prohyrax hendeyi* est Ie plus com¬mun des mammifères de taille moyenne d'Arrisdrift. Il est connu par plus de 2000 spécimens avec de nombreuses mandibules et maxillaires complets. Un crâne presque entier a été récolté et la plupart du squelette est conservé en tant qu'os isolés. L'anatomie osseuse a donc pu être reconstituée, montrant que cette forme était de 1,6 à 2 fois plus gran de que le daman des roc hers actuel, *Procavia capensis*. Son poids est estimé à 36 kg. L'articulation du coude montre que le membre antérieur était parfaitement redressé tandis que chez *Procavia* ce membre reste habituellement arqué. La locomotion se faisait avec un mode cursorial et l'espèce terrestre vivait dans un paysage ouvert.

La variabilité de taille de l'incisive supérieure centrale montre trois pics. La valeur la plus élevée représenté probablement les mâles, la valeur moyenne représenté les femelles, et la petite valeur indiqué les jeunes et les dents lactéales, mais il y a un recouvrement important entre ces trois groupes. Il faut se rappeler que l'incisive centrale supérieure des hyracoïdes est une dent à croissance continue et que la surface de la section s'accroît jusqu'à l'age adulte. Les dents juvéniles sont donc plus petites que celles des adultes confirmés. L'étude de la variabilité des dents jugales montre une répartition unimodale et monomorphe.

Prohyrax hendeyi est d'une taille supérieure à celle de *Prohyrax tertiarius* du Miocène inférieur de la Sperrgebiet du Nord (Elisabethfeld, Langental) mais d'une taille inférieure à celle des espèces de la fin du Miocene moyen *Parapliohyrax mirabilis* du Maroc, *Parapliohyrax ngororaensis* du Kenya, espèces à leur tour plus petites que celles du Miocène supérieur et du Pliocène d'Eurasie. Ainsi, les Pliohyracidés suivent parfaitement la lois de Depérét/Cope qui veut que les lignées augmentent de taille au cours du temps.

Introduction

Over 2,000 fossil hyracoid specimens have been recovered from Arrisdrift, 35 km upstream from the mouth of the Orange River, Namibia (Hendey, 1978). The size of the sample is unique for Hyracoidea, which are generally rather rare in the fossil record. For instance, fossil hyracoid postcranial bones are known from very few localities, but at Arrisdrift there are many specimens representing almost all parts of the skeleton. Thus the Arrisdrift collection provides a rare chance to document variability in a group of fossil hyracoids from a single deposit.

In a preliminary description and analysis of the Arrisdrift hyracoid, *Prohyrax hendeyi*, Pickford (1994) entered into some detail about variability within the species, including the contribution made by sexual dimorphism and growth history. The phylogenetic position of *Prohyrax* was examined in greater detail by Pickford *et al.*, (1997) who concluded that it belongs to the family Pliohyracidae (*sensu* Pickford & Fischer, 1987) separate from Procaviidae (extant hyracoids), Saghatheriidae, Geniohyidae and Titanohyracidae.

Prohyrax is likely to be the ancestral group from which the genera *Parapliohyrax*, *Pliohyrax*, *Kvabebihyrax*, *Sogdohyrax* and *Postschizotherium* evolved. The family probably emerged from the Saghatheriidae during the Oligocene period, but no fossil evidence has been discovered to throw light on the details of the transition.

The focus of this paper will be on variability within *Prohyrax hendeyi* but includes a summary of important points about the species and genus.

Systematic Description

Order Hyracoidea Huxley, 1869
Family Pliohyracidae Osborn, 1899
Genus *Prohyrax* Stromer, 1922
Species *Prohyrax hendeyi* Pickford, 1994

Description: A comprehensive description of the skull, mandible, upper and lower dentitions, and post-cranial skeleton of *Prohyrax hendeyi* was published by Pickford (1994). Numerous additional fossils recovered from Arrisdrift by the Namibia Palaeontology Expedition since 1993 provide additional information about variation in the species. It is not necessary to repeat detailed anatomical descriptions of parts that were already represented in the old collections. We here focus on body parts such as the talus, which were not hitherto known from the site, and examine metric variation within the species.

Skull (Fig. 1-2). The skull of *Prohyrax* is similar in many respects to that of living dassies such as *Procavia*, but it does have several peculiarities. The palate is shallow and extends caudally behind the third molars. The orbits in adults are located above the second and third molars and the intraorbital and nasomaxillary foramina are positioned above the fourth premolar. The nasomaxillary foramen leads to a groove that runs forwards, then upwards and backwards to the lachrymal slit in the anterodorsal margin of the orbit. The lachrymal bone is large with a wing-like projection. The nasals are long and project over the premaxillae. The orbit is closed posteriorly by processes of the frontal and jugal bones. The sagittal crest is small and the tympanic bulla is reduced in size compared with that of *Procavia* and it is sunken between the post-glenoid and paroccipital processes. The external auditory meatus opens obliquely upwards and backwards, unlike that of *Procavia* which

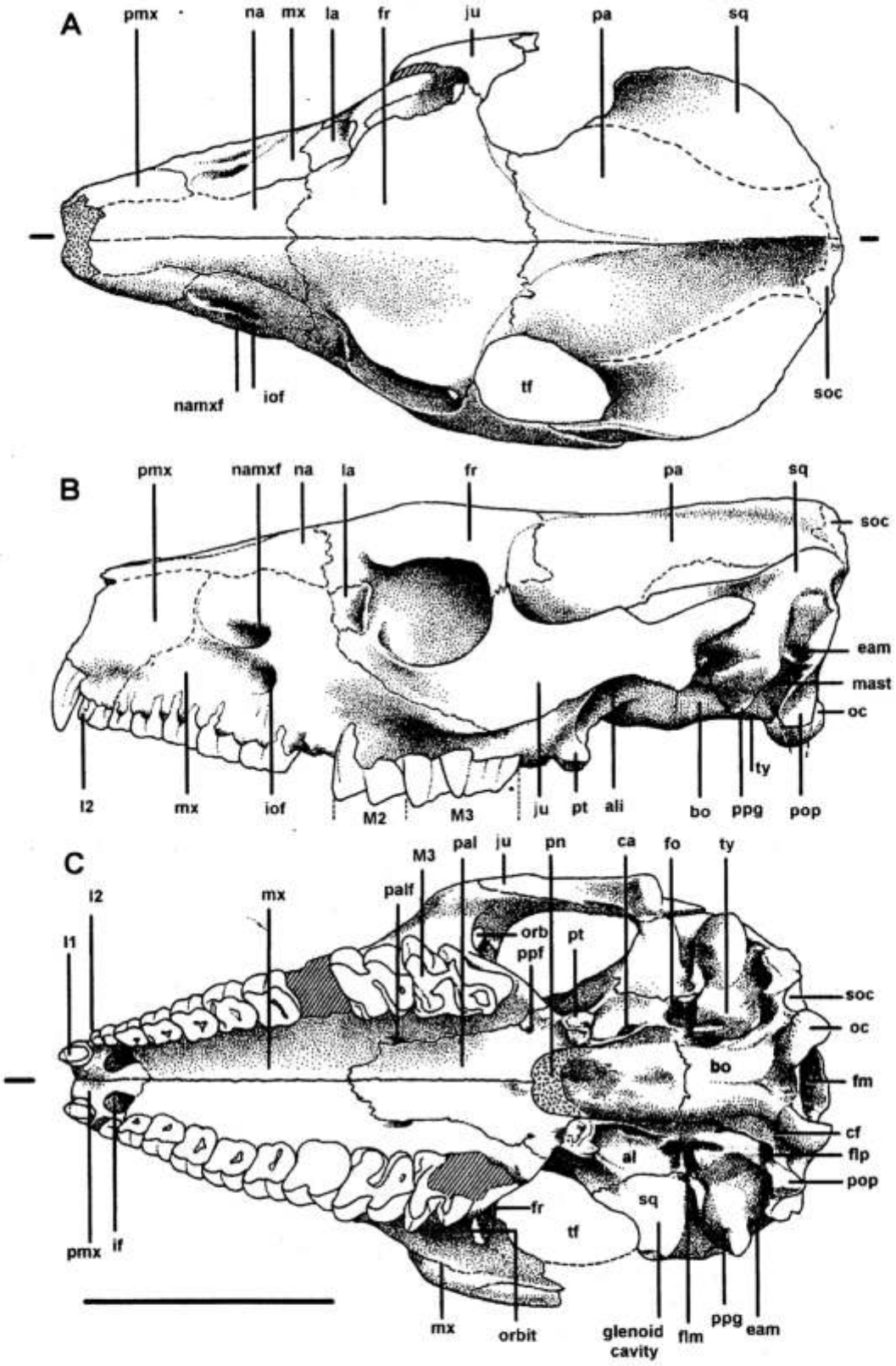

Figure 1: The skull of *Prohyrax hendeyi* Pickford, 1994 (PQAD 363) (dorsal, left lateral and palatal views) (scale bar 5 cm). Abbreviations : ali - alisphenoid, bo - basioccipital, ca - alisphenoid canal, cf - condylar foramen, eam - external auditory meatus, flm - foramen lacerum anterius, flp - foramen lacerum posterius, fm - foramen magnum, fo - foramen ovale, fr - frontal, if - incisive foramen, iof - infra-orbital foramen, ju - jugal, la - lachrymal, mast - mastoid, mx - maxilla, na - nasal, namxf - nasomaxillary foramen, oc - occipital condyle, orb - orbit, pa - parietal, pal - palatine, palf - palatine foramen, pmx - premaxilla, pn - posterior nares, pop - paroccipital process, ppf - posterior palatine foramen, ppg - post-glenoid process, pt - pterygoid, soc - supra-occipital, sq - squamosal, tf - temporal fossa, ty - tympanic.

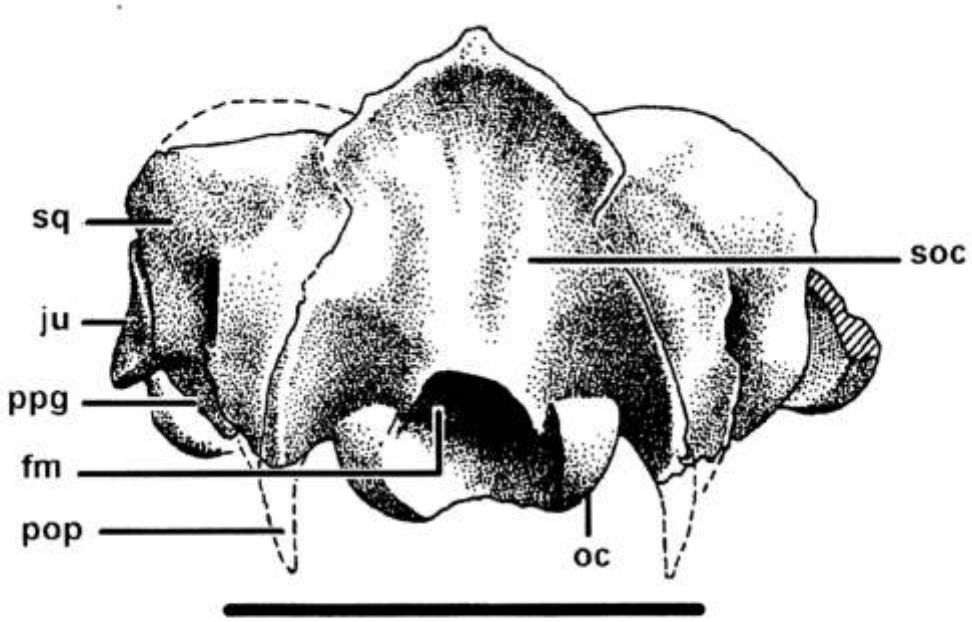

Figure 2: The skull of *Prohyrax hendeyi* Pickford, 1994 (PQAD 363) (posterior view) (scale bar 5 cm). Abbreviations : as for figure 1.

opens laterally or even slightly downwards.

The skull of the pliohyracid *Prohyrax hendeyi* differs from that of *Megalohyrax eocaenus* (Thewissen & Simons, 200 1) by being short-snouted - i.e. there are no diastemata between any of the teeth. *M. eocaenus* is a long-snouted form with gaps between the three incisors and the canine, as in other Titanohyracidae. Furthermore, the naso-frontal suture is located relatively far anteriorly in *M. eocaenus* compared to the position in *Prohyrax*. For this reason, the maxillo-frontal contact is short in *Prohyrax* and is thus closer to extant dassies such as *Procavia*, whereas it is considerably longer in *Megalohyrax*. In several ways, therefore, *Prohyrax* is intermediate in skull morphology between *Megalohyrax* and *Procavia*. Dentally, there are major differences between the three taxa, especially in the degree of hypsodonty of the ectoloph of the molars and pre-molars, and in the total number of teeth (reduced in *Procavia*).

Mandible (Fig. 3). The mandible is typical of dassies. The bodies are relatively slender and there is a coronoid foramen piercing the ascending ramus behind the third lower molar. The symphysis is relatively narrow and elongated and is solidly fused even in juveniles. There is a great deal of variation in the depth of the body below the molar row, and this may be related to sexual dimorphism (Pickford, 1994), the supposed mature males having deeper jaws than females and young males.

Dentition. A resume of dental features that characterize *P. hendeyi* (and *P. tertiarius* where known (Stromer, 1926; Pickford, 1994; Pickford *et al.*, 1997) indicates that the species possessed a full eutherian complement of teeth (3 incisors, a canine, four premolars and three molars in both upper and lower quadrants), but with a tendency for the lower third incisor to be expulsed in adult individuals. There are no diastemata in the toothrows. The first and second lower incisors are tripectinate at their apices, but the pectinations soon wear away with use. The lower central incisors possess crowns which are twisted from their apices towards the roots. When the crowns are still in their crypts the labial surfaces of the two central incisors lie parallel to each other (much as a pair of hands in prayer or the covers of a closed book). As they erupt the distal margins of the crowns diverge at the same time that the mesial margins remain close together (as in a book that is being opened). Thus, as the crown emerges from its crypt, what was initially the lingual most part of the crown rotates to become the distal edge. As the base of the crown and the root grow, the tooth no longer rotates, with the result that the apex of the crown appears twisted with respect to its base and the root.

The upper central incisor and the second lower incisor are permanently growing. The second and third upper incisors as well as the upper canine together with the third lower incisor and canine are premolariform. The premolars and molars increase in size distally, each of the lower teeth comprising two crescents, save for the third molar which has a well developed hypoconulid forming a third crescentid. The upper premolars and molars increase in size and complexity distally, the styles in the premolars being narrow whereas those of the molars are inflated. The third upper molar has a distal extension comprising a third loph. The ectoloph of the molars is considerably more hypsodont than the endoloph which is brachyodont. During wear the molar crowns rotate about a longitudinal axis running through the protocone and hypocone of each tooth.

Postcranial skeleton. Apart from a few features the postcranial skeleton of *Prohyrax* is an upscaled version of that of *Procavia* with the Arrisdrift fossils being 1.6 to 2 times larger than their counterparts in *Procavia*. There are however, several characters which indicate a more cursorial locomotor repertoire in *Prohyrax* than in the rock hyrax. For example, long bone diaphyses are straighter in *Prohyrax* than in *Procavia*,

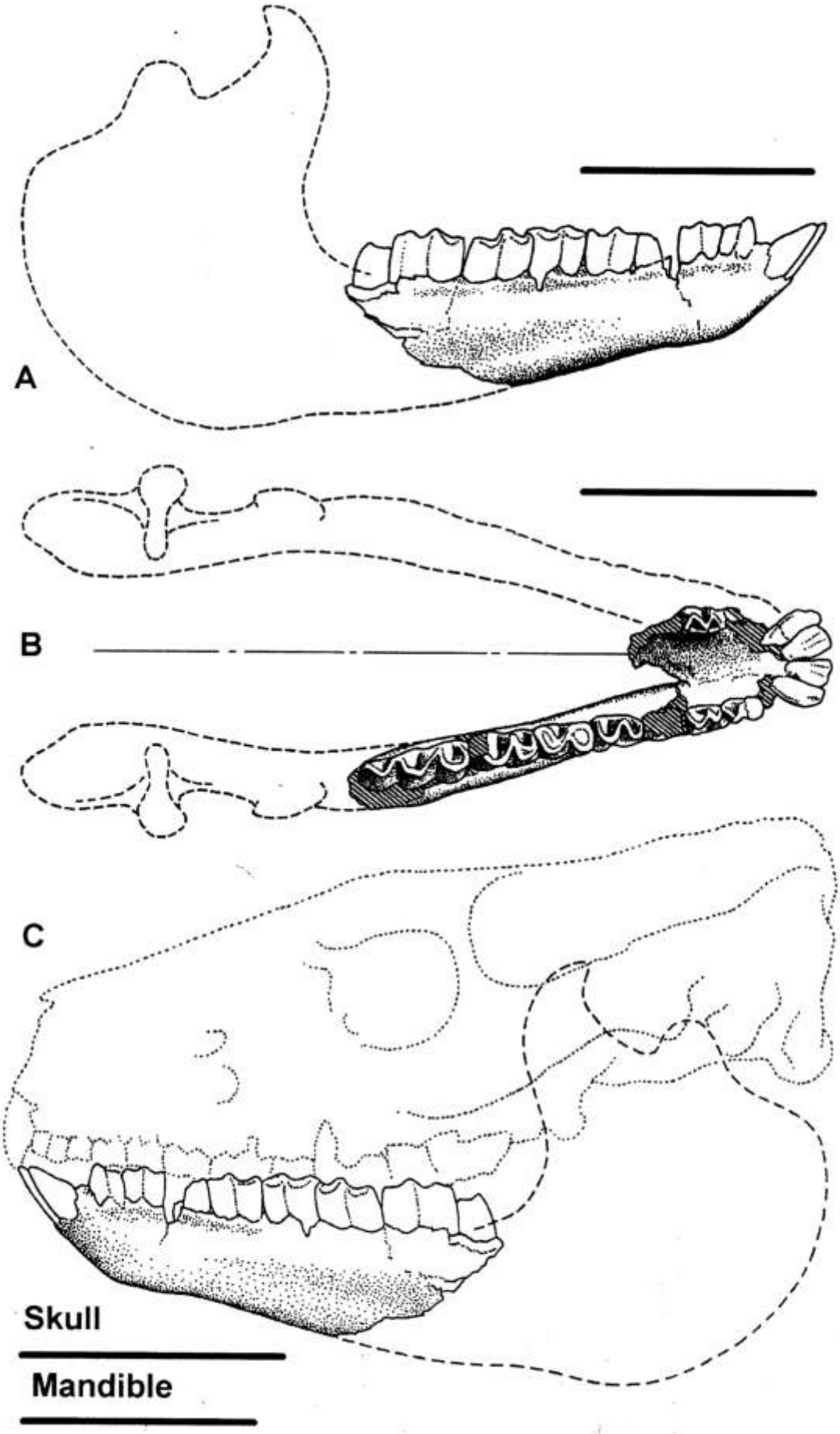

Figure 3: The mandible of *Prohyrax hendeyi* Pickford, 1994 (PQAD 2962) (right lateral and occlusal views and left lateral view in reconstruction to match the holotype skull) (scale bar 5 cm).

and the articular surfaces of the elbow and knee joints suggest that they were more strongly stabilised in extended positions than they are in *Procavia*. Strangely, in flexed positions the elbow joint of *Prohyrax* appears to have had greater potential for pronation than that of *Procavia*. The fibula and tibia are not fused in *Prohyrax*, suggesting perhaps that the ankle joint was not as stabilised as it is in *Procavia*.

Several hyracoid tali are now known from Arrisdrift. AD 683'97, a right talus, is well preserved and typical of the species. The body of the talus is offset from the tibial trochlea, much as in *Dendrohyrax*, the extant tree hyrax (Fischer, 1986). In dorsal view, the cotylar *fossa* for the medial malleolus of the tibia is large and deep, occupying about 40% of the width of the talus. The trochlea is pulley-like with a central groove bordered medially and laterally by rounded crests. The lateral crest is longer than the medial one. The pulley extends over an angle of just under 1800. On the lateral surface of the trochlea, there is a well developed facet for the fibula, which was well developed in this species. The body of the talus is offset from the trochlea and is more in line with the cotylar *fossa*, indicating that much of the body weight passed through the tibial maleolus and through the talo-navicular facet, the feet being located in a more medial position under the body than is the case in hyracoids such a *Megalohyrax championi* which possessed straight tali. In volar aspect, there is a mediolateral groove for the calcaneum which is oriented obliquely, running from the anterolateral corner of the bone to the rear of the cotylar *fossa*. The talo-navicular facet of *Prohyrax hendeyi* is almost flat, as in most other hyracoids where the talus is known, and as such it differs greatly from the talus of *Antilohyrax pectidens* from Quarry L41 of the Jebel Qatrani Formation, Fayum Egypt (Rasmussen & Simons, 2000) which posesses a trochlea-like talo-navicular facet.

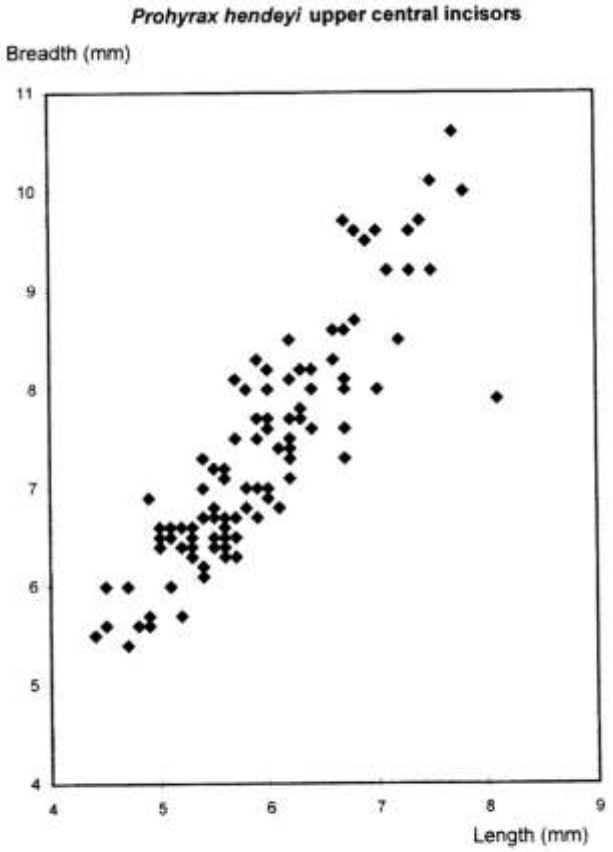

Figure 4: Bivariate plot of upper central incisors of *Prohyrax hendeyi* from Arrisdrift, Namibia, showing a cluster of very large specimens somewhat separated from the main cloud of points, interpreted as large males, and a cluster of small specimens probably representing deciduous teeth.

Discussion

Dental variation in *Prohyrax hendeyi*: Upper central incisors (Fig. 4). Pickford (1994) briefly discussed metric variation in upper central incisors of *Prohyrax hendeyi* which suggested the presence of sexual bimodality in the species. 24 specimens were used in the preliminary analysis. There are now 103 specimens available and a similar analysis reveals the presence of one peak in the mesiodistal length measurements as in the previous study, but three peaks in buccolingual breadth measurements rather than two that appeared in the 1994 study. The range of variation has increased somewhat, especially at the large end of the spectrum of measures. The previous study suggested that there was a large degree of overlap between the male and female ranges of variation, with the supposedly female mean breadth occurring between 5 and 5.5 mm and the supposedly male one between 6 and 6.5 mm. The new analysis indicates that the matter is not as clear cut as previously thought, because now the supposed female peak would span 6 to 7 mm and the male one 7.5 to 8.5 with a third peak at 9.5 to 10 mm. Part of the problem could be due to the fact that the upper central incisors of *P. hendeyi* are permanently growing and they increase gradually in size with increasing age. In order to standardize the data gathering, measurements were made near the enamel-root junction, but this is not always preserved, especially in *Prohyrax hendeyi* upper central incisors deeply worn specimens. There is also the problem of deciduous central incisors which, apart from their smaller dimensions, resemble their permanent counterparts, and if included in a study such as this one, would tend to skew the peak towards the low end of the histogram. It is concluded that there is a tendency for the upper central incisors of *P. hendeyi* to be sexually bimodal, but that determining the sex of individual specimens near the mean is not possible. The only specimens which can be determined with any degree of confidence are the largest ones (buccolingual breadth greater than 8.5 mm) which are likely to represent males (about 16% of individual teeth in the presently available sample).

Variation in dimensions of the lower third molar (Fig. 5). There are 118 lower third molars of *Prohyrax hendeyi* in the Arrisdrift collection. Bivariate plots of length against breadth reveals a single cluster of points with a few outliers. Separate analyses of breadth and length reveals the presence of a single peak in each measurement category. There are two points at the upper end of the length measurements which are well separated from the main cluster of points, and these are specimens with particularly well developed and elongated hypoconulids. At the low end of the length series there are five or six specimens with relatively short and poorly developed hypoconulids. The bulk of the length measures range between 21 and 25.5 mm (mean = 23.3) whilst the breadth measurements (taken across the base of the anterior loph) range between 7.5 and 10 mm (mean 8.8)

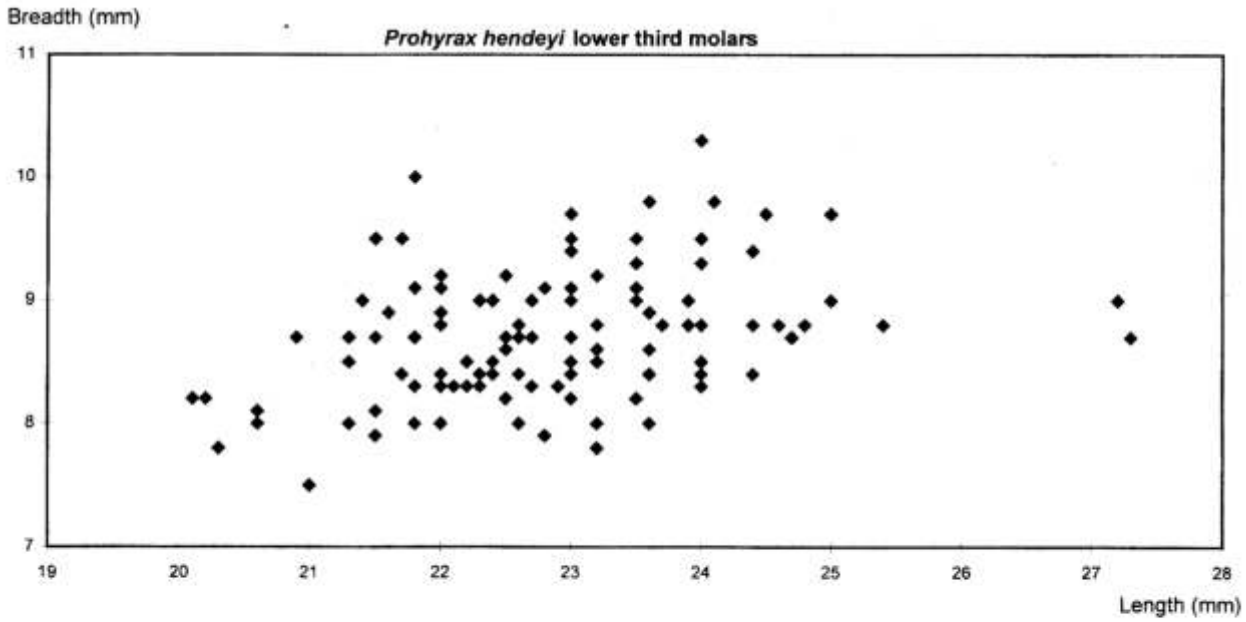

Figure 5: Bivariate plot of lower third molars of *Prohyrax hendeyi* from Arrisdrift, Namibia, showing a cloud of points with two outliers at the large end and five or six outliers at the small end of the main scatter of points. The outliers are not excessively wide or narrow, but they possess either extremely elongated or somewhat shortened hypoconulids, which explains their somewhat anomalous positions within the scatter diagram. The evidence suggests that there is only one species of hyracoid at Arrisdrift.

with no obvious outliers. It is therefore highly likely that all the Arrisdrift hyracoid fossils belong to a single species and that the outlying individuals represent nothing more than extremes of intraspecific variation.

The presence of i/3 in *Prohyrax hendeyi*. In the previously available samples from Arrisdrift, there were no specimens with the third lower incisor. In the new collections there are several specimens retaining this tooth, often on one side of the jaw only. AD 584'99 is typical in this respect, the third incisor being present on the left side, but absent on the right. It is a tiny tooth crowded between the second incisor and the canine. This individual was young at the time of death, with the third molar still emerging from its crypt. It is likely that if this individual had lived much longer its i/3 would have been expulsed from its alveolus, which is in any case very shallow. Forward migration of the cheek teeth occurs in hyracoids, and this would eventually eliminate the short diastema that occurs between the i/2 and the canine when the i/3 falls out. The third lower incisor is premolariform and possesses a lingual cingulum. The canine behind it is also premolariform, its crown being formed of two crescentids.

Body weight estimate of *Prohyrax hendeyi*

In most measurements the postcranial bones of *Prohyrax hendeyi* are about twice the size of those of *Procavia capensis* (ranging from 1.6 to 2.1 times larger depending on which bone is measured) (Pickford, 1994). *Procavia capensis* has a body weight of up to 4.5 kg, with females being lighter than males (Skinner & Smithers, 1990). Isometrically upscaling the body weight using the postcranial measurements, suggests that *P. hendeyi* had a body weight in the range of about 36 kg (23 x 4,5) which is similar to that of the Springbok (*Antidorcas marsupialis*) (Skinner & Smithers, 1990).

The preponderance of hyracoids at Arrisdrift

Prohyrax is by far the most common of the medium to large fossil mammals excavated at Arrisdrift. For example, out of 754 catalogue entries made during the 2000 field season, 307 (40.7%) represent *Prohyrax*, while all other medium to large mammals account for only 244 specimens (32.4%), the remainder (203 = 26.9%) being micromammals, crocodiles, squamates, birds, invertebrates and plants. The 1999 field season was similarly rich in *Prohyrax* in that out of 869 catalogue entries, 300 (34.5%) were hyracoids, 313 (36%) were other medium to large mammals and 256 (29.4%) the remainder. Other years were comparable (in 1994, 223 out of 750 catalogue entries (29.7%) were hyracoid; in 1995,175 out of 545 (32.1%); in 1996, 167 out of 480 (34.8%); in 1997,361 out of 1009 (35.8%) and 1998,248 out of 691 (35.9%). Thus throughout the excavations by the Namibia Palaeontology Expedition, 1781 hyracoid fossils were found out of a total of 5098 catalogue entries (34.9%). If we add the material discovered by G. Corvinus in 1976-1978, then the total number of specimens exceeds 2,000. In the preponderance of hyracoid remains over all other zoological groups, Arrisdrift, as a fossil site, is unique. Furthermore, all age groups are represented in the sample, from infants through to aged adults (Pickford, 1994). These facts and figures indicate that during the basal Middle Miocene not only was *Prohyrax hendeyi* a common animal in southern Namibia, but also that it probably inhabited the immediate vicinity of the fossil site in the lower Orange River Valley. Study of the locomotor apparatus suggested to Pickford (1994) that *Prohyrax hendeyi* was more cursorial than any of the extant dassies (*Procavia*, *Heterohyrax* and *Dendrohyrax*) and in some minor features it appears to be convergent on ruminants, but not to such an extent as *Antilohyrax pectidens* of the Fayum (Rasmussen & Simons,

2000). The combination of high numbers of individuals and the presence of sexual dimorphism in the species (apparently with relatively few males), raises the possibility that *Prohyrax hendeyi* was an animal that lived in herds consisting of greater numbers of females than males.

Systematic position of *Prohyrax*

Thewissen & Simons (2000) classified *Megalohyrax* in the Pliohyracidae. However, the differences in cranial, dental and postcranial morphology of *Prohyrax*, a typical pliohyracid, and *Megalohyrax* are greater than the differences between *Prohyrax* and *Procavia* (Procaviidae). It has been argued previously (Pickford *et al.*, 1997) that Pliohyracidae should contain the genera *Prohyrax*, *Parapliohyrax*, *Pliohyrax*, *Sogdohyrax*, *Kvaebihyrax* and *Postschizotherium*, all of which are characterized by possessing hypsodont ectolophs in the upper molars and premolars, among other cranial, dental and postcranial characters. Long-snouted, brachyodont hyracoids from the Miocene and Oligocene should be assigned to the family Titanohyracidae containing the genera *Megalohyrax*, *Titanohyrax*, *Microhyrax*, *Bunohyrax* and *Pachyhyrax* (Pickford *et al.*, 1997).

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