

## A new species of *Prohyrax* (Mammalia, Hyracoidea) from the middle Miocene of Arrisdrift, Namibia

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Abundant fossilized remains of a medium-sized hyracoid from Arrisdrift, Namibia, are assigned to a new species of *Prohyrax*, *P. hendeyi*. The dental morphology indicates affinities with *Paraplioxyrax* and *Plioxyrax*, and the genus *Prohyrax* is accordingly placed in the family Plioxyracidae (Pickford & Fischer, 1987). The absence of palatine pockets and external mandibular fossae indicate that the Arrisdrift hyracoid is a primitive member of this subfamily. The species *P. hendeyi* was about twice the size of the extant hyracoid *Procavia capensis*, on the basis of linear measurements of the skull and limb bones, and 30 per cent larger than *Prohyrax tertarius*. Among the distinctive features of the postcranial skeleton of *P. hendeyi* in comparison with that of *Procavia capensis* are the less stable elbow (in flexed positions) and ankle joints, combined with more stable knee and wrist joints. These differences are considered to represent adaptations to increased terrestrial cursoriality in *Prohyrax* compared with *Procavia*. The occurrence of two mandibular size groups in the sample is thought to represent variability due to sexual dimorphism in *Prohyrax*. Even though the sample of *Prohyrax tertarius* Stromer, 1922, does not permit extensive comparisons, it is suggested that *P. hendeyi* is closely related to it. *Prohyrax* differs from *Meroxyrax* Whitworth, 1954, of East Africa in its lack of internal mandibular chambers, absence of lingual fossae, and morphology of its cheek teeth. These differences refute Meyer's (1978) suggestion that the two are synonymous.

### Introduction

Abundant well-preserved remains of middle Miocene hyracoids were recovered during 1976 and subsequent years from Arrisdrift, a locality close to the Orange River in the southern part of Namibia (Hendey 1978). Preliminary descriptions of the locality, its geological sequence and the nature of the fossils' occurrence were given by Corvinus & Hendey (1978) and by Hendey (1978, 1984). The fossils occur in a gravel deposit with silt lenses that accumulated in a channel incised into bedrock. Of several thousand fossils found in the channel (many still remain *in situ*), several hundred were of hyracoids, and were the most common mammalian fossils found, together with abundant remains of the macroscelidean *Myoxyrax* and ruminants. Faunal lists are provided by Hendey (1978, 1984) and Corvinus & Hendey (1978). The family Varanidae has also been identified on the basis of vertebrae.

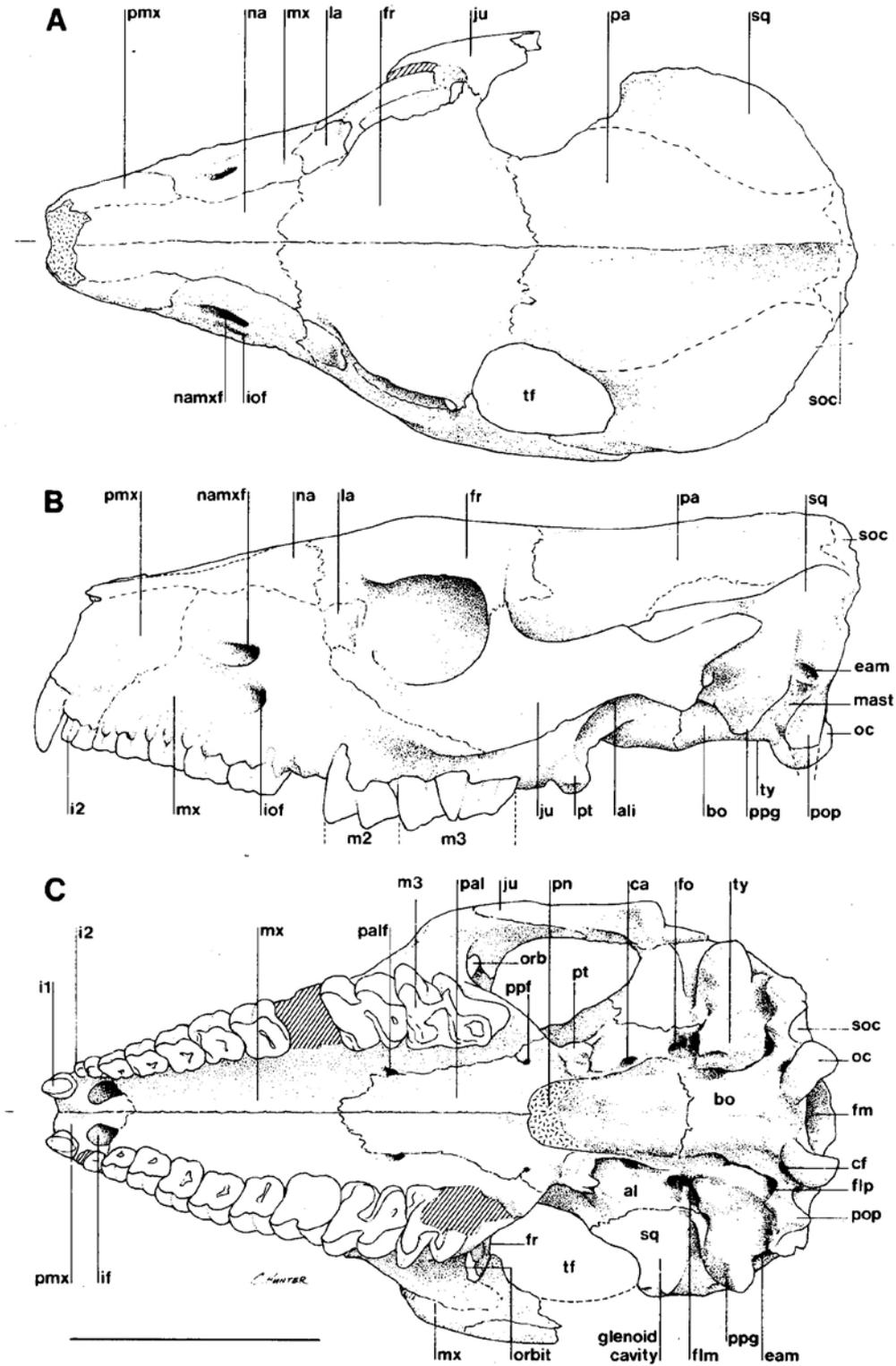
Current age estimates of the Arrisdrift fauna are of the order of 15-16 m.y. old on the basis of faunal comparisons with East Africa. While these estimates may be correct, the site could conceivably be as young as 14 m.y. or as old as 17 m.y. Such a wide margin of error exists because the early middle Miocene strata of Kenya, against which the biostratigraphic position of Arrisdrift is compared, are not yet precisely dated. Hendey (1978) observed that the Arrisdrift fauna is not an exact correlate of any of the early middle Miocene faunas of Kenya (e.g. Maboko, Nachola, Moruorot or Buluk (Harris & Watkins 1974; Pickford 1984)). However, despite the faunal differences between the Arrisdrift and East African middle Miocene faunas, I conclude that they cannot be widely temporally disparate from each other. The palaeoenvironmental conditions at Arrisdrift may have been similar to those reconstructed for East Af-

rican middle Miocene sites such as Maboko which, on the basis of its terrestrial gastropods, appears to have been relatively dry, open woodland with gallery forest fringing streams and rivers (Pickford 1985).

The value of the Arrisdrift fauna lies principally in that it is the first recorded middle Miocene assemblage from Africa south of the Equator, except for a few sites near Nyakach and Maboko, Kenya (Pickford 1984), which are within 30 km of it. It is equally important that it lies within the previously extensive palaeontological hiatus in the southern African fossil record which used to include the entire middle and upper Miocene periods from about 17 m.y. until about 5 m.y. ago. The zoogeographic implications of the Arrisdrift fauna have yet to be fully appreciated because much basic analysis remains to be done.

All specimens from Arrisdrift, housed in the Geological Survey of Namibia, Windhoek, are prefixed with the letters AD. Material housed in the South African Museum, Cape Town, has the prefix SAM-PQN followed by the catalogue number. The entire collection of Arrisdrift fossils has been rehoused at the Geological Survey of Namibia, where they will have the prefix GSN, followed by the letters AD and a number which will be the same as they were before. Abbreviations in the illustrations follow Grassé (1955), Deschaseaux (1958), and Sisson & Grossman (1953).

Measurements are in millimetres. In Tables 1-2, many isolated teeth have been omitted because of difficulties in determining their correct positions within the tooth rows. Measurements alone do not permit the determination of their positions since there is overlap in the ranges of variation of neighbouring teeth. Thus, even though omitting specimens biases the sample, this procedure introduces less uncertainty into subsequent analysis than would attempts to include every specimen.



**Figure 1:** *Prohyrax hendeyi* sp. nov. Holotype skull, AD363. A. Dorsal view. B. Lateral view. C. Palatal view. 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---lacrimal, 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. Scale bar = 5 cm.

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## Systematic description

Genus *Prohyrax* Stromer, 1922

**Type-species.** *Prohyrax tertarius* Stromer, 1922.

### Diagnosis

Small to medium-sized hyracoids with full eutherian dentition (lower  $I_3$  sometimes lost); upper central incisors widely separated mesially and separated from  $I^2$  by short diastema; upper  $I^2$ - $I^3$  and canine premolariform, not separated from rest of cheek teeth; molars with brachyodont lingual cusps and hypsodont buccal cusps; palate shallow, extending caudally behind the  $M^3$ ; orbits in adults situated above the  $M^2$ - $M^3$ ; infraorbital and nasomaxillary foramina located above  $P^4$ ; nasomaxillary foramen leads to a groove that runs forwards, then upwards and backwards to the lachrymal slit in the anterodorsal margin of the orbit; lachrymal bone large, with conspicuous wing-like projection on orbital margin; nasals long and projecting over premaxillae; descending process of frontal meets ascending process of jugal, thereby closing the orbit posteriorly; glenoid fossa formed on both squamosal and jugal (primitive hyracoid character); sagittal crest small; tympanic bulla reduced in comparison with that of *Procavia*, and sunken between the post-glenoid and paroccipital processes; external auditory meatus opens obliquely upwards and backwards; fibula not fused to tibia.

*Prohyrax hendeyi* sp. nov.

Figs 1-6, 7B-7F, 8-13; Tables 1-3.

*Prohyrax* sp. Hendey, 1978: 16, fig. 6; 1984: 91, table 1.

### Diagnosis

A species larger than *Prohyrax tertarius*; styles on upper molars more inflated; buccal cingulum less well defined;  $M^3$  with ectoloph elongated to form an extended talon.

### Holotype (Fig. 1A-C, 2)

AD363, virtually complete skull, lacking the right  $I^2$ , left  $M^1$ , part of left  $M^3$ , and part of the right zygomatic; from Arrisdrift, Namibia; illustrated by Hendey (1978, fig. 6).

### Paratypes

Numerous maxillae, mandibles and isolated teeth of adults, juveniles and infants of both sexes (Figs 2-6), as well as various postcranial elements, especially the long bones (Figs 12-13). These represent more than 40 individuals of all ontogenetic ages (Hendey 1978: 17).

### Type locality

Arrisdrift, Pit AD8/2, east of Oranjemund, Namibia.

## Age

Early Middle Miocene, ca  $16 \pm 1$  Ma

## Etymology

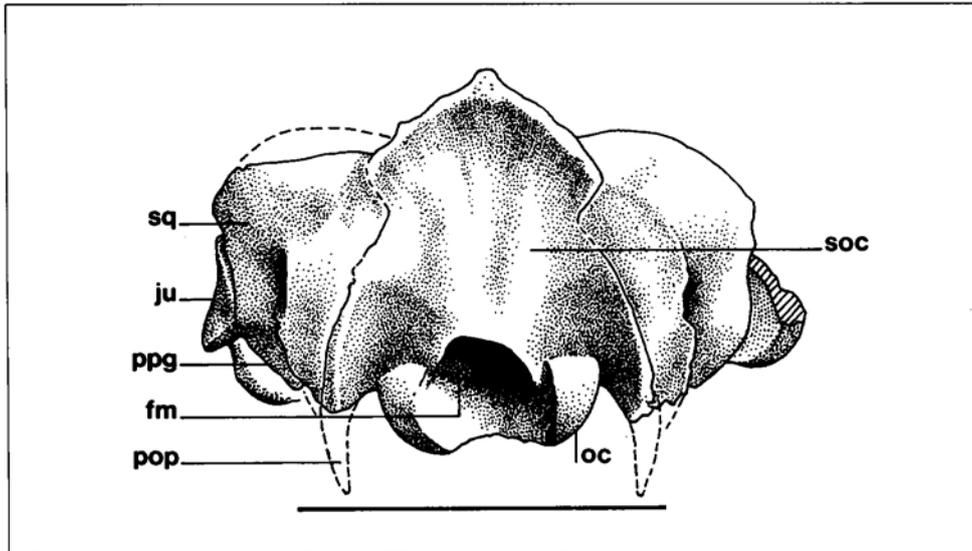
The specific name honours Dr Q. B. Hendey for his contributions to vertebrate palaeontology in southern Africa over the past two decades.

## Morphological description

### Skull (Fig. 1A-C, 2)

Hendey (1978, table 4) described, illustrated and gave measurements of the *Prohyrax* skull from Arrisdrift that is here designated holotype of *P. hendeyi* sp. nov. Among the characters noted by him were the posteriorly closed orbits, the nasomaxillary slit leading anteroventrally to the naso-maxillary foramen located immediately above the infra-orbital foramen; dental formula 3.1.4.3 in both uPRer and lower tooththrows, although the  $I_3$  is often lost;  $I^2$ - $M^3$  forming a closed series of cheekteeth; the premolariform upper canine and  $M^3$  with an elongated distal lobe. Hendey (1978) also noted the absence of mandibular fossae and fenestrae that occur in a variety of Tertiary hyracoids from other parts of Africa, including *Meroehyrax* and *Megalohyrax* (Whitworth 1954), and he concluded that *Prohyrax* differed from most other pliohyracids by its small size, less elevated orbits and narrower skull.

Additional features are also observable. The central upper incisors of *P. hendeyi* sp. nov. are separated by about two incisor widths in the available specimens. They are relatively small, and even though they appear to be in their life position, they project only a small distance beyond the occlusal plane (Fig. 1B). It is unlikely that they have rotated backwards into the alveolus post-mortem, and it seems likely that the holotype represents a female individual (see below). In *Procavia* the upper central incisors project relatively further. As in modern procaviids, the central upper incisors of *Prohyrax* were permanently growing with persistently open roots that extended back through the premaxilla to the maxilla above the  $P^1$ . There is a very short diastema between the  $I^1$  and  $I^2$ . The  $I^2$ ,  $I^3$  and canine are premolariform with the  $I^2$  being very small, succeeding teeth increasing in size and complexity of crown form distally. There is a definite change in crown outline between the  $P^4$  and  $M^1$ , which allows easy identification of tooth positions in fragmentary maxillae. It is difficult to assign isolated premolars to their correct position because of overlap in size and morphology between neighbouring teeth. The same applies to the first two molars. Such a change between  $P^4$  and  $M^1$  confirms Stromer's (1926) identification of teeth in the fragmentary holotype of *Prohyrax tertarius*. In *P. hendeyi* and *P. tertarius* the upper molars tend to be less square in occlusal outline than the premolars, with prominent and more inflated buccal styles. The molars of both species are characterized by the presence of brachyodont lingual cusps and ex-



**Figure 2:** *Prohyrax hendeyi* sp. nov. Holotype skull, AD363, posterior view. Abbreviations as for Figure 1. Scale bar = 5 cm.

tremely hypsodont buccal ones, as in typical pliohyracids such as *Paraplio-hyrax* and *Plio-hyrax* (Pickford & Fischer 1987). In this respect they differ markedly from other hyracoids such as *Megalohyrax*, *Pachyhyrax*, *Bunohyrax*, *Sagatherium* and living procaviids, in which the buccal cusps of the cheekteeth are brachyodont. The MI in the holotype is heavily worn, but its occlusal surface has remained in the occlusal plane with the other cheekteeth because, as it wore down, the hypsodont labial cusps rotated towards the sagittal plane in phase with tooth abrasion.

The palate in *P. hendeyi* is shallow and is not marked by any palatine pockeis such as occur in *Paraplio-hyrax mirabilis* Lavocat (1961) and *Paraplio-hyrax ngororaensis* Pickford & Fischer (1987). The palatine extends posteriorly behind  $M^3$  (Fig. 1C) and meets the pterygoid wings 17 mm from  $M^3$ . The orbits in adult specimens, such as the holotype, lie above  $M^2$  and the mesial two-thirds of  $M^3$ , but in young adults and juveniles they are situated relatively further forwards. For example, in a juvenile specimen with a lightly worn  $M^1$ , the rear of the zygomatic root is opposite the rear of  $M^2$ , whereas in the adult it is opposite the second lobe of  $M^3$ . In an infant specimen with worn  $dM^3$ - $dM^4$ , the rear of the zygomatic root is opposite the rear of  $dM^4$  (i.e. in front of  $M^1$ ). Such extensive forward growth of the maxilla carrying the cheekteeth forward relative to the orbit and zygomatic root during maturation, appears to be a normal growth phenomenon in hyracoids, as it also occurs in *Paraplio-hyrax* and *Procavia*.

On the facial aspect of the cranium (Fig. 1A-B) the nasomaxillary foramen (narnxf), which opens forwards level with  $P^4$ , leads into a groove that runs anteriorly to a level with  $P^2$  before turning dorsally towards the

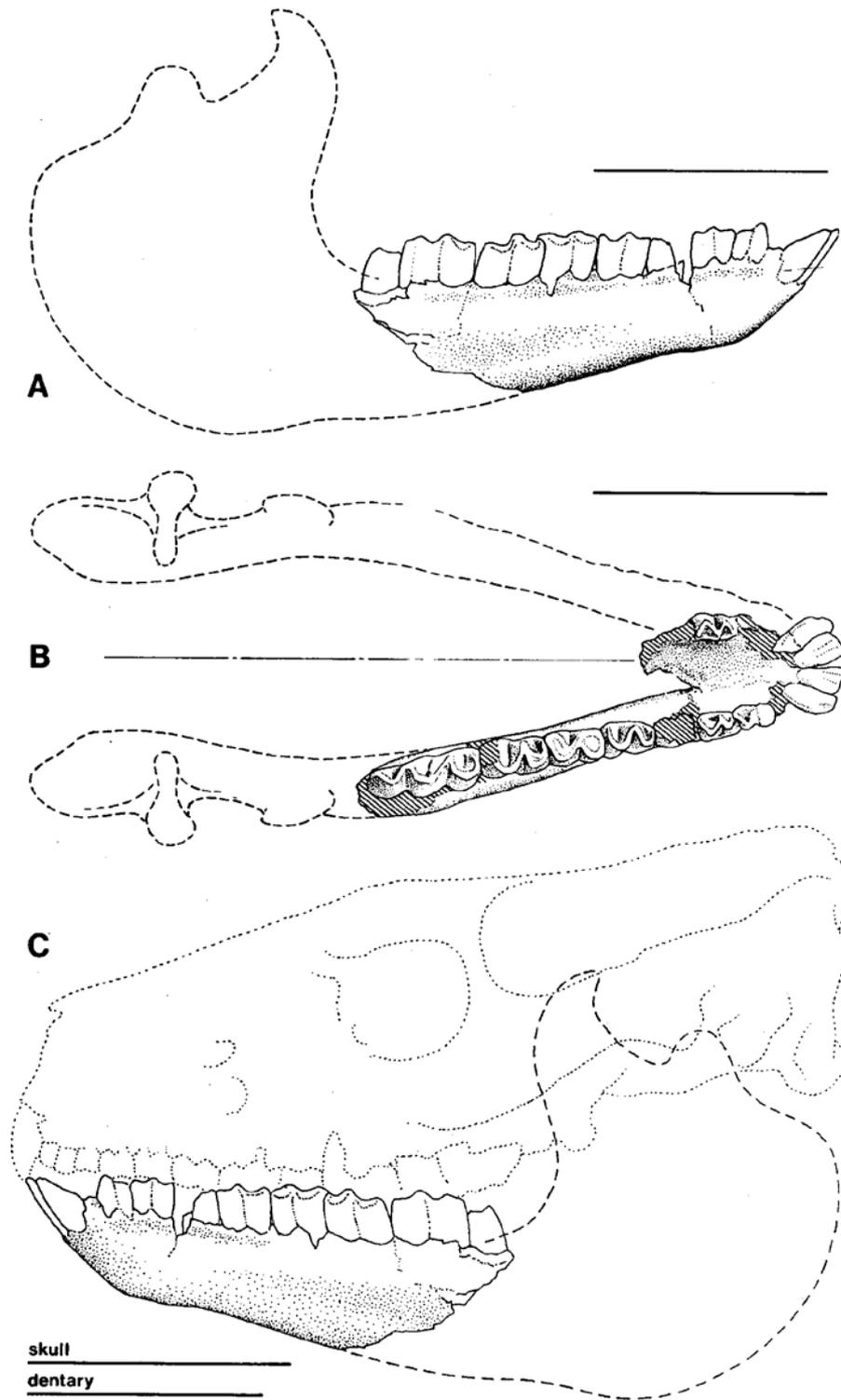
nasomaxillary suture and thence posteriorly towards the lachrymal slit situated in the orbit at its antero-dorsal margin. This morphology seems to be unique to the genus *Prohyrax*, although its form is unknown in *P. tertiarius*. The lachrymal bone is large, forming a conspicuous wing-like projection at the leading edge of the orbit. The nasal bones are long and project over the naso-premaxillary notch as in *Paraplio-hyrax*.

The glenoid cavity for articulation with the mandibular condyle is a compound of jugal and squamosal, as in modern and other fossil hyracoids. The sagittal crest in *Prohyrax* is low and small. The sutures in the holotype skull, AD363, are not fully closed and it is possible to discern most of the boundaries of the individual skull bones. The general relationships of these bones to each other are much as in modern hyracoids. The jugal has an extensive suture with the maxilla and comprises the entire lower half of the orbital margin (Fig. 1B-C). It also makes contact with the base of the wing-like lachrymal anteriorly, with the frontal bone in the post-orbital bar, and with the squamosal at the glenoid and laterally on the zygomatic arch.

The inter-frontal suture is straight (Fig. 1A) and the naso-frontal suture is moderately zigzag. The suture between the frontal and lachrymal occurs near the leading edge of the orbit. Extensive supraorbital sinuses can be seen in this region in some broken specimens. To the rear, the frontal bone makes a wavy contact with the parietal. The temporal fenestra is large and bordered distally by a large squamosal plate that ascends obliquely towards the dorsal part of the supra-occipital bone.

The general features of the basicranium are similar to those of *Procavia* (Fig. 1C) but significant points of difference are as follows:

- (a) The pterygoid wings are situated appreciably



**Figure 3:** *Prohyrax hendeyi* sp. nov. A–B. Mandible, AD2962. A. Lateral view. B. Occlusal view. C. Reconstruction with mandible reversed and matched to skull AD363. Scale bar = 5 cm.

Table 1

*Prohyrax hendeyi* sp. nov.  
Upper dentition  
measurements in millimetres  
(e = estimated)  
All specimens prefix AD

Spec.	Tooth	Length	Breadth
655	dC*	7.0	4.7
421	dM <sup>1</sup>	8.6	6.0
655		8.5	5.5
3126		8.7	6.6
653	dM <sup>2</sup>	10.5	7.6
754		10.4	7.1
1002		9e	7.0
3063		---	6.9
3126		9.4	7.7
653	dM <sup>3</sup>	12.3	9.0
754		12.0	8.4
944		11.8	8.9
1002		12.0	8.4
3126		11.6	9.4
383	dM <sup>4</sup>	13.4	10.2
944		14.4	10.7
949		13.1	10.1
1002		13.7	10.9
165	I <sup>1</sup>	6.3	5.4
232		5.8	5.2
239		6.2	5.3
245		6.9	5.9
292		7.7	6.5
300		6.6	5.3
311		6.6	5.3
370		7.4	6.1
380a		7.8	6.6
380b		7.6	6.7
385		5.1	4.5
428		7.4	6.1
470		6.3	5.6
823		6.8	5.0
872		7.1	5.5
943		4.3	4.8
1004		6.8	5.7
1196		5.7	4.7
1358		7.0	6.0
1908		6.9	6.3
2723		6.8	5.8
2777		4.7+	4.5+
2837		6.2	5.1
2882		7.6	6.3
943	I <sup>2</sup>	4.0	3.5
1196		3.0	3.2
943	I <sup>3</sup>	4.0	3.5
2777		4.2	3.3
429	C*	6.6	5.2
943		5.5	6.5
1196		5.1	5.8
2777		4.6	3.8
429	p <sup>1</sup>	7.3	6.7
943		6.2	7.3
2777		5.3	5.6
1196		6.3	6.8
2847		7.8	7.8
429	p <sup>2</sup>	9.0	8.0
943		7.7	8.1
1196		7.1	7.9
2777		6.9	6.4
2847		8.8	8.9
2878		7.6	8.4

further posteriorly than in *Procavia*.

(b) The posterior margin of the falatines, which forms the narial margin, lies behind the M<sup>3</sup>s, whereas in *Procavia* it lies level with the M<sup>3</sup>s and thus places the posterior nares more posteriorly.

(c) The tympanic bullae are relatively much smaller than those of *Procavia* and form the floor of a deep valley between the post-glenoid process of the squamosal and the paroccipital process of the basioccipital bone.

(d) The external auditory meatus of *Prohyrax* emerges posterodorsally, whereas in *Procavia* it emerges slightly posterolaterally and horizontally, or slightly ventrolaterally.

Apart from these significant differences, the morphology of the rest of the basicranium is similar in *Prohyrax* and *Procavia*, indicating that the basicranial morphology of hyracoids is basically conservative. In particular, the relationships of the various foramina to the principal bones appears to be entirely homologous in the two genera. In *Prohyrax* the condylar foramen, foramen lacernm posterius, foramen lacernm anterius, foramen ovale, and the alisphenoid canal, appear to be similar in position, shape and relative size to those of *Procavia*.

The palatine foramen (palf in fig. 1) in the adult of *Prohyrax* is opposite M<sup>2</sup> whereas in *Procavia* it is opposite M<sup>1</sup>. Near the distal end of the palatine-maxillary suture on the maxillary shelf there is generally a subsidiary posterior palatine foramen (ppf in fig. 1) in both *Procavia* and *Prohyrax*.

### Mandible

In the general morphology of its lower jaw, the Arisdrift hyracoid is similar to *Procavia* and to many other hyracoids. It has a steeply rising coronoid process pierced by a coronoid foramen behind M<sub>3</sub>. It is slim, without any significant lingual or buccal fossae, a feature which occurs in *Meroehyrax* and *Pachyhyrax* among other Miocene and Oligocene taxa. It is not fenestrated as is the mandible of *Megalohyrax championi* from the lower Miocene of East Africa (Whitworth 1954). The jaw is not inflated below the molars; as it is in *Paraplioehyrax*, in which a substantial chamber (a modified and enlarged mandibular canal) runs below the roots of the molars (Pickford & Fischer 1987). In AD 1749, the mandibular foramen is situated horizontally behind M<sub>3</sub>. The symphysis is relatively narrow and houses the first and second incisors of typical hyracoid morphology; I<sub>1</sub> with closed roots and a twisted crown; I<sub>2</sub> with a pennantly growing root and lacking enamel on mesial and distal edges. The tips of I<sub>1</sub> and I<sub>2</sub> are tripectinate when unworn, but the pectinations soon disappear with wear.

All the cheekteeth from I<sub>3</sub> to M<sub>2</sub> are comprised of two crescent-shaped lophs in series. M<sub>3</sub> is trilobed. On anterior teeth the crescents are angular in occlusal outline, whereas in posterior teeth they are more rounded. The cheektooth row is closed from I<sub>1</sub> to M<sub>3</sub>, but there is an occlusal gap between the tip of I<sub>2</sub> and the crown of I<sub>3</sub>, comprising the distal edge of I<sub>2</sub> (Fig. 3A). The

429	P <sup>3</sup>	9.6	9.1
943		8.7	9.4
1196		8.2	9.7
2777		8.0	7.8
2847		10.6	9.7
2878		8.7	9.3e
429	P <sup>4</sup>	9.9	10.2
1196		8.6	10.5
2777		9.0	8.4
2847		11.3	11.7
2878		9.9	10.7
383	M <sup>1</sup>	13.2	11.2
429		13.4	13.9
949		13.5	12.0
1196		9.9	12.5
2777		11.4	10.6
2847		15.2	12.8
2878		12.0	12.6
429	M <sup>2</sup>	15.5	15.3
449		15.8	14.7
1196		12.1	13.5
2777		14.2	12.0
2847		16.3	14.8
2878		13.6	14.8
2923		14.9	14.9
387	M <sup>3</sup>	20.7	14.7
416		20.8	16.5
418		20.4	17.0
432		22.5	16.5
449		22.8	15.4
1196		17.6	14.8
1399		19.4	15.6
2847		19.6	16.5
2878		22.3	16.1
2923		21.2	16.4
2963		21.5	16.8

cheektooth row between I<sub>3</sub> and M<sub>3</sub> is bowed outwards to a much lesser degree than is the cheektooth row of *Procavia* (Fig. 5D<sub>1</sub>).

### Sexual dimorphism

The sample of mandibles at Arrisdrift is large enough (40 ± individuals) that the observed variability in the fossils is probably approaching the actual variability of the species that lived in the middle Miocene. As such one can examine questions as to the nature and causes of variability. As already noted by Hendey (1978), there are individuals with deep mandibles and others with shallow ones (Fig. 6B-C). Measurements of the depth of 29 adult mandibles are listed in Table 3. These plot into two discrete fields separated by a distributional gap (Fig. 11A). There are approximately twice as many individuals in the shallow group as in the deeper one, suggesting at first glance that there may have been a skewed sex ratio in the Arrisdrift hyrax, with more females than males. However, during growth in many sexually dimorphic mammals, the sexes are metrically comparable until puberty, after which the males continue to grow until maturity, whereas females remain more or less the same size, a phenomenon known as bimaturism. The

measurements of young male individuals therefore tend to plot out within the female range of variability until they reach puberty and progress towards maturity, and it is therefore likely that some of the shallow mandibles belong to young males.

A plot of upper central incisors (Fig. 11B, second frame) provides support for the idea that the Arrisdrift hyrax was a sexually dimorphic species, rather than two species within a genus, the array of breadth measurements being bimodal.

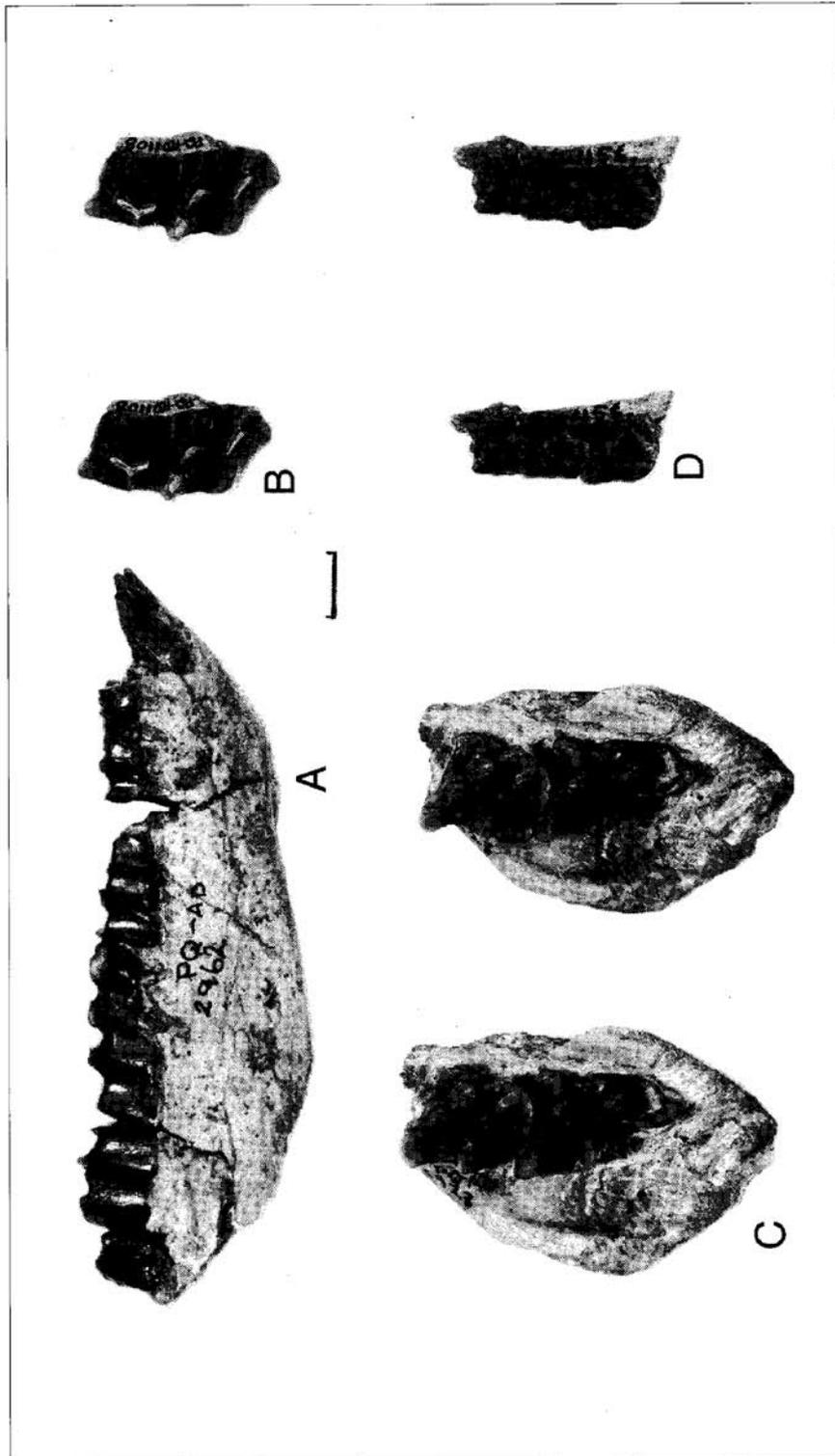
In order to test for the presence of two sexes as opposed to two species in the sample, it is necessary to examine the nature of the variability in other parts of the body. In mammals in general, middle-of-the-row cheekteeth are usually the least dimorphic. Thus, if there is only one species in the sample the P<sub>4</sub> and M<sub>1</sub>, for example, should show a single-peaked Gaussian distribution pattern. In *Prohyrax hendeyi* the metric data obtained from the cheekteeth do indeed plot out as a single-peaked pattern (Fig. 11, lower two frames), indicating the presence of a single species in the sample. It is difficult to evade the conclusion that at Arrisdrift we are dealing with a single species of dimorphic hyrax.

### Deciduous dentition

**Upper dentition.** AD655 is a left maxilla with dC<sup>1</sup>-dP<sup>1</sup> (Fig. 5B) that deserves description. The deciduous upper canine is an elongated molariform tooth with an anteriorly projecting ectostyle. It possesses an anterior fossette, a structure that does not occur in the upper permanent dentition. The large main fossette is closed lingually by a strong crest that runs between the two lingual cusps. The ectoloph is large with clear but not greatly inflated stelar crests. There is a basal swelling in the ectoloph near its cervix, and the ectoloph is appreciably taller than the brachyodont lingual cusps. The dM<sup>1</sup> is similar in morphology to the dC<sup>1</sup>, but is slightly larger than it.

**Lower dentition.** There are several juvenile lower dentitions in the sample from Arrisdrift. AD634 is an infant right mandible, unfused at the symphysis, containing dM<sub>2</sub>, half of dM<sub>3</sub> and complete dM<sub>4</sub>, both in wear, while M<sub>1</sub> is still in the crypt (Fig. 7B-D). The dM<sub>2</sub> is more elongate than its permanent replacement and has a pointed mesial end. The buccal crest is fairly sharply angled. The front half of dM<sub>3</sub> is comparable to that of dM<sub>2</sub> but its buccal crest is weakly developed and its anterior projection not so elongate. It also has a sloping anterior cingulum. In dM<sub>4</sub> the buccal crest is absent and the ectoloph is smoothly curved at its base. The enamel in this tooth is slightly wrinkled and the two crests at the occlusal surface possess angles, and are not smoothly curved as in permanent molars. It has an anterior descending cingulum and a distally extended hypoconulid, as in permanent molars. In the basal portion of the buccal valley there is a small cingular fold.

AD1163 has a worn dM<sub>4</sub> and permanent P<sub>2-3</sub>, M<sub>1-2</sub>; dM<sub>4</sub> is worn flat and only the buccal and lingual enamel



**Figure 4:** *Prohyrax hendeyi* sp. nov. A. AD2962, right mandible and symphysis, lateral view. B. AD1108, right maxilla with P<sup>4</sup>--M<sup>1</sup>, stereo view of occlusal surface. C. AD2923, right maxilla with M<sup>2</sup>--M<sup>3</sup>, stereo view of occlusal surface. D. AD456, right P<sup>1</sup>--P<sup>3</sup>, stereo view of occlusal surface. Scale bar 10 mm.

remains. P<sub>2</sub> has sharply angled ectoloph crescents, and the anterior-sloping cingulum is well formed and swollen. Its lingual cingulum is continuous from mesial to distal, but is sharp and low. P<sub>3</sub> is similar to P<sub>2</sub> but the buccal crests are not so sharply angled. M<sub>1</sub> and M<sub>2</sub> have evenly curved buccal crescent surfaces, weak lingual cingula and prominent hypoconulids.

**Dental eruption sequence**

By cross-correlating various mandibles at different stages of development, it is possible to determine the sequence of eruption of the teeth. *Prohyrax hendeyi* seems to be similar in this respect to *Parapliohyrax ngororaensis* Pickford & Fischer (1987). As far as the sample permits us to determine, the sequence is as follows: dM<sub>2</sub>/dM<sub>3</sub>/dM<sub>4</sub>/M<sub>1</sub>+P<sub>2</sub>/P<sub>3</sub>+I<sub>2</sub>+M<sub>2</sub>/P<sub>4</sub>+M<sub>3</sub>.

**The postcranial skeleton**

**Forelimb**

**Scapula.** There are several fragmentary scapulae from Arrisdrift that are assigned to *Prohyrax hendeyi* because of their hyracoid morphology and size. The best preserved of these is AD462, a left scapula lacking parts of the blade (Fig. 12A) but which otherwise is in reasonable condition. The glenoid, which is not as well developed in the fossils as it is in *Procavia*, is an oval dorsoventrally compressed cavity, as in living hyraxes. The coracoid process is shorter proportionally than in *Procavia*, but the tuber scapulae is similar to that of *Procavia*. The same may be said of the neck, which is long and narrow, but slightly more flattened in the fossil species.

Measurements of the scapula (in mm) are as follows:

Scapular neck	Width	Height
AD462	12,7	7,0
<i>Procavia</i>	7,7	4,5

**Humerus.** There are several humeral fragments in the collection, but none of them is complete. In the most complete specimen, AD59, an adult right humerus lacking the proximal end, the shaft is basically a scaled-up version of the modern hyrax humeral diaphysis, except that the deltoid tuberosity is not as well developed, and the teres tuberosity, which is well defined in *Procavia*, is difficult to discern in the fossil.

AD500 is the distal end of a left humerus (Fig. 12B-C). The lateral and medial condyles have a more rounded profile in the fossil, whereas in *Procavia* the condyles are sharp edged, and in this respect they recall the distal humerus of *Megalohyrax championi* from the lower Miocene of Kenya. The coronoid and olecranon fossae of the humerus are similar in *Prohyrax* and *Procavia*. Both genera possess humeral olecranal foramina. In

**Table 2**  
*Prohyrax hendeyi* sp. nov.  
Lower dentition  
measurements in millimetres  
(e = estimated)  
All specimens prefix AD

Spec.	Tooth	Length	Breadth
115	dM <sub>1</sub>	5.6	3.6
115	dM <sub>2</sub>	7.2	4.2
634		7.9	4.0
906		7.2	4.3
10	dM <sub>3</sub>	---	5.0
115		8.6	5.2
368		8.7	5.6
634		8.8e	4.6e
906		8.1	4.8
1164		9.1	4.8e
3	dM <sub>4</sub>	10.2	6.2
10		9.7	5.3
115		9.9	5.3
255		9.4	5.0
368		10.2	6.3
404		9.3	5.2
634		9.9	4.7
906		9.5	5.2
1163		9.8	6.0
1164		10.2	5.6e
1166		9.8	5.6
2962	I <sub>1</sub>	6.0	4.1
1636	I <sub>2</sub>	6.0	4.6
2962		6.5	4.8
3091		6.0	5.8
1636	C*	6.5	4.8
3091		6.2	4.7
3	P <sub>1</sub>	7.4	5.1
1636		7.7	5.5
3091		7.7	5.6
3	P <sub>2</sub>	8.3	5.7
373		7.5	5.3
1163		8.4	5.3
1636		9.2	6.1
2522		7.5	5.5
2623		7.7	5.8
2962		9.5	6.0
3091		8.6	6.1
3	P <sub>3</sub>	9.8	6.8
16		8.6	6.6
120		9.1	6.4
373		9.0	6.8
1163		9.0e	6.2e
1636		10.3	7.1
2522		8.5	6.5
2623		9.4	6.9
2876		9.0	7.2
3091		9.4	7.0
3101		9.8	6.5
8	P <sub>4</sub>	9.0	7.4
16		9.7	7.0
120		9.5	7.0
172		10.0	7.0
373		9.5	7.3
432		11.0	7.3
1636		11.5	8.1
2088		10.2	7.8
2522		9.7	6.7
2623		9.8	7.4
2778		9.2	7.5
2876		9.2	7.6
2962		12.8	7.6
3101		10.2	6.5

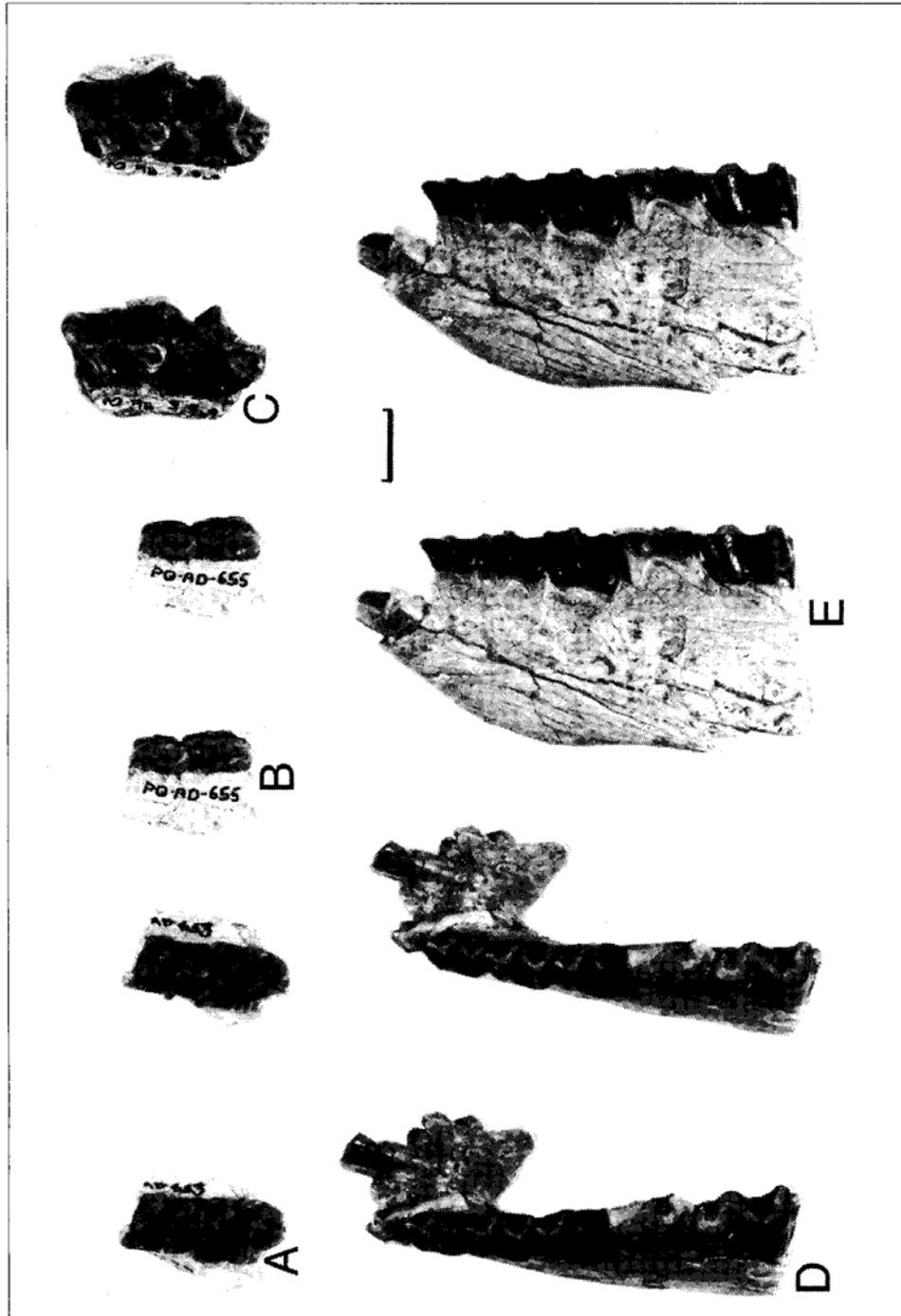
1	M1	12.7	7.2
3		12.0	6.6
8		10.2	8.0
10		12.0	---
15		12.3	6.8
16		11.6	7.3
115		11.6	6.2
279		12.0	6.0
368		11.3	6.9
372		11.5	7.0
373		10.3	7.4
415		13.0	8.0
432		13.5	7.3
1163		11.8	6.5
1164		12.3	6.3
1166		12.2	6.5
1636		14.7	8.1
1974		---	7.2
2088		11.9	7.7
2522		11.4	6.8
2632		11.0	7.3
2778		11.0	---
2876		10.8	8.1
2962		13.0	7.6
3091		---	8.1
3101		13.3	8.0
<hr/>			
1	M2	14.8	8.0
8		13.4	8.7
15		14.3	7.5
16		14.5	8.0
172		11.8	7.3
372		13.2	7.0
373		13.5	8.5
415		14.0	7.8
422		15.5	8.0
437		15.0	7.9
454		14.8	8.6
482		12.1	7.7
948		14.3	7.9
1163		13.7	7.2
1636		16.7	9.0
1883		14.1	8.6
1974		13.8	7.9
2088		14.3	8.3
2522		13.1	7.5
2623		14.3	8.4
2624		15.0	8.1
2746		13.7	8.5
2778		13.1	8.5
2779		11.6	8.7
2876		13.5	8.8
2877		12.3	8.6
3091		15.4	8.2
3101		15.2	8.5
3119		12.5	8.0
<hr/>			
1	M3	23.0	8.6
7		21.3	7.5
8		21.0	8.5
120		21.1	8.2
172		22.2	8.2
284		22.0	9.0
290		22.5	8.7
350		20.5	8.4
367		22.5	8.4
373		21.7	8.4
415		21.2	8.6
422		24.5	8.4
437		21.4e	8.1
454		22.0	8.6
482		20.2	7.8
581		20.5	7.9
651		21.7	8.0

907	23.9	9.3
908	25.5	9.8
948	22.6	8.4
1172	20.4	8.4
1193	22.0	8.2
1636	25.6	---
1640	21.9	8.3
1648	21.8	10.2
1883	23.4	8.9
1974	25.0	8.8
2088	23.2	---
2148	24.5	8.9
2522	21.7	8.2
2623	20.6	8.7
2624	23.7	8.8
2633	22.4	8.9
2656	22.5	8.5
2746	24.1	8.8
2778	21.5	8.7
2779	22.3	8.7
2800	22.5	---
2876	21.8	9.0
2877	23.0	9.2
2962	22.9	8.6
3018	22.7	8.0
3101	24.1	8.3
3119	22.4	8.1

*Prohyrax* the part of the medial epicondyle to which the medial ligament is attached is weak and flat, in marked contrast to its morphology in *Procavia*, in which it is large and projecting. The positions of attachment of the insertions of the flexor and extensor muscles of the carpus and digits are situated more posteriorly in the fossil, so that the epicondyle is antero-posteriorly enlarged. This makes it larger than the lateral condyle, whereas the opposite is the case in *Procavia*. In addition, the articular surface extends further into the olecranon fossa in the fossil, suggesting that a greater degree of ulnar extension was possible in *Prohyrax* than in *Procavia*.

The rounded condylar edges in the fossil suggest that when it was in the flexed position, the elbow joint was more flexible in pronation than is the case in *Procavia*, in which the action of the elbow is effectively confined to the parasagittal plane, with little or no rotational possibilities for the radius. The insertions of the extensor muscles of *Prohyrax* are enlarged compared with those of *Procavia*, suggesting the existence of a more developed extensor function in *Prohyrax*, perhaps with greater elbow stability in the fully extended position, but allowing slight pronation when the elbow was flexed. In the olecranon fossa; there is a notch in its lateral pillar for reception of the lateral eminence of the anconeal process. This feature would also serve to stabilize the joint while it was in the fully extended position.

Specimen	Measure	Dimension (mm)
AD59	length of humerus lacking distal end	7,4
AD500	maximum width of distal articulation	16,8
<i>Procavia</i>	maximum width of distal articulation	9,1



**Figure 5:** *Prohyrax hendeyi* sp. nov. A. AD653, right maxilla with  $dM^2$ -- $dM^3$ , stereo view of occlusal surface. B. AD655, left maxilla with  $dC$ -- $dM^1$ , stereo view of occlusal surface. C. AD949, left maxilla with  $dM^4$ -- $M^1$ , stereo view of occlusal surface. D--E. AD3, left mandible and symphysis with right  $I_1$ , left  $P_1$ -- $P_3$ ,  $dM_4$ , and  $M_1$ . D. Stereo view of occlusal surface. E. stereo view of lateral surface. Scale bar 10 mm.

**Radio-ulna.** Apart from size, the radio-ulnae of *Prohyrax* are remarkably similar to those of *Procavia*. Among important differences are the inclination of the superior edge of the olecranon process, which in *Prohyrax* slopes appreciably away from the long axis of the shaft. In *Procavia* it is more or less in line with the shaft, so that when extended the elbow joint is still slightly bent. Such angulation of the elbow is a common feature of cursorially adapted mammals, such as bovids and equids, suggesting that *Prohyrax* was probably more cursorial than *Procavia*. The radius and ulna are strongly fused proximally and distally, both in the fossil and living forms (Fig. 12D&H). Their shafts are robust and, in distal view, the articular surfaces are closely comparable in morphology (Fig. 12H). However, in *Prohyrax* the facet for the radial carpal bone is separated from that of the intermediate carpal by a more vertically oriented facet. The groove for the tendon of the digital extensors is much better defined in *Prohyrax* than in *Procavia*, suggesting that extension was relatively more important in the fossil form. The more angled, or sharply defined, distal facets of the fossil radio-ulna suggest that the stability of the joint would have been greater than it is in *Procavia*.

Measurements of the radio-ulna are as follows:-

Specimen	Measure	Dimension (mm)
AD2715	length from proximal radius to distal end	99,6
<i>Procavia capensis</i>	length from proximal radius to distal end	51,7
AD2715	width of proximal articular surface	15,5
<i>Procavia capensis</i>	width of proximal articular surface	8,7
AD2715	maximum width of distal end radio-ulna	19,3
<i>Procavia capensis</i>	maximum width of distal end radio-ulna	13,0

### Hind limb

**Pelvis.** Among the several Arrisdrift pelvic fragments assignable to hyracoids, there is only one which is more than a small fragment. AD2498 (Fig. 13A) is basically a scaled-up version of the pelvis of *Procavia*, but the depressions for the attachment of the m. rectus femoris are better developed in the fossil. In other respects, the acetabulum and acetabular surfaces are similar in *Procavia capensis* and *Prohyrax*.

Measurements of the pelvis are as follows:

Specimen	Measure	Dimension (mm)
AD2498	max. diameter of the acetabular fossa (ant.-post.)	12,3
<i>Procavia capensis</i>	max. diameter of the acetabular fossa (ant.-post.)	17,3

**Femur.** The femora assigned to *Prohyrax* are basically similar to those of *Procavia* (Fig. 13B-C), although the greater trochanter in the fossil is relatively expanded anteriorly so that the anterior part of the trochanter is as wide as the posterior part (Fig. 13C). In *Procavia capensis* the anterior part of the greater trochanter is very reduced. The trochanteric fossa is similar in both

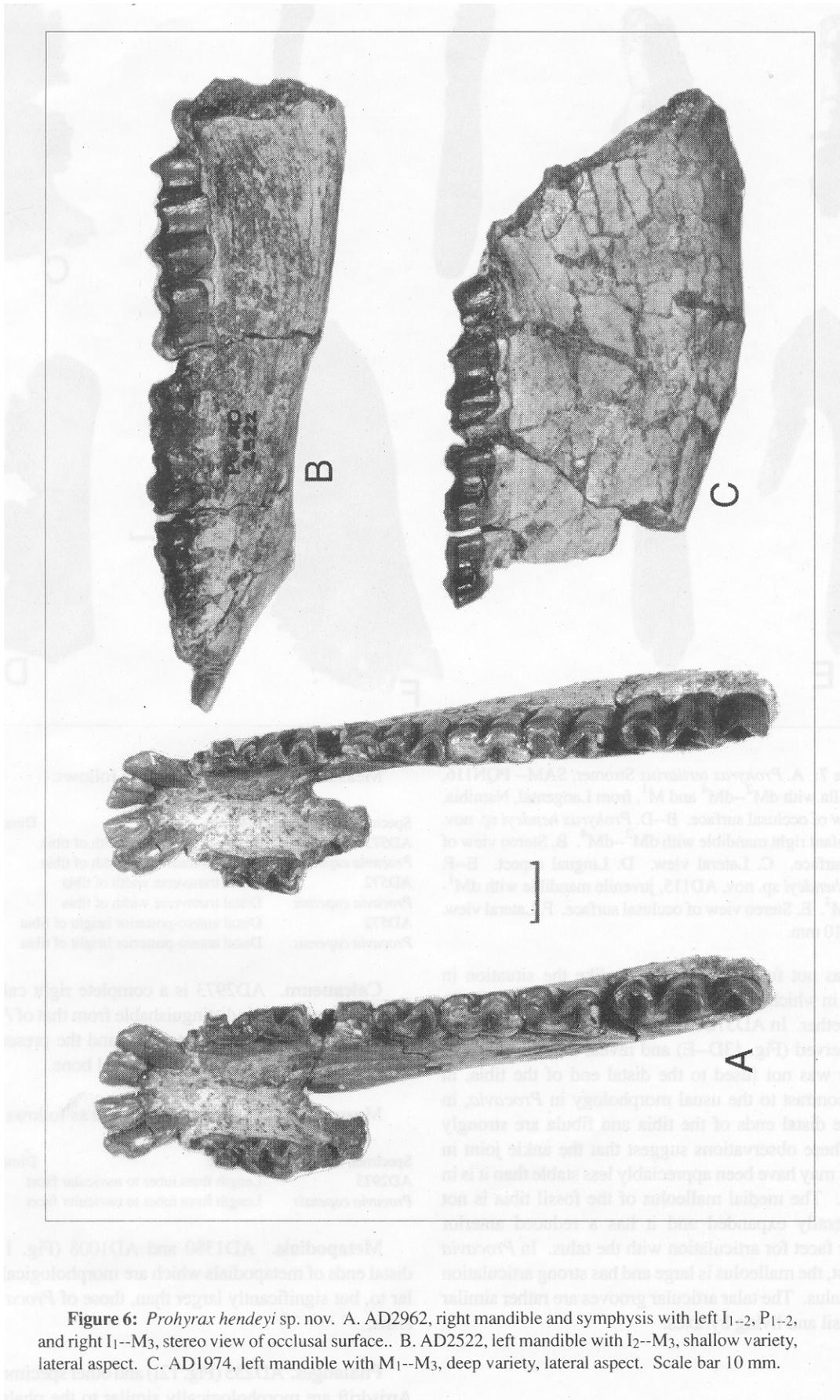
the living and the fossil forms, but the lesser trochanter is proximo-distally expanded in *Prohyrax* and extends as a sharp ridge up the neck towards the femoral head (Fig. 13B). In *Procavia capensis* on the other hand, the lesser trochanter does not extend greatly onto the neck of the femur. The anterior surface of the shaft between the neck and the major trochanter in the fossil is flattened, whereas it is more rounded in *Procavia*. The third trochanter in the fossil (Fig. 13C) is situated appreciably more distally on the shaft than it is in *Procavia*, in which it is almost opposite the lesser trochanter.

The distal end of the femur in *Prohyrax hendeyi* is flatter antero-posteriorly than it is in *Procavia capensis*. The distal articular surfaces are relatively narrower and taller in *Prohyrax* than in living hyraxes; thus the patellar groove in the fossil is narrow and tall compared with the same portion of a *Procavia* femur, suggesting a greater cursorial adaptation in *Prohyrax* than in *Procavia*. This is reflected in the measurements; in *Prohyrax* the patellar groove is only slightly wider than it is in *Procavia capensis* (12,2 mm versus 10,0 mm), whereas the height of the distal end of the femur is considerably larger (27,5 mm versus 16,4 mm). The lateral supracondylar fossa of the femur is much more evident in the fossil and the tibial facets are slightly offset, which contrasts with the smaller fossa and nearly opposing facets in *Procavia*. The antero-posterior enlargement and the medio-lateral narrowing of the distal articular facets suggests a more cursorial life-style for the fossil species; indeed, the femur has converged to some extent towards the morphology usually found in bovids. The relatively higher and narrower patellar groove suggests that *Prohyrax* had a more stable knee joint in all positions from fully flexed to fully extended, than is the case in *Procavia*,

Measurements of the femur are as follows:-

Specimen	Measure	Dimension (mm)
AD1133	femur head diameter	13,7
<i>Procavia capensis</i>	femur head diameter	9,4

**Tibia.** AD475, a proximal end of a tibia (Fig. 12E-F) is very similar in general morphology to that of *Procavia capensis* but is less curved antero-posteriorly along the shaft, i.e. the fossil shaft is straighter. The proximal attachment of the fibula is not at all obvious in the fossil, indicating that it was not fused to the tibia, unlike the situation in *Procavia* in which the proximal fibula and tibia are strongly fused together. In AD572+573, the shaft and distal end are well preserved (Fig. 13D-E) and reveal that the fibula of *Prohyrax* was not fused to the distal end of the tibia, in marked contrast to the usual morphology in *Procavia*, in which the distal ends of the tibia and fibula are strongly fused. These observations suggest that the ankle joint in *Prohyrax* may have been appreciably less stable than it is in *Procavia*. The medial malleolus of the fossil tibia is not mediolaterally expanded and it has a reduced anterior malleolar facet



**Figure 6:** *Prohyrax hendeyi* sp. nov. A. AD2962, right mandible and symphysis with left I<sub>1-2</sub>, P<sub>1-2</sub>, and right I<sub>1</sub>--M<sub>3</sub>, stereo view of occlusal surface. B. AD2522, left mandible with I<sub>2</sub>--M<sub>3</sub>, shallow variety, lateral aspect. C. AD1974, left mandible with M<sub>1</sub>--M<sub>3</sub>, deep variety, lateral aspect. Scale bar 10 mm.

**Table 3**

*Prohyrax hendeyi* sp. nov. Mandibular depth below M<sub>3</sub> measurements in millimetres (e = estimated)  
All specimens prefix AD

Specimen Number	Depth of Jaw
1	29.7
4	28.0
5	32.0
8	23.3
16	25.6
120	28.5
172	27.2
290	28.0
350	33.9
373	26.5
415	29.7
437	25.8
454	32.3
908	34 <sub>e</sub>
1197	25.2
1648	28.0
1974	37.0
2088	25.5
2148	33.2
2522	22.8
2623	26.0
2746	28.7
2778	27.9
2779	25.0
2876	29.3
3018	36.0
3082	34.8
3112	27.0

for articulation with the talus. In *Procavia* in contrast, the malleolus is large and has strong articulation with the talus. The talar articular grooves are rather similar in the fossil and living hyraxes.

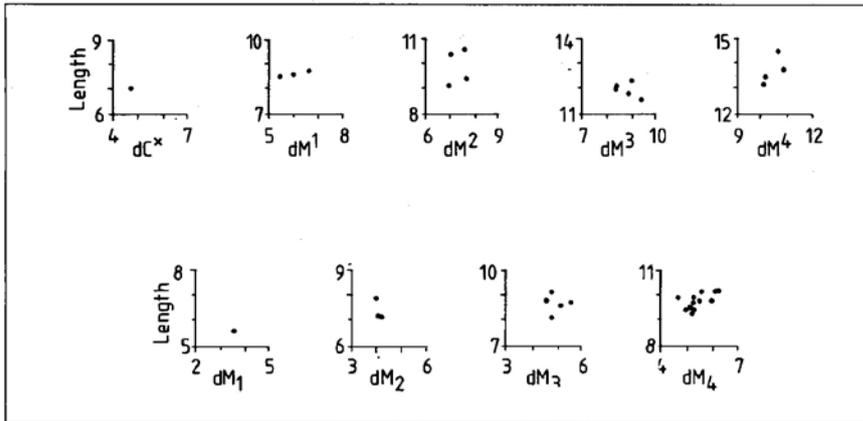
Measurements of the tibia are as follows:

Specimen	Measure	Dimension (mm)
AD573	Proximal transverse width of tibia	24,5
<i>Procavia capensis</i>	Proximal transverse width of tibia	16,0
AD572	Distal transverse width of tibia	14,2
<i>Procavia capensis</i>	Distal transverse width of tibia	12,2
AD572	Distal antero-posterior height of tibia	11,5
<i>Procavia capensis</i>	Distal antero-posterior height of tibia	6,9

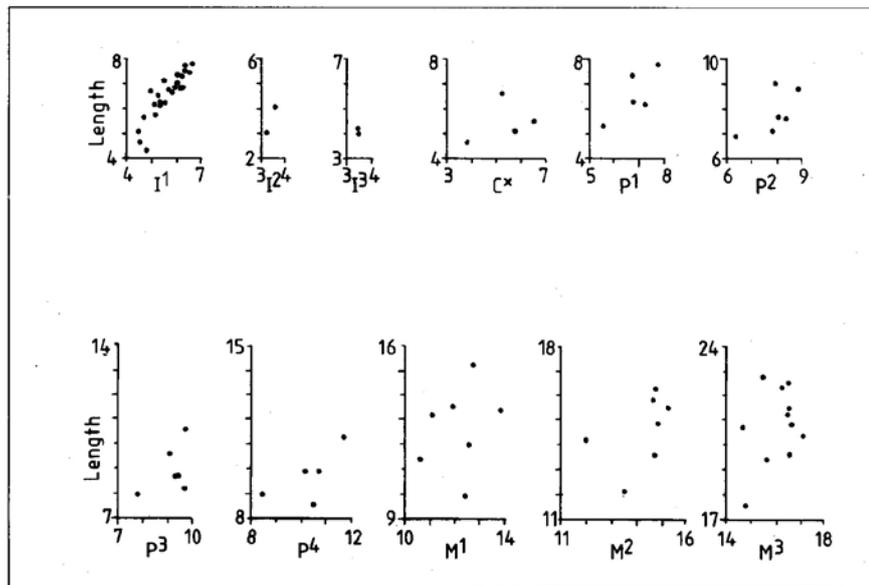
**Calcaneum.** AD2973 is a complete right calcaneum (Fig. 13F), which is indistinguishable from that of *Procavia capensis* apart from its greater size and the presence of a slightly larger facet for the fourth tarsal bone.

**Figure 7:** A. *Prohyrax tertarius* Stromer, SAM-PQN116, right maxilla with dM<sup>2</sup>-dM<sup>4</sup> and M<sup>1</sup>, from Langental, Namibia, stereo view of occlusal surface. B-D. *Prohyrax hendeyi* sp. nov. AD634, infant right mandible with dM<sup>2</sup>-dM<sup>4</sup>. B. Stereo view of occlusal surface. C. Lateral view. D. Lingual aspect. E-F. *Prohyrax hendeyi* sp. nov. AD115, juvenile mandible with dM<sup>1</sup>-dM<sup>4</sup> and M<sup>1</sup>. E. Stereo view of occlusal surface. F. Lateral view. Scale bar 10 mm.

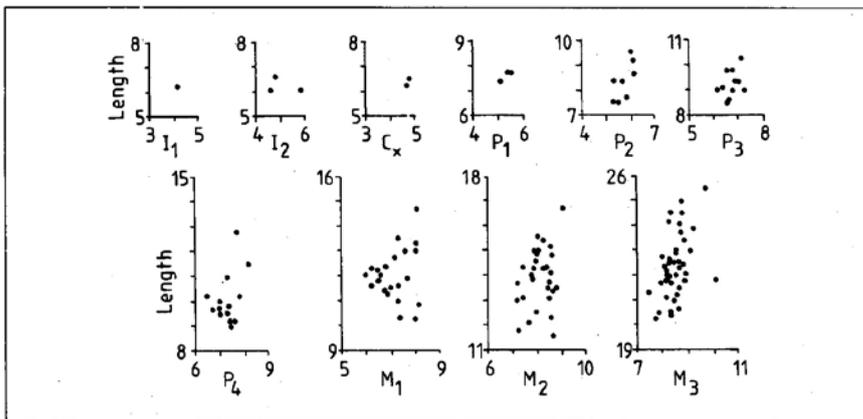




**Figure 8:** Bivariate plots (length and breadth) of the milk teeth of *Prohyrax hendeyi* sp. nov. Scale in mm.



**Figure 9:** Bivariate plots (length and breadth) of the upper permanent teeth of *Prohyrax hendeyi* sp. nov. Scale in mm.



**Figure 10:** Bivariate plots (length and breadth) of the lower permanent teeth of *Prohyrax hendeyi* sp. nov. Scale in mm.

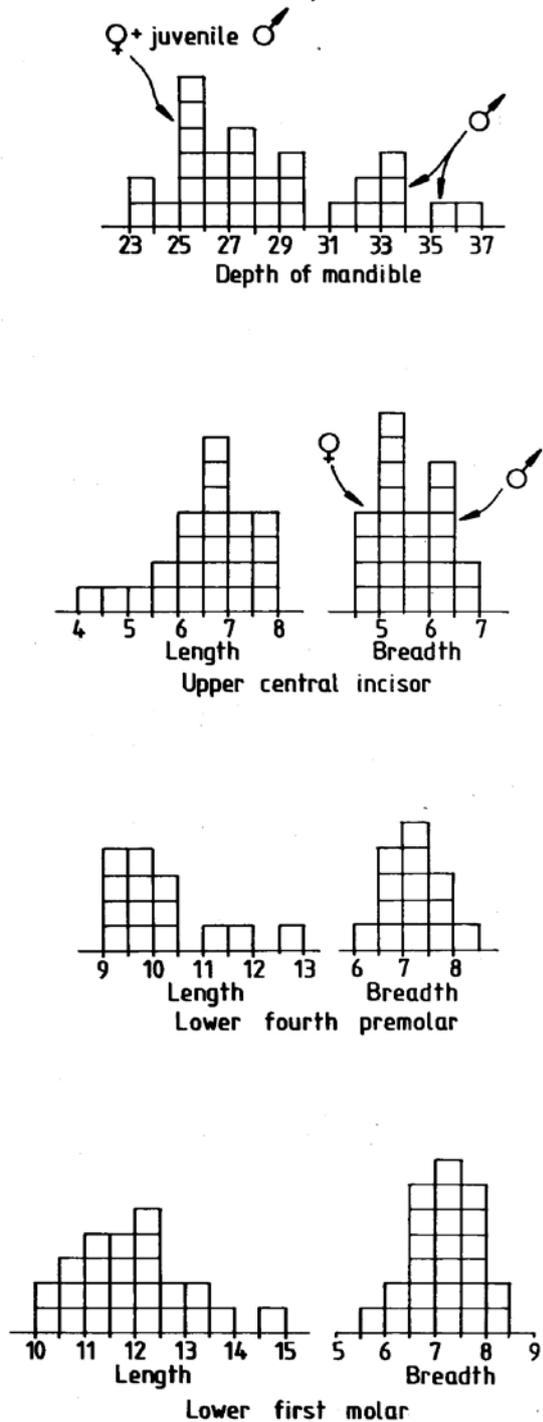


Figure 11: *Prohyrax hendeyi* sp. nov. Variability and sexual dimorphism in depth of mandible (upper frame), upper central incisors, and P and M<sub>1</sub>. Note bimodal distribution in mandibular depth measures and I<sup>1</sup> widths, but unimodal distribution in widths of P<sub>4</sub> and M<sub>1</sub>. Such data suggest that the sample represents a single species marked by sexually dimorphic mandibles and upper central incisors.

Measurements of the calcaneum are as follows:-

Specimen	Measure	Dimension (mm)
AD2973	Length from tuber to navicular facet	35,2
<i>Procavia capensis</i>	Length from tuber to navicular facet	21,2

**Metapodials.** AD1380 and AD1008 (Fig. 12G) are distal ends of metapodials which are morphologically similar to, but significantly larger than, those of *Procavia capensis*.

**Phalanges.** AD235 (Fig. 121) and other specimens from Arrisdrift are morphologically similar to the phalanges of *Procavia capensis* but are appreciably larger.

**New fossil of *Prohyrax tertarius* Stromer**

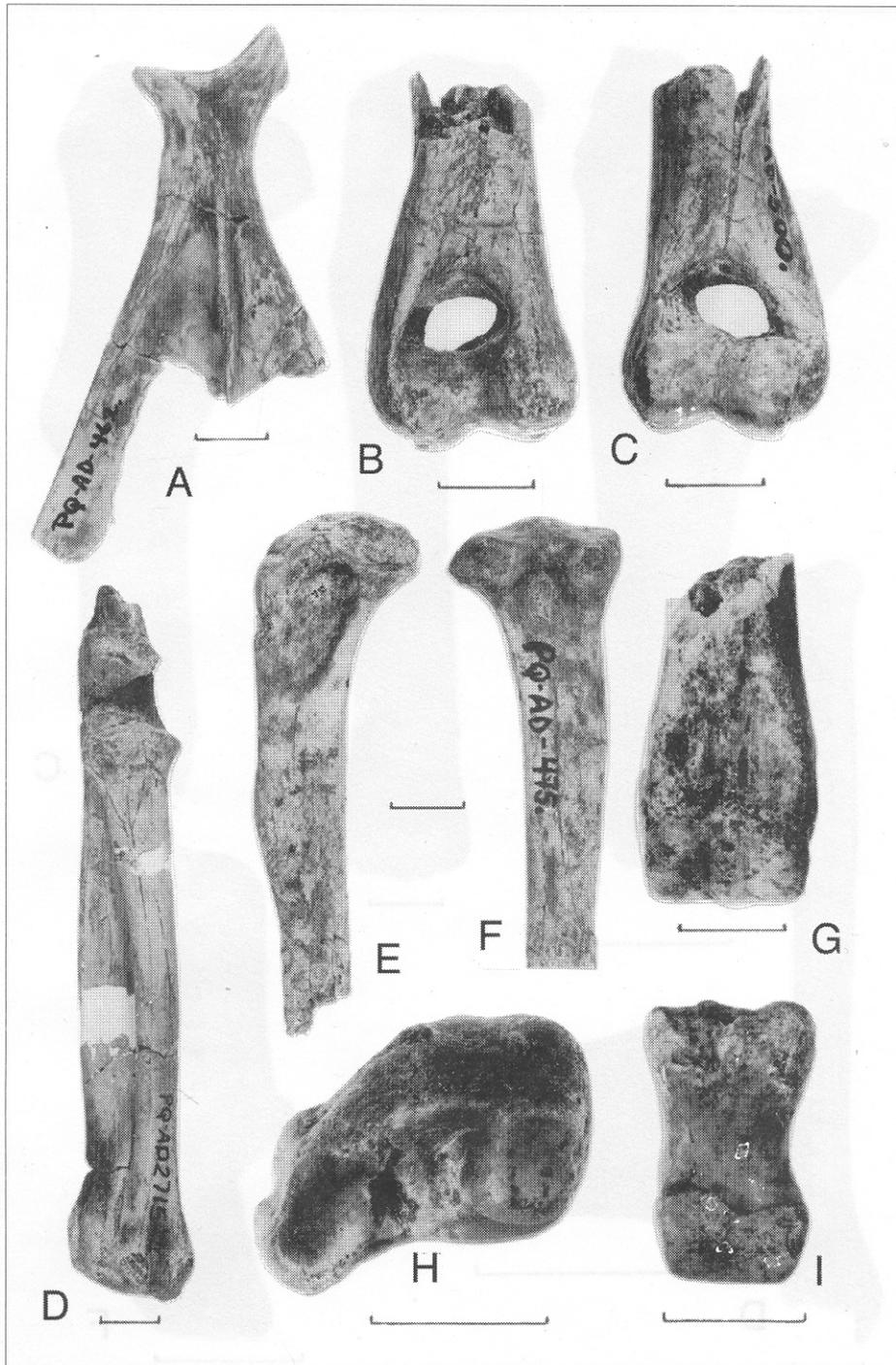
SAM-PQN116 is a right maxilla with dM<sup>2</sup>-M<sup>4</sup> and M<sup>1</sup> from the Lower Miocene beds of the northern Sperrgebiet at Langental (Fig. 7A). The orbit in this juvenile specimen is above the dM<sup>4</sup>-M<sup>1</sup>, as in individuals of *Prohyrax hendeyi* of the same ontogenetic age. Styles in the ectoloph of the deciduous upper molars increase in size from mesial to distal, until in dM<sup>4</sup>, the crown is similar in appearance to permanent molars. The M<sup>1</sup> has erupted but is little worn. Apart from being much smaller than that in *P. hendeyi*, the teeth in this specimen differ by having less inflated styles. Nevertheless, the two species are probably closely related, at least on the basis of the known parts.

Measurements of the teeth of *Prohyrax tertarius* and *P. hendeyi* are as follows:-

Tooth	Species	Length	Breadth	
dM <sup>2</sup>	<i>P. tertarius</i>	6,0	5,4	
dM <sup>2</sup>	<i>P. hendeyi</i>	9,4-10,5	6,9-7,6	n=5
dM <sup>3</sup>	<i>P. tertarius</i>	6,8	6,3	
dM <sup>3</sup>	<i>P. hendeyi</i>	11,6-12,3	8,4-9,4	n=5
dM <sup>4</sup>	<i>P. tertarius</i>	8,1	7,5	
dM <sup>4</sup>	<i>P. hendeyi</i>	13,1-14,4	10,1-10,9	n=4
M <sup>1</sup>	<i>P. tertarius</i>	9,7	8,8	
M <sup>1</sup>	<i>P. hendeyi</i>	9,9-15,2	10,6-13,9	n=7

**Discussion**

**Skull and mandible.** Comparison of *P. hendeyi* and the few available fragments of *Prohyrax tertarius* (the holotype and SAM-PQN116, a right maxilla with dP<sup>2-4</sup> and M<sup>1</sup>) indicates that Hendey's assignment of the Arrisdrift fossils to *Prohyrax* is probably correct. A perennial problem with the genus has been the inadequate nature of the holotype, and several problems have arisen. Meyer (1978), for example, thought that *Meroehyrax* Whitworth (1954) might be a synonym of *Prohyrax*, because the former was known only by lower dentitions, whereas the latter was known only by the maxillae. However, the shapes of the jaw and teeth in *Meroehyrax bateae*, the type species from Rusinga Island, Kenya (Whitworth 1954), do not closely resemble



**Figure 12:** *Prohyrax hendeyi* sp. nov. A. AD462, left scapula, lateral aspect. B-C. AD500, distal end of left humerus, posterior and anterior aspects. D&H. AD2715, right radio-ulna lacking the head of the olecranon, anterior and distal aspects. E-F. AD475, proximal end of left tibia, lateral and posterior aspects. G. AD1008, distal end of metapodial, volar aspect. I. AD235, first phalanx, volar aspect. All scale bars 10 mm.

the jaws and teeth of *P. hendeyi*. In *Meroehyrax* there is a large mandibular chamber below the cheekteeth on the lingual side of the body, a structure that is unknown in the Arrisdrift sample. In effect it is difficult to decide whether the few upper teeth from Loperot, Kenya, or Gebel Zelten, Libya (Meyer 1978), belong to *Meroehyrax* or to *Prohyrax*. Unless the exact position of isolated

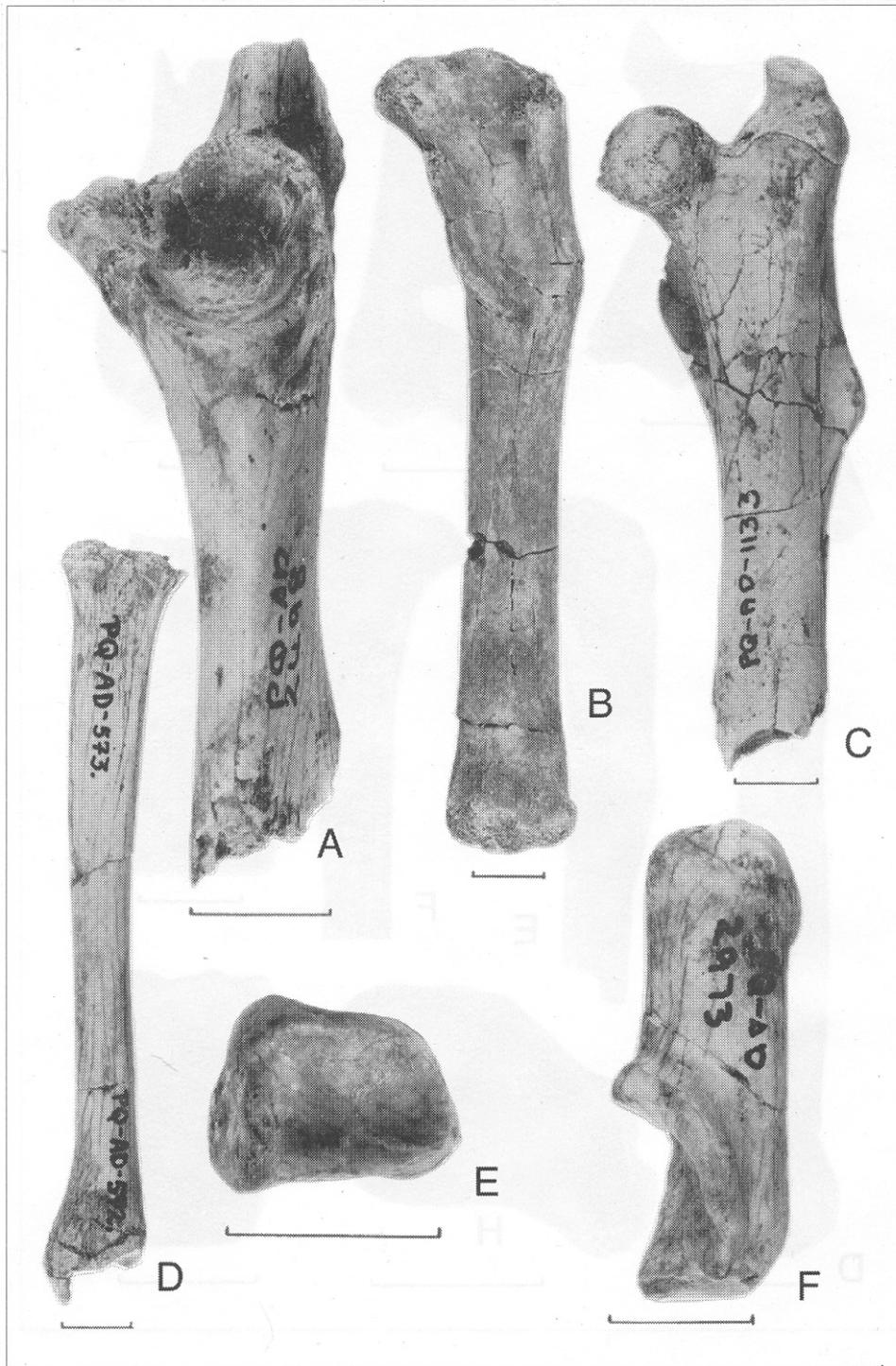
teeth within the toothrow is known, it will continue to be a problem to determine to which taxon they belong.

The newly available fossil of *Prohyrax tertarius* from Namibia provides more information about the species (Fig. 7 A) but no  $M^3$  has been collected, so the most characteristic tooth of *P. hendeyi* cannot be compared with *Prohyrax tertarius*. Apart from this, the only sig-

nificant differences, other than size, are that the styles on the upper molars are less inflated and the basal cingulum on the upper molars is less developed, but both these features are possibly allometric in nature. In other respects the Arrisdrift species is merely an enlarged version of *Prohyrax tertarius*.

There are several similarities between the dentition

of *P. hendeyi* and *Paraplioxyrax* (Pickford & Fischer 1987), including upper molars that possess brachyodont lingual cusps and hypsodont buccal ones. Furthermore, the M<sup>3</sup> of *Prohyrax* has an extension of the ectoloph distally, which forms a third lobe as in *Paraplioxyrax*, but it lacks the distal bifurcation found in that genus. Tri-lobed upper third molars are not found in any of the



**Figure 13:** *Prohyrax hendeyi* sp. nov. A. AD2498, right pelvic fragment, acetabular aspect. B. Right femoral diaphysis, juvenile, posterior aspect. C. AD 1133, proximal end of left femur, anterior aspect. D-E. AD572+573, right tibia, posterior aspect and distal articular view. F. AD2973, right calcaneum, medial aspect. All scale bars 10 mm.

Fayum hyracoids, nor in the lower Miocene species. of East Africa, nor does such a structure occur in living hyracoids. This morphology is therefore unique to Pliohyracidae (Pickford & Fischer 1987).

Unfortunately, the Arrisdrift species appears to throw little light on the origins of modern hyracoids, its dentition being too highly derived for it to be in the ancestry of *Procavia*, *Dendrohyrax* or *Heterohyrax*. However, *Prohyrax* could well represent the ancestral group from which *Parapliohyrax*, *Pliohyrax*, and other Eurasian pliohyracids such as *Kvabebihyrax* and *Postschizotherium*, emerged, as discussed by Pickford & Fischer (1987).

The type species of *Parapliohyrax* is from Beni Mellal, Morocco (Lavocat 1961; Ginsburg 1977). Recently, some isolated teeth assignable to *Parapliohyrax mirabilis* were collected by B. Loiret from a locality south of Kerouan in Tunisia, from sediments identified as part of the Beglia Formation. In the same collection there are fossils belonging to *Hipparion*, so these specimens are probably slightly younger than the type series from Beni Mellal. Judging by their size and the angular labial edge of the crescents, the two Tunisian teeth are premolars, probably P<sub>3</sub> and P<sub>4</sub>. They are characterized by prominent labial flare and by the rear loph being appreciably wider than the anterior one.

Measurements of the Kerouan *Parapliohyrax* specimens are as follows:

Specimen right	Length	Breadth
?P <sub>3</sub> right	11,0	8,6
?P <sub>4</sub>	14,3	11,6

#### *Postcranial skeleton*

The available postcranial elements of *Prohyrax hendeyi* are, generally speaking, scaled-up versions of their counterparts in *Procavia capensis*, being 1,6-2,1 times larger. They are by no means exact enlarged replicas, however, their muscle scars usually being more marked, their long bone shafts being straighter and the elbow and knee joints showing features suggesting greater joint stability in fully extended positions. In flexed positions, in contrast, the elbow joint apparently had greater possibilities for enhanced pronation movements. The ankle joint also seems to have been less stable in *Prohyrax* than in *Procavia capensis*, the tibial malleolus of *Prohyrax* being relatively reduced and the fibula unfused to the tibia. Taken as an assemblage, this combination of limb bone features suggests that *Prohyrax* had a more cursorial mode of locomotion than does *Procavia capensis* but that, in flexed postures, there was a requirement for a certain amount of flexibility at the elbow and ankle joints.

#### **Conclusions**

*Prohyrax hendeyi* sp. nov., a middle Miocene hyra-

coid from Arrisdrift, Namibia, was nearly twice the size of *Procavia capensis* and about 33 per cent larger than *Prohyrax tertarius*. It is represented by abundant cranial, dental and postcranial elements, which reveal that even though in its skeleton it was basically an enlarged version of *Procavia capensis*, in detail it possessed features that indicate its distinctiveness, not only at the specific and generic levels, but probably also at the sub-family level.

Among the dental features that distinguish *Prohyrax* from *Procavia* are the presence of a full eutherian dentition (although the I<sub>3</sub> may be lost in some or most individuals, a point which requires further study), upper molars with brachyodont lingual cusps and hypsodont buccal ones comparable to those of *Parapliohyrax* and *Pliohyrax*, and a well developed third lobe in the upper M<sup>3</sup>.

*Prohyrax* differs from *Parapliohyrax* in a number of features. It lacks the external mandibular fossa, the mandibular chamber and the palatine pocket while the third lobe in the M<sup>3</sup> is not bifurcate. It differs from *Pliohyrax* in its lack of cementum on the molars, by its smaller size and by having unreduced nasal bones and its nasal opening directed forwards rather than upwards.

In the skull of *Prohyrax* there are several specialized features, including the presence of a nasomaxillary foramen and its associated groove which leads eventually into the orbit above the lacrimal. Other distinctive characters include the posteriorly extended palatines and the sunken tympanic bullae.

Postcranially the resemblances between *Prohyrax* and *Procavia* are more marked, but the shafts of the long bones tend to be straighter in *Prohyrax* and the fibula is not fused to the tibia, neither proximally nor distally.

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