J. du P. Bothma

Recent Hyracoidea (Mammalia) of Southern Africa

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RECENT HYRACOIDEA (MAMMALIA) OF SOUTHERN AFRICA

By J. DU P. BOTHMA

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INTRODUCTION

The order Hyracoidea has long been a source of speculation and confusion to naturalists and zoologists alike. This is especially evident in the speculations of earlier authors regarding the morphological and phylogenetic affinities of the Hyracoidea to the other mammalian orders, cf. Gregory (1910: 360).

Gregory (1910: 45-93) thoroughly reviewed the nomenclatural history of the order Hyracoidea, and from his work it is evident that T. H. Huxley first credited the Hyracoidea with separate ordinal rank in his Introduction to the Classification of Animals of 1869. At present the dassies still resort under the order Hyracoidea, their correct taxonomic position (Simpson, 1945: 40-134) being:

Class: Mammalia
Subclass: Theria
Infraclass: Eutheria
Cohort: Ferungulata
Superorder: Paenungulata
Order: Hyracoidea

It is currently believed that in South Africa the dassie was first mentioned by Kolbe in 1719 (Shortridge, 1934: 382), but Van Riebeeck already mentioned this animal in his Journal between 1652 and 1655 (Bosman & Thom, 1952: 85). It was only in 1766, however, that the first description of the dassie was published by Pallas (1766: 30), who named it Cavia capensis. Since this description by Pallas a multitude of species and subspecies have been described, with the result that the taxonomy of this order is as confusing as the morphological relationships of the animals themselves.

Twenty-eight years ago Allen (1939: 442-52) listed 10 African and Arabian species with 79 subspecies. Roberts (1951: 252-63) described seven new subspecies and recognized 22 subspecies in Southern Africa alone. Ellerman, Morrison-Scott & Hayman (1953: 157-62) increased this number to 27 subspecies in their concept of Southern Africa (including also northern Mozambique, Malawi, Zambia and Angola). No new species or subspecies have been described in Southern Africa since 1953.

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In 1934 Hahn undertook the task of revising the taxonomy of the Procaviidae. However, he based his results mainly on minor colour differences and did not take normal population variation into account. Although Roberts (1951: 252–63) tried to sort out and to simplify matters, he succeeded in complicating the hyracoidan taxonomy by adding seven new Southern African subspecies. One of these, *Procavia capensis klaaverensis*, occurs geographically so near to another, *P. c. marlothi* Brauer, that it is almost impossible to separate their type localities on a normal map.

Ellerman et al. (1953: 157–62) present nothing new to clarify the picture. In fact, by naming one of the Kaokoveld dassies *Procavia capensis welwitschii* (Gray), while related animals from the same area are named *Dendrohyrax (Heterohyrax) brucei tsuambensis* (Roberts) and *D. (H.) brucei otjiwarongensis* (Roberts) respectively, taxonomic chaos is compounded.

The present paper is an attempt to revise this order, at least where Southern Africa is concerned. However, the revision does include a number of references to certain extralimital specimens in order to compare them with Southern African forms in geographical proximity to them. Southern Africa is taken here as the part of Africa south of the Cunene and the Zambesi Rivers.

Unfortunately certain parts of Southern Africa have not been surveyed as thoroughly as others, and these areas may yet prove to contain specimens quite distinct from those discussed here. This is especially true of the north-eastern parts of Southern Africa: the eastern part of Rhodesia, the whole of Mozambique south of the Zambesi River and also Bechuanaland, Swaziland and Basutoland.

Colour was used extensively in the past as a taxonomic criterion in the Hyracoidea. However, the only colour criterion constant enough to be of value in this respect is the colour of the dorsal spot. This spot is situated in the mid-dorsal lumbar region of the dassie and its colour is constantly different from species to species. This is especially of importance in the dassies from South West Africa, where the Cape dassie, *Procavia capensis* (Pallas), with its black dorsal spot, is replaced by the Kaokoveld dassie, *P. welwitschii* (Gray), with a yellow dorsal spot.

No new forms are described. Recognition of species and subspecies is based on morphological grounds, which in one case include a constant difference in colour.

**Material**

A total of 620 specimens was studied, consisting of:

- *Procavia capensis* 485 specimens
- *P. welwitschii* 63 specimens
- *Heterohyrax brucei* 63 specimens
- *Dendrohyrax arboreus* 9 specimens

Specimens from the following collections were examined:

- Transvaal Museum, Pretoria
- Kaffrarian Museum, King William's Town
- Natal Museum, Pietermaritzburg
- National Museum, Bulawayo
- South African Museum, Cape Town
- McGregor Memorial Museum, Kimberley
- Medical Ecology Centre, Johannesburg
- Port Elizabeth Museum, Snake Park and Oceanarium, Port Elizabeth
- Private collection, now in the Transvaal Museum
The following type specimens were examined:


*P. c. coombesi* Roberts, 1924, TM 3489, ♂, collected: 17. iii. 1923, Hennops River, Pretoria Dist., Transvaal.


*P. c. vanderhorsti* Roberts, 1946, TM 7793, ♂, collected: May 1936, Graaff Reinet, Cape Province.

*P. c. griqueae* Roberts, 1946, TM 8738, ♀, collected: July 1937, Fauresmith, Orange Free State.

*P. c. klaverensis* Roberts, 1946, TM 2145, ♀, collected: 1. x. 1917, Klaver, Cape Province


*H. w. otjiwarongensis* Roberts, 1946, TM 5355, ♂, collected: 3. viii. 1928, Farm Tweekopjes, Otjiwarongo, South West Africa.


**Method**

The following measurements were used:

**Field measurements**

1. **Head and body length**: from the tip of the nose to the posterior end of the vertebral column, dorsally.
2. **Hind foot length**: from the heel to the end of the longest toe, including the claw.
3. **Ear length**: from the lower inside corner of the rim to the tip of the ear.

**Skull measurements**

1. **Greatest length**: from the anterior edge of the premaxilla to a point directly above the extreme posterior dorsal extension of the foramen magnum.
2. **Height of the braincase**: taken from the suture between the basi-occipital and the basisphenoid, to the highest point vertically above it on the dorsal surface of the skull.
3. **Width of the braincase**: horizontally, across the widest part of the braincase, parallel to and approximately at the level of the dorsal edge of the zygomatic arch.
4. **Width of nasals anteriorly**: dorsally across the most anterior suture between the premaxillae and the nasals.
5. **Length of nasals**: medially.
6. **Width of zygomatic arch**: extreme width.
7. **Length of upper diastema**: from the posterior edge of the upper incisor to the anterior edge of the first upper premolar, at the alveolar level.
8. **Length of upper toothrow**: from the anterior edge of the first premolar to the posterior edge of the third molar, at cingulum level.
9. **Length of upper molars one to three**: buccal length, from the anterior edge of the first molar to the posterior edge of the third molar, at cingulum level.
10. **Width of first upper molar**: measured bucco-lingually across the centre of the tooth.

11. **Distance between upper incisors**: measured between the lingual edges of the upper incisors, at the alveolar level.

12. **Width of upper incisor**: measured bucco-lingually at the level of the alveolus.

For skull measurements a Helios steel sliding caliper measuring to 0.1 mm was used. Unless otherwise stated all measurements are expressed in millimetres.

**Sexual dimorphism.** In the Hyracoidea sexual dimorphism is present mainly in the muzzle area. The degree of dimorphism was determined in samples of *Procavia capensis* only, as the available material of the other Southern African species did not allow similar calculations. Whatever was evident from *P. capensis* was then considered to be also true for *P. welwitschii, Heterohyrax brucei* and *Dendrohyrax arboreus*.

For the sake of statistical comparisons, the sexes are separated in the following measurements: length of the premaxilla, width of the nasals anteriorly, length of the upper diastema and width of the first upper incisor, all of which show sexual dimorphism. In the remaining measurements, as no evidence of sexual dimorphism was apparent, values for males and females were combined. A further obvious difference exists between males and females in the upper incisor. In both sexes the upper incisor is more or less triangular in shape when viewed in cross-section, with the apex of the triangle pointing anteriorly. In males the two anterior surfaces are more or less equal in width, being divided by a definite and well-developed centrally situated ridge. In females this ridge occurs more medially, with the result that the inner of the two anterior surfaces is markedly narrower than the outer one (Fig. 1).

![Fig. 1. Schematic cross-sections to illustrate sexual dimorphism in the upper incisors.](image)

**Age determination.** The age groupings of the Hyracoidea in this paper are based on the criteria suggested by Thomas (1892: 53). The following growth stages are recognized in the dentition:

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I</td>
<td>Before the milk dentition is fully in place.</td>
</tr>
<tr>
<td>Stage II</td>
<td>Milk dentition all erupted and in use (incisors, canines and premolars).</td>
</tr>
<tr>
<td>Stage III</td>
<td>M.1 erupted but M.2 still below the level of the bone.</td>
</tr>
<tr>
<td>Stage IV</td>
<td>M.2 just appearing or partly erupted.</td>
</tr>
<tr>
<td>Stage V</td>
<td>M.2 nearly or fully erupted, M.3 below the level of the bone.</td>
</tr>
<tr>
<td>Stage VI</td>
<td>Tip of M.3 appearing.</td>
</tr>
</tbody>
</table>
Stage VII M₃ fully erupted but with occlusal surface unworn.
Stage VIII M₃ fully erupted and in use.

It will be noticed that in the definition of stage II canines are mentioned. Although the adult dassie displays no canines, the milk dentition includes a canine tooth in each hemi-jaw.

Stages V–VIII are considered adult, while the juveniles cover stages I–IV, i.e. animals with milk dentition. Attention is given only to adults in this study. Statistical comparisons showed that stages V and VI differ from each other in size to such an extent that they cannot be used together as a homogeneous sample. Stages VI, VII and VIII, however, represent a homogeneous sample in all the measurements taken, except for the greatest length of the skull and the width of the zygomatic arch. In the latter two measurements only specimens of stage VIII are used in taxonomic comparisons.

Most of the extralimital specimens and synonyms discussed in this study were not examined personally.

**ABBREVIATIONS**

**Collections**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>TM</td>
<td>Transvaal Museum</td>
</tr>
<tr>
<td>KM</td>
<td>Kaffrarian Museum</td>
</tr>
<tr>
<td>NM</td>
<td>Natal Museum</td>
</tr>
<tr>
<td>ME</td>
<td>Medical Ecology Centre</td>
</tr>
<tr>
<td>RM</td>
<td>National Museum</td>
</tr>
<tr>
<td>SA</td>
<td>South African Museum</td>
</tr>
<tr>
<td>MM</td>
<td>McGregor Memorial Museum</td>
</tr>
<tr>
<td>PE</td>
<td>Port Elizabeth Museum, Snake Park and Oceanarium</td>
</tr>
<tr>
<td>JB</td>
<td>Private collection</td>
</tr>
</tbody>
</table>

**Measurements and statistical terms**

- H.B. Head and body length
- H.F. Length of the hind foot
- E. Ear length
- G.L. Greatest length of the skull
- H.B.C. Height of the braincase
- W.Z.A. Width of the zygomatic arch
- L.N. Length of the nasals
- W. M₁ Width of the first upper molar
- L. P+M Length of the upper tooth-row
- L. M₁–₃ Length of the upper molar row
- L.U.D. Length of the upper diastema
- W.N.A. Width of the nasals anteriorly
- D. I Distance between upper incisors
- W. I₁ Width of the first upper incisor
- N. Number of specimens per sample
- M. Arithmetic mean of a sample
- S.D. Standard deviation. \( \sigma = \sqrt{\frac{\sum a^2 - (\sum a)^2/N}{N-1}} } \)
- C.V.* Coefficient of variation. \( \text{C.V.} = \frac{\text{S.D. (100)}}{\text{M}} \)

* Conventionally a C.V. of 4% indicates that the S.D. of the sample is too small to reflect the actual degree of natural population variation (i.e. the sample is too small). A value of 10% usually indicates a heterogeneous population, e.g. where sexual dimorphism, differences between age groups, etc., exist in statistically significant degrees in the sample which is tested. In the Hydracoidea, however, a range of 1-7%, instead of the conventional 4-10%, seemed to indicate the normal limits of variation of S.D. in a homogeneous population.
Standard error of the mean. $S.\ E_m = S.D./\sqrt{N}$

Coefficient of difference. $C.D. = (M_1 - M_2)/(SD_1 + SD_2)$

Percentage joint non-overlap.

A value distributed in a definite way, used to calculate possibilities in comparisons of several parameters calculated from samples.

$$t = \frac{M_1 - M_2}{\sqrt{\left(\frac{(N_1SE_{M1})^2 + (N_2SE_{M2})^2}{N_1 + N_2 - 2}\right)}}$$

Probability that a difference can be ascribed to chance.
THE RECENT GENERA

All the extant genera of the Hyracoidea are present in Southern Africa. The genus *Procavia* Storr consists of two species which occur extensively throughout the area under discussion (see below). *Heterohyrax* Gray has a more limited distribution in Southern Africa, where it occurs only in the northern parts. *Dendrohyrax* Gray is even more limited in its distribution, as it occurs only in the evergreen forests of the eastern Cape Province and Natal.

As far as external morphology is concerned there is little to distinguish *Procavia*, *Heterohyrax* and *Dendrohyrax*. The animals are all more or less uniform in shape and size, but *Dendrohyrax* has longer and more velvety fur, and usually a smaller number of mammae than *Procavia* and *Heterohyrax*. In their skulls, however, considerable differences exist between the various genera (see later).

**PROCAVIA** Storr

*Procavia* Storr, 1780. Prodromus methodi mammalium: 39 and tab. B.
Typus generis: *Cavia capensis* Pallas, 1766.
Locality: Cape of Good Hope.

Typus generis: *Cavia capensis* Pallas, 1766.
Locality: Cape of Good Hope.

Typus generis: *Hyrax habessinicus* Hemprich & Ehrenberg, 1832.
Locality: Abyssinia.

This genus occurs extensively throughout Africa. It is the only genus of the Hyracoidea occurring in Syria, its range extending farther north and farther south than that of any other living genus. It occupies very diverse areas and is commonly called a rock 'rabbit', indicating the type of shelter it usually frequents. The only Southern African area where it apparently does not occur is the Kalahari-sandveld of the north-western Cape Province and Bechuanaland. In these areas the habitat is entirely unsuitable for any of the Hyracoidea.

*Cavia capensis* was originally described by Pallas (1766). In 1780 it was placed in the genus *Procavia* by Storr. In 1783 it was named *Hyrax* by Hermann, and by this name it was referred to in many of the older works. In 1868 Gray described a new genus, *Euhyrax*, based on a specimen collected in Abyssinia. From the description it seems to have been *Procavia habessinica* (≡ *Hyrax habessinicus* of Hemprich & Ehrenberg, 1832).

The following species are included under *Procavia*:

*P. capensis* (Pallas, 1766). In Rhodesia, South West Africa, South Africa and Swaziland.

*P. welwitschii* (Gray, 1868). Confined to the Kaokoveld of Angola and South West Africa.

*P. johnstoni* Thomas, 1894. Malawi, Kenya, Tanzania and the Congo Republic.

*P. ruficeps* (Hemprich & Ehrenberg, 1832). The Sudan, south-western Cameroons, northern Nigeria, Tchad, Senegal, Gambia and the central Sahara.

*P. habessinica* (Hemprich & Ehrenberg, 1832). Abyssinia, Sudan, Egypt, Somaliland, Shoa, Red-Sea coast and Syria.

As only *P. capensis* and *P. welwitschii* occur in Southern Africa they will be discussed in this work.
HETEROHYRAX Gray

Hyrax Schreber, 1792. Säugetiere in Abbildungen..., etc. 4: 923.
Typus generis: Hyrax syriacus Schreber, 1792.
Locality: Mounts Lebanon and Sinai, Egypt.
Typus generis: Dendrohyrax blainvillii Gray, 1868.
Locality: no information.

The genus Heterohyrax Gray includes all species of rock dassies in Southern Africa with a yellow dorsal spot, except the Kaokoveld rock dassie, Procavia welwitschii. This genus is confined to the eastern parts of Africa, with the exception of an occurrence in Angola, and although Schreber (1844: 315) described its range as extending from '...die Gebirge um die Küsten des rothen Meeres herum bis nordwärts nach Syrien', I could find no proof of this. The furthest recorded northern limits of distribution for Heterohyrax are Mount Lebanon in Syria and Mount Sinae in the Sinai Province of Egypt (Schreber, 1792: 923).

Heterohyrax is regarded by Ellerman et al. (1953: 160) as a subgenus of Dendrohyrax, particularly on the grounds of the remarkable dental resemblances between these two forms. Their reasons are basically the same as those of Ellerman & Morrison-Scott (1951: 334), i.e. '...other authors recognize a third genus, Heterohyrax, which does not differ from Dendrohyrax in dentition, but which has the orbit not ringed by bone. But as the character is not strictly constant in South African Dendrohyrax, it is difficult to see how Heterohyrax could be more than a subgenus of Dendrohyrax.' In my opinion, however, the marked differences between Heterohyrax and Dendrohyrax exist in some cranial aspects (e.g. the length of the molar row as compared with the length of the premolar row; a sagittal crest only in the former, against separate temporal crests in the latter; length of the upper diastema shorter in Heterohyrax than in Dendrohyrax) coupled with the differences in mammary formula (usually 0+1 = 2 in Dendrohyrax, varying to 1+1 = 4 and 1+2 = 6 in D. arboreus; and 1+2 = 6 in Heterohyrax) and habitat differences (the former rock, and the latter tree dwellers) are valid reasons for separating them generically.

The following species are included under Heterohyrax:
H. brucei (Gray, 1868): Abyssinia, the west bank of the Nile, Egypt, Sudan, Somaliland, Kenya, Tanzania, Malawi, Angola, Zambia, Rhodesia, Mozambique north of the Zambesi and Gorongoza Mountains, and the northeastern Transvaal (South Africa).
H. antineae Heim de Balsac and Béguen, 1932: Ahaggar in the central Sahara.
H. chapini Hatt, 1933: Loadi Hill, Congo.

Only H. brucei occurs in Southern Africa.

DENDROHYRAX Gray

Typus generis: Hyrax arboreus A. Smith, 1827.
Locality: the forests of South Africa.
Typus generis: Hyrax arboreus A. Smith, 1827.
Locality: the forests of South Africa.

The tree dassie of Southern Africa is confined to the evergreen forests of the eastern Cape Province and Natal. In other areas of Africa the species occur in
most of the tropical and subtropical forests. They are especially abundant in the Congo rain forests.

Phylogenetically it is the oldest of the extant genera. Both *Procavia* and *Heterohyrax* are later descendants of the original *Dendrohyrax dorsalis* Fraser.

The name *Dendrohyrax* was first used by Gray (1868: 48). Prior to Gray, however, A. Smith (1827: 468) had already described the tree dassie as a species of *Hyrax*, while Thomas (1892: 74), Schlater (1900: 314) and Lydekker (1916: 125) regarded the tree dassies as a *Procavia* species.

*Dendrohyrax* includes three recent species:

*D. arboresus* (A. Smith, 1827): South Africa, Zambia, Congo, Malawi, Kenya, Mozambique, Tanzania and possibly the central and eastern Caprivi Strip.

*D. dorsalis* Fraser, 1852: the western equatorial coastal areas of Africa (including the island of Fernando Po), Nigeria, Congo, Uganda, Angola, Guinea, Cameroon, Ghana and Liberia.

*D. validus* True, 1890: Tanzania and Pemba Island.

Only *D. arboresus* occurs in Southern Africa.

The recent species

*Procavia capensis* (Pallas)

*Cavia capensis* Pallas, 1766. Miscellanea zoologica: 30.

Type locality: Cape of Good Hope; type not in existence.


Type locality: no information; type: British Museum (Natural History), no. 724 h.


Type locality: vicinity of Windhoek, South West Africa; type: Berlin Museum.


Type locality: Chamis, Great Namaqualand; type: Berlin Museum.


Type locality: vicinity of Windhoek, South West Africa; type: Berlin Museum.


Type locality: Meadows, Orange Free State; type: Transvaal Museum, TM 6884.


Type locality: Meadows, Orange Free State; type: Transvaal Museum, TM 6884.


Type locality: Kranshoek, Clanwilliam District, C.P., type: Berlin Museum.


Type locality: Pigg's Peak, Swaziland; type: Transvaal Museum, TM 2005.


Type locality: Hennops River, Pretoria; type: Transvaal Museum, TM 3489.


Type locality: Mount Fletcher, East Griqualand; type: Transvaal Museum, TM 4861.


Type locality: Meadows, Orange Free State; type: Transvaal Museum, TM 6884.


Type locality: Meadows, Orange Free State; type: Transvaal Museum, TM 6884.


Type locality: Fir Glen, Grahamstown; type: Transvaal Museum, TM 6751.


Type locality: Graaff Reinet, Cape Province; type: Transvaal Museum, TM 7793.

Procavia capensis, the Cape rock dassie, is the oldest species of the Hyracoidea from Southern Africa. It was described by Pallas in 1766 as Cavia capensis, being mistakenly associated with Cavia and its related forms. Storr (1780) called it Procavia capensis. In 1783 Hermann named it Hyrax capensis and placed the Cape dassie along with Hystrix, Castor, Cavia, Mus, Sciurus and Lepus in the subdivision Glires of the Digitata. Thomas (1892: 51) again followed Storr.

Procavia capensis is regarded as monotypic and none of the described subspecies appear to be valid. It is by far the commonest species of dassie in Southern Africa. Its range extends from Cape Agulhas in the south to Damaraland in South West Africa and the Chimanimani Mountains of Rhodesia (Fig. 2). From the available evidence it may not occur in Mozambique.

The Hyracoidea do not inhabit the Kalahari-sandveld of the northern Cape Province and Bechuanaland. The single broken skull of a P. capensis which was found in the National Kalahari Gemsbok Park was probably washed down the Nossob River from much higher up in South West Africa where these dassies do occur. The floods of 1963 in these areas seem to support this hypothesis.

Diagnostic characters. This is the largest of the species of Procavia in Southern Africa. Head and body length 420–762 mm, mean = 501 mm. Fur short and
coarse; dorsal spot black; P 1 constantly absent; lower incisors unicuspid in adults and tricuspid in juveniles; postorbital process constantly open; mean length of upper diastema in males = 10.29 mm, and in females = 9.44 mm. See also Table 3.

**Skull.** The skull of *P. capensis* is longer than those of *P. welwitschi* and *Heterohyrax brucei*, but shorter than that of *Dendrohyrax arbores*. In the skull of *P. capensis* the muzzle is short and broad, the frontals are flat dorsally and the temporal ridges sometimes form a sagittal crest, zygomatic arch wide. The upper diastema is short and there is an increase in size of the individual premolars and molars from anterior to posterior as far as approximately M 1, the widest tooth. From this point backwards, the molars again decrease in size, with the result that when viewed from behind the upper tooth-row gives the impression of bulging outwards near the middle. The upper incisors are large and usually situated less than the width of an individual incisor apart. The lower incisors are tricuspid in juveniles and unicuspid in adults. The molars are hypsodont and
bilophodont. The length of the upper tooth-row exceeds that of any other Southern African species. The upper P 1–4 (mean = 16·18 mm) is much shorter than the upper M 1–3 (mean = 20·95 mm), a characteristic common for Procavia. A very constant feature in the skulls of P. capensis and P. welwitschii is the absence of the first premolar in the lower jaw.

**Colour.** The colour of all Southern African Hyracoidea shows considerable individual variation; P. capensis is no exception. Generally, the colour of the Cape dassie may be described as beige to reddish-brown dorsally, paling on the flanks with off-white to reddish-yellow bellies, dorsal spot black. There appears to be some correlation between the mean annual rainfall of the habitat and the intensity of the dorsal colour. The darkest specimens usually occur in the relatively higher rainfall areas and vice versa. There are no subspecifically significant differences in colour.

Table 1. The size of Procavia capensis

<table>
<thead>
<tr>
<th>Size</th>
<th>M. (mm)</th>
<th>S.D. (mm)</th>
<th>N.</th>
</tr>
</thead>
<tbody>
<tr>
<td>H.B.</td>
<td>420–762</td>
<td>—</td>
<td>78</td>
</tr>
<tr>
<td>H.F.</td>
<td>58–73</td>
<td>66</td>
<td>41</td>
</tr>
<tr>
<td>E.</td>
<td>23–40</td>
<td>32</td>
<td>38</td>
</tr>
<tr>
<td>G.L.</td>
<td>79‘1–101’7</td>
<td>88·53</td>
<td>120</td>
</tr>
<tr>
<td>H.B.C.</td>
<td>27‘5–35’6</td>
<td>31·09</td>
<td>180</td>
</tr>
<tr>
<td>W.Z.A.</td>
<td>46‘9–64’0</td>
<td>52·08</td>
<td>117</td>
</tr>
<tr>
<td>L.N.</td>
<td>14‘1–25’4</td>
<td>18·91</td>
<td>123</td>
</tr>
<tr>
<td>W.M. 1</td>
<td>4‘9–8’0</td>
<td>6·740</td>
<td>193</td>
</tr>
<tr>
<td>L. P+M</td>
<td>32‘4–42’3</td>
<td>37·13</td>
<td>164</td>
</tr>
<tr>
<td>L.M. 1–3</td>
<td>18‘0–23’7</td>
<td>20·95</td>
<td>180</td>
</tr>
<tr>
<td>W.N.A.</td>
<td>6‘9–12’1</td>
<td>8·740</td>
<td>68</td>
</tr>
<tr>
<td>(53)</td>
<td>6·6–10·2</td>
<td>8·140</td>
<td>64</td>
</tr>
<tr>
<td>L.U.D.</td>
<td>6‘9–13’8</td>
<td>10·29</td>
<td>58</td>
</tr>
<tr>
<td>(66)</td>
<td>6·0–13‘5</td>
<td>9·440</td>
<td>67</td>
</tr>
<tr>
<td>D. I/F/W I 1</td>
<td>0‘43–1·54</td>
<td>0·830</td>
<td>58</td>
</tr>
<tr>
<td>(55)</td>
<td>0‘48–1·25</td>
<td>0·820</td>
<td>65</td>
</tr>
</tbody>
</table>

**Taxonomy.** P. capensis is regarded as polytypic by most authors. However, there is considerable controversy as to the exact degree to which it is polytypic. Hahn (1934: 288–91) recognizes five subspecies, i.e. P. c. capensis, P. c. windhuki, P. c. schultzei, P. c. marlothi and P. c. welwitschii in Southern Africa. Allen (1939: 442–52) adds three more subspecies to Hahn’s list; Roberts (1951: 256–9) recognizes sixteen subspecies in Southern Africa, while Ellerman et al. (1953: 157–62) recognize fifteen subspecies of P. capensis in their concept of Southern Africa which also includes northern Mozambique, Malawi, Zambia and Angola. The latter authors include P. c. welwitschii and P. c. volkmanni in their list, but as will be pointed out later I prefer to regard welwitschii as a specifically distinct form of Procavia.

Concerning the other subspecies of P. capensis, it was found that they should all be synonymized with P. c. capensis. Although this implies a considerable alteration and simplification of the existing taxonomy of this species, this appears to be justified, as specimens from a large number of localities were examined and compared statistically in a number of measurements before this decision was reached. These comparisons revealed no basis upon which to support the retention of any of the subspecies as valid (Fig. 3).

Specimens collected from Pigg's Peak in Swaziland and from Windhoek in South West Africa are subspecifically separable from the typical P. c. capensis.
(Cape Agulhas). However, closer inspection revealed a gradual decrease in size in the specimens from Cape Agulhas along the eastern and the western coasts to the types of *P. c. natalensis* (Pigg's Peak) and *P. c. windhuki* (Windhoek) respectively. These clines eliminate the validity of *natalensis* and *windhuki* as subspecies of *P. capensis*, which appear to be correlated with the vegetation (Bothma, 1966: 687).

Consequently, *P. capensis* is regarded as a monotypic species of the Hyracoidea, showing considerable variation and occurring commonly but exclusively through subspecies of *P. welwitschii*.

**List of localities from which specimens were examined.** Rooikrans, Waterberg, 1 (TM); Copperfontein, Waterberg, 3 (TM); Okosongomingo, Waterberg, 4 (TM); Waterberg, 2 (TM); Ombu, Erongo Mountain, 4 (TM); Ameib, Erongo Mountain, 1 (ME); Khan Mountain, 1 (TM); Khan River, Onguati, 3 (TM); Karibib, 4 (TM); Okahandja, 1 (TM); Namib, 1 (TM); Neudamm, 3 (TM); Windhoek, 1 (TM); Kobos, Rehoboth, 1 (TM); Naracus, 1 (TM); Noah, Rehoboth, 1 (KM); Samkubis, Rehoboth, 1 (TM); Barby, Helmeringhausen, 2 (TM); Brukkaros Mountain, 1 (TM); Berseba, 8 (KM); Seeheim, 1 (TM); Kraikluft, Keetmanshoop, 1 (TM); Goodhouse, 1 (TM); Aughrabies Falls, Orange River, 2 (TM, KM); Leeuwdril, Twee Rivieren, 1 (ME); Waterlooo, Vryburg, 3 (TM); Orange River, Upington, 2 (KM); Campbell, 2 (TM); Enenriet, Steinkopf, 2 (KM); Heuningneskloof, Herbert, 1 (JB); Modder River 10 (KM); Hopetown, 1 (TM); Kameelboom, Garies, 2 (KM); Eelfontein, Little Namaqualand, 10 (KM, PE); Witwater Plateau, Kamiesberg, 9 (KM, PE), Britstown, 2 (JB); Deelfontein, Karoo, 19 (PE, KM, MM); Lady Grey, 11 (PE, KM); Mount Fletcher, 1 (TM); Vanrhynsdorp, 10 (JB); Klaver, 4 (TM); Hantam Range, Calvinia, 1 (KM); Biesiespoort, 4 (KM); New Bethesda, 2 (ME); Middelburg, C.P., 4 (PE, KM); Coetzeesfontein, Middelburg, C.P., 6 (JB); Elliot, 3 (JB); Lamberts Bay, 3 (TM); Compagnies Drift, 21 (KM); Kliphuis, Clanwilliam, 3 (KM); Redelinghuis, 1 (TM); Olifants River, Clanwilliam, 1 (KM); Pakhuise Pass, 1 (KM); Traveller's Rest, 6 (NM, KM); Middelpos, 1 (KM); Beaufort West, 2 (JB); Leeu Gamka, 8 (JB); Broederstroef, Graaff Reinet, 8 (TM); Waterkloof, Pearston, 3 (JB); Mortimer, 1 (KM); Somerset East, 1 (JB); Bedford, 15 (TM, KM); Kaggasmondt, Bedford, 8 (PE, KM); Balderja, Post Retief, 14 (KM); Kat River Valley, Stockenstrom, 7 (KM); Fort Beaufort, 2 (KM); Farm Lowestowe, Cathcart, 12 (JB); Frankfort, King William's Town, 2 (KM); Pirie Forest, King William's Town, 1 (KM); Ntsikini, King William's Town, 1 (KM); Lower Kanaansie, King William's Town, 1 (KM); Kaffarians, 5 (KM); Mount Coke, 3 (KM); Kei Road, 1 (KM); Komga, 3 (KM); Table Mountain, 4 (SA); Kirstenbosch, 1 (SA); Grootvadersbos, 1 (TM); Garcia Forest, 2 (TM); Jonkersberg, 1 (TM); Centlivres, Uitenhage, 1 (TM); Ruford, Uitenhage, 3 (PE); Yellowwoods, Van Stadens, 2 (PE); Uitenhage, 1 (TM); Orinway Farm, Grahamstown, 1 (KM); Atherstone, Grahamstown, 3 (KM); Kleinpoort, Grahamstown, 4 (TM); Fir Glen, Grahamstown, 6 (TM); Naterall, Grahamstown, 3 (TM); Peddie District, 1 (KM); Zoetendalsvlei, 1 (TM); Breë River Mouth, Cape Infante, 4 (JB); Stilbaai, Knysna, 3 (TM); Belvedere, Knysna, 3 (TM); Knysna, 2 (TM); Plettenberg Bay, 1 (RM); Waterpoort, 1 (TM); Sentinel Ranch, Limpopo River, 5 (RM); Soutpansberg, 2 (TM); Njelele Dam, 1 (JB); Wyliespoort, 1 (TM); Tamboekieskloof, Mogol River, 2 (TM); Leipzig Mission, Blouberg, 1 (TM); Mokeetsi, Soutpansberg, 6 (TM); Great Letaba River, Soutpansberg, 3 (TM); Mochudi, Bechuanaland, 1 (TM); Schurweberg, 2 (TM); Potgietersrus, 1 (TM); Blyde River, Mariepskop, 2 (TM); Koster, 1 (TM); Koperfontein, Rustenburg, 2 (TM); Rustenburg district, 4 (TM); Vliegepoort, Rustenburg, 1 (TM); Rooikrans, Rusten-
Procavia welwitschii (Gray)


Type locality: Maiomba River, Mossamedes, Angola; type: Lisbon Museum.


Type locality: Franzfontein, Outjo District; type: Berlin Museum.


Type locality: Kaokoveld, South West Africa; type: Berlin Museum.


Type locality: Guinas Waterhole, Tsumeb; type: Transvaal Museum, TM. 8329.


Type locality: Farm Tweekopjes, Otjiwarongo; type: Transvaal Museum, TM. 5335.

The Kaokoveld rock dassie, _Procavia welwitschii_, was first described as _Hyrax welwitschii_ by Gray (1868: 43) from specimens collected by Dr Welwitsch on the banks of the river Maiomba, in the Mossamedes district of Angola. However, as no specimens from this type locality were available for study, I followed Roberts (1951: 574) in regarding the specimens from Kamanjab and Kalkfeld in South West Africa as typical for _P. welwitschii_.

_P. welwitschii_ is monotypic and is confined to the Kaokoveld of South West Africa and the south-western tip of Angola. However, as no specimens from this type locality were available for study, I followed Roberts (1951: 574) in regarding the specimens from Kamanjab and Kalkfeld in South West Africa as typical for _P. welwitschii_.

P. welwitschii is confined to the Kaokoveld of South West Africa and the south-western tip of Angola. However, as no specimens from this type locality were available for study, I followed Roberts (1951: 574) in regarding the specimens from Kamanjab and Kalkfeld in South West Africa as typical for _P. welwitschii_.

The Kaokoveld rock dassie replaces _P. capensis_ in the Kaokoveld. In South West Africa the latter species does not occur farther north than Damaraland. Where these two species come into contact with each other, an almost perfect jigsaw distributional pattern is found, but no overlap has yet been reported (Fig. 2). For the present study only one specimen from Angola was available. This is a very young male (stage III, TM. 13422) which was collected from Caracul, 45 miles east of Mossamedes. It is too young to be of any value other than for colour comparison.

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most southern recorded occurrence of *P. welwitschii* seems to be along the 21° S latitude.

**Diagnostic characters.** This species is smaller than *P. capensis*. Head and body length 365–500 mm, mean = 464 mm. Fur short and coarse; dorsal spot light yellow; P1 constantly absent, lower incisors tricuspid in adults as in juveniles; postorbital process open or closed; length of upper diastema mean = 8.35 mm in males and 7.37 mm in females. See also Table 4.

**Skull.** In the original description Gray (1868: 43) already pointed out that the skull of *P. welwitschii* is different from the other species in being broader in proportion to its length. However, another criterion often said to be diagnostic of this species, a constantly closed postorbital process, was found to be just as often open as closed. A cranial characteristic by means of which separation of *P. welwitschii* from *P. capensis* proves practical is the retention of the tricuspidity of the lower incisors in adult *P. welwitschii*. In old specimens with worn teeth two grooves on the inner surface of each incisor might be the only indication of the tricuspidity. Apart from this the dentition of *P. welwitschii* closely resembles that of *P. capensis*. The first premolar in the lower jaw is usually absent or present as a small splint-like tooth only. The upper incisors are narrower than in *P. capensis* and the space between them is larger on the average than the width of an individual incisor. The molars are hypsodont, but less than in *P. capensis*, and also bilophodont. The upper P1-4 (mean = 15.86 mm) much shorter than the upper M1-3 (mean = 19.22 mm).

**Colour.** As in the other species the colour of *P. welwitschii* is subject to considerable individual variation. In general, however, the Kaokoveld rock dassie is fawn to yellow-brown dorsally, liberally flecked with pale yellow, and paling on the flanks. The belly is off-white with a yellowish tint. The dorsal spot light to creamy-yellow. There are no subspecifical differences.

**Taxonomy.** Several authors regard the Kaokoveld rock dassie as a species of the genus *Heterohyrax*, amongst others Shortridge (1934) and Roberts (1951). Ellerman et al. (1953) consider the typical *welwitschii* a species of the subgenus *Heterohyrax* of the genus *Dendrohyrax*, regarding the related *tsumebensis* and *otjiwarongensis* as subspecies of *Dendrohyrax* (*Heterohyrax*) *brucei*. Others such as Thomas (1892), Hahn (1934) and Allen (1939) place it under *Procavia*.

The authors who favour the inclusion of *welwitschii* under *Heterohyrax* are probably prompted by the colour of the dorsal spot, which in both groups is yellow. However, the colour of this spot varies from species to species in the same genus; it is orange in *P. ruficeps*. An analysis of the skull, particularly the hypsodont molars and the P1–4 length which is much shorter than that of the M1–3, reveals a closer relationship with *Procavia*. Consequently I am inclined to support the authors placing *welwitschii* in this genus.

From comparisons of their skulls it is also evident that in all the major dentitional features *P. welwitschii* is more closely related to *P. capensis* than to *Heterohyrax brucei*. In the general size of the skull elements on the other hand, such as greatest length, width of the zygomatic arch, height of the braincase, etc., there is a closer relationship with *H. brucei*. This is illustrated in the multiple-unit network relationships (Fig. 4). The only dentitional characteristic in which *P. welwitschii* resembles *H. brucei* more than it does *P. capensis* is the fact that adults of both former species have tricuspid incisors in the lower jaw. However, so has almost all the other species of Hyracoidea, including extralimital species of *Procavia*.

As dentition is considered genetically more constant than the relative sizes of the various skull components, I am inclined to attach more importance to the similarities in dentition between *P. capensis* and *P. welwitschii* than to similarities in size between the skull components of *P. welwitschii* and *H. brucei*. Further-
more, the highly characteristic absence of the first premolar in the lower jaw of both *P. capensis* and *P. welwitschii* lend considerable support to a closer relationship with *P. capensis* than with *H. brucei*.

With regard to the colour of the dorsal spot, it may further be pointed out that Mollison (1905) linked this spot with the sexual activity of the animals.

![Network relationships of: Dendrohyrax arboreus with Procavia capensis, P. welwitschii and Heterohyrax brucei respectively. --, P. welwitschii with P. capensis and with Heterohyrax brucei. A, Procavia capensis; B, P. welwitschii; C, Heterohyrax brucei; D, Dendrohyrax arboreus. 1, Width of the first upper molar. 2, Greatest length of the skull. 3, Length of the upper tooth-row. 4, Distance between upper pair of incisors/width of one upper incisor. 5, Length of upper diastema. 6, Width of the zygomatic arch. 7, Anterior width of the nasals (males). 8, Anterior width of the nasals (females). 9, Height of the braincase. 10, Length of upper molars one to three. 11, Length of the nasals. 12, Inner pair of lower incisors tricuspid in adults. 13, First premolar in lower jaw present. 13°, First premolar in lower jaw absent. 14, Colour of the dorsal spot.](image_url)

Thus *welwitschii* and *capensis* are two valid species of *Procavia*. Furthermore, by placing *welwitschii* under *Procavia* there at once emerges a clearer picture of the interrelationships of the rock dassies in West Africa as the southern *P. capensis* is now no longer separated geographically from the more northern *P. ruficeps* by representatives of a totally different genus, *Heterohyrax*, but by another species, *P. welwitschii*, of the same genus.

The subspecies of *P. welwitschii* are *P. w. welwitschii* from Angola (Gray, 1868: 43), and Kamanjab and Kalkfeld (Roberts, 1951: 574); *P. w. tsuembensis* from Guinas Waterhole near Tsumeb (Roberts, 1938: 326); and *P. w. otjiwaron-
\textit{gensis} from the farm Tweekopjes near Otjiwarongo (Roberts, 1946: 328). Shortridge (1934: 384) recognizes three subspecies of \textit{P. welwitschii}, but these differ from the ones listed above as they include a \textit{welwitschii}, a \textit{volkmanni} and a \textit{flavimaculata}.

Table 2. \textit{Comparison of Procavia volkmanni with P. johnstoni, P. capensis and P. welwitschii to illustrate their relationships}

<table>
<thead>
<tr>
<th></th>
<th>W.Z.A.</th>
<th>L.N.</th>
<th>H.B.C.</th>
<th>W. Mt.</th>
<th>L. P+M</th>
<th>L.U.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{P. volkmanni}</td>
<td>49.0</td>
<td>16.2</td>
<td>29.2</td>
<td>6.0</td>
<td>36.3</td>
<td>8.3</td>
</tr>
<tr>
<td>\textit{P. welwitschii}</td>
<td>48.9</td>
<td>18.3</td>
<td>28.9</td>
<td>6.2</td>
<td>—</td>
<td>8.0</td>
</tr>
<tr>
<td>\textit{P. capensis}</td>
<td>50.9</td>
<td>15.0</td>
<td>31.3</td>
<td>5.8</td>
<td>33.1</td>
<td>9.3</td>
</tr>
<tr>
<td>\textit{P. johnstoni}</td>
<td>54.1</td>
<td>22.4</td>
<td>32.5</td>
<td>6.5</td>
<td>36.1</td>
<td>12.7</td>
</tr>
</tbody>
</table>

Both Hahn (1934: 292) and Allen (1939: 451) place \textit{P. volkmanni} under an extralimital species, \textit{P. johnstoni}. Hahn does so mainly on the basis of a definite first premolar which Brauer (1914) observed in the lower jaw of the specimen he described. It has been found, however, that in \textit{P. welwitschii} and in \textit{P. capensis} there sometimes does exist a small splint-like \textit{P\textsubscript{1}} in adults, and it is my belief that this may possibly have misled Brauer in the specimen which he examined.

Table 3. \textit{Comparison of the means of some skull measurements (mm) for Procavia flavimaculata with those for P. welwitschii to indicate relationships}

<table>
<thead>
<tr>
<th></th>
<th>W.Z.A.</th>
<th>L. P+M</th>
<th>W. Mt.</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{P. flavimaculata}</td>
<td>50.6</td>
<td>32.8</td>
<td>6.0</td>
</tr>
<tr>
<td>\textit{P. welwitschii}</td>
<td>49.9</td>
<td>34.8</td>
<td>6.4</td>
</tr>
</tbody>
</table>

In the present revision no material was available for study from the type locality of \textit{P. volkmanni} (Franzfontein, S.E. 2015 Ac) in South West Africa. A comparison of the measurements of \textit{P. volkmanni} and \textit{P. johnstoni} which are listed in Hahn, with the corresponding measurements for \textit{P. welwitschii} from the immediate vicinity of Franzfontein, shows very little difference. Further comparisons of the measurements of \textit{P. volkmanni} and \textit{P. johnstoni} with those of the nearest \textit{P. capensis} (Rooikrans, S.E. 2017 Ca), show that \textit{P. volkmanni} is definitely more closely related to \textit{P. welwitschii} than to \textit{P. capensis}, and closer to \textit{P. capensis} than to \textit{P. johnstoni}.

Furthermore, the yellow dorsal spot of \textit{P. volkmanni} correlates closely with that of \textit{P. welwitschii}. Although no material from the type locality of \textit{P. volkmanni} was examined, I consider it improbable that this form is valid and therefore follow recent authors who synonymize it with \textit{Procavia welwitschii} instead of following Hahn in placing it under a species otherwise extralimital to Southern Africa.

From the original description by Brauer (1917: 303) I also agree to synonymize \textit{P. flavimaculata} with \textit{P. welwitschii}. As the type locality of \textit{P. flavimaculata} is described very vaguely as the northern Kaokoveld by Brauer, it is almost impossible to compare any samples of this form with \textit{P. welwitschii}. The following characteristics of \textit{P. flavimaculata}, which Brauer regarded as typical of this form, correlate with \textit{P. welwitschii}: both have a yellow dorsal spot and no first premolar in the lower jaw. The other differences concern colour, a feature which is highly variable in the Hyracoidea.
Fig. 5. Subspecific comparison of the *Procapra welwitschii* specimens. A, Erombe Mountain; B, Rua Cana Falls; C, Sanitatas; D, Ombombo; E, Sesfontein; F, Kovares; G, Kamanjab; H, Guinas Waterhole; I, Nosib, Tsumeb; J, Karochos; K, Huab River; L, Kalkfeld; M, Otjiwarongo; N, Canas, Okawa. Sample-size is given on the left of each graph.

Table 4. The size of *Procapra welwitschii*

<table>
<thead>
<tr>
<th></th>
<th>Size (mm)</th>
<th>M. (mm)</th>
<th>S.D. (mm)</th>
<th>N.</th>
</tr>
</thead>
<tbody>
<tr>
<td>H.B.</td>
<td>365-500</td>
<td>464</td>
<td>—</td>
<td>24</td>
</tr>
<tr>
<td>H.F.</td>
<td>60-76</td>
<td>66</td>
<td>—</td>
<td>24</td>
</tr>
<tr>
<td>E.</td>
<td>23-34</td>
<td>24</td>
<td>—</td>
<td>26</td>
</tr>
<tr>
<td>G.L.</td>
<td>74.5-93.4</td>
<td>83.90</td>
<td>6.062</td>
<td>6</td>
</tr>
<tr>
<td>H.B.C.</td>
<td>27.5-32.5</td>
<td>30.15</td>
<td>1.854</td>
<td>15</td>
</tr>
<tr>
<td>W.Z.A.</td>
<td>44.5-54.1</td>
<td>49.05</td>
<td>3.499</td>
<td>7</td>
</tr>
<tr>
<td>L.N.</td>
<td>13.6-22.4</td>
<td>17.44</td>
<td>2.361</td>
<td>17</td>
</tr>
<tr>
<td>W. M. 1.</td>
<td>5.3-6.90</td>
<td>6.320</td>
<td>0.340</td>
<td>18</td>
</tr>
<tr>
<td>L. P + M</td>
<td>33.1-37.2</td>
<td>35.08</td>
<td>1.770</td>
<td>17</td>
</tr>
<tr>
<td>L.M. 1-3</td>
<td>17.6-20.5</td>
<td>19.22</td>
<td>0.850</td>
<td>18</td>
</tr>
<tr>
<td>W.N.A.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(δ3)</td>
<td>7.5-10.5</td>
<td>8.350</td>
<td>1.031</td>
<td>7</td>
</tr>
<tr>
<td>(ε2)</td>
<td>6.2-8.00</td>
<td>7.370</td>
<td>0.607</td>
<td>10</td>
</tr>
<tr>
<td>L. U.D.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(δ3)</td>
<td>9.3-12.7</td>
<td>10.71</td>
<td>1.285</td>
<td>7</td>
</tr>
<tr>
<td>(ε2)</td>
<td>7.4-10.1</td>
<td>8.920</td>
<td>0.907</td>
<td>10</td>
</tr>
<tr>
<td>D. (W. I. (upper)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(δ3)</td>
<td>0.81-1.34</td>
<td>1.110</td>
<td>0.251</td>
<td>7</td>
</tr>
<tr>
<td>(ε2)</td>
<td>0.72-1.45</td>
<td>1.000</td>
<td>0.228</td>
<td>11</td>
</tr>
</tbody>
</table>
The skull measurements of *P. flavimaculata* listed by Brauer do not seem to present any basis upon which to separate this form subspecifically from *P. welwitschii*. As there is no direct reference to the exact type locality, I compared the few skull measurements given by Brauer for *P. flavimaculata* with those taken for *P. welwitschii* in the present study. Although this method is not very desirable, it did not indicate any taxonomic basis upon which to separate these two forms subspecifically (see below). Consequently *P. flavimaculata* is here synonymized with *P. welwitschii*, as in Allen (1939: 449).

Roberts described *P. w. tsumebensis* and *P. w. otjiwarongensis* in 1938 and 1946 respectively. Once again the main basis for separating these forms from *P. welwitschii* concerns minor colour differences. The amount of individual colour variation in *P. welwitschii* and the lack of statistically significant morphological differences (Fig. 5) suggest that both *P. tsumebensis* and *P. otjiwarongensis* are synonyms of *P. welwitschii*.

Thus *P. welwitschii* is a monotypic species confined to the Kaokoveld of Southern Africa.

*List of localities from which specimens were examined.* Caracul, Angola 1 (TM); Otjimbundu, 2 (KM); Ehombe Mountain, 1 (RM); Rua Cana Falls, Cunene River, 5 (KM); Oropembe, 1 (KM); Sanitatas, 9 (KM, RM, TM); Hoarusib, 1 (SA); Kaoko-Otavi, 4 (KM, RM, TM); Ombombo, 3 (KM); Otjitundua, 1 (KM); 21.5 miles east of Sesfontein, Kaokoveld, 1 (ME); Kovares, 10 (TM, KM); Kamanjab, 8 (TM); Farm Vryheid 267, 18 miles south of Franzfontein, 1 (ME); 50 miles east of Kamanjab, 1 (TM); Guinas Waterhole, Tsumeb, 4 (TM); Nosiib, near Tsumeb, 2 (TM); Mount Aukas, 18 miles north-east of Grootfontein, 1 (KM); Karochos, Otjo, 2 (TM); Huab River, 1 (TM); Ugab, 1 (TM); Kalkfeld, 1 (TM); Farm Tweekopjes, Otjiwarongo, 1 (TM); Canas, Okawa, 1 (KM).

*Heterohyrax brucei* (Gray)


- Type locality: Abyssinia; type: no information.

_H. syriacus* Schreber, 1792. *Saugethiere in Abbildungen, etc.* 4: 923.

- Type locality: Lebanon, Mt Sinai; type: no information.

*Dendrohyrax blainvilli* Gray, 1868. *Ibidem* (4) 1: 50.

- Type locality: Abyssinia; type: no information.


- Type locality: Abyssinia; type: no information.


- Type locality: Angola; type: no information.


- Type locality: Cabaceira peninsula, Mozambique; type: no information.


- Type locality: Latiko, 3° N.; type: no information.


- Type locality: Quissange, Angola; type: no information.


- Type locality: Sudan; type: no information.


- Type locality: 50 miles south-east of Berbera, Somaliland; type: no information.


- Type locality: south-east of Iringa, Tanganyika; type: no information.


- Type locality: Bismarckburg, Tanganyika; type: no information.


- Type locality: Mwakate, Tanganyika; type: no information.


Type locality: Tambarara, Gorongoza Mountains, Mozambique; type: British Museum (Natural History), no. B.M. 8.1.1.116.


Type locality: Matibi District, Southern Rhodesia; type: Transvaal Museum, TM. 1348.

The name *Heterohyrax* was first used by Gray (1868: 51). In the same work Gray (p. 44) described another species, *Hyrax brucei* from Abyssinia, which has since proved to be a species of *Heterohyrax*. However, Gray was not the first author who described this species.

*Heterohyrax syriacus* was described by Schreber as *Hyrax syriacus* in 1792, but as pointed out by Ellerman & Morrison-Scott (1951: 335) no *Heterohyrax* occurs in Syria. According to Hahn (1934: 271) the specimen described by Schreber was collected in Abyssinia, while Schreber himself never saw Syrian Hyracoidea. In addition Schreber (1792: 924) admits that his description of *Hyrax syriacus* is mainly a repetition of the facts given by Bruce (1791: 175), who actually described this dassie from Abyssinia, but who apparently did not name it scientifically. Schreber refers to the animal(s) described by Bruce as Bruce's hyrax, and proceeds to name it *Hyrax syriacus*. Thus Bruce was the first author to describe this dassie, while Schreber was the first to give it a scientific name.
In view of the uncertainty surrounding the name *syriacus* I prefer to follow Ellerman *et al.* (1953: 160) in using the name *Heterohyrax brucei* (Gray) for this species, although *syriacus* has priority and may in fact be more correct.

*H. brucei*, a yellow-spotted rock dassie, is confined to the northern, central and north-eastern parts of Southern Africa (Fig. 6). It apparently does not occur south of 25°S. latitude, and although it is sympatric with *P. capensis* it is a browser while the latter is a grazer. Therefore it is not unusual to see young of both kinds playing together as observed by Roberts (1951: 254).

**Diagnostic characters.** This species is the smallest of the recent Hyracoidea in Southern Africa. Head and body length 269–540 mm, mean = 452 mm. Fur short and coarse; dorsal spot reddish-yellow to ochre; P1 constantly present and the lower incisors tricuspid in adults and juveniles. Postorbital process open; temporal ridges often form a sagittal crest; frontals flat dorsally; length of upper diastema mean = 12·38 mm in males and 12·86 mm in females. See also Table 5.

**Table 5. The size of Heterohyrax brucei**

<table>
<thead>
<tr>
<th>Size (mm)</th>
<th>M. (mm)</th>
<th>S.D. (mm)</th>
<th>N.</th>
</tr>
</thead>
<tbody>
<tr>
<td>H.B.</td>
<td>269–540</td>
<td>160</td>
<td>24</td>
</tr>
<tr>
<td>H.F.</td>
<td>58–80</td>
<td>32</td>
<td>23</td>
</tr>
<tr>
<td>E.</td>
<td>25–38</td>
<td>20</td>
<td>24</td>
</tr>
<tr>
<td>G.L.</td>
<td>76·7–90·7</td>
<td>85·92</td>
<td>16</td>
</tr>
<tr>
<td>H.B.C.</td>
<td>27·2–32·1</td>
<td>20·29</td>
<td>21</td>
</tr>
<tr>
<td>W.Z.A.</td>
<td>43·1–53·4</td>
<td>49·75</td>
<td>13</td>
</tr>
<tr>
<td>L.N.</td>
<td>16·6–20·2</td>
<td>18·37</td>
<td>16</td>
</tr>
<tr>
<td>W.M. 1.</td>
<td>4·8–6·0</td>
<td>5·290</td>
<td>24</td>
</tr>
<tr>
<td>L. <em>P + M</em></td>
<td>30·2–35·5</td>
<td>32·37</td>
<td>24</td>
</tr>
<tr>
<td>L.M. 1–3</td>
<td>15·4–18·3</td>
<td>16·42</td>
<td>22</td>
</tr>
<tr>
<td>L.U.D.</td>
<td>9·3–15·5</td>
<td>12·38</td>
<td>10</td>
</tr>
<tr>
<td>W.N.A.</td>
<td>11·4–15·8</td>
<td>12·86</td>
<td>11</td>
</tr>
<tr>
<td>D. I/W. 1. (upper)</td>
<td>5·4–8·5</td>
<td>7·270</td>
<td>9</td>
</tr>
<tr>
<td>D. (lower)</td>
<td>6·7–9·0</td>
<td>7·570</td>
<td>8</td>
</tr>
<tr>
<td>D. 1/W. 1. (upper)</td>
<td>1·09–2·37</td>
<td>1·430</td>
<td>10</td>
</tr>
<tr>
<td>D. (lower)</td>
<td>1·07–1·83</td>
<td>1·410</td>
<td>9</td>
</tr>
</tbody>
</table>

**Skull.** More elongate than that of *P. weiwitschii*. Postorbital process always open. Lower incisors tricuspid in adults and juveniles. The molars are bilophodont and more brachyodont than hypsodont. In this respect the skull of *H. brucei* closely resembles that of *Dendrohyrax arboreus*. In *H. brucei* the upper tooth-row does not seem to bulge outwards near the middle as much as in *P. capensis* and *P. weiwitschii*, when viewed from behind. However, the characteristic separating *H. brucei* from the latter two species is the constant retention of the first premolar of the lower jaw. The upper incisors of *H. brucei* are relatively narrower than those of *P. capensis*, about equal to those of *P. weiwitschii* and wider than those of *D. arboreus*. The space between the upper incisors of *H. brucei* exceeds the width of one individual incisor. The molars are relatively narrower than in *P. capensis* and *P. weiwitschii*. The length of P1–4 (mean = 15·95 mm) just a little less than that of M1–3 (mean = 16·42 mm).

**Colour.** The colour of *H. brucei* is difficult to describe. This is principally due to the great individual variation of the specimens in this species and its subspecies. In general, however, it may be said that in *H. b. ruddi* Wroughton the colour is a coarse mixture of brown and whitish, paling to light brownish on the flanks but nevertheless separated from the pure white belly. The dorsal spot is creamy-white to creamy-buff. In *H. b. granti* Wroughton, on the other
hand, it may be described as somewhat darker than *ruddi*. Dorsal colour is blackish-brown, grizzled with buff, paler on the flanks, with a dirty-white belly. The dorsal spot here is reddish-ochre.

**Taxonomy.** *H. brucei* is most closely related to *D. arboreus*, the tree dassie. *H. brucei* is polytypic and consists of the two above-mentioned subspecies in Southern Africa, based mainly upon statistically significant differences in the upper tooth-row.

![Graph comparing Heterohyrax brucei granti (the localities Mokeetsi and Malta) with H. b. ruddi (the other localities below).](image)

**Fig. 7.** Comparison of *Heterohyrax brucei granti* (the localities Mokeetsi and Malta) with *H. b. ruddi* (the other localities below). A, Macequece; C, Mchabesi; D, Bulawayo; H, Magalakwin/Limpopo River confluence; J, Soutpansberg; K, Matibi district; L, Motale River; M, Njelele River; N, Moatlateng; (O, Mokeetsi; P, Malta); Q, Maribashoek; R, Moorddrif; S, Blyde River. Sample-size is given on the left of each graph.

Hahn (1934: 282) and Allen (1939: 446) also recognize these two subspecies. Roberts (1946: 327) adds another subspecies, *H. b. rhodesiae*, which occurs in the Matibi District of Rhodesia, north of Malala Drift on the Limpopo River, Motale River, Njelele River, Magalakwin River and Moorddrif in the Waterberg District. Roberts (1951: 261) and Ellerman et al. (1953: 361) retain *rhodesiae* as a subspecies. However, I could find no statistical evidence to support the retention of *H. b. rhodesiae* (Fig. 7), and propose to synonymize it with *H. b. ruddi*.

In the original description of *H. b. ruddi*, Wroughton (1910: 108) quotes the type locality as the Gorongoza Mountains in Mozambique, locus S.E. 1834 Ca.
The specimens geographically nearest to these which were available for study in the present paper were collected at Macequece, locus S.E. 1832 Db, in the same territory. These specimens were consequently considered typical of *H. b. ruddi* and were compared statistically with those from the type locality of *H. b. rhodesiae* and the other localities regarded as typical by Roberts (1946: 327).

No adult specimens of *H. b. granti* from Woodbush were available for study, but the specimens from Mokeetsi and Malta are undoubtedly larger than those of *H. b. ruddi* in a significant degree as is evident from Fig. 7.

Unfortunately the samples from Mokeetsi and Malta do not contain enough specimens to allow the calculation of population variation. The result is that only the means of samples of *H. b. granti* in any measurement could be compared with those of samples of *H. b. ruddi*. This implies the assumption that the means of the samples from Mokeetsi and Malta, in any given measurement, represent the mean of the entire *granti* population in the same measurement.

It is especially in the length of the upper tooth-row and the length of the upper molar row that the skull of *H. b. granti* differs significantly from that of *ruddi*. If one compares *H. b. granti* with specimens of *H. b. ruddi* from Motale River and Njelele River, the differences between the subspecies in length of the upper tooth-row are well above the required \( \pm 4.5 \times S.D. \) level when the mean of a sample of less than five specimens is compared with the mean of a larger sample. In the length of the upper tooth-row the sample mean of *H. b. granti* from Mokeetsi is separated by a distance equal to \( \pm 5.54 \times S.D. \) of the mean of *H. b. ruddi*. In the Malta sample this distance is \( \pm 5.38 \times S.D. \). In the length of the upper molar row the difference between the mean of the sample of *H. b. ruddi* and that of *H. b. granti* from Mokeetsi is \( \pm 5.19 \times S.D. \), and \( \pm 7.29 \times S.D. \) for *H. b. granti* from Malta (Fig. 7). It is evident that the specimens from Mokeetsi and Malta represent the distinct subspecies *H. b. granti*.

Specimens from Soutpansberg are also somewhat larger than the average *H. b. ruddi*. However, they are well below the level for subspecific separation. Closer inspection reveals that they are situated geographically between *H. b. ruddi* in its typical form, and *H. b. granti*. Therefore it is possible that with larger samples the specimens from Soutpansberg may be taxonomically intermediate between *H. b. ruddi* and *H. b. granti*, in which case the two forms will become synonyms. It is also possible that the Soutpansberg specimens may belong to *H. b. granti*. If this is the case the question arises how they can represent a subspecies which is otherwise restricted to areas with a higher annual rainfall than that found in their own habitat. One can assume, however, that the Soutpansberg may form an isolated area of higher relative humidity than the areas surrounding it.

I am therefore of the opinion that in Southern Africa *Heterohyrax brucei* consists of two subspecies only, the smaller and more common *H. b. ruddi* and the larger, less common *H. b. granti*.

*Heterohyrax brucei ruddi* (Wroughton)


Type locality: Mazoe District, Southern Rhodesia; type: no information.


Type locality: Tambarara, Gorongoza Mountains, Mozambique; type: British Museum (Natural History), no. B.M. 8.1.1.116.


Type locality: Limpopo Hills, Southern Rhodesia; type: no information.


Type locality: Matibi District, Southern Rhodesia; type: Transvaal Museum, TM. 1348.
This subspecies was possibly mentioned for the first time by Sclater (1900: 315) when he described P. brucii, and was said to be found throughout East Africa, from Abyssinia to Malawi and Mozambique. The same applies to the specimens of P. brucei which were collected by the Rudd exploration of the Gorongoza Mountains in 1908, and which Thomas & Wroughton (1908: 172) tentatively thought to be Hyrax mossambicus Peters, though they identified the specimens as P. brucii. In 1910 Wroughton described the specimens from Tambarara in the Gorongoza Mountains as a distinct subspecies from those of the Woodbush area.

Table 6. The size of Heterohyrax brucei ruddi

<table>
<thead>
<tr>
<th></th>
<th>Size</th>
<th>M.</th>
<th>S.D.</th>
<th>N.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(mm)</td>
<td>(mm)</td>
<td>(mm)</td>
<td></td>
</tr>
<tr>
<td>H.B.</td>
<td>380-498</td>
<td>453</td>
<td>—</td>
<td>19</td>
</tr>
<tr>
<td>H.F.</td>
<td>58-70</td>
<td>64</td>
<td>—</td>
<td>21</td>
</tr>
<tr>
<td>E.</td>
<td>25-38</td>
<td>30</td>
<td>—</td>
<td>21</td>
</tr>
<tr>
<td>G.L.</td>
<td>76-7-89.3</td>
<td>85-28</td>
<td>3:174</td>
<td>13</td>
</tr>
<tr>
<td>H.B.C.</td>
<td>26-4-30.4</td>
<td>28-60</td>
<td>1:072</td>
<td>27</td>
</tr>
<tr>
<td>W.Z.A.</td>
<td>43-1-52.6</td>
<td>49-35</td>
<td>2:733</td>
<td>11</td>
</tr>
<tr>
<td>L.N.</td>
<td>13-1-20.2</td>
<td>17-30</td>
<td>1:987</td>
<td>28</td>
</tr>
<tr>
<td>W.M. 1.</td>
<td>4-5'-5'7</td>
<td>5-130</td>
<td>0:366</td>
<td>28</td>
</tr>
<tr>
<td>L. P+M</td>
<td>30.2-34.3</td>
<td>31-90</td>
<td>1:179</td>
<td>19</td>
</tr>
<tr>
<td>L.M. 1-3</td>
<td>15.4-17.2</td>
<td>16-21</td>
<td>0:569</td>
<td>19</td>
</tr>
</tbody>
</table>

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>L.U.D.</td>
<td>(♀♂)</td>
<td>(♀♂)</td>
<td>(♀♂)</td>
</tr>
<tr>
<td></td>
<td>9.4-13.7</td>
<td>11.98</td>
<td>1:306</td>
</tr>
<tr>
<td>W.N.A.</td>
<td>10.3-14.0</td>
<td>12.47</td>
<td>1:319</td>
</tr>
<tr>
<td>D. 1</td>
<td>(♀♂)</td>
<td>5.4-8.5</td>
<td>5-880</td>
</tr>
<tr>
<td></td>
<td>(♀♂)</td>
<td>5-8-8.5</td>
<td>7-200</td>
</tr>
<tr>
<td>W. I.</td>
<td>(♀♂)</td>
<td>3-8-6.4</td>
<td>5-04</td>
</tr>
<tr>
<td></td>
<td>(♀♂)</td>
<td>4-4-6.0</td>
<td>5-06</td>
</tr>
<tr>
<td></td>
<td>(♀♂)</td>
<td>2.5-4.1</td>
<td>3-24</td>
</tr>
<tr>
<td></td>
<td>(♀♂)</td>
<td>2-5-4.2</td>
<td>3-29</td>
</tr>
</tbody>
</table>

Diagnostic characters. Colour dorsally a coarse mixture of brown and white, paling to light brownish-white on the flanks, but nevertheless sharply separated from the pure white belly (Wroughton, 1910: 108). Dorsal spot creamy-white to creamy-buff. Length of the upper tooth-row and the upper molar row seldom more than 34.0 and 17.3 mm respectively. On the whole a smaller animal than granti, but with interspace between the upper incisors wider than in granti.

Distribution. The subspecies is distributed in Southern Africa over most of the central, eastern and north-eastern parts (Fig. 6). It almost encircles H. b. granti geographically, occurring to the north, the west and the south of it. In the Moketsi, Woodbush and Malta areas ruddi is replaced by granti. See also Table 6.

List of localities from which specimens were examined. Macequece, Mozambique, 2 (TM); Senkwe, Zambesi River, 1 (RM); Sanyati Estuary, Kariba, 1 (RM); Plumtree, 2 (TM); Matopos, 3 (TM, RM); Mchabesi, Matopos, 1 (RM); Lower Hillside Dam, Bulawayo, 1 (RM); Cyrene, Bulawayo, 1 (RM); Bulawayo 1 (RM); Filabusi, 1 (RM); Maporomo Hills, Sabi Valley, 1 (RM); Matibi, District, 2 (TM); road between Palapye and Francistown, Bechuanalnd, 1 (RM); Makossa Hills, Sabi River east bank, 1 (RM); Magalakwin/Limpopo confluence, 1 (TM); Greeswald, Limpopo River, 1 (TM); Soutpansberg, 6 (TM); Motale River, 15 (TM); Njelle River, Soutpansberg, 4 (TM); Motlateng, Blouberg Mission, 2 (TM); Moordrif, 1 (TM); Maribashoek, 2 (TM); Blyde River, Mariepskop, 3 (TM).
Heterohyrax brucei granti (Wroughton)

Type locality: Woodbush, Transvaal; type: British Museum (Natural History), no. B.M. 6-4-3-102.

This subspecies is a somewhat larger and darker form than ruddi, and is confined almost entirely to the areas in the vicinity of the Woodbush Forest Reserve in the Transvaal which is the type locality. Thus its habitat is situated in a region with a mean annual rainfall of more than 50 in. (1251 mm).

Diagnostic characters. Colour dorsally blackish-brown grizzled with buffy, fading on the flanks and with a dirty-white belly (Wroughton, 1910: 109). Dorsal spot reddish-ochre. Length of the upper tooth-row and upper molar row seldom less than 34.0 and 17.3 mm respectively. Upper incisors situated closer to each other than in ruddi. See also Table 7.

Table 7. The size of Heterohyrax brucei granti

<table>
<thead>
<tr>
<th>Size</th>
<th>M.</th>
<th>N.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(mm)</td>
<td>(mm)</td>
<td></td>
</tr>
<tr>
<td>H.B.</td>
<td>495-533</td>
<td>507</td>
</tr>
<tr>
<td>H.F.</td>
<td>69-80</td>
<td>73</td>
</tr>
<tr>
<td>E.</td>
<td>34-35</td>
<td>34</td>
</tr>
<tr>
<td>G.L.</td>
<td>86.4-90.7</td>
<td>88.5</td>
</tr>
<tr>
<td>H.B.C.</td>
<td>28.8-33.1</td>
<td>30.6</td>
</tr>
<tr>
<td>W.Z.A.</td>
<td>50.5-53.4</td>
<td>51.9</td>
</tr>
<tr>
<td>L.N.</td>
<td>16.1-19.8</td>
<td>18.5</td>
</tr>
<tr>
<td>W.M.</td>
<td>5.5-6.0</td>
<td>5.7</td>
</tr>
<tr>
<td>L. P+M</td>
<td>34.9-35.5</td>
<td>35.1</td>
</tr>
<tr>
<td>L.M.</td>
<td>17.3-18.3</td>
<td>17.7</td>
</tr>
<tr>
<td>L.U.D.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(23)</td>
<td>11.9-13.6</td>
<td>12.7</td>
</tr>
<tr>
<td>(23)</td>
<td>12.0-13.3</td>
<td>12.6</td>
</tr>
<tr>
<td>W.N.A.</td>
<td>8.0-8.5</td>
<td>8.25</td>
</tr>
<tr>
<td>(22)</td>
<td>7.1-9.0</td>
<td>8.00</td>
</tr>
<tr>
<td>D. 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(23)</td>
<td>4.7-5.3</td>
<td>5.00</td>
</tr>
<tr>
<td>(24)</td>
<td>2.9-5.1</td>
<td>4.00</td>
</tr>
<tr>
<td>W.I. 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(22)</td>
<td>4.3-4.7</td>
<td>4.50</td>
</tr>
<tr>
<td>(22)</td>
<td>3.9-3.9</td>
<td>3.90</td>
</tr>
</tbody>
</table>

Distribution. Its known range includes Woodbush, Mokeetsi and Malta, near Leydsdorp, although it may possibly also occur in the Soutpansberg area (Fig. 6).

List of localities from which specimens were examined. Mokeetsi, 4 (TM); Woodbush Forest Reserve, 1 (TM); Malta, Leydsdorp, 4 (TM).

Dendrohyrax arboreus (A. Smith)

Type locality: the forests of South Africa; type: no information.

Type locality: Bukoba, Tanganyika; type: no information.

Dendrohyrax scheelei Matschie, 1895. Die Säugerthiere Deutsch-Ost-Afrikas: 90.
Type locality: Khutu, Tanganyika; type: no information.

Type locality: Nyasa-Tanganyika Plateau; type: no information.

Type locality: Western slope of Mount Kenya, Kenya; type: no information.
In Southern Africa *Dendrohyrax arboreus* is monotypic, although at least one other subspecies occurs in Zambia (Solwezi Boma, the Kabompo/Mukundwishi junction, Luawamala River and Sichili River).

The tree dassies of Southern Africa are limited in their distribution to the evergreen tropical and subtropical forests of the eastern Cape Province and the Natal Midlands (Fig. 8). The species was described by A. Smith (1827: 49) as *Hyrax arboreus*, but was renamed *Dendrohyrax arboreus* by Gray (1868: 49).
The value of more intensive collections in otherwise poorly represented areas is illustrated remarkably well by Bigalke and Bateman (1962: 87), who supplement the five localities in the eastern Cape Province from which tree dassies had been collected previously by 33 new sight records. However, I am of the opinion that on a number of occasions rock dassies which are also known to climb into trees may have been mistaken for tree dassies in these sight records. This especially applies to areas in the arid Karoo whence sight records have come.

**Diagnostic characters.** A fairly large animal, living mainly in trees. Fur soft, long and velvety; dorsal spot creamy-white; belly creamy-white to pure white; dorsal colour mottled grey and white, sometimes with a brownish tint. Frontals concave dorsally; each parietal has a definite dorso-lateral temporal ridge, absent in all other Southern African Hyracoidea. Length of the upper diastema: mean = 18·6 mm in males and 16·58 mm in females. See also Table 8.

**Table 8. The size of Dendrohyrax arboreus**

<table>
<thead>
<tr>
<th>Size</th>
<th>M.</th>
<th>S.D.</th>
<th>N.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(mm)</td>
<td>(mm)</td>
<td>(mm)</td>
<td></td>
</tr>
<tr>
<td>H.B.</td>
<td>428-520</td>
<td>475</td>
<td>---</td>
</tr>
<tr>
<td>H.F.</td>
<td>59-67</td>
<td>63</td>
<td>---</td>
</tr>
<tr>
<td>E.</td>
<td>29-36</td>
<td>32</td>
<td>---</td>
</tr>
<tr>
<td>G.L.</td>
<td>85·4-98·6</td>
<td>91·41</td>
<td>3·524</td>
</tr>
<tr>
<td>H.B.C.</td>
<td>26·3-29·8</td>
<td>28·17</td>
<td>1·232</td>
</tr>
<tr>
<td>W.Z.A.</td>
<td>43·7-53·7</td>
<td>50·60</td>
<td>3·197</td>
</tr>
<tr>
<td>L.N.</td>
<td>15·7-21·3</td>
<td>18·01</td>
<td>2·234</td>
</tr>
<tr>
<td>W.M. 1</td>
<td>4·9-5·6</td>
<td>5·200</td>
<td>0·209</td>
</tr>
<tr>
<td>L. P+M</td>
<td>31·5-33·7</td>
<td>32·30</td>
<td>0·688</td>
</tr>
<tr>
<td>L.M. 1-3</td>
<td>15·6-17·0</td>
<td>16·10</td>
<td>0·419</td>
</tr>
<tr>
<td>L.U.D.</td>
<td>17·0-19·5</td>
<td>18·60</td>
<td>1·289</td>
</tr>
<tr>
<td>(s)</td>
<td>13·9-18·0</td>
<td>16·58</td>
<td>1·537</td>
</tr>
<tr>
<td>W.N.A.</td>
<td>8·4-10·9</td>
<td>9·500</td>
<td>1·258</td>
</tr>
<tr>
<td>(s)</td>
<td>7·3-10·6</td>
<td>8·820</td>
<td>1·106</td>
</tr>
<tr>
<td>D. I/W. 1 (upper)</td>
<td>1·14-1·85</td>
<td>1·610</td>
<td>0·400</td>
</tr>
<tr>
<td>(s)</td>
<td>1·60-2·43</td>
<td>1·980</td>
<td>0·284</td>
</tr>
</tbody>
</table>

**Skull.** Relatively longer but flatter dorsally than those of the rock dassies. Frontals concave dorsally, each one with a ridge-like dorso-lateral edge. Greatest length of the skull and length of the upper diastema the largest of any of the Southern African Hyracoidea, in contrast with the height of the braincase, which is less than in the other species. Post-orbital process usually closed. If open, the gap is very narrow. Lower incisors always tricuspid; molars brachydont and bilophodont; first premolar in the lower jaw present and the upper tooth-row not seeming to bulge outwards near the middle when viewed from behind. The length of the P 1-4 (mean = 16·20 mm) longer that of the M 1-3 (mean = 16·10 mm).

**Colour.** A colour cline correlated with the mean annual rainfall exists with the relatively darkest specimens in the north (rainfall 1000-1500 mm) and the palest ones in the south (rainfall 750-1000 mm). In general the tree dassie has a mottled grey and white dorsal colour, sometimes with a brownish tint. The dorsal spot is constantly creamy-white while the belly is creamy-white to pure white.

**Taxonomy.** As tree dassies require tropical to subtropical forest conditions for habitat, and as these forests are not very abundant in Southern Africa,
**D. arboreus** is the rarest of the Hyracoidea from Southern Africa. In its distribution it is confined almost entirely to the eastern coastal and near-coastal areas and has been collected most extensively in the vicinity of King William's Town in the eastern Cape Province.

Its habitat requirements have effectively isolated the Southern African tree dassies from the more northern representatives of the species. Therefore it is not surprising that the Southern African **D. arboreus arboreus** is subspecifically distinct from **D. a. braueri** of the north-western parts of Zambia (Ansell, 1960: 51), as was found when this extralimital form was compared statistically with the Southern African form (see Fig. 9). Thus the tree dassies of Southern Africa have been isolated geographically for a period of sufficient duration to have allowed subspeciation to take place. Even in the colour of the fur, differences indicating more than just individual variation seem to exist between **D. a. arboreus** and **D. a. braueri**. The subspecies from Zambia exhibits a greater dominance of white hair over grey hair, compared with the Southern African form, with the result that as a whole **D. a. braueri** appears paler and more mottled than **D. a. arboreus**.

Specimens from Mlanje in Malawi also appear to differ noticeably from both the Southern African and the Zambian **D. arboreus**. Although the Mlanje specimens were compared superficially only with the other two forms, it was found that they are almost entirely dark brown dorsally, with the belly pure white and the dorsal spot creamy-white. The skulls of the Mlanje specimens seem smaller than the Southern African ones, are less robust and without the characteristic thickened dorso-lateral ridge on the frontals which also occurs in the Zambia specimens. The temporal ridges of the skulls from Mlanje also seem ill-developed in comparison with the Southern African form. Therefore more thorough comparisons may prove the Mlanje specimens to be subspecifically distinct from both the Southern African and the Zambian subspecies, in which case the name **D. arboreus mimus** Peters should be used.

Colour variation occurs, but is subject to so much fluctuation in correlation with the mean annual rainfall of the habitat that it is not considered a useful subspecific criterion. Therefore the tree dassies of Southern Africa represent only the nominate subspecies **Dendrohyrax arboreus arboreus** (Fig. 10).

*List of localities from which specimens were examined.* Colbourne, Karkloof, 3 (NM); Pirie Forest, King William’s Town, 9 (KM); Mimosa, 1 (PE); Addo, 1 (PE); Sinangwana, Ngqeleni District, 1 (TM); Ngqeleni District, 1 (TM); Nateyall, Grahamstown, 1 (TM).
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Fig. 10. Subspecific comparison of the Dendrohyrax arboreus specimens from Southern Africa. A, Karkloof; B, Ngqeleni; C, Sinangwana; D, Pirie Forest; E, Nateyall. Sample-size is given on the left of each graph.
The quarter degree locus system of plotting localities as introduced by Davis (1948) is followed. The following localities have been plotted according to this system:

<table>
<thead>
<tr>
<th>Locality</th>
<th>Co-ordinates</th>
<th>Locus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aberdeen</td>
<td>32° 28' S., 24° 02' E.</td>
<td>3224 Ac</td>
</tr>
<tr>
<td>Addo</td>
<td>33° 32' S., 25° 44' E.</td>
<td>3325 Da</td>
</tr>
<tr>
<td>Adelaide</td>
<td>32° 42' S., 26° 20' E.</td>
<td>3226 Cb</td>
</tr>
<tr>
<td>Alexandria</td>
<td>33° 36' S., 26° 28' E.</td>
<td>3326 Cb</td>
</tr>
<tr>
<td>Aliwal North</td>
<td>30° 45' S., 26° 45' E.</td>
<td>3026 Dd</td>
</tr>
<tr>
<td>Allemansgras, Harrismith</td>
<td>28° 16' S., 29° 07' E.</td>
<td>2829 Ac</td>
</tr>
<tr>
<td>Ameib, Erongo Mountain</td>
<td>21° 49' S., 15° 32' E.</td>
<td>2115 Dc</td>
</tr>
<tr>
<td>Atherstone, Grahamstown</td>
<td>33° 19' S., 26° 23' E.</td>
<td>3326 Ad</td>
</tr>
<tr>
<td>Aughrabies Falls</td>
<td>28° 37' S., 20° 21' E.</td>
<td>2820 Cb</td>
</tr>
<tr>
<td>Balderja, Post Retief</td>
<td>32° 30' S., 26° 32' E.</td>
<td>3226 Da</td>
</tr>
<tr>
<td>Barby, Helmeringhausen</td>
<td>25° 30' S., 16° 34' E.</td>
<td>2516 Dc</td>
</tr>
<tr>
<td>Barkly East</td>
<td>30° 58' S., 27° 33' E.</td>
<td>3027 Dc</td>
</tr>
<tr>
<td>Barkly West</td>
<td>28° 05' S., 24° 31' E.</td>
<td>2824 Ba</td>
</tr>
<tr>
<td>Bathurst</td>
<td>33° 30' S., 20° 55' E.</td>
<td>3326 Db</td>
</tr>
<tr>
<td>Bedford</td>
<td>33° 41' S., 26° 06' E.</td>
<td>3226 Ca</td>
</tr>
<tr>
<td>Belvedere, Knysna</td>
<td>34° 02' S., 22° 58' E.</td>
<td>3422 Bb</td>
</tr>
<tr>
<td>Benguela, Angola</td>
<td>12° 37' S., 13° 25' E.</td>
<td>1213 Cb</td>
</tr>
<tr>
<td>Berseba</td>
<td>26° 00' S., 17° 47' E.</td>
<td>2617 Bb</td>
</tr>
<tr>
<td>Biesiespoort</td>
<td>31° 42' S., 23° 11' E.</td>
<td>3123 Ca</td>
</tr>
<tr>
<td>Bloemfontein</td>
<td>20° 07' S., 28° 11' E.</td>
<td>2026 Aa</td>
</tr>
<tr>
<td>Blyde River, Mariepskop</td>
<td>24° 35' S., 30° 50' E.</td>
<td>2430 Db</td>
</tr>
<tr>
<td>Botslaan, Leeu Gamka</td>
<td>32° 43' S., 21° 29' E.</td>
<td>3221 Bb</td>
</tr>
<tr>
<td>Breé River Mouth</td>
<td>34° 07' S., 20° 54' E.</td>
<td>3420 Bd</td>
</tr>
<tr>
<td>Britstown</td>
<td>30° 37' S., 23° 30' E.</td>
<td>3023 Da</td>
</tr>
<tr>
<td>Broedersstrom</td>
<td>32° 15' S., 24° 32' E.</td>
<td>3224 Bc</td>
</tr>
<tr>
<td>Brukkaros Mountain</td>
<td>25° 50' S., 17° 48' E.</td>
<td>2517 Dd</td>
</tr>
<tr>
<td>Bulawayo</td>
<td>20° 09' S., 28° 35' E.</td>
<td>2028 Ba</td>
</tr>
<tr>
<td>Burgersdorp</td>
<td>31° 00' S., 26° 20' E.</td>
<td>3126 Ab</td>
</tr>
<tr>
<td>Campbell</td>
<td>28° 49' S., 23° 44' E.</td>
<td>2823 Dc</td>
</tr>
<tr>
<td>Canas, Okawa</td>
<td>20° 28' S., 17° 10' E.</td>
<td>2017 Ac</td>
</tr>
<tr>
<td>Caracul</td>
<td>15° 12' S., 12° 09' E.</td>
<td>1512 Aa</td>
</tr>
<tr>
<td>Carter’s Nursery, Pietermaritzburg</td>
<td>29° 35' S., 30° 25' E.</td>
<td>2930 Cb</td>
</tr>
<tr>
<td>Cathcart</td>
<td>32° 18' S., 27° 10' E.</td>
<td>3227 Ac</td>
</tr>
<tr>
<td>Centlivres, Uitenhage</td>
<td>33° 29' S., 25° 28' E.</td>
<td>3325 Cb</td>
</tr>
<tr>
<td>Chase Valley, Pietermaritzburg</td>
<td>29° 35' S., 30° 25' E.</td>
<td>2930 Cb</td>
</tr>
<tr>
<td>Chibis ur Sada</td>
<td>15° 10' S., 13° 50' E.</td>
<td>1513 Bb</td>
</tr>
<tr>
<td>Chimanimani Mountains</td>
<td>19° 40' S., 32° 56' E.</td>
<td>1932 Db</td>
</tr>
<tr>
<td>Coetzeesfontein, Middelburg (C.P.)</td>
<td>31° 30' S., 25° 00' E.</td>
<td>3125 Ca</td>
</tr>
<tr>
<td>Colbourne, Karkloof</td>
<td>30° 25' S., 23° 16' E.</td>
<td>2030 Ad</td>
</tr>
<tr>
<td>Colesberg</td>
<td>30° 45' S., 25° 05' E.</td>
<td>3025 Cc</td>
</tr>
<tr>
<td>Compagnies Drift</td>
<td>32° 07' S., 18° 28' E.</td>
<td>3218 Ab</td>
</tr>
<tr>
<td>Copperfontein, Waterberg</td>
<td>20° 30' S., 17° 14' E.</td>
<td>2017 Ca</td>
</tr>
<tr>
<td>Cradock</td>
<td>32° 08' S., 25° 36' E.</td>
<td>3225 Ba</td>
</tr>
<tr>
<td>Cyrene, Bulawayo</td>
<td>20° 09' S., 28° 35' E.</td>
<td>2028 Ba</td>
</tr>
<tr>
<td>Dartford, Underberg</td>
<td>29° 48' S., 29° 32' E.</td>
<td>2929 De</td>
</tr>
<tr>
<td>Dastfontein, Beaufort West</td>
<td>32° 13' S., 23° 30' E.</td>
<td>3221 Ba</td>
</tr>
<tr>
<td>De Aar</td>
<td>30° 39' S., 24° 00' E.</td>
<td>3024 Ca</td>
</tr>
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<td>3023 Dd</td>
</tr>
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<td>Dordrecht</td>
<td>31° 20' S., 27° 07' E.</td>
<td>3127 Ac</td>
</tr>
<tr>
<td>East London</td>
<td>33° 00' S., 27° 55' E.</td>
<td>3327 Bb</td>
</tr>
<tr>
<td>Eenriet, Steinkopf</td>
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<td>2917 Bb</td>
</tr>
<tr>
<td>Eensam, Wepener</td>
<td>29° 42' S., 27° 03' E.</td>
<td>2927 Ca</td>
</tr>
<tr>
<td>Eholmbe Mountain</td>
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<td>3713 Db</td>
</tr>
<tr>
<td>11 miles south of Middelpos</td>
<td>32° 04' S., 20° 12' E.</td>
<td>3220 Aa</td>
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<td>Elliott</td>
<td>31° 18' S., 27° 50' E.</td>
<td>3127 Bd</td>
</tr>
<tr>
<td>Eselfontein</td>
<td>30° 27' S., 18° 13' E.</td>
<td>3018 Ac</td>
</tr>
<tr>
<td>Fauresmith</td>
<td>29° 45' S., 25° 19' E.</td>
<td>2925 Cd</td>
</tr>
<tr>
<td>15 miles north of Okahandja</td>
<td>21° 45' S., 16° 55' E.</td>
<td>2116 Dd</td>
</tr>
<tr>
<td>Locality</td>
<td>Co-ordinates</td>
<td>Locus</td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>50 miles east of Kamanjab</td>
<td>19°38'S., 15°41'E.</td>
<td>1915</td>
</tr>
<tr>
<td>Filabusi</td>
<td>20°30'S., 29°15'E.</td>
<td>2020</td>
</tr>
<tr>
<td>Fir Glen, Grahamstown</td>
<td>33°18'S., 26°32'E.</td>
<td>3326</td>
</tr>
<tr>
<td>Fort Beaufort</td>
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</tr>
<tr>
<td>Fourniesburg</td>
<td>28°38'S., 28°14'E.</td>
<td>2826</td>
</tr>
<tr>
<td>Frankfort, King William's Town</td>
<td>32°44'S., 27°28'E.</td>
<td>3227</td>
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<tr>
<td>Gansfontein, Ficksburg</td>
<td>28°51'S., 27°53'E.</td>
<td>2837</td>
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<tr>
<td>Garcia Forest</td>
<td>33°57'S., 21°14'E.</td>
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<td>Giant's Castle Game Reserve</td>
<td>29°15'S., 29°30'E.</td>
<td>2920</td>
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<tr>
<td>Gonaakraal, Somerset East</td>
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<td>28°54'S., 18°15'E.</td>
<td>2815</td>
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<td>Gordonia</td>
<td>28°13'S., 21°10'E.</td>
<td>2821</td>
</tr>
<tr>
<td>Graaff Reinet</td>
<td>32°15'S., 24°32'E.</td>
<td>3224</td>
</tr>
<tr>
<td>Great Letaba River, Soutpansberg</td>
<td>23°40'S., 30°45'E.</td>
<td>2330</td>
</tr>
<tr>
<td>Greefswald, Limpopo</td>
<td>22°12'S., 29°23'E.</td>
<td>2229</td>
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<tr>
<td>Groblersdal</td>
<td>25°15'S., 29°25'E.</td>
<td>2320</td>
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<tr>
<td>Grootvadersbos, Swellendam</td>
<td>33°50'S., 20°53'E.</td>
<td>3320</td>
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<tr>
<td>Guinas Waterhole, Taumeb</td>
<td>21°14'S., 17°20'E.</td>
<td>1917</td>
</tr>
<tr>
<td>Hanover</td>
<td>31°04'S., 24°29'E.</td>
<td>3124</td>
</tr>
<tr>
<td>Hantam Range, Calvinia</td>
<td>31°21'S., 19°57'E.</td>
<td>3110</td>
</tr>
<tr>
<td>Heerenlogementberg, Vanrhynsdorp</td>
<td>31°36'S., 18°44'E.</td>
<td>3118</td>
</tr>
<tr>
<td>Hennops River, Pretoria</td>
<td>25°51'S., 27°38'E.</td>
<td>2527</td>
</tr>
<tr>
<td>Herschel</td>
<td>30°37'S., 27°10'E.</td>
<td>3027</td>
</tr>
<tr>
<td>Hoarusib River, Kaoko-Otavi</td>
<td>18°12'S., 13°45'E.</td>
<td>1815</td>
</tr>
<tr>
<td>Hofmeyr</td>
<td>31°39'S., 25°36'E.</td>
<td>3125</td>
</tr>
<tr>
<td>Hopetown</td>
<td>29°34'S., 24°03'E.</td>
<td>2924</td>
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<tr>
<td>Huab River, Kaokoveld</td>
<td>20°34'S., 14°06'E.</td>
<td>2014</td>
</tr>
<tr>
<td>Humansdorp</td>
<td>34°02'S., 24°46'E.</td>
<td>3424</td>
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<td>Inyati</td>
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<td>1928</td>
</tr>
<tr>
<td>Jansenville</td>
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</tr>
<tr>
<td>Jonkersberg</td>
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<td>3322</td>
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<tr>
<td>Kabompo/Mukundwishi Junction</td>
<td>13°36'S., 24°30'E.</td>
<td>1324</td>
</tr>
<tr>
<td>Kafferedstad Station, Warden</td>
<td>28°01'S., 29°00'E.</td>
<td>2829</td>
</tr>
<tr>
<td>Kaffirrria (King William's Town)</td>
<td>32°53'S., 27°23'E.</td>
<td>3227</td>
</tr>
<tr>
<td>Kaggasmondt, Bedford</td>
<td>32°50'S., 26°14'E.</td>
<td>3226</td>
</tr>
<tr>
<td>Kalkfeld</td>
<td>20°41'S., 16°20'E.</td>
<td>2016</td>
</tr>
<tr>
<td>Kamanjab</td>
<td>19°38'S., 14°51'E.</td>
<td>1914</td>
</tr>
<tr>
<td>Kameelboom, Garies</td>
<td>30°27'S., 17°41'E.</td>
<td>3017</td>
</tr>
<tr>
<td>Kaoko-Otavi</td>
<td>18°12'S., 13°45'E.</td>
<td>1815</td>
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<tr>
<td>Waterberg</td>
<td>20° 30' S., 17° 14' E.</td>
<td>Ca</td>
</tr>
<tr>
<td>Waterkloof, Pearston</td>
<td>32° 12' S., 25° 13' E.</td>
<td>Aa</td>
</tr>
</tbody>
</table>
**GAZETTEER (cont.)**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Co-ordinates</th>
<th>Locus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Waterloo, Vryburg</td>
<td>26° 47' S., 24° 45' E.</td>
<td>2624 Dd</td>
</tr>
<tr>
<td>Waterpoort, Soutpansberg</td>
<td>22° 54' S., 28° 37' E.</td>
<td>2228 Dc</td>
</tr>
<tr>
<td>Weltevreden, Parys</td>
<td>26° 51' S., 27° 39' E.</td>
<td>2627 Dc</td>
</tr>
<tr>
<td>Willem Pretorius Reserve</td>
<td>28° 18' S., 27° 08' E.</td>
<td>2827 Ac</td>
</tr>
<tr>
<td>Willowmore</td>
<td>33° 15' S., 23° 30' E.</td>
<td>3324 Bc</td>
</tr>
<tr>
<td>Windhoek</td>
<td>22° 34' S., 17° 06' E.</td>
<td>2217 Ca</td>
</tr>
<tr>
<td>Witwater Plateau, Kamiesberg</td>
<td>30° 28' S., 18° 05' E.</td>
<td>3018 Ac</td>
</tr>
<tr>
<td>Woodbush Forest Reserve</td>
<td>23° 50' S., 30° 00' E.</td>
<td>3419 Db</td>
</tr>
<tr>
<td>World’s View, Matopo Hills</td>
<td>33° 53' S., 25° 13' E.</td>
<td>3325 Cc</td>
</tr>
<tr>
<td>Wyliespoort, Soutpansberg</td>
<td>22° 54' S., 29° 56' E.</td>
<td>2229 Dd</td>
</tr>
<tr>
<td>Willowoods, Van Stadens River</td>
<td>30° 28' S., 18° 08' E.</td>
<td>3325 Cc</td>
</tr>
<tr>
<td>Zoetendalsvlei, Cape Agulhas</td>
<td>34° 43' S., 19° 58' E.</td>
<td>3419 Db</td>
</tr>
</tbody>
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