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Fossil hyraxes (Hyracoidea: Mammalia) from the Late Miocene and Plio-Pleistocene of Africa, and the phylogeny of the Procaviidae

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A palate with much of the dentition from Aragai, Lukeino Formation (6 Ma) Kenya, is the most complete known specimen of a Late Miocene procaviid hyracoid. It shares several features with *Dendrohyrax.* The specimen is as large as the western tree hyrax, *Dendrohyrax dorsalis,* but it is attributed to a new species. *D. dorsalis* ranges through the tropical forests of Central and Western Africa, from Uganda to Gambia. As such the presence of a similar species at Lukeino provides evidence of the humid forest nature of the palaeoenvironment in the Tugen Hills during the Late Miocene. The fossil hyracoid specimens from the Early Pliocene of Langebaanweg, South Africa, are close in morphology to, but somewhat larger than, the extant bush hyrax, *Heterohyrax brucei,* but have some derived characters found in *Procavia capensis.* The cheek teeth are brachyodont, the lower premolar row is complete with a well-developed p/1 and there is a long diastema between the second incisor and the first premolar, all features recalling *Heterohyrax.* However, the depth of the mandible, the hypsodonty of the lower incisor, and the length of the premolar row relative to the length of the molar row are similar to the condition in *Procavia* and attest to the onset of molar enlargement relative to the rest of the dentition. In the overall context of the Procaviidae, *Procavia* is the most derived genus, and the presence of a few *Procavia*-like features in the Langebaanweg fossils indicate that the species concerned was probably already evident on the *Procavia* lineage, but the presence of several plesiomorphic characters reveals that it is a primitive member of the lineage. These also reveal that the specimens do not belong to *Procavia* cf. *antiqua* into which they were previously tentatively classified by Hendey (1976) as they are somewhat more derived. The detailed systematic status of the large extinct hyracoid *Gigantohyrax maguirei,* Kitching, 1965, from Pliocene cave fillings at Makapansgat, South Africa, has not previously been satisfactorily demonstrated, even though it is clear that most authors have considered it to be a procaviid closely related to *Procavia.* Kitching (1965) compared it only to species of *Procavia.* Re-study of the original sample, as well as additional fossils (three partial skulls, isolated upper premolar, fragment of mandible with a premolar) reveal that *Gigantohyrax* shares many features with the genus *Dendrohyrax,* fewer with *Heterohyrax* and even fewer with *Procavia.* It is concluded that among the Procaviidae, *Gigantohyrax* is most closely related to *Dendrohyrax.* The new discoveries of Late Miocene and Pliocene procaviids in Kenya and South Africa, when added to recently described associated upper and lower dental elements of *Meroehyrax bateae* from the base of the Middle Miocene of Uganda, permit a reappraisal of procaviid phylogeny. It is concluded that procaviids probably descended from Saghatheriidae, and that Pliohyracidae did not give rise to procaviids as previously thought by some authors.

Keywords: Procaviidae phylogeny, Lukeino Formation, Makapansgat, Langebaanweg.

INTRODUCTION

Fossil Procaviidae are known from many Plio-Pleistocene localities in East and South Africa (Churcher 1956; Jaeger & Wesselman 1976; Kitching 1965; McMahon & Thackeray 1994; Schwartz 1996, 1997; Schwartz *et al.* 1995; Zeally 1916) but Miocene occurrences are rare, for the moment the only published ones being from Namibia (Rasmussen *et al.* 1996) and Kenya (Fischer 1986). In both the latter occurrences, the procaviids were identified as *Heterohyrax.*

Procaviids have recently been collected at two additional Late Miocene sites in Kenya, Lukeino in the Tugen Hills, and Lemudong'o, near Narok (Hlusko *et al.* 2002). The Lukeino dassies, represented by a palate and some isolated teeth, belong to *Dendrohyrax,* the earliest record of this genus. The Lemudong'o specimens are more fragmentary than the Lukeino material, but they too belong to *Dendrohyrax* (Pickford & Hlusko, in press).

Hyracoids from Langebaanweg were originally attributed to *Procavia* cf. *antiqua* (Hendey 1976, 1981) but no detailed descriptions of the specimens have been published. Examination of the collection, stored in the South African Museum, reveals that they belong to a species that is larger than *P. capensis* (and its probable synonyms *P. antiqua* and *P. robertsi*), but smaller than *P. transvaalensis.* In many features, such as the brachyodonty of the cheek teeth and the presence of p/1 (or lower canine, if Luckett 1990 is correct), the Langebaanweg dassies are close to *Heterohyrax,* but since brachyodonty is probably the primitive condition for procaviids, the decision to classify the remains in *Procavia* is based on the derived morphology of the mandible and dentition which is *Procavia*-like, rather than *Heterohyrax,* even though the quantity of features is not very great. It is possible that *Procavia* diverged from the other extant procaviid genera sometime during the Late Miocene.

The detailed affinities of the giant Late Pliocene procaviid *Gigantohyrax maguirei* from Makapansgat, South Africa, have never been elucidated. Kitching (1965) compared it only to fossil and extant species of *Procavia,* and pointed out a number of ways that the fossils differ morphologically from them. The combination of large size and the morphological differences from *Procavia* provided the basis for erecting the genus *Gigantohyrax.* However, almost all the characters that were used to distinguish *Gigantohyrax* from *Procavia,* occur in the genus *Dendrohyrax.* The only features noted by Kitching that, if true, would continue to distinguish the two genera are the 'massive hypsodont teeth', and the presence of a sagittal

crest, neither of which occur in *Dendrohyrax.* A curved maxillo-palatine suture was also listed as a character that distinguished *Gigantohyrax* from *Procavia.*

The aim of this paper is to describe new procaviid fossils and then to review the systematic affinities of the Late Miocene to Pleistocene dassies from East and South Africa. The subject will be tackled in five parts – a general overview of the problems of distinguishing the three extant procaviid genera from each other, as there is a dearth of recent information in the literature, followed by three sections on the fossil hyracoids treated by locality in geochronological order, followed by a section of discussion and conclusions in which the phylogeny of the Procaviidae will be evoked.

MATERIALS AND METHODS

Three hundred and forty seven extant, fully adult procaviid skulls and mandibles were measured with vernier callipers (63 *Dendrohyrax,* 86 *Heterohyrax* and 198 *Procavia*) housed in the Natural History Museum, London, the Transvaal Museum, Pretoria, the Iziko South African Museum, Cape Town, the Bernard Price Institute (Johannesburg) and the Muséum National d'Histoire Naturelle, Paris. Measurements taken included lengths of premolar row, molar row, diastemata, gap between upper incisors, depth of mandible beneath the rear of the first lower molar and temporal crest separation. Dental measurements (length × breadth) of fewer specimens were undertaken. The only measurements that need explanation are mandibular depth and upper molar row length. Because procaviid mandibles increase in depth posteriorly, the callipers were placed with one of its jaws parallel to the base of the mandible, the other jaw being positioned at gingival level between m/1 and m/2. Upper molar row length was measured from the antero-buccal projection of the parastyle of M1/ to the rear of M3/.

Fossils measured included material in the Community Museums of Kenya (*Dendrohyrax samueli*), the Transvaal Museum (*Procavia antiqua, Procavia transvaalensis*), the Bernard Price Institute (*Gigantohyrax*) and the Iziko South African Museum (*Procavia pliocenica* sp. nov.).

Measurements were analysed using Excel to produce bivariate plots (Figs 1–8) the ones retained for this paper being those that showed clear patterns of differences between the three extant genera. Available fossils, except for *Gigantohyrax,* were plotted on these diagrams.

PART I. DIVERSITY OF EXTANT PROCAVIIDAE

The question of generic diversity in extant Procaviidae has been addressed on numerous occasions over the past century and a half (Allaerts *et al.* 1982; Bothma 1967; Brauer 1913; Ellerman & Morrison-Scott 1951; Hahn 1934; Lataste 1886, 1892; Thomas 1892). All authors are agreed that there are at least two genera (*Procavia* and *Dendrohyrax*) and many authors agree that there are three (*Heterohyrax*). Others, however, consider that *Heterohyrax* should be treated as a subgenus of *Dendrohyrax* (Ellerman & Morrison-Scott 1951; Roche 1972, 1978) while yet others have noted morphological and behavioural affinities between *Heterohyrax* and *Procavia* (Hoeck 1978), some even raising the possibility of occasional hybridization between these two genera (Kingdon 1974). The current consensus is that there are three genera, with behaviour [daily life rhythm (nocturnal versus diurnal activity), vocalization], soft anatomy (perineal anatomy, mammary formula) and craniodental, and to a lesser extent skeletal, anatomy (Fischer 1986; Rasmussen *et al.* 1996) serving to distinguish them. Morphometric analysis of several hundred extant procaviids from many parts of Africa and Arabia reveal the presence of three clear groups (*Dendrohyrax, Heterohyrax* and *Procavia*) with a fourth group from Liberia and Nigeria that blends characters and proportions of *Dendrohyrax* and *Procavia.* This group is probably to be referred to *Dendrohyrax,* but the possibility of a fourth genus of extant procaviid requires examination.

For a palaeontologist, only the skeletal source of evidence can be used, but the distinctiveness in cranio-dental morphology between the three genera is not always as clearcut as one would wish. This is because, for many morphological and metric features, *Heterohyrax* is intermediate between *Dendrohyrax* and *Procavia.* An added difficulty is that there is a great deal of geographic variation within each of the genera such that some East African species traditionally attributed to *Procavia* (*ruficeps, johnstoni*) are closer in some dental and cranial features to *Heterohyrax* than they are to the South African species *Procavia capensis.* Churcher (1956), for instance, reported that the p/1 was almost always absent in extant *P. capensis,* and concluded that its presence in the fossil species *P. transvaalensis* and *P. antiqua* was an indication of the primitive status of these two Plio-Pleistocene species. However, in extant East African species of *Procavia,* p/1 is almost always present, and furthermore, the molars are often less hypsodont than those of South African *P. capensis,* and in isolation can easily be confused with those of *Heterohyrax* and even *Dendrohyrax.*

The following features (Table 1) have often been used by neontologists and palaeontologists to distinguish between the skulls and mandibles of the three genera of Procaviidae (Allaerts *et al.* 1982; Bothma 1967; Churcher 1956; Hahn 1934; Skinner & Smithers 1990).

South African specimens of *Procavia capensis* show a wide range of variation in molar hypsodonty, temporal crest anatomy and other craniodental features. This variability is not due to sexual dimorphism, as both males and females are variable in the same way, and it is not solely due to ontogeny, since young adults and aged individuals are also quite variable in these features.

Some distinctions between the mandibles of *Heterohyrax* and *Dendrohyrax*

The mandibles of *Heterohyrax* and *Dendrohyrax* are superficially similar to each other, not only in their dental features but also in most of the mandibular morphology. However, there are a few consistent differences between the mandibles of the two genera. In general, the jaws of *Heterohyrax* are shallower than those of *Dendrohyrax.* This appears to be related to the development of stronger temporalis musculature in the tree hyrax, which often possess well-developed temporal ridges on the dorsal

Table 1. Features often used to distinguish the three extant genera of Procaviidae.

Feature	*Procavia*	*Heterohyrax*	*Dendrohyrax*	Comments
Basal length: jugal breadth	169.7: 100	174.0: 100	180.8: 100	Rarely available in fossil samples, and somewhat variable
Sagittal crest	Often present in adults	Not present	Not present	Varies with age, but overall is a useful criterion, but many *Procavia* do not have one
Frontal bone morphology	Raised close to midline	Raised close to midline	Hollowed near midline	Rarely available in fossils, and in any case somewhat variable in *Procavia*
Infra-orbital foramen position	Above posterior root of P3/	Above contact between P2/ and P3/	Above posterior root of P2/	Somewhat subjective due to difficulties in orienting specimens
Post-orbital bar	Open	Open but some individuals closed	Closed	Not often preserved in fossils, but generally reliable for *Dendrohyrax*
Temporal ridges	Unbeaded	Unbeaded	Beaded	Sometimes incipiently beaded in *Heterohyrax* and even occasionally in *Procavia*
Dorsal profile of skull	Convex	Convex to straight	Concave	Not often preserved in fossils
Premaxillary palatal fossa	Small, shallow	Small, shallow	Large, deep	Not often preserved in fossils
Fossa beneath upper incisive jugum	Small, shallow	Small, shallow	Large, deep	Not often preserved in fossils
Tooth row convergence	Convergent anteriorly	More or less parallel	Convergent posteriorly	Somewhat variable in all genera
Ventral surface of symphysis	Usually smooth	Usually smooth	Often rugose with a basal promontary separated from the rest of the symphysis by grooves	Useful for identifying *Dendrohyrax*
p/1	Usually absent	Present	Present	Tropical species of *Procavia* usually possess this tooth, as do several fossil species
Wear on lower incisors	Tines obliterated rapidly	Tines lost in old age	Tines seldom lost	Not reliable in very worn teeth
Lower incisor hypsodonty	High	Low	Low	Deciduous incisors of *Procavia* are low crowned
Gap between lower central incisor apices	None or narrow (0–1.6 mm)	Narrow to wide (1.3–2.5 mm)	Narrow to wide	Not often preserved in fossils
Upper diastema length	Short	Medium	Long	Some overlap between *Heterohyrax* and *Dendrohyrax*
Upper incisor dimorphism	Strong	Weak	Weak	More difficult to assess in *Heterohyrax* and *Dendrohyrax* than in *Procavia*
Upper molar ectoloph morphology	Almost flat	Undulating	Strongly undulating	Somewhat subjective due to variation caused by wear
Upper molar cingula	Weak	Moderate to weak	Moderate to strong	Not very reliable
Interparietal fusion	None	Yes	Yes	Ontogenetically variable
Gap between upper incisors	Less than width of incisor	Greater than width of incisor	Greater than width of incisor	*Heterohyrax* and *Dendrohyrax* are similar
Molar hypsodonty	Moderate to high	Moderate to low	Low	*Procavia* quite variable, with some individuals overlapping *Heterohyrax*
Upper molar row: premolar row	Premolar row shorter than molar row	Premolar row subequal to molar row	Premolar row longer than molar row	Overlap between *Heterohyrax* and *Dendrohyrax*
Lower molar row: premolar row	Premolar row shorter than molar row	Premolar row subequal to molar row	Premolar row longer than molar row	Generally reliable taking into account loss of p/1
Stylar prominence in upper molars	Weak	Medium	Strong	Variable but reasonably reliable
Dental metrics	Medium to small	Medium to small	Large to medium	Much overlap between the three genera

surface of the skull. Measurements of the mandibular depth below the rear of the first molar plotted against the length of the lower molar row generally differentiates the two genera, at least the adult specimens (Fig. 1). Other measures proposed in the literature concern the length of the premolar row relative to the molar row (Skinner & Smithers 1990) (Figs 2 & 5). There are however, overlaps in the range of variation, so that a few individuals are difficult to classify. Indeed, some specimens appear to be intermediate in morphology between the two genera, blending features of both. Under the circumstances, the identification of some of the extant specimens by the collectors could be in error (many museum labels are inaccurate). In *Dendrohyrax* the ventral part of the symphysis is often marked by rugose bone and two swollen ridges of bone, whereas in *Heterohyrax* the symphysis is smoother

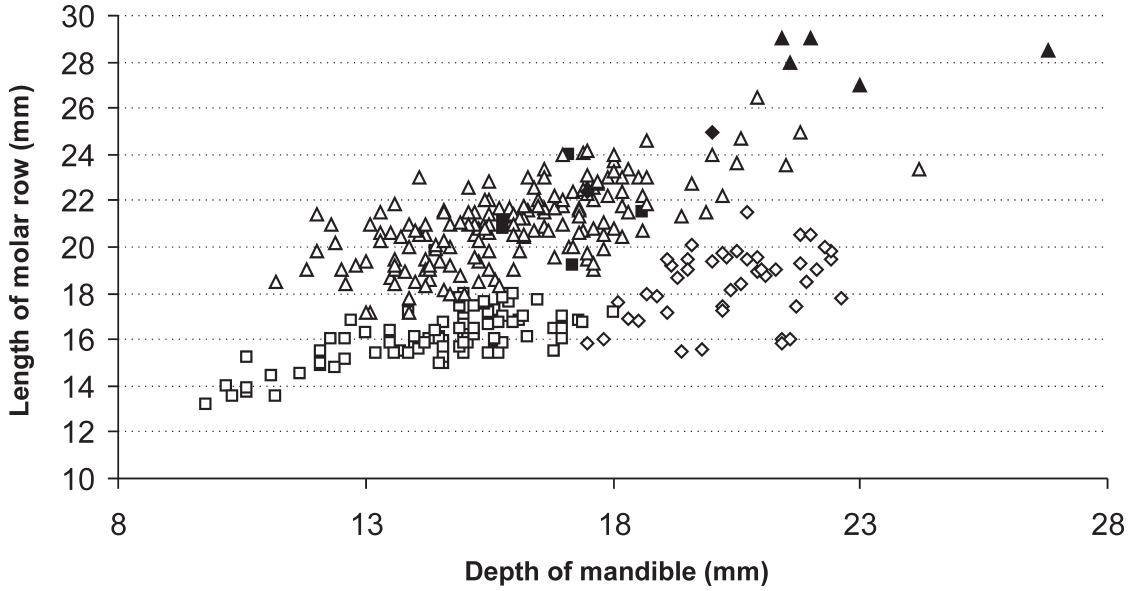


Figure 1. Bivariate plot of depth of mandible beneath the rear of m/1 against length m/1–m/3 in extant and fossil Procaviidae (open symbols, extant species; filled symbols, fossil species) (Δ = *Procavia* species; ✧ = *Dendrohyrax* species; ❑= *Heterohyrax* species; ▲ = *Procavia transvaalensis*; ■ = *Procavia antiqua*; ◆ = *Procavia pliocenica*; ● = *Dendrohyrax samueli*).

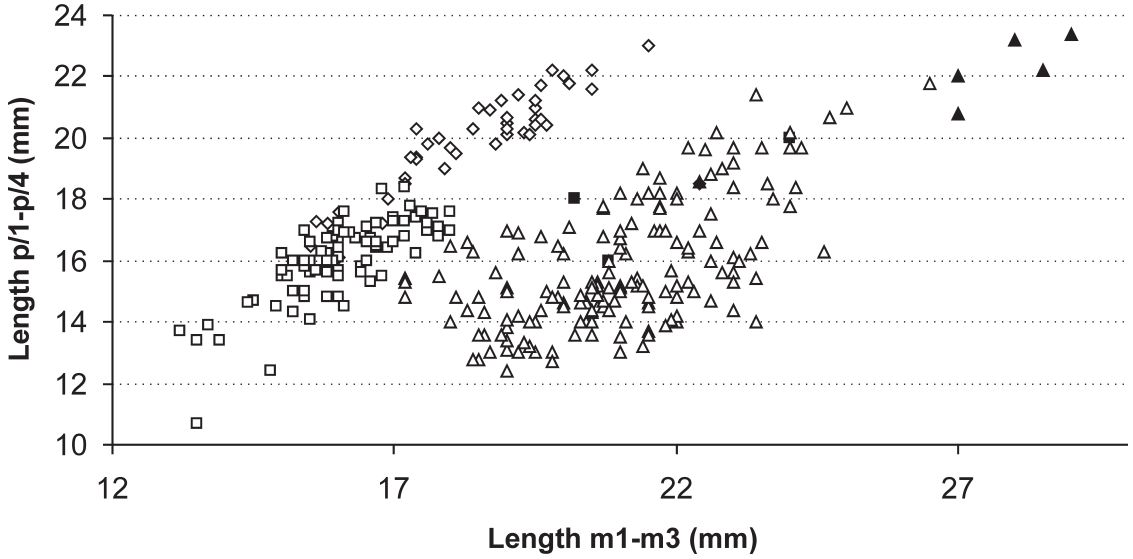


Figure 2. Bivariate plot of length of lower molar row versus length of lower premolar row in extant and fossil Procaviidae (symbols as in Fig. 1).

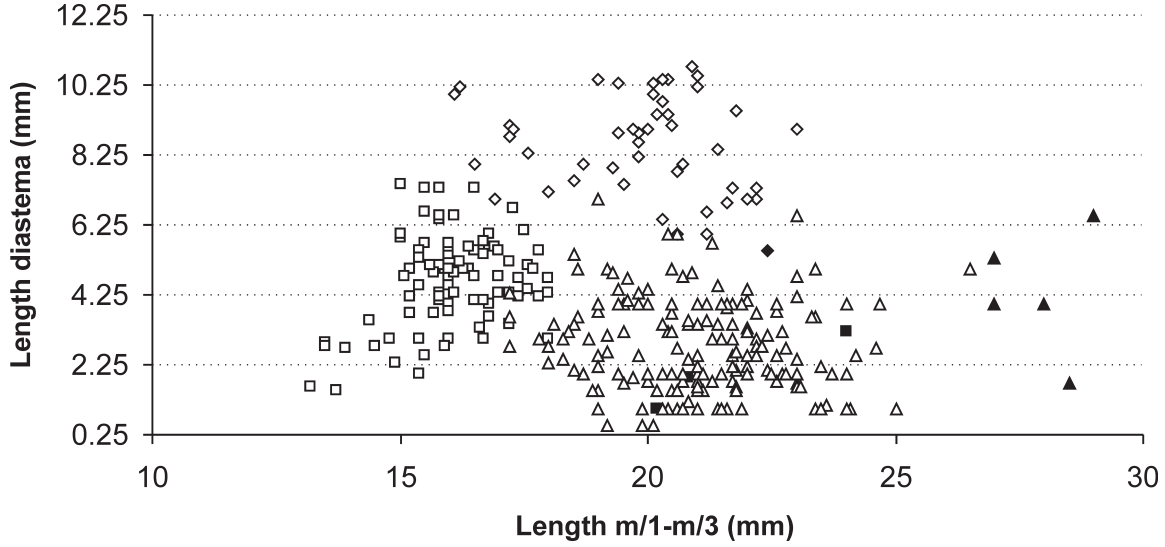


Figure 3. Bivariate plot of length m/1–m/3 versus lower diastema in extant and fossil Procaviidae (symbols as in Fig. 1).

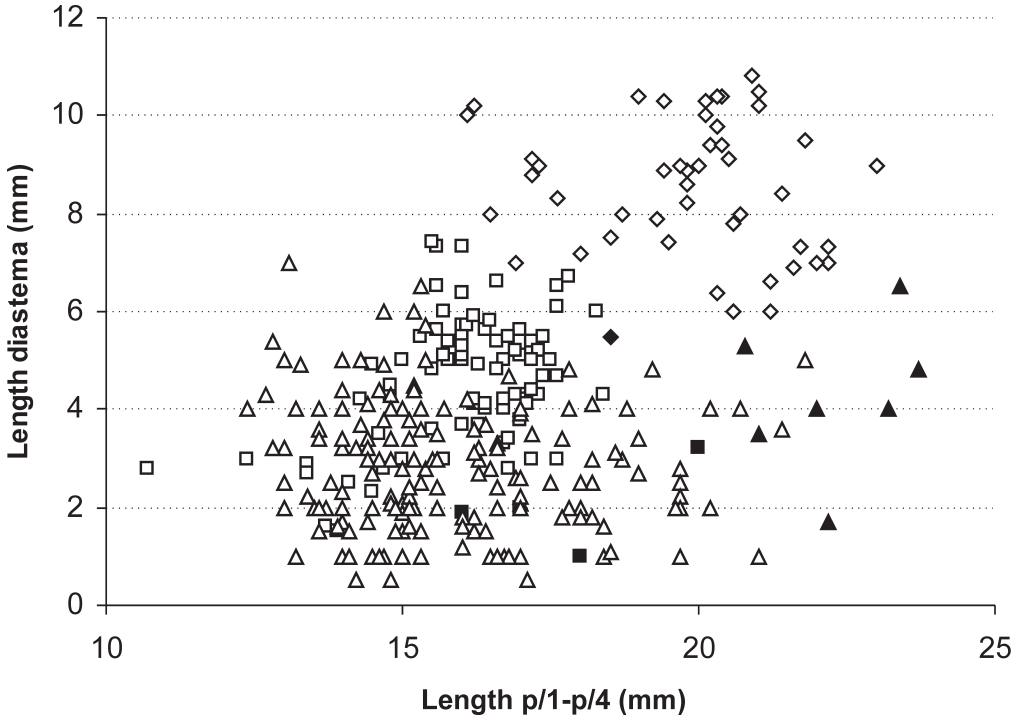


Figure 4. Bivariate plot of lower premolar row versus length of lower diastema in extant and fossil Procaviidae (symbols as in Fig. 1).

and has no ridges. A few specimens of *Dendrohyrax,* especially juveniles, lack the ridges, but if they are present, then the identification of the individuals as *Dendrohyrax* is reliable.

Figures 1–4 are plots of mandibular and dental parameters. Figure 1 deals with mandibular depth against length of lower molar row and reveals the pattern which can be used to distinguish the three genera of extant dassies. The mandibles of *Heterohyrax brucei* are uniformly shallower relative to the length of the molar row than those of *Dendrohyrax* species, which scatter around a separate regression line. The mandibles of *Procavia* species are even shallower relative to the length of the molar row, and they scatter about a third regression line.

Some distinctions between the genera *Procavia* and the *Heterohyrax*/*Dendrohyrax* pair

Because the Langebaanweg dassies combine features of both *Heterohyrax* and *Procavia,* it is necessary to revisit the question of how to distinguish between them and the tree hyrax, *Dendrohyrax.*

Procavia differs in many respects from both *Heterohyrax* and *Dendrohyrax* (Hahn 1934; Sale 1960; Roche 1972). Dentally, the latter two genera are similar to each other, but there are minor differences in premolar-molar proportions, mandibular depth, and cranial morphology. It is difficult, if not impossible, to distinguish isolated lower teeth of these two genera from each other. Table 2 summarizes the main differences between extant *Procavia*

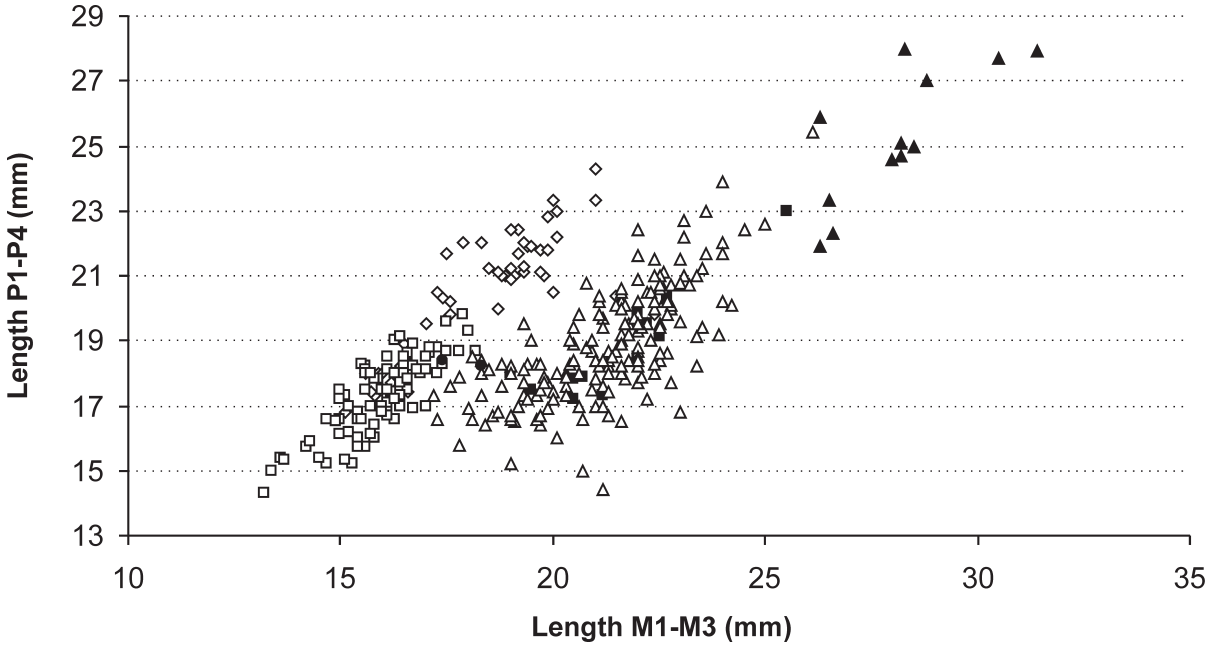


Figure 5. Bivariate plot of length of upper molar row versus length of upper premolar row in extant and fossil Procaviidae (symbols as in Fig. 1).

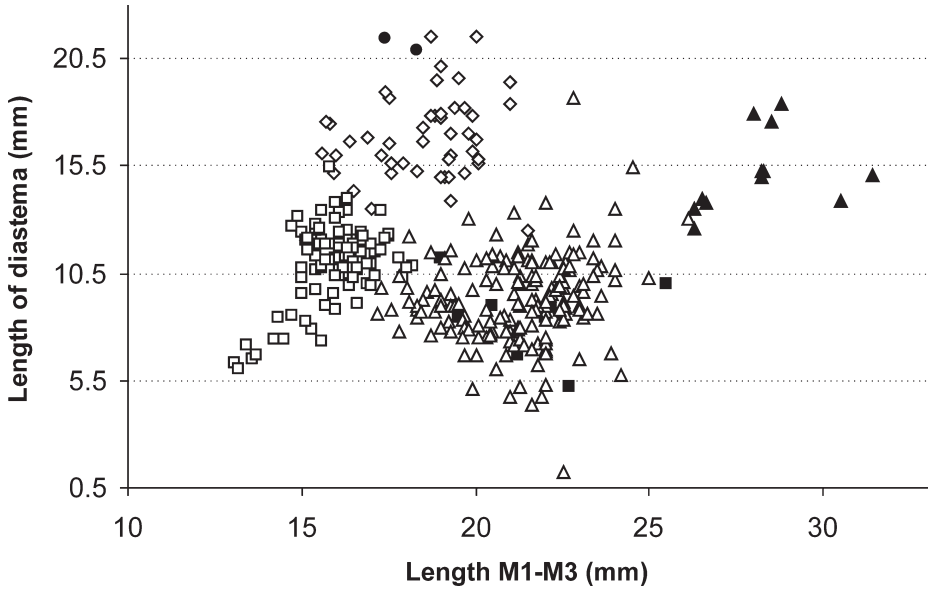


Figure 6. Bivariate plot of length upper diastema versus length of upper molar row in extant and fossil Procaviidae (symbols as in Fig. 1).

on the one hand and the *Heterohyrax/Dendrohyrax* pair on the other.

Variation in fossil and extant *Procavia*

The large degree of morphological variability in *Procavia* has led to some confusion in the literature. Broom (1934, 1936), for instance, created two species of *Procavia* for fossils from karst deposits of South Africa (*Procavia (Prohyrax) antiqua* from Taung, and *P. robertsi* from Uitkomst (= Gladysvale)). The differences between these species related to the hypsodonty of the molars, curvature of the cheek tooth rows and the distance between buccal and lingual cusps in the upper cheek teeth. Some of these features, such as the distance between the buccal and lingual cusps, vary with wear (McMahon & Thackeray 1994) and thus do not represent real morphological differences, but the other features that Broom cited are part of the normal range of variation of the species. Broom appears to have been influenced by the extremes of variation that exist in the extant rock hyrax, his species *P. antiqua* being similar to the more brachyodont specimens of *P. capensis* (which generally have the temporal crests far apart, as in *Heterohyrax*), and *P. robertsi* being similar to the more hypsodont individuals of *P. capensis* (in which the temporal crests are often closer together, even to the extent of forming a sagittal crest). As was demonstrated by McMahon & Thackeray (1994), all the material attributed to *P. antiqua* (including *P. robertsi*) falls within the range of metric variation of *P. capensis,* and on this basis they concluded that all the small fossil dassies from cave deposits

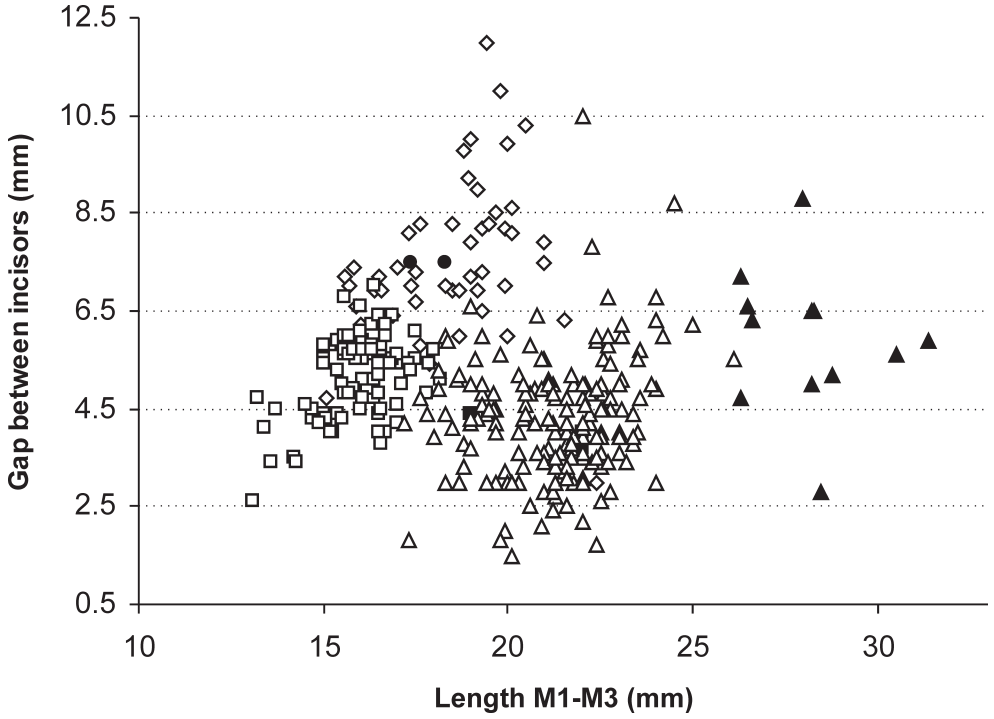


Figure 7. Bivariate plot of length of upper molar row versus length of gap between upper incisors in extant and fossil Procaviidae (symbols as in Fig. 1).

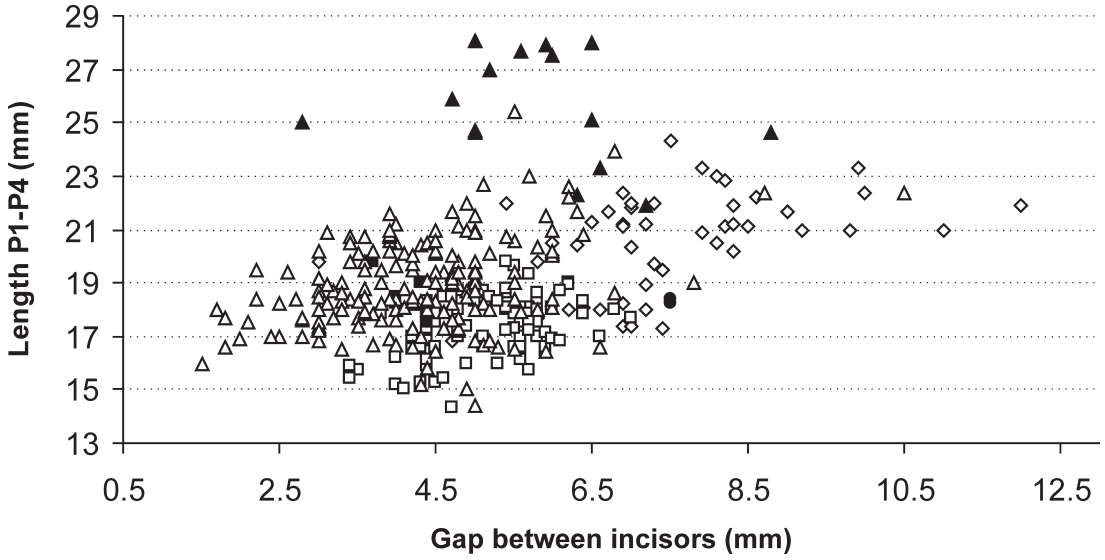


Figure 8. Bivariate plot of length of upper premolar row versus length of incisor gap in extant and fossil Procaviidae (symbols as in Fig. 1).

of South Africa belonged to the extant species *Procavia capensis*. By contrast, Schwartz (1997) upheld Broom's species *P. antiqua,* citing its brachyodonty, a few other odontological features and some metric differences (ratio of ectoloph length to lingual length of upper molars).

While the conclusion of McMahon & Thackeray (1994) is well-founded for the characters that they selected to analyse from a statistical point of view, it does not address the issue of the presence of both brachyodont and hypsodont individuals (populations) in the same species. Nor does it explain the presence of straight and curved tooth rows in the same species, nor of the temporal crest development (wide apart or close together) and other morphological variation. Many of the differences observed are related directly or indirectly to mastication (hypsodonty versus brachyodonty, size of temporal musculature (temporal crest development), loss or retention of p/1, position of the infra-orbital foramen, relative proportions of premolar row to molar row, length of diastemata), from which it is deduced that the diets of the species contain a wide range of plants, with some populations devouring only small quantities of grass, and other populations much more. It is surely no coincidence that the individuals with the most hypsodont molars are also those with the largest areas of origins of the temporal musculature (as reflected in closer temporal crests), and those with the most brachyodont molars tend to have the temporal crests further apart (i.e. smaller areas of origin of the temporal musculature).

Churcher (1956) concluded that *P. antiqua* and *P. robertsi* were synonymous, and reconstructed the cranial and mandibular anatomy of the species on the basis of various fragmentary fossils from a variety of localities. In doing so, he appears to have combined elements of more hypsodont and more brachyodont individuals (see Churcher 1956, p. 496, the list of specific characters is clearly a mixture drawn from hypsodont and brachyodont individuals). Partly because of this the fossil species was considered by him to be a primitive member of the genus, and he positioned it near the base of the *P. capensis* lineage. However, because the fossils possess almost the same range of variation as the extant species, it is in reality just as derived. For this reason, the author agrees with McMahon &

Table 2. Summary of features that have been used to separate *Procavia* from the *Heterohyrax/Dendrohyrax* pair.

Feature	*Heterohyrax/Dendrohyrax*	*Procavia*
p/1	Well formed, two-rooted	Simple peg, tiny single root, often absent except in East African populations
Diastema between i/2 and anterior premolar	Long	Short or absent
Lower incisors	Brachyodont, long times	Hypsodont, short tines
Diastema between lower central incisors	Medium to wide	Absent to short
Distal transverse lophs of lower molars	Short, at right angles to long axis of tooth row	Long, oblique to long axis of tooth row
Mental foramina	Below p/1	Below p/3
Styles on upper molars	Well developed, extending to cervix	Weak, fading out above cervix
Ectolophs of upper molars	Brachyodont	Hypsodont
Buccal cingulum of upper molars	Sub-parallel to occlusal surface	Steeply angled
Increase in size of upper cheek teeth	Regular from anterior to posterior, M3/ slightly smaller than M2/.	Molars abruptly larger than premolars. M3/ large.
Lower molars	Brachyodont	Hypsodont
Premolar row	Long relative to molar row	Short relative to molar row

Thackeray (1994) that *P. antiqua, P. robertsi* and *P. capensis* have similar ranges of metric variation in the dentition, but it is noted that the range of variation in temporal crest separation is greater in the fossil sample than it is in the extant one. This could be due to either of two things; a) the fossil sample is a mixture of two or more species in which case the material from the various sites should not be pooled together into a single species, b) the range of variation in dassies was different in the Plio-Pleistocene than it is today, in which case we cannot use actualism to explain variation in fossil dassies. The former explanation is probably more likely than the latter.

Schwartz (1997) did not mention the fact that extant South African dassies attributed to *P. capensis* are variable in terms of hypsodonty and brachyodonty. My own observations reveal that the species is highly variable, both in terms of hypsodonty and other cranio-dental features, such as the disposition of the temporal crests and curvature of the tooth rows in occlusal view. Fossils from the Gauteng Cave Sites attributed to *P. antiqua* by Churcher (1956) and Schwartz (1997) span a similar range of morphometric variation as *P. capensis.* More detailed analysis of the collections, including undescribed fossils that have been collected in the past two decades may lead to a better understanding of the situation. Pending the results of such a study, I consider that the fossils identified as *P. antiqua* by Churcher (1956) and Schwartz (1997) are better classified as *P. capensis,* but for the purposes of metric analyses which follow, the fossils will be kept separate from extant specimens in order to prevent mixing of material of different geological ages (Figs 1–8).

Even though the more brachyodont individuals of *P. capensis* fall comfortably within the range of metric variation of the species, in terms of some morphological characters they are closer to *Heterohyrax* than to the hypsodont individuals of *P. capensis.* The strong development of the styles and cingula on the ectolophs of the upper molars, for example, is closer to the condition in *Heterohyrax* than to that of hypsodont individuals of *Procavia* in which the ectoloph is flatter (Allaerts *et al.* 1982). The straightness of the palatal tooth rows is another feature by which brachyodont *P. capensis* recall *Heterohyrax,* and there are others, including the relatively great separation of the temporal crests. Because of these similarities, it is sometimes confusing to work on fragmentary material or isolated teeth, and it is possible that some inferences regarding hybridization between *Procavia* and *Heterohyrax* (Kingdon 1974) may be due to the intermediate nature of the brachyodont individuals of *Procavia.*

Inclusion of *Heterohyrax* and *Dendrohyrax* in the analyses reveals an even more complicated situation, with a great deal of overlap in metric and morphological features. Thus, whilst there is little difficulty in correctly identifying complete skulls of *Dendrohyrax* and *Heterohyrax* due to the great differences in temporal crest morphology, post-orbital bar development, length of diastemata relative to the tooth rows, post-orbital closure and proportions of premolar rows to molar rows, it is considerably more difficult to identify fragments of jaws and isolated teeth. This is especially evident when individuals from many populations in different countries and habitats are considered. It is undoubtedly this aspect of *Heterohyrax* and *Dendrohyrax* that underlies the decisions of some researchers to consider *Heterohyrax* to be a subgenus of *Dendrohyrax* (Ellerman & Morrison-Scott 1951; Roche 1972). Nevertheless, there can be little doubt that *Heterohyrax* and *Dendrohyrax* represent separate genera – their biology is so divergent that it is difficult to conceive of them as being congeneric. Not only are their daily rhythms different (diurnal in *Heterohyrax,* nocturnal in *Dendrohyrax*), but also their calls are widely divergent and their social structures dissimilar.

As concerns fossil procaviids, the gradation of morphological features between the three extant genera poses particular problems, especially in fragmentary material. Historically, there has been a tendency to identify brachyodont fossil procaviid remains as *Heterohyrax* (Fischer 1986; Rasmussen *et al.* 1996), but the possibility exists that some of the material could represent *Dendrohyrax* or *Procavia* instead. Only the collection of more substantial specimens will resolve the matter.

At Lukeino, the Aragai palate is complete enough to reveal with little doubt that it belongs to *Dendrohyrax.* The Lemudong'o, Kenya, fossils in contrast are fragmentary and most of the features that are diagnostic for separating *Heterohyrax* from *Dendrohyrax* are lacking. However, a base of a mandibular symphysis preserves morphology that is usually only found in *Dendrohyrax* (presence of a roughened promontary separated from the body of the symphysis by grooves). Metrically the dental remains from Lemudong'o plot within the ranges of variation of both *Dendrohyrax* and *Heterohyrax.* If they are *Heterohyrax* then they represent a large species of the genus, but if they are attributed to *Dendrohyrax,* then they would denote a small species of the genus. The assumption is that only one genus is present at the site, which, if true, means that it should be attributed to *Dendrohyrax* (Pickford & Hlusko, in prep.).

The Langebaanweg (South Africa) dassie possesses mandibular proportions of the genus *Procavia,* and because this morphology is derived among procaviids, the remains are attributed to *Procavia,* even though in several features of the dentititon, they resemble *Heterohyrax.* As such, the Langebaanweg *Procavia* is the earliest known member of the genus in the fossil record. The primitive nature of the cheek dentition, allied to the derived proportions of the mandible suggest that the *Procavia* lineage diverged from those of the other procaviids sometime during the Late Miocene.

PART 2. THE LATE MIOCENE PROCAVIID FROM LUKEINO, KENYA

The site of Aragai in the southern extremity of the Lukeino Basin, Baringo District, Kenya, which is at the base of the Lukeino Formation (Sawada *et al.* 2002) yielded an almost complete palate of a hyrax of modern aspect (Fig. 9). The fossil was collected from rust-coloured sands comprising a palaeosol near the base of the formation. The specimen was heavily encrusted in a hard, red ironstone sand rich in phosphate. The neurocranium is missing and

much of the naso-maxillary region is crushed into the nasal cavity but the lateral surfaces of the maxilla are well preserved.

The same site yielded abundant colobine cranial and mandibular material, as well as a juvenile suid mandible (*Nyanzachoerus tulotos*) and remains of impala (*Aepyceros* sp.). The nature of the assemblage and the damage to the specimens indicates that the fossils were probably concentrated in the area by a bird of prey, such as Verreaux's eagle or the crowned eagle, as similar damage has been described in extant bone assemblages recovered from the ground below the nests of the crowned eagle (Sanders *et al.* 2003).

Systematic description

Order Hyracoidea Huxley, 1869
Family Procaviidae Thomas, 1892
Genus *Dendrohyrax* Gray, 1868

Species *Dendrohyrax samueli* sp. nov., Fig. 9

Diagnosis. Upper diastema longer relative to premolar and molar rows than is usual in *Dendrohyrax*. Hypocone of M3/ not greatly reduced, incisive jugum terminates above the P1/.

Holotype. Bar 961'01, palate with much of the dentition.

Type locality. Aragai, Lukeino Formation, Tugen Hills, Kenya.

Age. 6 Ma, Late Miocene.

Etymology. Named in honour of Mr Samuel Chetalam of Rondinin Village and member of the Community Museums of Kenya, who found the holotype.

Description

Lukeino hyrax palate *(Bar 961'01)*

The specimen consists of a palate that was heavily encrusted in a hard red sandstone (Fig. 9). It has the bases of both upper central incisors, the roots of the left P1/ and the right P1/–P3/, the other premolars and all the molars being complete or only slightly damaged and heavily to moderately worn.

The snout is slightly distorted and has suffered a bit of plastic deformation and displacement of bones, especially the nasals which have been pushed into the nasal cavity. The snout flares out abruptly above the P1/ and the zygomatic arch departs from this flared part of the snout at the level of P2/ (Fig. 9). There is a well-developed buccinator ridge just above the roots of the cheek teeth, while on the palatal side of the cheek teeth, especially opposite the molars there is a small shelf of bone, forming a prominent alveolar process. The posterior choanae are broadly U-shaped and invaginate up to the level of the front of M3/ (Fig. 9). The rear of the root of the zygomatic process of the maxilla lies above the middle of M2/.

The upper incisors are triangular in section, the antero-mesial and antero-lateral sides being slightly concave indicating that the individual was probably a male. The lingual surface of the incisor is devoid of enamel, and is slightly convex lingually. The distance between the incisors (7.5 mm) is much wider than the mesio-distal diameter of each of the incisors (4.2–4.5 mm). The central incisors occupy a prominent jugum which extends in the arc of a circle as far back as the P1/ (Fig. 9). The fact that this jugum terminates above the P1/ indicates that it is a relatively long snouted form, unlike *Prohyrax tertiarius* and *Prohyrax hendeyi*, in which the incisor root terminates above the P3/ and other species of *Dendrohyrax* in which it ends above the P2/.

The diastema between the upper incisors and the anteriormost premolar is *c.* 18 mm. The premolar row is *c.* 19.8 mm on the left and 20.5 mm on the right, which is longer than the molar row (18.9 mm left and 19.6 mm right) (Fig. 9; Table 3).

The P1/ roots suggest that the tooth was about the same length as the P2/, and was thus not reduced.

The ectoloph of P2/ is broken and the tooth is heavily worn, but the remaining part of the crown reveals that it was molariform with well-developed protocone and hypocone with large anterior crests leading antero-buccally from each cusp forming prominent protoloph and metaloph, respectively, with a deep valley between them.

P3/ is larger than P2/ and has a well-developed basal cingulum running the length of the ectoloph. The parastyle is strong and projects anteriorly of the rest of the tooth. The paracone and metacone are large and are joined to the ectoloph by well-developed protoloph and metaloph. The parastyle and metastyle form low relief rounded ridges on the outer surface of the tooth. The protoloph and metaloph are separated on their lingual sides by a deep transverse valley, but are strongly joined to the ectoloph.

P4/ is similar to P3/ but is larger, and because it is less worn it is possible to observe an anterior shelf-like cingulum, and a posterior cingulum which overhangs the distal roots. The buccal cingulum is well developed.

The M1/ is larger than the P4/ and differs from it by possessing better developed and more angular styles on

Table 3. Measurements of the teeth (in mm) of Bar 961'01 are as follows.

Tooth	Mesio-distal length	Bucco-lingual breadth
I1/ left	4.5	4.8
I1/ right	4.2	4.8
Gap between I1/s	7.5	–
Diastema left	18.0	–
Diastema right	18.3	–
P2/ left	4.3	–
P3/ left	5.1	6.2
P4/ left	5.6	6.1
P4/ right	5.6	–
M1/ left	6.1	6.3
M1/ right	6.2	6.7
M2/ left	7.1	6.9
M2/ right	7.5	7.7
M3/ left	6.0	6.4
M3/ right	6.3	–
P1/–P4/ left	19.8	–
P1/–P4/ right	20.5	–
M1/–M3/ left	18.9	–
M1/–M3/ right	19.6	–

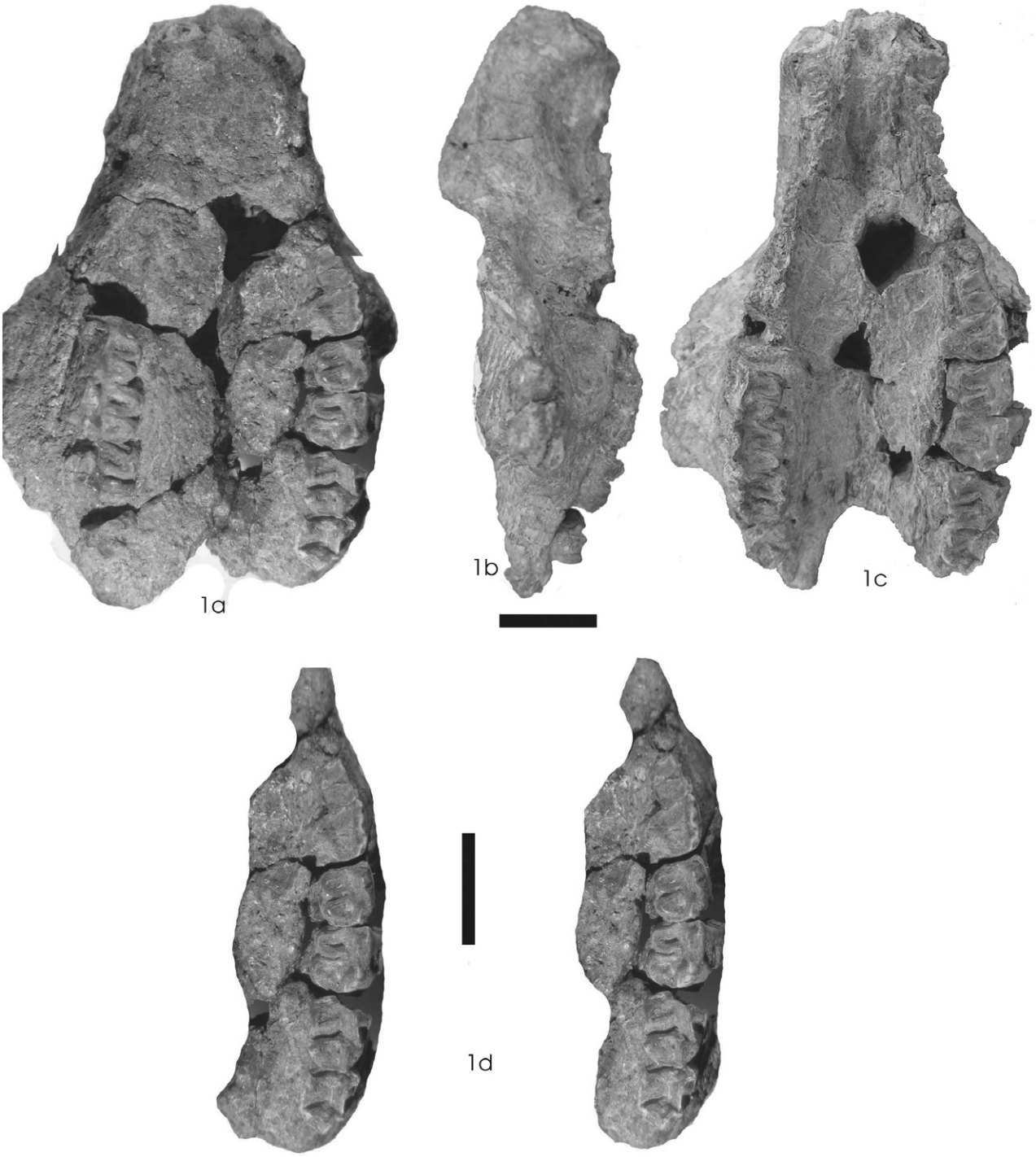


Figure 9. Bar 961'01, *Dendrohyrax samueli* sp. nov. palate with partial dentition from Aragai, Late Miocene (6 Ma), Lukeino Formation, Tugen Hills, Kenya. **1a**, palatal view before cleaning. **1b**, Right lateral view to show incisor jugum. **1c**, Palatal view after cleaning. **1d**, Stereo occlusal view of left cheek tooth row (scale bars = 10 mm).

the ectoloph. It too is deeply worn to the stage where the protoloph and metaloph are confluent with the ectoloph, but still separated from each other lingually. There is a small style at the distal extremity of the ectoloph, and the distal cingulum is well developed. The parts of the ectoloph anterior and posterior to the mesostyle lie in the same plane.

M2/ is the largest tooth in the dentition. It closely resembles the M1/ in morphology, but being less worn reveals that the transverse valley between the protoloph and metaloph is deep. The ectoloph morphology is similar to that of the M1/.

The M3/ is the smallest of the molars and tapers distally more rapidly than the other two, the hypocone being reduced compared with the other cusps. The distal cingulum is much narrower bucco-lingually than it is in M2/, but it still closes off a small fovea between the metaloph and the distal end of the tooth. Despite the reduction of the metacone, the two parts of the ectoloph either side of the metastyle lie in the same plane.

The lingual margins of the tooth rows are virtually parallel, being *c.* 17 mm apart throughout their length. The buccal margins of the toothrow bow outwards slightly, the outer surfaces being 26 mm apart at P4/, 31 mm at M1/ and

Table 4. Comparison of premolar row to molar row proportions of *Dendrohyrax samueli* sp. nov. with other procaviids.

Feature	*Procavia*	*Heterohyrax*	*Dendrohyrax*	Bar 961'01
Premolar row. molar row length (means)	16.18–20.95	15.95–16.42	16.20–16.10	21.2–18.2
Ratio premolars – molars	77%	97%	100.6%	116%

Data for extant hyracoids from Skinner & Smithers 1990.

29 mm at the front of M3/.

In lateral view the occlusal surface of the cheek teeth is slightly convex ventrally.

Comparisons among Procaviidae

Bar 961'01 is definitely not a *Procavia* (the premolar row is longer than the molar row; the molars are brachyodont and have prominent styles, ribs and cingulum; the upper incisors are far apart; the tooth rows are not markedly bowed outwards; I1/ is narrow; the diastema is longer than the length of M2/+M3/, and the molars are more brachyodont than in *Procavia,* in the upper molars the parts of the ectoloph either side of the mesostyle lie in the same plane) (Figs 5–8). Some of these differences in extant genera have been quantified, and it is clear that there is minor overlap in the ranges of variation of these parameters. As a general rule, however, the differences appear to be valid for most individuals.

In overall aspect the Aragai palate and upper dentition is similar to both *Dendrohyrax* and *Heterohyrax.* The craniodental differences between these two genera are subtle, and some are not reliable on a continental basis. However, for southern Africa, where the most thorough comparative work has been done (Bothma 1967; Hahn 1934; Roche 1972), the following criteria are usually valid:

Heterohyrax has the premolar row more or less equal in length to the molar row, the anterior premolars are closer together relative to the molar row and the diastema is much shorter than the length of M2/+M3/. In East Africa there is significant overlap in the range of variation of the premolar/molar measurements, to the extent that a large number of individuals cannot be identified on the basis of the premolar-molar row relationships alone. The length of the diastema relative to the premolar row is a more consistent criterion for distinguishing the genera (Table 4), but there is some overlap in the range of variation. *D. dorsalis* has an elongated diastema that is consistently longer than that in any species of *Heterohyrax.* However, in these features many individuals of *Dendrohyrax arboreus* fall within the range of variation of *Heterohyrax brucei.*

Environmental significance of *Dendrohyrax*

According to Corbet & Hill (1991) there are three extant species of tree hyrax. The largest is *Dendrohyrax dorsalis* which occurs in rainforests extending from Uganda to Gambia. The smaller *Dendrohyrax arboreus* inhabits more seasonal forests and well-wooded areas from Kenya to South Africa, and the coastal species, *Dendrohyrax validus,* is found in Eastern Tanzania and Zanzibar. This distribution translates into a size cline, with large tree hyraxes occurring in rainforest, medium-sized ones in seasonal forests and small ones in woodland and drier areas. When individuals from the three vegetation categories are plotted on bivariate plots a relatively clear pattern emerges supporting the observation. Adding the Aragai specimen onto the same bivariate graph reveals that it plots out consistently with the rainforest individuals.

This identification accords with other evidence that the Tugen region was covered in rainforest during the Late Miocene and Early Pliocene (Pickford *et al.* 2004). Other indications that the Lukeino Formation accumulated under humid climatic conditions are the presence of the water chevrotain, *Hyemoschus aquaticus,* the palm civet (*Nandinia*), the monkey fauna which consists only of colobines, and the bovid fauna which contains duikers, bushbuck and impala. The suids from Lukeino are bunodont, as are some of the proboscideans, including *Anancus kenyensis.* Large browsing mammals are present, including *Ancylotherium cheboitense,* and small giraffids. By contrast, mammals that are classically considered to be adapted to savanna and steppe, such as equids, are rare at Lukeino. Some of the Lukeino mammals are semi-hypsodont, with weak cementum on the cheek teeth (*Primelephas, Ceratotherium, Hippopotamus*). Fossil leaves from the formation are generally large, and many have drip points. Abundant small shards of fossil grass occur in diatomaceous shales (probably disaggregated hippopotamid faeces). The palaeoenvironmental picture that emerges for the Late Miocene of the Tugen Hills, is one of rainforest with open patches of grassland near water bodies, somewhat like parts of the western Rift Valley in eastern Congo and western Uganda.

Lukeino procaviid

The Lukeino hyrax palate is closest in morphology and proportions to the extant genus *Dendrohyrax.* In most measurements it falls within the range of variation of the western tree hyrax *Dendrohyrax dorsalis,* which occurs in rainforest extending from Uganda to Gambia. It is larger than the eastern tree hyrax *Dendrohyrax arboreus,* and the coastal species, *Dendrohyrax validus.* It is definitely not *Procavia,* and is unlikely to represent *Heterohyrax.* This is the first fossil record of *Dendrohyrax.* Because it has a relatively long upper diastema, an unreduced M3/ and the incisive jugum terminates in a position more anterior than is the case in other species of *Dendrohyrax,* the Aragai specimen is classified as a new species, *Dendrohyrax samueli.*

Dendrohyrax, as its name implies, is indicative of trees. It is arboreal, except in a few places where it lives in rocky areas with abundant crannies within forested areas (Corbet & Hill 1991; Roberts 1951). It is mostly nocturnal, but does have some diurnal activity when conditions are

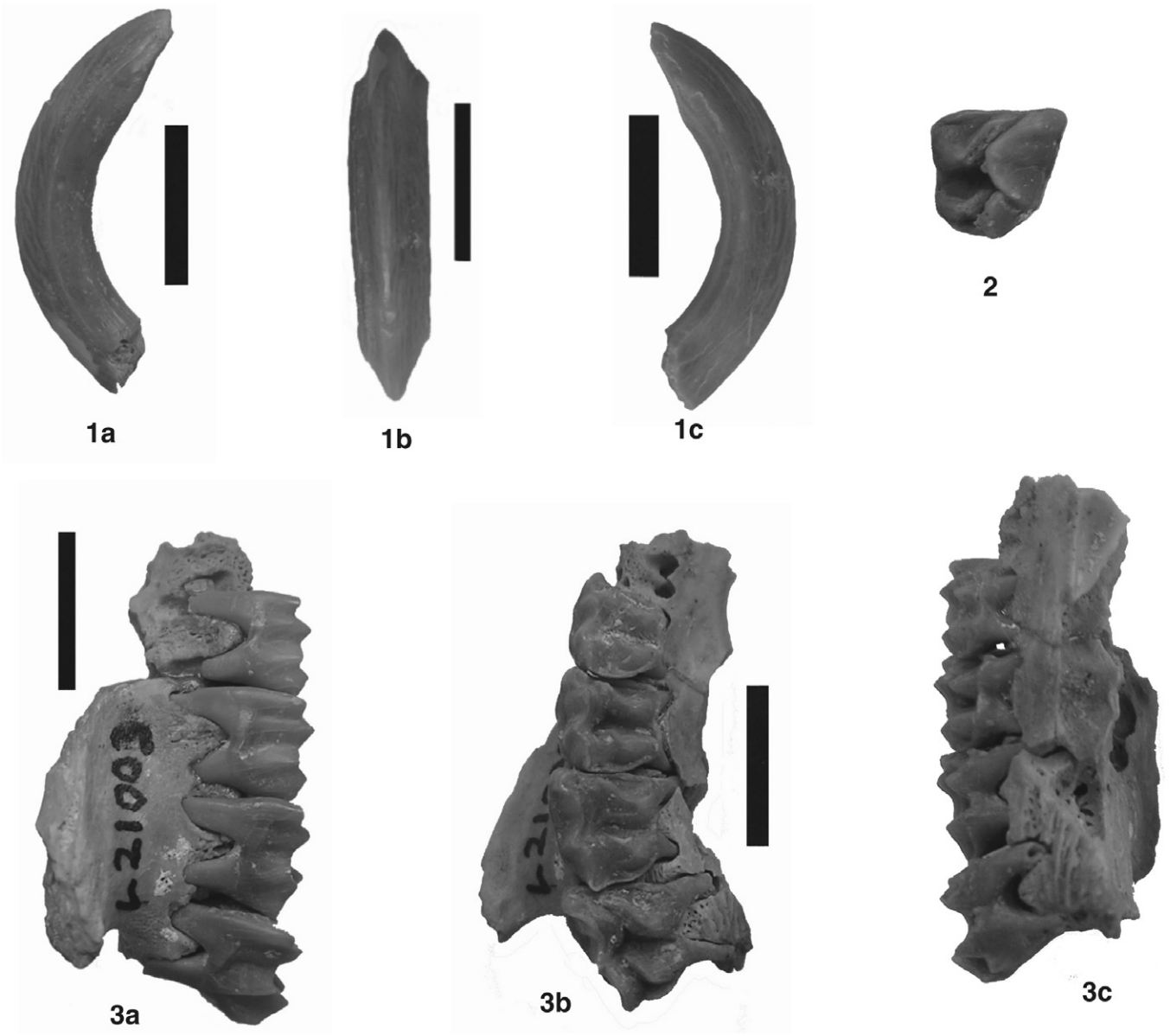


Figure 10. *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa (scale bars = 1 cm). **1**, PQ L 11189, left I1/, **a**) mesial; **b**) anterior and **c**) distal views. **2**, PQ L 21003, left M3/, occlusal view. **3**, PQ L 21003, right maxilla with P3/–M2/ and alveoli of P2/, **a**) buccal; **b**) occlusal and **c**) lingual views.

suitable (Sale 1960). On the basis of the hyrax and other faunal and floral evidence, it is postulated that the Tugen Hills were covered in rainforest during the Late Miocene.

PART 3. THE LANGEBAANWEG PROCAVIID

Langebaanweg is an Early Pliocene site in Western Cape Province, South Africa from which a restricted sample of dassies was attributed to *Procavia* cf. *antiqua* by Hendey (1976, 1981). The bulk of the fossils described herein (Figs 10 & 11), came from the Quartzose Sand Member of the Varswater Formation.

Systematic description

Genus *Procavia* Storr, 1780

Species *Procavia pliocenica* sp. nov., Figs 10 & 11

Diagnosis. Species of *Procavia* with two rooted p/1, species 20% larger than *Procavia capensis* (and its probably synonymous species *P. antiqua* and *P. robertsi*); smaller than *Procavia transvaalensis*.

Synonymy

1976 *Procavia* cf. *antiqua* Broom, 1934 – Hendey, pp. 236, 242.

1981 *Procavia* cf. *antiqua* Broom, 1934 – Hendey, pp. 52, 90.

Holotype. PQ L 23564, mandible with both bodies, but lacking incisors, the right p/1 and ascending rami (Fig. 11.1).

Type locality. Langebaanweg, Cape Province, South Africa.

Stratigraphy. Quartzose Sand Member, Varswater Formation.

Age. Lower Pliocene

Etymology. The species name refers to the Early Pliocene age of the deposits from which the fossils were obtained.

Paratypes

Upper jaws and teeth

L 11189/21, left I1/ (Fig. 10.1).

L 21003, right maxilla with P3/–M2/, plus two isolated upper cheek teeth (Fig. 10.2, 10.3).

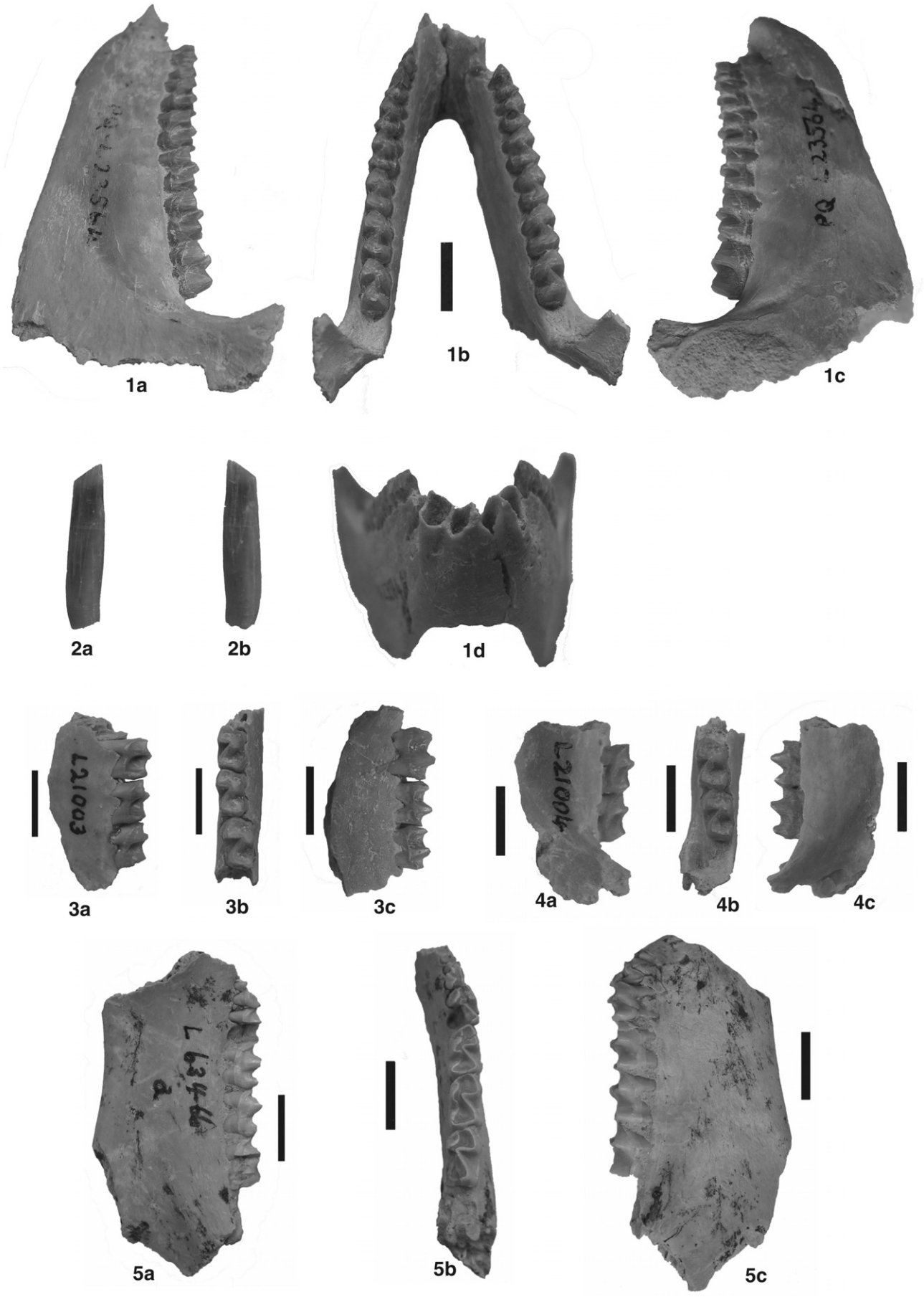


Figure 11. *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa (scales: 1 cm). **1**, PQ L 23564, mandible lacking incisors, right p/1 and ascending rami, **a**) left lateral, **b**) occlusal, **c**) right lateral and **d**) anterior views. **2**, PQ L 21003, right i/2, **a**) anterior and **b**) posterior views. **3**, PQ L 21003, left mandible fragment with p/4–m/2, **a**) buccal, **b**) occlusal and **c**) lingual views. **4**, PQ L 21004, left mandible fragment with m/2–m/3, **a**) buccal, **b**) occlusal and **c**) lingual views. **5**, PQ L 63455, right mandible with p/3–m/2, **a**) lingual, **b**) occlusal and **c**) buccal views.

L 50522, right P3/.
L 63466f, right maxilla with two fragmentary cheek teeth.

Lower jaws and teeth
L 13633, right m/2.
L 21003 (see above) right i/2, plus left mandible fragment with p/4–m/2 (Fig. 11.2).
L 21004, left mandible with m/2–m/3 (Fig. 11.3).
L 24016, left m/2.
L 24605, left mandible fragment with p/2.
L 63466a, right mandible with p/3–m/2, roots p/2 (Fig. 11.5).
L 63466b, left mandible with rear half of m/3.
L 63455c, right mandible with m/1–m/2.
L 63466d, right mandible with p/1–p/2 and front part of p/3.
L 63466e, left mandible fragment with m/2.

Description

Maxilla. The only piece of hyracoid maxilla preserved at Langebaanweg consists of the alveolar process from P2/ to M2/ and part of the root of the zygomatic process of the maxilla (Fig. 10.3). As in *Heterohyrax brucei,* the two lingual roots of the P2/ are close together, being fused near cervix, while those in the P3/ to M2/ are wide apart. In the fossils the rear of the root of the zygomatic process of the maxilla is opposite the rear of M1/, which is further forwards than it usually is in adults of *H. brucei,* in which it is opposite the midline of M2/. However, during ontogeny the dental battery in dassies migrates forwards with respect to the zygomatic arch, and its forward position in the Langebaanweg specimen is due to the youthful status of the individual (M3/ was probably still in its crypt) rather than to a specific difference.

The morphology of the maxillary dentition of the Langebaanweg hyrax is similar to that of extant *Heterohyrax brucei* (Fig. 10.2, 10.3). The cheek teeth differ markedly from those of *Procavia capensis* by having well-developed styles and buccal ribs on the ectoloph. The ectoloph is brachyodont rather than hypsodont as in *Procavia.* In the extant rock hyrax the styles are usually weak and the ribs low and rounded (although the molars are variable in these respects), whereas in the Langebaanweg species the styles project more strongly buccally and the ribs are more prominent and are sharper. The styles in the fossil species are pinched in and sharp apically and swell towards cervix where they are more rounded in profile. The cingula on the buccal surfaces of the upper cheek teeth are sharper and more prominent than they are in the extant species. The hypocone of the M3/ in the Langebaanweg dassie is complete, though relatively smaller than it is in the other molars. In *Procavia capensis,* the hypocone of the M3/ is reduced to absent but similar reduction also occurs frequently in *Heterohyrax* and *Dendrohyrax.* Measurements of the upper teeth are provided in Table 5. In other respects the upper cheek teeth of the Langebaanweg dassie are close to those of the extant bush hyrax.

Mandible. There are several mandible fragments of dassies from Langebaanweg, and one specimen, the holotype (Fig. 11.1), consists of a lower jaw lacking only the ascending rami and the incisors. The diastema between the i/2 and p/1 is longer in the Langebaanweg specimen (5.5 mm) than it is in the extant rock hyrax (usually 1–2 mm only). This together with the fact that p/1 is present in the fossil species, and is reduced to absent in *P. capensis,* means that the Langebaanweg species has a proportionally longer mandible than extant rock hyrax, somewhat similar to those of *Heterohyrax* and *Dendrohyrax.* Related to this is the position of the mental foramina, which occur below the p/3 and p/4 in *P. capensis,* but beneath the p/1 and p/2 in *P. pliocenica.* In most other respects the mandibles of the Langebaanweg and extant bush hyrax are similar to each other.

Table 5. Measurements (in mm) of the upper dentition of *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa.

Catalogue No.	Tooth	Length	Breadth
L 11189/21	I1/	5.0	4.8
L 21003 right side	P3/	5.8	6.2
	P4/	6.4	6.9
	M1/	7.4	7.3
	M2/	7.9	8.0
L 21003 left side	M1/	7.3	7.3
	M3/	7.1	7.6
L 50522	P3/	6.4	6.2

Apart from its greater dimensions, the mandibular dentition of *P. pliocenica* is similar to that of *Heterohyrax brucei.* It differs in several important ways from extant *Procavia capensis* – the p/1 is large and possesses two roots in the Langebaanweg species, whereas in South African *P. capensis* the p/1 is usually absent, or if present is a tiny, single rooted tooth with a single cusp (most individuals of East African *Procavia* retain the p/1). In *P. pliocenica* the p/1 has two crescentic lophs, being a smaller and narrower version of the p/2. The i/2 from Langebaanweg has three terminal pectinations as in the extant species. The lower cheek teeth of *P. pliocenica* have sharp buccal cingula, whereas in South African specimens of *Procavia capensis* buccal cingula are usually absent or are represented by a low rounded swelling near the base of the crown. In East African specimens of *Procavia* there can be sharp buccal cingula in the lower cheek teeth, and the p/1 is more often present than it is in South African populations.

The rear loph of the m/3 in *P. pliocenica* is as well-developed as it is in the m/1 and m/2, whereas in South African *Procavia capensis* it is usually slightly reduced (lower when unworn) in size relative to those of the m/1 and m/2 as well as to the anterior loph of the m/3. A further difference between the lower cheek teeth of the Langebaanweg species and extant *Procavia capensis* is that in *P. pliocenica* the rear loph of the molars is oriented almost at right angles to the long axis of the tooth row, whereas in *P. capensis* it is more oblique, being angled at about 60° to the long axis of the tooth row.

However, the relative depth of the mandible is similar to the situation in *Procavia* rather than *Heterohyrax* and *Dendrohyrax,* the jaw being relatively shallow compared

to the length of the molar row. Measurements of the lower teeth are given in Table 6.

Comparisons with other *Procavia* species

Procavia antiqua. The lower cheek teeth of *Procavia pliocenica* are about 20% larger than the mean of *Procavia antiqua* Broom, 1934 (Churcher 1956) (Fig. 1, 2). Some features of the dentition of *P. antiqua* described by Churcher suggest that this species is intermediate between *Heterohyrax* and *Procavia.* In particular, the more brachyodont molars, and the position of the protocone and hypocone relative to the ectoloph are primitive features, as is the presence of a well-formed p/1. However, the smooth ectoloph of the upper molars, the very short lower diastema, the single-rooted nature of the p/1 and the shape and narrow gap between the upper central incisors, and the close proximity of the lower central incisors, are all features typical of the genus *Procavia.*

McMahon & Thackeray (1994) concluded that *P. antiqua* and *P. robertsi* were synonyms of *P. capensis,* as the material is metrically and morphologically similar to the extant dassies from South Africa, but this view was challenged by Schwartz (1997), who considered the differences between the populations to be great enough to warrant separation at the species level. He therefore reinstated *P. antiqua.* However, there are still residual problems with the fossil species, in that the range of morphological variation in dental and cranial features seems to be rather large for a single species, and there may in fact be two species of dassies in the Plio-Pleistocene deposits of South Africa.

Procavia transvaalensis Shaw (1937) and its synonym (*Procavia obermayerae* Broom, 1936) is about 150% the size of *P. capensis* (i.e. 1.5 times larger) (Churcher 1956). It appears to be morphologically close to *P. capensis.*

Table 6. Measurements (in mm) of the lower dentition of *Procavia pliocenica* sp. nov. from Langebaanweg, South Africa.

Catalogue No.	Tooth	Length	Breadth
L 13633	m/2	7.2	3.8
L 21003	i/2	4.3	2.3
	p/4	6.0	4.4
	m/1	7.4	4.1
	m/2	7.3	4.7
L 21004	m/2	7.9	4.8
	m/3	7.6	4.7
L 23564 left side	p/1	3.4	2.3
	p/2	5.0	3.2
	p/3	5.2	3.9
	p/4	5.6	4.5
	m/1	7.2	3.8
	m/2	7.4	4.5
	m/3	6.8	4.3
L 23564 right side	p/2	4.9	3.2
	p/3	5.5	3.9
	p/4	6.0	4.5
	m/1	7.6	4.3
	m/2	7.2	4.5
	m/3	7.6	4.6
L 24016	m/2	7.1	4.5
L 24605	p/3	5.3	3.6
L 63466a	p/3	5.6	–
	p/4	6.8	5.3
	m/1	7.6	4.9
	m/2	7.6	5.0e
L 63466b	m/3	–	4.7*
L 63466c	m/2	–	4.4
	m/3	7.1	4.4
L 63466d	p/1	3.6	2.3
	p/2	4.5	3.2
L 63466e	m/2	7.3	4.7

*Rear loph of m/3.

Identification of the Langebaanweg hyracoids

The dentition of the Langebaanweg dassie differs in several respects from those of extant *Procavia.* The upper and lower molars are brachyodont, the p/1 is not reduced, the diastema is long, and the ectolophs of the upper molars possess well-developed styles and ribs which extend to the cervix, all features that do not occur in extant *Procavia,* but are present in *Heterohyrax* and *Dendrohyrax.* In addition the molar ectolophs are not as hypsodont as they are in living *Procavia.* The main feature by which the Langebaanweg dassie resembles *Procavia* is the depth of the mandible relative to the length of the molar row, the shape of the symphysis and the hypsodonty of the lower incisor.

There are few differences between the upper dentitions of *Heterohyrax* and *Dendrohyrax,* and even traditionally used criteria for distinguishing between them, such as length of the upper premolar row relative to molar row (Bothma 1967; Skinner & Smithers 1990) are sometimes inconclusive for some individuals. Unfortunately there is no complete upper cheek tooth row from Langebaanweg, so this 'test' cannot be applied.

There are differences in cranial morphology, principally related to the development of the temporal crests, which are strongly developed in *Dendrohyrax* and weak in *Heterohyrax.* Correlated to this difference, which suggests that *Dendrohyrax* possesses more powerful masseter and temporal musculature than *Heterohyrax,* is the presence of a deeper mandible in the tree hyrax than in the bush hyrax and the rock hyrax. The functional meaning of this is not clear, as it seems not to be related to chewing power or duration, since the teeth of the two genera are closely similar to each other. It is possible that these features are related to the loud and prolonged calling that typifies *Dendrohyrax,* and the softer, less common calling that occurs in *Heterohyrax.* When tree hyraxes call, they extend the head upwards, tightening the skin beneath the mandible, which, together with the enlarged hyoid apparatus, forms an efficient resonance chamber and 'drum skin'.

Be that as it may, the deeper mandible in *Dendrohyrax* generally serves to distinguish it from both *Heterohyrax* and *Procavia.* The Langebaanweg specimens (two can be measured) indicate that the mandibles are shallow relative to the length of the molar row, and they thus accord better with *Procavia* than with *Dendrohyrax* or *Heterohyrax.* The ventral surface of the symphysis is similar to that of *Procavia,* and the central incisor roots are close together, as in the rock hyrax, and unlike the situation in *Dendrohyrax* and *Heterohyrax.* Furthermore, the lateral lower incisor from Langebaanweg is hypsodont, and the tines are worn

off well above the cervix, as in *Procavia,* markedly different from the lower crowned incisors of *Heterohyrax* and *Dendrohyrax.*

Phylogenetic implications of the Langebaanweg dassie

The species *P. pliocenica* provides a link between the extant *Procavia capensis* on the one hand and the genus *Heterohyrax* on the other, including *Heterohyrax auricampensis* from the Late Miocene of Berg Aukas, Namibia (Rasmussen *et al.* 1996). The overall similarity in size and morphology of these species indicates that the procaviids have experienced slow evolution for the past 10 million years.

In four features – the depth of the jaw relative to the length of the molar row, the morphology of the ventral part of the symphysis, the lack of a diastema between the lower central incisors, and the hypsodont i/2 with short tines – the Langebaanweg hyrax falls within the range of variation of *Procavia.* Because of this it is possible that the population is an early member of the *Procavia* lineage, retaining a large quantity of primitive features in the dentition. If this is so, then the genus *Procavia* originated in the Late Miocene rather than earlier. In this case the genus did not evolve its distinctive hypsodont dentition (molars in particular) until the Late Pliocene or Pleistocene. As Churcher (1956) pointed out, the Middle to Late Pliocene species *Procavia antiqua* retains a number of features of the dentition that are present in *Heterohyrax* but not in *Procavia,* including a well-formed p/1, and clear buccal styles and ribs on the upper molars, which are brachyodont (but see discussion above about *P. robertsi* and the results of McMahon & Thackeray 1994).

Geographic origin of the genus *Procavia*

The earliest known member of the *Procavia* lineage is from South Africa (this paper; Churcher 1956), where it has a more or less continuous fossil record from *c.* 5 Ma to the present. In East Africa, *Procavia* is unknown until the Late Pleistocene to Holocene, where it has been found in archaeological contexts at Kapthurin, Bromhead's Site and Gamble's Cave, Kenya (Hopwood 1931, 1939), while in Zimbabwe its earliest known record is Bulawayo (Zeally 1916). It is thus likely that the genus *Procavia* evolved in southern Africa, where it survived for a substantial period before spreading northwards during the late Pliocene, first to Eastern Africa, and eventually to parts of northeast Africa and even the Arabian Peninsula. Undoubtedly, the adaptations of *Procavia* for surviving in semi-arid and arid environments enabled it to colonize East Africa as this region became drier during the Pliocene before local lineages of hyraxes (*Dendrohyrax* and *Heterohyrax*) could themselves adapt to them. Tree hyraxes are still restricted to well-wooded to forested environments, but the bush hyrax (*Heterohyrax*) has managed to adapt to somewhat arid environments, and often occurs side-by-side with *Procavia.* However, in extremely arid regions, such as the Sahara and the Arabian Peninsula, the only hyracoid found is *Procavia.*

Extant South African rock hyraxes are more derived than those that occur in the tropics. In *P. capensis* the molars are more hypsodont, the upper diastema shorter, and the p/1 is generally absent, whereas in the East African species, p/1 is almost always present, the molars are often more brachyodont and the upper diastema longer. Thus, even the extant *Procavia* populations of South Africa are more evolved than those of East Africa.

Langebaanweg procaviids

The fossil dassie from the early Pliocene deposits at Langebaanweg belongs to the *Procavia* lineage, being similar in size to extant *Procavia capensis,* but it retains a large number of primitive features of the cheek dentition usually associated with the genera *Heterohyrax* and *Dendrohyrax.* It is larger than extant *Heterohyrax brucei* and the extinct *H. auricampensis,* and is attributed to a new species, *Procavia pliocenica.* In some features of its dentition it approaches the extinct early Miocene species *Meroehyrax bateae,* indicating that among all the known early Miocene hyracoids, the procaviids are more closely linked to *Meroehyrax* than to any other known genus, *Prohyrax* included. It is thus more likely that procaviids descended from saghatheriids than from any other family of hyracoids.

PART 4. AFFINITIES OF *GIGANTOHYRAX* AMONG THE PROCAVIIDAE

The detailed affinities of the large hyrax from Makapansgat, South Africa, *Gigantohyrax maguirei,* have never been elucidated. Examination of the fossils housed at the Bernard Price Institute (University of the Witwatersrand), South Africa, reveals that the resemblances between *Gigantohyrax* and *Dendrohyrax* are pervasive (Figs 12–14). The cheek teeth are large, concomitant with the dimensions of the skull, but they are by no means hypsodont, being upscaled versions of the teeth in *Dendrohyrax,* with well-formed buccal cingulum, large para-, meso- and metastyles, and relatively low-crowned ectoloph, and the parts of the ectoloph either side of the mesostyle lie in the same plane (Allaerts *et al.* 1982) (Fig. 14). Since Kitching's report, additional material has been collected from Makapansgat, consisting of two partial adult skulls, a juvenile skull that has been severely crushed, an isolated upper premolar and a fragment of lower jaw carrying a premolar. The undescribed fossils are useful in that they reveal variation in temporal crest morphology, some individuals having them close together and others wide apart. Thus the two features that could be taken to distinguish *Gigantohyrax* from *Dendrohyrax* were either incorrectly reported (hypsodont teeth) or are variable (degree of separation of the temporal crests).

Table 7 summarizes the main features of cranial morphology that distinguish adults of the three genera of Procaviidae and *Gigantohyrax.* The list contains observations by Allaerts *et al.* 1982; Hahn 1934; Kitching 1965, and the author.

The position of the infra-orbital foramen in *Gigantohyrax* was evoked by Kitching (1965) as a difference from *Procavia,* but the scoring of this character is somewhat subjective because of difficulties in orienting the reference plane (in lateral view, curvature of the toothrows differs in the three extant genera). In any case the supposed differ-

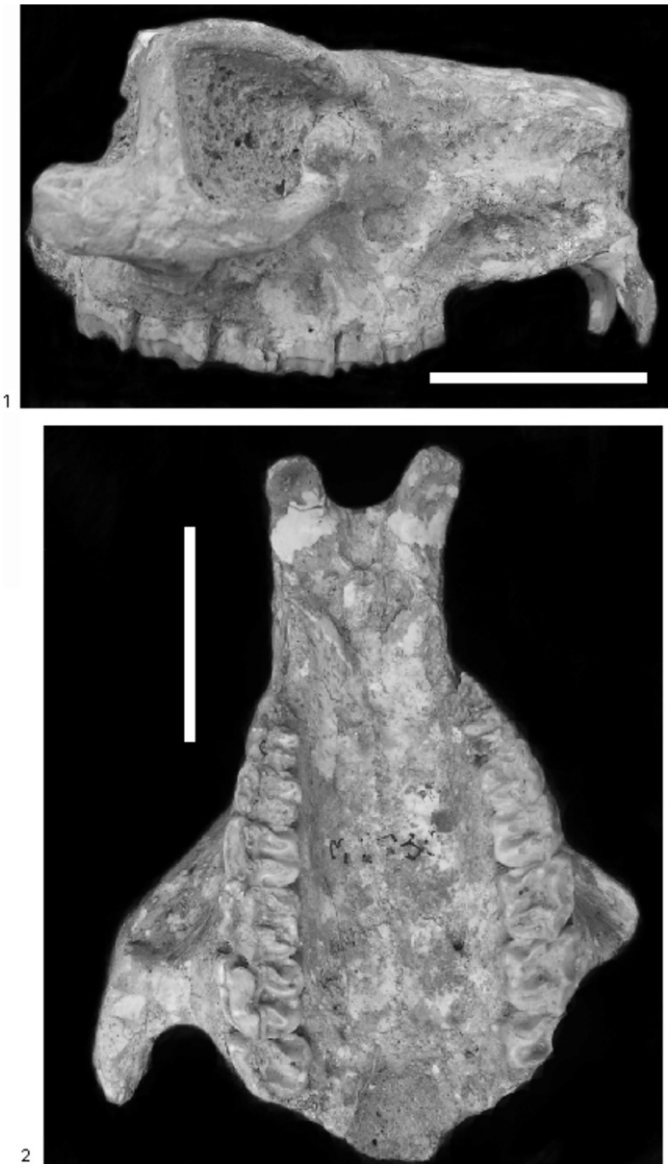


Figure 12. M 8230, snout of *Gigantohyrax maguirei* Kitching, 1965, from the Pliocene of Makapansgat, South Africa ((scale bars = 5 cm). **1**, right lateral view. **2**, Palatal view.

ences between the three extant genera are not great. Likewise, the anterior convergence of the tooth rows in *Gigantohyrax* is not markedly different from that in other procaviids, at least when measured between the lingual edges of the cheek teeth. Hypsodont specimens of *Procavia* sometimes have toothrows that converge more sharply than brachyodont specimens, but in any event the degree of convergence is quite variable in all three extant genera.

Determination of sex in *Gigantohyrax*

In extant procaviids, the upper incisors are sexually dimorphic. In both sexes the incisors are tusk-like, but in males the section is almost an equilateral triangle, often with the two anterior surfaces slightly concave in section, whereas in females, the section is an inequilateral triangle, in which the antero-lateral surface is appreciably broader than the antero-mesial one, and the anterior surfaces are convex.

The incisors in the holotype snout (M 8230) (Fig. 12) are

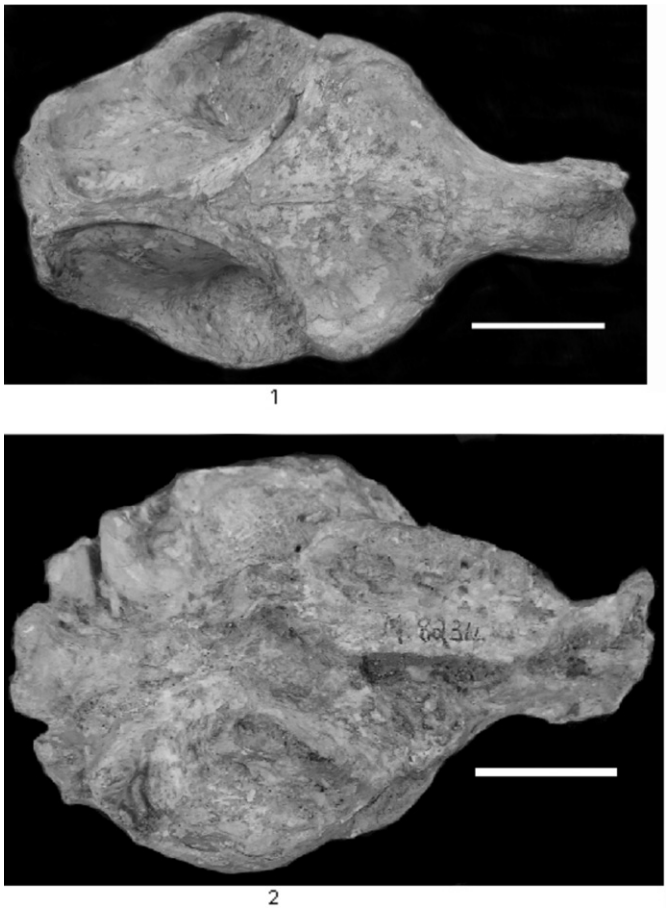


Figure 13. M 8234, skull of *Gigantohyrax maguirei* Kitching, 1965, from the Pliocene of Makapansgat, South Africa (scale bars = 5 cm). **1**, Dorsal view. **2**, Palatal view.

tusk-like and in section have a short mesial side and a long slightly convex labial one as in females of extant procaviids. The other specimens of *Gigantohyrax* lack incisors, so it is not possible to determine their sex.

Discussion and conclusions on *Gigantohyrax*

Of the 19 features listed in the table, *Gigantohyrax* shares only a few with *Heterohyrax* (anterior position of incisive foramina, large gap between upper incisors, brachyodont cheek teeth). It shares none with *Procavia*. By contrast, it shares most of them with *Dendrohyrax.* The question that poses itself is whether the Makapansgat fossils should not be classified as *Dendrohyrax* rather than as a separate genus. Apart from the obvious size differences, there are two features by which the fossils described by Kitching (1965) differ from *Dendrohyrax,* the presence of a sagittal crest or temporal crests that are close to each other (Fig. 13.1) and the relative proportion of the lengths of the premolar and molar rows. An undescribed skull of *Gigantohyrax* (M 8416) has the temporal crests separated from each other, thereby not forming a sagittal crest, but they are not as wide apart as is generally the case in *Dendrohyrax.* The difference between the lengths of the molar and premolar rows (molars are 101% of premolars in M 8415, and 110% in M 8230) is less that is usual in *Dendrohyrax* (88–91%), and is closer to *Heterohyrax* (*c.* 100%) and *Procavia* (109–118%).

The fact that adults of *Gigantohyrax* and *Dendrohyrax*

Table 7. Summary of comparison between *Gigantohyrax* and the three extant genera of Procaviidae.

Character	*Procavia*	*Heterohyrax*	*Dendrohyrax*	*Gigantohyrax*
Anterior ventral zygomatic depression	Small or absent	Often present	Variable but often strong	Strong
Maxillo-palatine suture	Usually square (some individuals curved)	Usually square (some individuals curved)	Square to curved	Curved (one specimen)
Orbital margin	Not thickened	Not thickened	Thickened	Thickened
Temporal crest	Not beaded	Not beaded	Beaded	Beaded
Interparietal	Rarely completely fused	Rarely fused	Fused	Fused
Parietal and supra-occipital suture	Not fused	Early fusion	Variable fusion	Fused
Post orbital bar	Open	Open	Closed	Closed
Frontal surface	Convex	Convex	Collapsed	Collapsed
Dorsal profile of cranium in lateral view	Convex	Convex	Concave	Concave
Molar cingula	Weak	Moderate	Strong	Strong
Molar styles	Weak	Moderate	Strong	Strong
Molar ectolophs	Hypsodont	Brachyodont	Brachyodont	Brachyodont
Diastema	Short (length less than P1/–P2/)	Long (length = P1/–P3/)	Long (length = P1/–P3/)	Long (length = P1/–P4/)
Anterior termination of nasals	Behind premaxilla tip	Behind premaxilla tip	Slightly behind premaxilla tip	Above premaxilla tip (one specimen)
Diastemal ridge	Weak	Moderate	Strong	Strong
Gap between incisors	Small	Large	Large	Large
Depression in palatal part of premaxilla	Shallow, small	Shallow, small	Deep, large	Deep, large
Incisive foramina	Opposite or slightly anterior to P1/	Well anterior to P1/	Well anterior to P1/	Well anterior to P1/
Fossa beneath upper incisive juga	Shallow	Shallow	Deep	Deep

show fusion of the sutures of the back of the neurocranium, whereas adults (and even senile) *Procavia* usually do not, indicates that the former two genera are remarkably close, not only in osteology and odontology, but also in growth variables such as fusion of sutures. There can be little doubt that *Gigantohyrax* and *Dendrohyrax* are more closely related to each other than either is to *Procavia* or *Heterohyrax.* By all the cranial criteria listed above, *Gigantohyrax* is furthest morphologically from *Procavia* among the procaviids.

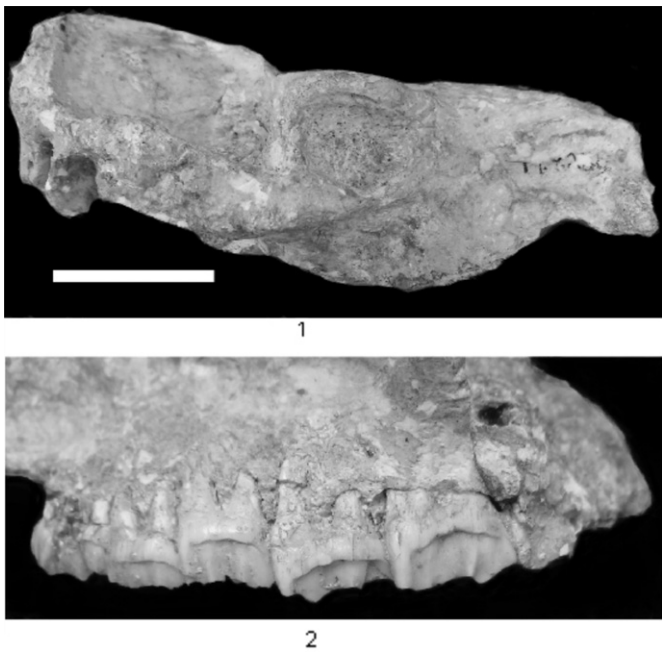


Figure 14. *Gigantohyrax maguirei* Kitching, 1965, from the Pliocene of Makapansgat, South Africa (scale bars = 5 cm). **1**, M 8234, skull, lateral view (note the concave dorsal profile). **2**, M 8230, enlargement of buccal aspect of upper left cheek dentition, P2/ to left, damaged M3/ to right (note strongly developed cingulum and styles).

If *Heterohyrax* is considered to be a subgenus of *Dendrohyrax,* as was suggested by Ellerman & Morrison-Scott (1951) and Roche (1972), then one would be forced to consider *Gigantohyrax* a synonym of *Dendrohyrax.* However, I take the view that *Gigantohyrax* is generically distinct from, although closely related to *Dendrohyrax,* and that *Heterohyrax* deserves full generic rank.

PART 5. DISCUSSION

The earliest known hyraxes of modern aspect (Procaviidae) are from Nakali (Kenya) (Fischer 1986) and Berg Aukas (Namibia) (Rasmussen *et al.* 1996) aged about 10 Ma. Prior to this date all the known African hyracoids were of archaic affinities including forms such as *Parapliohyrax* from Namibia, Kenya and the Maghreb (Pickford *et al.* 1997). Plio-Pleistocene East African hyracoids have been attributed to *Heterohyrax* and *Gigantohyrax* (Jaeger & Wesselman 1976) although, in the absence of complete tooth rows, the identification of the remains as *Heterohyrax* as opposed to *Dendrohyrax* must remain in doubt. *Gigantohyrax* Kitching 1965, first

described from South Africa, appears to be most closely related to *Dendrohyrax* among the modern genera (thickened frontal above the orbits; depressed frontals; strongly developed post-orbital bar fused to the jugal; beaded temporal crests; premolar row longer than molar row; upper central incisors wide apart, molars brachyodont, dorsal profile of skull concave in lateral view). The Lukeino hyrax specimen is thus the first tropical African Late Miocene hyrax to be confidently identified to genus (*Dendrohyrax*).

Churcher (1956) considered that the genus *Procavia* included *P. tertiarius* from the Early Miocene of Namibia, which he erroneously thought was Pleistocene, but the discovery of more complete specimens of *Prohyrax tertiarius* and *Prohyrax hendeyi* (Pickford 1994, 2003) indicate that the similarities once considered to link these Early Miocene forms to the extant ones are outweighed by the abundant dissimilarities. As such the few comparable features (such as small size, some aspects of molar morphology) are probably symplesiomorphies, whereas the differences including the presence of hypsodont curved ectolophs with inflated styles in *Prohyrax* are apomorphies that do not occur in procaviids. However, the presence of a distally directed fifth root in the M3/ of some procaviids suggests that the ancestral form may have possessed a third lobe in the M3/ as in pliohyracids, although this lobe no longer occurs in any of the extant procaviids. In procaviids, the upper molars generally have a small fifth root distally, located between the distal pair of roots. Only in the third molars is the fifth root enlarged, inclined and positioned distally from the second pair of roots. The relationships of the procaviids to other East African Early Miocene hyracoids, such as *Afrohyrax* and *Brachyhyrax* (Whitworth 1954; Pickford 2004) are more distant than they are to Pliohyracidae. *Meroehyrax*, however, is of interest, as recent discoveries in the Early Miocene of Uganda (Pickford 2004) reveal that its upper dentition is morphologically intermediate between that of procaviids on the one hand and *Saghatherium* on the other. Out of all the known Early Miocene hyracoids, *Meroehyrax* is the most likely lineage from which the procaviids evolved.

Comparisons with Middle and Late Miocene Pliohyracidae (Pickford & Fischer 1987) and Procaviidae reveal few similarities between them. *Parapliohyrax* is considerably larger than any procaviid, with the exception of *Gigantohyrax,* and it has extremely hypsodont curved ectolophs in the upper molars. There are also major differences in cranial morphology.

The Aragai (Lukeino) tree hyrax palate is much more complete than the fossil from Nakali (a single lower tooth of doubtful position in a mandible fragment) (Fischer 1986). As such it provides useful data about the Late Miocene members of the Procaviidae, and reveals that by this time they were almost modern in most aspects of the upper dentition and in size. This contrasts strongly with the Eurasian hyracoids of the Late Miocene and Plio-Pleistocene which were all pliohyracids of large to gigantic size; Chinese *Postschizotherium* for example, was about the size of a rhinoceros.

Phylogenetic origins of the Procaviidae

In order to uncover the origins of the procaviids, it is necessary to explore the extinct Early Miocene species *Meroehyrax bateae* (Pickford, 2004). The main features that are of interest in a phylogenetic sense are the development of the styles, ribs and cingula on the buccal side of the upper cheek teeth, which in *H. auricampensis* and *P. pliocenica* are well formed, imparting a strongly undulating buccal surface to the teeth, reminiscent of the genera *Saghatherium* and *Meroehyrax.* In particular, the styles in *Meroehyrax* and *Heterohyrax* are pinched in at their apices and bulbous or swollen near cervix, unlike the styles in other hyracoids such as *Prohyrax, Afrohyrax* and *Brachyhyrax* (Pickford 2004).

Despite the resemblances to *Meroehyrax,* there are major differences between the Early Miocene form and *Heterohyrax* including the absence of a third lobe in the lower m/3 in *Heterohyrax.* There is a distal cingulum in the m/3 of *P. pliocenica* which may represent a trace of this structure, which has completely disappeared or is weakly developed in the extant species *H. brucei* and *P. capensis* but is present in Late Miocene *Dendrohyrax* from Lemudong'o, Kenya (Pickford & Hlusko, in press).

In conclusion, the most likely group from which procaviids evolved is the Saghatheriidae, in particular the genus *Meroehyrax* from the Early Miocene of East Africa, the dentition of which is similar enough to that of procaviids to have given rise to them, principally by loss of the third incisor and canine in the upper and lower toothrows, the loss of the upper second incisor and suppression of third lophids in the m/3.

CONCLUSIONS

This revision of the Late Miocene to Pleistocene hyracoids of East and South Africa, fills in some of the gaps that used to exist between the 10-million-year-old *Heterohyrax auricampensis* from Berg Aukas, Namibia, and *Procavia antiqua* of the Plio-Pleistocene of South Africa. The most crucial fossils for throwing light on procaviid phylogeny are from two localities in Kenya which have yielded the earliest known well-identified fossils of *Dendrohyrax,* and material from Langebaanweg of Early Pliocene age which represents an extremely primitive stage of the *Procavia* lineage, retaining a number of plesiomorphic features similar to those that occur in *Heterohyrax.* The inclusion of *Gigantohyrax* from the Middle Pliocene of Makapansgat, South Africa, to the debate provides additional evidence of the affinities of the various genera of procaviids, showing, as it does, many features close to *Dendrohyrax.* For example, if *Heterohyrax* is considered to be a subgenus of *Dendrohyrax* (Ellerman & Morrison-Scott 1951; Roche 1972), then *Gigantohyrax* would have to be identified as *Dendrohyrax,* since it is much closer morphologically to this genus than *Heterohyrax* is. Given its gigantic size, and the presence of a few morphological characters that distinguish it from *Dendrohyrax,* such as the presence of a sagittal crest in some specimens, I accept its generic distinctiveness, in which case, I am forced to agree with most authors (Allaerts *et al.* 1982; Bothma 1967; Hahn 1934; Skinner &

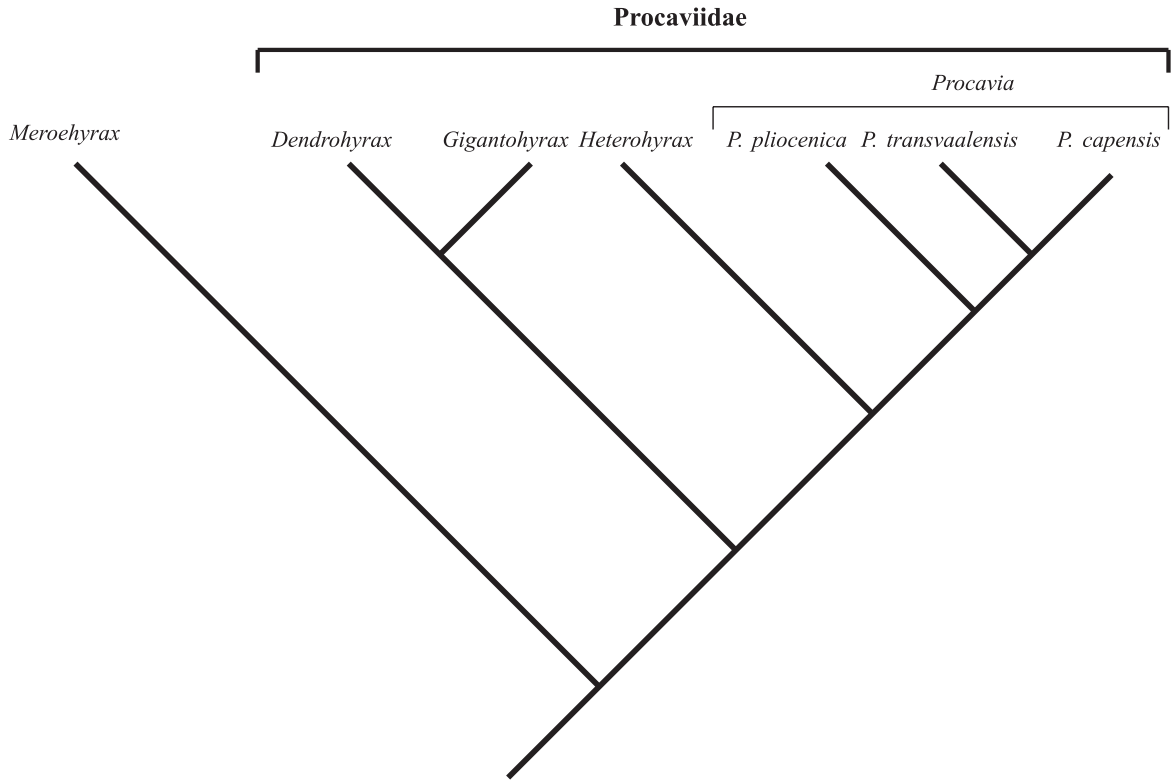


Figure 15. Relationships among Procaviamorpha excluding Pliohyracidae.

Smithers 1990) that *Heterohyrax* is indeed generically distinct from *Dendrohyrax.*

As a result of this study, the relationships between the four known genera of Procaviidae are clearer (Fig. 15). What remains to be determined is the origin of the family Procaviidae. Most recent papers have looked to the Pliohyracidae for the origins of this family (Pickford & Fischer 1987; Pickford *et al.* 1997) despite major differences in cheek tooth morphology. Recent finds, including the discovery of associated upper and lower dental elements of the saghatheriid *Meroehyrax bateae,* from Moroto, Uganda, (Pickford 2004) opens up new possibilities. In several features of the cheek teeth, *Meroehyrax* presages the dental morphology of procaviids. The third lobe in the M3/ and m/3 of *Meroehyrax* is reduced in size. It is absent in the M3/ of procaviids, but in m/3 of *Dendrohyrax* from Lemudong'o, there is a low vertical ridge on the distal surface of the m/3 that could represent the final stages in the disappearance of the third lobe. In *Procavia pliocenica* the distal cingulum rises slightly in the m/3 but does not form a ridge, which could represent an even later stage in its suppression. Very occasionally, extant dassies will grow an m/4 in the mandible, and if so then it is a narrow pillar lodged closely behind the m/3, in a position analogous to the third lobe in *Meroehyrax bateae* (Whitworth, 1954). On the basis of the Moroto fossils, it now seems more likely that the procaviids descended from Saghatheriidae, than from any other family, including the Pliohyracidae (Fig. 15).

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