

Plio-Pleistocene Hyracoidea from Swartkrans Cave, South Africa

McMahon, C.R.

Mammal Research Institute, University of Pretoria, Pretoria, 0002

J.F. Thackeray

Department of Palaeontology and Palaeoenvironmental Studies, Transvaal Museum, P.O. Box 413, Pretoria, 0001

Received 1 February 1993; accepted 15 July 1993

Swartkrans Cave, an important Pleistocene hominid site in the Sterkfontein valley, has yielded abundant fossil hyracoid remains. Two extinct taxa, *Procavia antiqua* and *P. transvaalensis*, have been previously reported to occur at the site in deposits postdating 1,8 million years before the present (B.P.). The extant taxon, *P. capensis*, has been reported in the most recent deposits, thought to include the Terminal Pleistocene. However, statistical analyses of teeth suggest that *P. antiqua* and *P. capensis* are conspecific. *P. transvaalensis* differs from *P. capensis* by being larger and more hypsodont. The coexistence of these taxa in palaeoenvironments of the Sterkfontein valley is attributed to dietary differences: *P. transvaalensis* being dependent primarily on grass foliage in grassland habitats, *P. capensis* being a generalist, feeding on a range of different kinds of vegetation in rocky habitats. Hypoconid-metaconid distances, previously used by Broom to distinguish taxa, are shown to be related to individual age. Crown height data of molars are used to generate age distributions, and incisors are used to obtain sex ratios. Predation on adults of *P. transvaalensis*, from populations associated with a sex ratio biased towards males, may have contributed to the decline in relative abundance and ultimate extinction of this species towards the end of the Pleistocene. Predators can have included leopards, black eagles and/or hominids.

Swartkrans is 'n belangrike grot in die Sterkfontein vallei, met waardevolle fossiele uit die Pleistoseentydperk. Bone en tande van twee uitgesterwe dassiespesies, *Procavia antiqua* en *P. transvaalensis*, word in afsettings van minder as 1,8 miljoen jaar voor hede aangetref. Fossiele van die huidige spesie, *P. capensis*, is in die mees onlangse afsettings gevind, moontlik uit die eind-Pleistoseen. Statistiese tandanalises het egter aan die lig gebring dat *P. antiqua* en *P. capensis* dieselfde spesie is. Die maaltande van *P. transvaalensis* is groter en langer as dié van *P. capensis*. Die gelyktydige bestaan van hierdie twee spesies in die paleo-omgewing van die Sterkfontein-vallei word aan 'n verskil in eetgewoontes toegeskryf: *P. transvaalensis* is hoofsaaklik op grasagtige voedsel aangewese, terwyl *P. capensis* op algemene plantegroei in rotsagtige omgewings leef. Metings van spasies tussen tandkroone, voorheen deur Robert Broom geneem om spesies te onderskei, het eerder die ouderdom van individue aangetoon. Hoogte van tandkroone kan ook aangewend word om ouderdomsverspreiding te bepaal. Die vorm van snytande word gebruik om geslagte van mekaar te onderskei. Predasie op volwassenes van *P. transvaalensis* uit populasies waar die vroulike diere in die minderheid was, mag tot die uiteindelijke uitsterwing van hierdie spesie aan die einde van die Pleistoseen gelei het. Roofdiere kon luiperds, swart arende en hominide ingesluit het.

Swartkrans is an important Pleistocene site in the Sterkfontein valley, well known for its hominid fossils (*Australopithecus* and early *Homo*) in deposits dated between about 1,8 and 1,0 million years before the present (B.P.) (Brain 1981; Brain *et al.* 1988). The site also contains abundant hyracoid remains which may have been brought to the site by various agents of accumulation, including leopards, black eagles and/or hominids. The principle aim of this study is to examine all specimens of *Procavia* that have been recorded from Swartkrans, and to determine how many species are actually represented at the site. Particular attention is given to specimens previously attributed to *P. antiqua*; *P. transvaalensis* [extinct, larger than *P. antiqua* and with *P. obermeyerai* as a junior synonym (Broom 1936; Churcher 1956)]; and *P. capensis* (extant, comparable in size and morphology to specimens attributed to *P. antiqua*). Sex ratios and age distributions are potentially useful for purposes of assessing possible factors that can have contributed to the extinction of *P. transvaalensis*.

Broom (1934) had attempted to distinguish *P. antiqua* from the extant form, *P. capensis*, on the basis of crown height of molars, the distance between hypocone and metacone cusps, and the bunodont condition for the protocone. He claimed that these were primitive characteristics, and

suggested that *P. antiqua* was ancestral to modern dassies. There is, however, a major problem with Broom's analysis. Apart from not compiling metric data, he did not consider individual age and tooth wear in relation to variables such as hypocone-metacone distance which he had used to distinguish *P. antiqua* from *P. capensis*. Churcher (1956:499) had in fact noted similarities between these two taxa, but begged the question of their synonymy. It is therefore relevant to reconsider the taxonomic status of *P. antiqua* from Swartkrans.

If it is possible to demonstrate that *P. antiqua* and *P. capensis* are conspecific, it would still be necessary to consider evidence for the coexistence of at least two species of *Procavia* at Swartkrans in the Pleistocene: the larger *P. transvaalensis* and a smaller taxon, previously attributed to *P. antiqua*, comparable in size to *P. capensis*. In this paper the differences in dentition that could possibly reflect differences in diet are looked at, thereby helping to account for the coexistence of two species of *Procavia* in the Sterkfontein valley in the Pleistocene.

Materials and Methods

Modern specimens of *P. capensis*, measured for compara-

tive purposes, were made available from collections at the Transvaal Museum. For purposes of this study, we accept the taxonomy of extant hyracoid species as reviewed by Meester, Rautenbach, Dippenaar & Baker (1986), who regard *P. capensis* as the only extant species of *Procavia*, whereas Bothma (1971) accepted five. All of the fossil material used in the present study comes from the Swartkrans cave in the Sterkfontein Valley, within 10 km north of Krugersdorp (Brain 1981; Brain *et al.* 1988).

Brain has recognized five depositional units at Swartkrans. Members 1, 2 and 3 are thought to have been deposited between about 1.8 and 1.5 million years B.P. Member 4 dates to the Late Pleistocene and has stone artefacts attributable to the Middle Stone Age. However, Member 4 contains few faunal remains. Member 5 is thought to include the Terminal Pleistocene, and has been dated to about 11 000 B.P. by the radiocarbon dating technique (Brain *et al.* 1988). All the other members have been dated using faunal remains, compared to securely dated East African sequences (Vrba 1975; Brain *et al.* 1988). *P. capensis* was reported by Brain *et al.* (1988) to occur only in Member 5. *P. antiqua* was documented in Members 1, 2 and 3, together with *P. transvaalensis* which has been found in Member 5. No hyraxes were recorded in Member 4.

Unfortunately the type specimen of *P. antiqua* from Taung was reported missing after it was described by Broom (Churcher 1956). In its absence, a well-preserved cranium of another specimen, St 105 from Sterkfontein (formerly *P. robertsi*, a junior synonym of *P. antiqua*), is used here as a substitute for the missing type. St 106 from Uitkomst (also known as Gladysvale) has been listed as the type specimen of *P. obermeyerae*, but as a junior synonym for *P. transvaalensis* (Shaw 1937; Churcher 1956), it is used as a reference specimen for the latter. St 105 and St 106 are housed at the Transvaal Museum.

Churcher (1956:482) drew attention to morphological differences between *P. transvaalensis* and *P. capensis*, notably to the occurrence of double-rooted milk canines with complex crowns in at least two specimens of the larger taxon. However, in this study attention is focussed on metric data (mesiodistal and bucco-lingual diameters) for purposes of making distinctions between *P. transvaalensis* and other specimens of *Procavia*. Tooth dimensions were measured according to criteria given by von den Driesch (1976). All measurements were recorded in millimetres. For taxonomic purposes attention is focussed on M¹ or M², since the characteristics initially used by Broom (1934) for distinguishing *P. antiqua* are best found in upper molars.

Broom (1934) used hypo-metacone distance in M¹ and M² (Figure 1) to distinguish *P. antiqua* from other dassies, but remarkably he never published metric data. In this study we provide measurements of hypocone-metacone distances together with data on crown height in the same specimens.

On account of small sample sizes for each member, data for Members 1, 2 and 3 were combined in some instances to form one early Pleistocene sample, for comparison with Late Quaternary material from Member 5.

Sexing specimens and age estimation

First maxillary incisors of *P. capensis* provide a means of

sexing hyraxes. Males are characterized by having first incisors which are triangular in cross-section, whereas those of females are more rounded (Thomas 1892). The dichotomy between triangular and rounded incisors in specimens attributed to *P. antiqua* and *P. transvaalensis* is assumed to reflect sexual differences, as in *P. capensis*. Minimum numbers of individuals (MNI) were calculated for species in each member by counting the number of upper incisors in each assemblage, and dividing by two in order to take left and right sides into account.

Studies of *P. capensis* have also shown that degree of tooth wear and eruption sequences can be used to estimate individual age (Millar 1971; Fairall 1980; Fourie 1983). Fourie's non-linear relationships between age and crown height are certainly useful for purposes of studies of specimens attributed to *P. capensis*, but difficulties arise when attempting to apply such relationships to extinct taxa such as *P. transvaalensis* which is larger than *P. capensis*. Although Fourie's equations cannot be used to obtain reliable age estimates for both taxa, crown height and wear patterns can be used to place specimens within relative age classes.

Results

Table 1 presents the number of upper incisors (left and right), and minimum numbers of individuals (MNI) for male

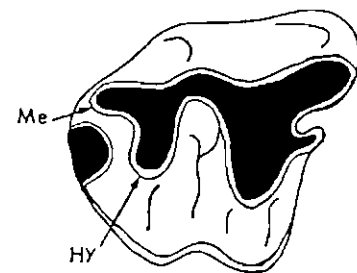


Figure 1 M¹ of *P. capensis*, indicating hypocone (HY) and metacone (Me) cusps, used by Broom (1934) for taxonomic purposes.

Table 1 Numbers of first upper incisors of male and female fossil dassies attributed to *P. antiqua* from Members 1, 2 and 3, *P. capensis* from Member 5 and *P. transvaalensis* from Members 1, 2, 3 and 5 at Swartkrans; minimum numbers of individuals (taking right and left incisors into account) indicated in parentheses

Member	<i>P. antiqua</i>		<i>P. transvaalensis</i>	
	Males	Females	Males	Females
1	35 (18)	16 (8)	6 (3)	2 (1)
2	15 (8)	9 (5)	1 (1)	0 (0)
3	11 (6)	9 (5)	3 (2)	3 (2)
	<i>P. capensis</i>		<i>P. transvaalensis</i>	
5	23 (12)	21 (11)	3 (2)	2 (1)

and female specimens previously attributed to *P. antiqua*, *P. transvaalensis* and *P. capensis* in each member. Males consistently outnumber females with the exception of a small sample of *P. transvaalensis* from Member 3, in which there are equal numbers of males and females (Table 1).

Table 2 presents means and standard deviations for M² dimensions of modern and fossil specimens, plotted in Figure 2.

Table 3 lists the number of individuals within six age classes, based on wear patterns previously described by Fourie (1983). Most specimens attributed to *P. capensis* and *P. antiqua* are represented in age class 2 (young individuals). By contrast, most of the individuals of *P. transvaalensis* are represented in age classes 4 and 5 (older individuals).

Crown height measurements of M¹ and M² have been placed within arbitrary age classes, in which the youngest

Table 2 Means and standard deviations of M² dimensions (mesiodistal length and buccolingual width) for specimens attributed to *P. antiqua* from Members 1, 2 and 3 (combined sample) and Member 5; *P. capensis* from Member 5; modern specimens of *P. capensis*; and *P. transvaalensis* from Members 1, 2, 3 and 5. Measurements in mm

	Mesiodistal length		Buccolingual width		n
	mean	s.d.	mean	s.d.	
<i>P. antiqua</i>					
Members 1-3	8,31	1,19	7,74	1,25	29
<i>P. capensis</i>					
Member 5	7,88	0,68	7,30	0,51	17
Modern sample	8,51	0,30	7,87	0,52	23
Member 5 and modern sample	8,24	0,58	7,63	0,60	40
<i>P. transvaalensis</i>					
(Members 1-5)	10,32	0,70	9,53	0,66	18

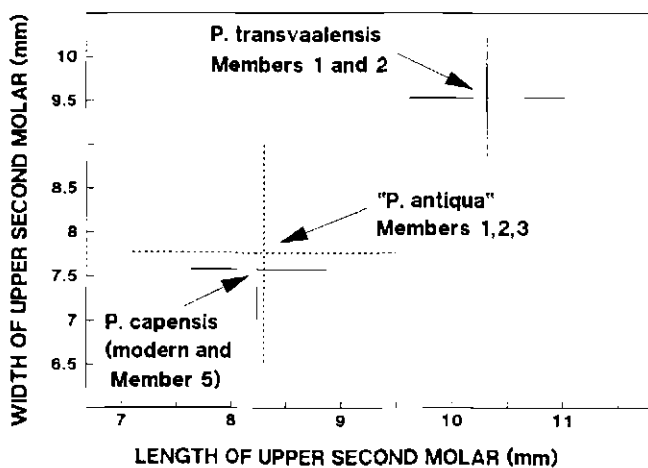


Figure 2 Mean and standard deviations of M² lengths and M² widths for modern *P. capensis* ($n = 23$), fossil *P. antiqua* from Members 1, 2 & 3 Swartkrans ($n = 29$), fossil *P. capensis* from Member 5 Swartkrans ($n = 17$), and *P. transvaalensis* from Members 1 & 2 Swartkrans ($n = 18$)

individuals for each taxon are placed in age class 1 and the oldest in age class 10. The results are plotted as histograms in Figure 3 (combining data from both M¹ and M²). The

Table 3 Minimum numbers of individuals of hyraxes in age classes based on wear patterns described by Fourie (1983); age classes of *P. transvaalensis* not directly comparable to those of *P. antiqua* and *P. capensis* on account of size differences

	<i>P. antiqua</i>	<i>P. capensis</i>	<i>P. transvaalensis</i>
Class 1 (young)	2	0	0
Class 2	16	4	2
Class 3	7	1	2
Class 4	8	1	5
Class 5	1	0	5
Class 6 (old)	0	0	0
Totals	34	6	14

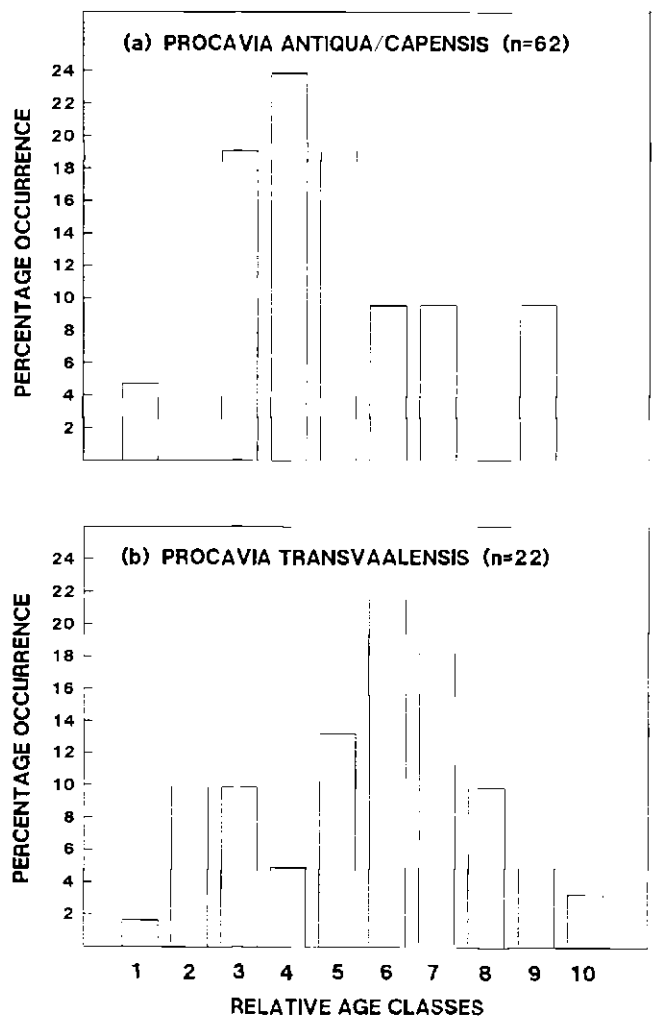


Figure 3 Histograms of age distributions based on crown height measurements in M¹ and M² of (a) 62 molars attributed to *P. antiqua* and *P. capensis*; (b) 22 molars attributed to *P. transvaalensis*. Age distributions are expressed in relative age classes ranging from 1 (youngest individuals in assemblage) to 10 (the oldest individuals).

results confirm the observation that *P. antiqua* and *P. capensis* are represented by higher frequencies of relatively young individuals.

Figure 4 shows relationships between crown height and hypocone-metacone distance (HMD) of upper molars (M^1 and M^2) of *P. antiqua*, *P. capensis*, and *P. transvaalensis* from Swartkrans. These figures show linear relationships between the two variables, reflecting the fact that HMD increases with individual age.

The following regression equation has been obtained for the relationship between crown height (x) and the hypocone-metacone distance (y), for M^1 and M^2 of specimens previously identified as *Procavia antiqua*, from Members 1, 2 and 3 at Swartkrans:

$$y = -0,549x + 5,670 \quad (r = 0,8; n = 36) \quad \text{Equation 1.}$$

The following equation was obtained for modern specimens of *P. capensis*:

$$y = -0,564x + 6,669 \quad (r = 0,8; n = 74) \quad \text{Equation 2.}$$

The following equation was obtained for *P. antiqua* from Members 1, 2, 3 and *P. capensis* from Member 5 (combining samples):

$$y = -0,578x + 5,821 \quad (r = 0,8; n = 62) \quad \text{Equation 3.}$$

The relationship obtained for specimens of *P. transvaalensis* from Members 1, 2, 3 and 5 is as follows:

$$y = -0,776x + 9,635 \quad (r = 0,9; n = 23) \quad \text{Equation 4.}$$

Discussion

Morphologically, specimens from Swartkrans attributed to *P. transvaalensis* are indistinguishable from St 106, here used as a reference specimen for this species. A t test indicates that the mean length of M^2 of specimens attributed

to *P. transvaalensis* (Table 2) is significantly larger than the mean value obtained for modern specimens of *P. capensis* ($t = 5,91$; $df = 40$; $p = 0,05$). However, the mean value for modern specimens of *P. capensis* is not significantly different from mean values for specimens attributed to *P. antiqua* ($t = 0,65$; $df = 51$; $p = 0,05$). Morphologically, all of the specimens from Swartkrans attributed to *P. antiqua*, as well as St 105 (a specimen used for reference purposes in this study) are indistinguishable from modern *P. capensis*. As shown in Figure 3, there is also a striking similarity between measurements of *P. antiqua* and *P. capensis* when crown height is examined in relation to hypocone-metacone distance, a variable which Broom (1934) had previously used to distinguish the two as distinct species. Clearly, HMD varies as a function of age. For HMD to be at all meaningful it should be analysed in conjunction with crown height.

Analyses of HMD and crown height in this study serve to show that there is no marked difference between the relationship of these two variables in specimens attributed to *P. antiqua* and *P. capensis*. By contrast, there are striking differences when data for *P. transvaalensis* are compared with measurements obtained from specimens attributed to *P. capensis* or *P. antiqua*. These results suggest that specimens attributed to *P. antiqua* and *P. capensis* could have belonged to populations of the same species, distinct from those of *P. transvaalensis*.

The range of variation in crown height of *P. antiqua* from Members 1, 2 and 3 is about 7 mm (ranging between approximately 1 mm for the oldest individuals to 8 mm for the youngest individuals at Swartkrans), corresponding closely to the known range of variation in modern *P. capensis*. The range in both *P. antiqua* and *P. capensis* is similar to the range of variation in crown height found in *P. transvaalensis* (3–10 mm). The implication is that, by taking

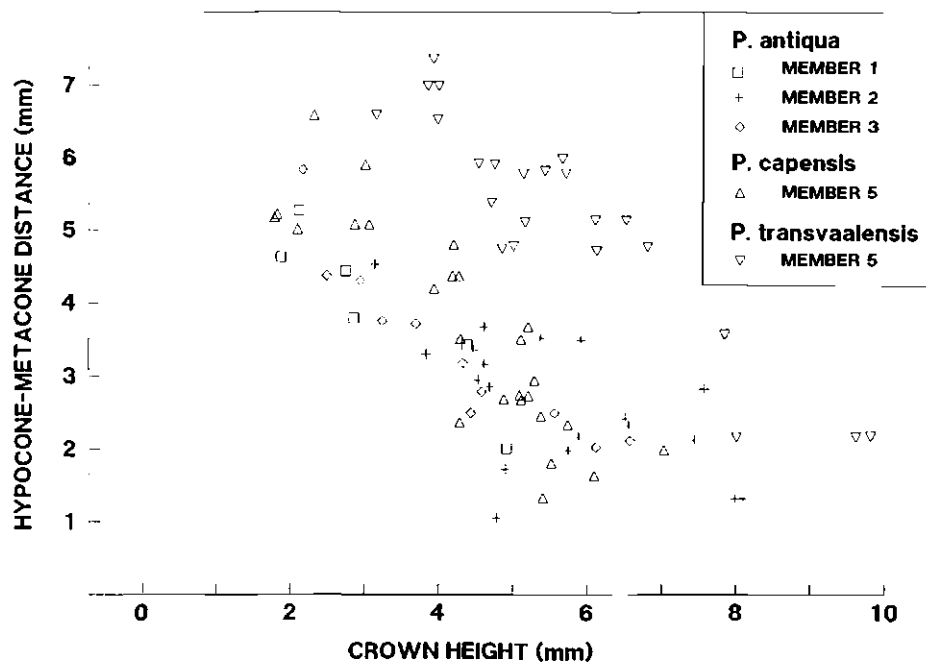


Figure 4 Relationship between hypocone-metacone distance and crown height of M^2 , for *P. antiqua* from Members 1, 2 & 3 at Swartkrans; *P. capensis* from Member 5; and *P. transvaalensis* from Members 1, 2, 3 and 5.

relative age into account, *P. transvaalensis* had teeth that were more hypsodont than those of *P. antiqua* and *P. capensis*.

Hypsodonty has previously been associated with a specialization towards grazing (for example, equids and alcelaphines are highly hypsodont and both are essentially grazers). The case for *P. transvaalensis* being a hyracoid that fed primarily on grass leaves would seem to be supported by strontium:calcium ratios in bones of this species from Swartkrans (Sillen 1992).

Variability in dental morphology of extant hyracoid genera has been studied by Hahn (1934) and Allaerts, van der Audenaerde & van Neer (1982). They noted that *Procavia* is more hypsodont than *Heterohyrax* and *Dendrohyrax*. This is not surprising considering the fact that *Heterohyrax* and *Dendrohyrax* are browsers. Of interest in this study is the observation that the extinct species of *Procavia* represented at Swartkrans, *P. transvaalensis*, is distinctly more hypsodont than the extant species *P. capensis*. Earlier hyracoids such as *Saghatierium* from the Oligocene are likely to have been browsers associated with wooded environments. Perhaps the hypsodont condition of *P. transvaalensis* is a late specialization associated with the opening up of grassland environments during cool intervals in the Pleistocene.

Differences in age distributions of *Procavia* at Swartkrans can be addressed in the context of questions concerning cave taphonomy. The fact that *P. transvaalensis* is represented by a relatively high proportion of adults is of interest in relation to the possibility that it was preyed upon primarily by leopards. This warrants attention since such carnivores will prey upon hyraxes if larger prey are not available (Thackeray 1990; Pienaar 1969); in areas in the western Cape in the absence of large ungulate prey, *P. capensis* can form up to 80% of the vertebrates taken by leopards (Norton, Lawson, Henley & Avery 1986). If given a choice between two hyracoid species, one might expect leopards to have preyed preferentially on individuals of the larger taxon, and of these they could have preferentially taken adults. This could account for the high proportion of adults of the larger species, *P. transvaalensis*, in the early Pleistocene deposits at Swartkrans. In support of this suggestion, mandible fragments of *P. transvaalensis* show the kind of damage that Brain (1981) has documented in a study of leopard feeding behaviour.

There is no reason to discount the possibility that leopards may have preyed on *P. capensis*. However, was the species also preyed upon by black eagles? This possibility deserves attention since it is known to be an important food item of these large birds of prey (Ginn, McIlhenny & Millstein 1989), and at least some fossil hyrax from Swartkrans have damage of the kind known to be associated with the feeding behaviour of black eagles which open up the foramen magnum of hyrax crania with their talons (Brain 1981). Black eagles may have found it easier to prey upon young rather than on older individuals of the small species; this could account for the relatively high proportion of young individuals of *P. antiqua/capensis* represented at Swartkrans.

In the case of early Pleistocene samples from Members 1, 2 and 3, males of *P. transvaalensis* outnumber females by a

ratio of 2 : 1. The relatively low proportion of females is of interest in relation to age distribution data which show that this species is represented by a high proportion of adults. Predation on adults of *P. transvaalensis* in populations with relatively low abundances of females could perhaps have meant that this species had a higher probability of extinction than the smaller *Procavia antiqua/capensis*.

In all members, *P. antiqua/capensis* is relatively more abundant than *P. transvaalensis*. The ratio of *P. antiqua/capensis* to *P. transvaalensis* (based on incisors) is circa 6 : 1 in Members 1, 2 and 3 (combined sample), increasing to circa 8 : 1 in Member 5. This shift suggests an increase in relative abundance of *P. capensis* at a time when populations of *P. transvaalensis* were in a state of decline.

Conclusions

It is concluded that *P. antiqua* and *P. capensis* are conspecific, the latter having precedence according to international rules of zoological nomenclature. *P. transvaalensis* remains a valid taxon, distinct from the smaller species at Swartkrans which may now be referred to as *P. capensis*.

The co-existence of two species of *Procavia* in the early Pleistocene is understandable in view of the observation that *P. transvaalensis* had hypsodont dentition, suggesting that it fed primarily on grass leaves, a possibility supported by strontium:calcium ratios in bone samples of this species (Sillen 1992). Since *P. capensis* is known today to be a generalist, feeding on leaves of bushes, shrubs, tubers, roots as well as grass (Skinner & Smithers 1991), the two species could have co-existed without undue competition for the same resources.

Analyses of fossil Bovidae from Swartkrans (Vrba 1975; Brain *et al* 1988) provide some indication of the nature of Pleistocene paleoenvironments at Swartkrans. The bovid faunal assemblages are generally dominated by alcelaphines which are indicative of open grassland conditions. Such environments would certainly have suited *P. transvaalensis* if it fed primarily on grass foliage, as suggested here from its hypsodont dentition.

The extinction of *P. transvaalensis* towards the end of the Pleistocene, apparently some time around 11 000 years B.P., is of interest since this is the period when large ungulates became extinct on a global scale (Martin 1967; Klein 1974). Remarkably it is the larger of the *Procavia* species, evidently a grazer, that became extinct. Of the ungulates that died out in southern Africa, it was grazers (many of them large) that became extinct at the end of the Pleistocene (Klein 1974; Thackeray 1981). Perhaps *P. capensis*, as a smaller hyracoid species and more of a generalist, had an adaptive advantage over *P. transvaalensis*.

Age distributions and sex ratios obtained from this analysis of Hyracoidea at Swartkrans are of potential value for understanding the factors contributing to the extinction of *P. transvaalensis* and the survival of the smaller species, *P. capensis*. Although it cannot be determined with certainty that the sex ratios of hyraxes represented in the fossil faunal assemblages reflect the ratios in past populations, there is some suggestion from the early Pleistocene samples that males outnumbered females by a ratio of 2 : 1. In the case of *P. transvaalensis*, there is also evidence that adult indivi-

duals were selected by one or more predators. Predation on adult individuals of *P. transvaalensis* from populations with relatively lower frequencies of females could have contributed to the decline and ultimate extinction of this species.

In a recent study of mitochondrial DNA in modern hyraxes from various regions of southern Africa, Prinsloo & Robinson (1992) found genetic differences between samples of *P. capensis*, in the absence of morphological differences. They suggested that two taxa diverged approximately 2 million years ago, leaving two relict populations: one in the Karoo near Beaufort West and the other in Malawi. Consequent migrations north and south are believed to be responsible for the extant populations of *Procavia* (Prinsloo & Robinson 1992). The present study has shown that at least two species of *Procavia* did in fact exist in the Transvaal within the last 1,8 million years before the present. It would be extremely interesting if analysis of DNA in fossils previously attributed to *P. antiqua* and *P. transvaalensis* from Swartkrans could shed further light on genetic and morphological variability in *Procavia*.

Acknowledgements

We would like to thank C.K. Brain, E. de Wet, E. Herold, I. Plug, T. Robinson, and V. Watson for their help in this study which was supported in part by an FRD grant awarded to J.F.T. Two anonymous referees kindly provided helpful comments.

References

- ALLAERTS, W., VAN DER AUDENAERDE, T. & VAN NEER, W. 1982. Dental morphology and the systematics of the Procaviidae (Mammalia: Hyracoidea). *Annals. Soc. r. zool. Belg.* 112: 217–225.
- BOTHMA, J. DU P. 1971. Order Hyracoidea. In: The Mammals of Africa, an Identification Manual, eds J. Meester & H.W. Setzer. Part 12. Smithsonian Institution Press, City of Washington.
- BRAIN, C.K. 1981. The hunters or hunted? An introduction to cave taphonomy. Chicago University Press.
- BRAIN, C.K., CHURCHER, C.S., CLARK, J.D., GRINE, F.E., SHIPMAN, P., SUSMAN, R.L., TURNER, A. & WATSON, V. 1988. New evidence of early hominids, their culture and environment from the Swartkrans cave, South Africa. *S. Afr. J. Sci.* 84: 828–835.
- BROOM, R. 1934. On the fossil remains associated with *Australopithecus africanus*. *S. Afr. J. Sci.* 31: 472.
- BROOM, R. 1936. On some new Pleistocene mammals from limestone caves of the Transvaal. *S. Afr. J. Sci.* 33: 766.
- CHURCHER, C.S. 1956. The fossil Hyracoidea of the Transvaal and Taung deposits. *Ann. Transv. Mus.* 22: 477–501.
- FAIRALL, N. 1980. Growth and age determination in the hyrax *Procavia capensis*. *S. Afr. J. Zool.* 15: 745–780.
- FOURIE, L.J. 1983. The population dynamics of the rock hyrax *Procavia capensis* (Pallas, 1766) in the Mountain Zebra National Park. Unpubl. Ph.D. thesis, Rhodes University, Grahamstown.
- GINN, P.J., MCILLERON, W.G. & MILLSTEIN, P. LE S. 1989. The complete book of Southern African birds. Struik Winchester, Cape Town.
- HAHN, H. 1934. Die Familie der Procaviidae. *Z. Säugetierk.* 9: 207–358.
- KLEIN, R.G. 1974. A provisional statement on the terminal Pleistocene mammalian extinctions in the Cape Biotic Zone (southern Cape Province, South Africa). *S. Afr. Archl. Soc. Goodwin Series* 2: 39–45.
- MARTIN, P.S. 1967. Pleistocene overkill. In: Pleistocene extinctions: the search for a cause, (eds) Martin, P.S. & Wright, H.E. pp. 75–120. Yale University Press, New Haven.
- MEESTER, J.A.J., RAUTENBACH, I.L., DIPPENAAR, N.J. & BAKER, C.M. 1986. Classification of southern African mammals. Transvaal Museum Monograph Np. 5.
- MILLAR, R.P. 1971. Reproduction in the rock hyrax (*Procavia capensis*). *Zool. Afr.* 6: 243–261.
- NORTON, P.M., LAWSON, A.B., HENLEY, S.R. & AVERY, G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *S. Afr. J. Wildl. Res.* 16: 47–52.
- PIENAAR, U. de V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12: 108–187.
- PRINSLOO, P. & ROBINSON, T.J. 1992. Geographic mitochondrial DNA variation in the rock hyrax, *Procavia capensis*. *Mol. Biol. Evol.* 9: 447–456.
- SHAW, J.C.M. 1937. Evidence concerning a large fossil hyrax. *J. Dent. Res.* no. 1, 16: 37.
- SILLEN, A. 1992. Strontium-calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans. *J. Hum. Evol.* 23: 495–516.
- SKINNER, J.D. & SMITHERS, R.H.N. 1991. The mammals of the southern African subregion. University of Pretoria, Pretoria.
- THACKERAY, J.F. 1981. The Holocene cultural sequence in the northern Cape Province, South Africa. Ph.D. thesis, Yale University.
- THACKERAY, J.F. 1990. Carnivore activity at Klasies River mouth: A response to Binford. *Palaeont. afr.* 27: 101–109.
- THOMAS, O. 1892. On the species of Hyracoidea. *Proc. Zool. Soc. Lond.* 50–76.
- VON DEN DRIESCH, A. 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Mus. Bull.* Harvard University.
- VRBA, E.S. 1975. Some evidence of chronology and paleoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* 254: 301–304.