

A TAXONOMIC AND ECOLOGICAL STUDY OF THE LIVING AND FOSSIL
HYSTRICIDAE WITH PARTICULAR REFERENCE TO SOUTHERN AFRICA

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8 THE CRANIAL MORPHOLOGY OF HYSTRIX AFRICAEAUSTRALIS

The external morphology of the cranium of H. africaeaustralis is well illustrated in Figs. 45, 47, 49, 51 and 53 and will not be discussed further here. The parameters measured are illustrated in Figs. 46, 48, 50, 52 and 54, and are defined in sections 7.2.1 to 7.2.11.

8.1 The analysis of general cranial characters used as diagnostic criteria in the description of new species of porcupine

1. Greatest length of skull above (Fig. 46 A, 7.2.1.1; Appendix V Table I pp.60, 61) (mm)

(Max. = 158,5; Min. = 101,8; $\bar{X}$ = 139,40; SD = 16,03; N = 20)

The length of the skull above increases steadily with age, from $\bar{X}$ = 107,07 at g/s 2 to $\bar{X}$ = 139,40 at g/s 6. Although there is no data for g/s 3 it is obvious that the maximum rate of growth occurs between g/s 2 and 3, or possibly between stages 3 and 4, in order to bring the mean up to 139,27 by g/s 4. Growth slows by the time the latter growth stage is reached, least growth occurring between this stage and g/s 5. There is a difference of 56,7mm between the skull lengths of the largest and smallest specimens available, and the sample SD is thus predictably high. The standard deviations for the various growth stages are also moderately high.

2. Occipitonasal skull length (Fig. 46 B, 7.2.1.2; Appendix V Table I pp. 60, 61) (mm)

(Max. = 150,3; Min. = 94,5; $\bar{X}$ = 130,92; SD = 16,19; N = 30)

The same growth trends as those that occur in character 1) are experienced by the occipitonasal skull length, with the period of maximum growth between stages 2 and 3 and least between stages 4 and 5. The sample range is 55,8mm and the sample SD is high, as are the SDs for individual growth stages.

3. Condylolincisive length (Fig. 48 R; 7.2.1.3; Appendix V Table I pp. 60, 61) (mm)

(Max. = 159,0; Min. = 113,8; $\bar{X}$ = 143,17; SD = 11,27; N = 18)

Exactly the same pattern of growth as occurs in greatest skull length and occipitonasal length is experienced by the condylolincisive length.

The sample range is somewhat lower than in the first two characters (45,2mm as opposed to 56,7 and 55,8mm respectively) and the sample SD is also lower (11,27 as opposed to 16+). The SDs for the individual growth stages are as high as those for 1) and 2).

4. Basilar length (Fig. 48 S; 7.2.1.4; Appendix V Table I pp.60,61) (mm)
(Max. = 147,1; Min. = 98,7; $\bar{X}$ = 131,82; SD = 13,29)

The basilar length experiences the same pattern of growth as that of characters 1), 2) and 3). The sample range of 48,14mm and the sample SD of 13,29 for this parameter are intermediate between those for the condyloincisive length and those for the occipitonasal and greatest skull lengths. The standard deviations for the individual growth stages are approximately the same as those for 1), 2) and 3).

5. Greatest width of the skull (Fig. 46 C; 7.2.1.5; Appendix V Table II pp. 62, 63) (mm)

(Max. = 96,4; Min. = 60,3; $\bar{X}$ = 80,74; SD = 9,47; N = 18)

Although no data is available for growth stage 3, it is apparent that the greatest width of the skull must increase more between growth stages 2 and 3 and possibly growth stages 3 and 4 than at or between growth stages 4 and 5 or 5 and 6. The difference between the greatest and least skull width measurements is 36,1mm which is less than any of the ranges for the various measurements of cranial length. This is reflected in a somewhat lower standard deviation, although this is still high (9,47).

6. Smallest skull breadth behind zygomatic arch (Fig. 46 D, 7.2.1.6; Appendix V Table II pp. 62, 63) (mm)

(Max. = 50,7; Min. = 39,1; $\bar{X}$ = 45,47; SD = 3,43; N = 20)

Once again it appears that the period of most rapid growth is between growth stages 2 and 4. The sample range of 11,6mm indicates that less growth takes place in this region of the skull than in any area discussed under points 1) to 5). The sample standard deviation (3,43) is also far lower than for characters 1) to 5).

7. Skull width at condyles (Figs. 46 E, 54 A²; 7.2.1.7; Appendix V Table II pp. 62, 63) (mm)

(Max. = 48,6; Min. = 25,8; $\bar{X}$ = 30,84; SD = 4,98; N = 18)

The growth trend suggested by the numerical data available indicates a different pattern of growth from that of all the characters discussed above. With the skull width at the condyles, the maximum expansion is achieved at g/s 4 ($\bar{X} = 31,70$); this decreases to a mean of 30,18 by g/s 6. No explanation could be found for this phenomenon. The sample range for this parameter is 12,8 and the sample SD is relatively low (4,98).

8. Interorbital distance at lachrymal edge (Fig. 46 F; 7.2.1.8; Appendix V Table II pp. 62, 63) (mm)

(Max. = 80,8; Min. = 49,7; $\bar{X} = 67,52$; SD = 7,80; N = 18)

The interorbital breadth of the cranium at the lachrymo-frontal suture increases systematically with age, with the period of most rapid growth taking place between stages 2 and 4. Least growth takes place between the latter growth stage and stage 5, after which there is a slight growth acceleration. This is reflected in the differences between the means of the growth stages in question - 16,22mm between g/s 2 and 4; only 1,93mm between g/s 4 and 5 and 4,72mm between g/s 5 and 6. The sample range is moderately high (31,1mm) indicating that a considerable degree of expansion takes place in this region.

9. Interorbital width at rudimentary post-orbital process (Fig. 46 G; 7.2.1.9; Appendix V Table II pp. 62, 63) (mm)

(Max. = 78,0; Min. = 49,9; $\bar{X} = 65,40$; SD = 7,33; N = 21)

This character shows a similar growth trend to the previous one, with maximum growth occurring between stages 2 and 3, least between stages 4 and 5 and a slight acceleration between stages 5 and 6. The sample range (28,1mm) and the sample SD are moderately high.

10. Height of skull from palate to posterior end of nasals (Fig 50 E¹; 7.2.1.10; Appendix V Table III pp.64-66) (mm)

(Max. = 74,5; Min. = 42,0; $\bar{X} = 59,88$; SD = 8,20; N = 25)

The skull height at this point increases gradually with age, with a difference of 32,5mm between the largest and smallest specimens. As with most other cranial parameters, the period of fastest growth is between growth stages 2 and 3, but unlike some of them, there is no growth lag between stages 4 and 5 or an acceleration after the latter

growth stage. The sample SD (8,20) and the SDs for individual growth stages are moderately high.

11. Height of skull from palate between M¹ (Fig. 50 F¹; 7.2.1.11; Appendix V Table III pp.64-66) (mm)

(Max. = 73,0; Min. = 52,0; $\bar{X}$ = 59,60; SD = 8,68; N = 21)

Growth proceeds in a similar manner to the above except that less expansion takes place in this region, as indicated by the lower sample range (21,0mm as opposed to 32,5mm). Up to g/s 4 the mean measurements for skull height from the palate between M¹ are slightly higher than those taken from the palate to the naso-frontal suture, but after this growth stage the measurements taken at these more posterior reference points exceed those taken from the palate between the M¹, indicating that the cranium is inflating more at the posterior end of the nasals than anterior to this point. This is well illustrated in the profile view of the cranium shown in Fig. 49. The sample and individual growth stage SDs compare favourably with those of character 10.

12. Least breadth of bony bridge between orbit and foramen infra-orbitale (Fig. 50 G¹; 7.2.1.12; Appendix V Table III pp.64-66) (mm)

(Max. = 19,6; Min. = 11,2; $\bar{X}$ = 16,12; SD = 2,06; N = 23)

There is a tendency for the dimensions of this parameter to increase gradually with age, the mean measurement for g/s 3 being somewhat high. Judging by the mean measurements, most growth appears to occur between g/s 5 and 6. The sample range is low (8,4mm) indicating that less growth occurs in this region than at other parts of the cranium hitherto mentioned. This is also reflected in the relatively low SD (2,06) which is lower than any of those obtained for the cranial criteria considered above.

13. Breadth of choanae (Fig. 52 P¹; 7.2.1.13; Appendix V Table III pp. 64-66) (mm)

(Max. = 34,4; Min. = 20,5; $\bar{X}$ = 29,99; SD = 4,50; N = 25)

There is a tendency for the diameter of the combined choanae to increase gradually with age, the sample range being 16,9mm.

14. Length, breadth and prominence of sagittal crest (Fig 46 H ;
7.2.1.14, 15; Appendix V Table III pp. 64-66) (mm)

(Max. = 20,1; Min. = 9,0; $\bar{X}$ = 14,22; SD = 3,80; N = 15)

The length, breadth and degree of development of the sagittal crest proved to be very variable in H. africae australis. The crest does not develop until growth stage 4 is reached, after which there is a tendency for it to increase its length gradually. The crest varies from broad and flat to high and blade-like. It may terminate abruptly anteriorly (particularly true of the blade-like variety) or the walls of the crest may diverge gradually and the crest flatten anteriorly. The parameter has not been adequately defined in the existing literature and it is therefore not known whether or not the published measurements of this parameter incorporate the thickness of the transverse occipital crest, as done by the present author. The sample range for this parameter is 11,1mm.

15. Prominence of lambdoid (occipital) crest (Fig. 45; 7.2.1.16)

As with the sagittal crest, the length, thickness and degree of development of the lambdoid crest proved highly variable.

16. Position of 'sphenopalatine foramen' (Fig. 47; 7.2.1.17;
Appendix V Table III pp. 64-66) (mm above alveolar rim of
maxillary teeth)

(Max. = 13,0; Min. = 6,5; $\bar{X}$ = 8,89; SD = 1,34; N = 28)

The distance of the opening of the 'sphenopalatine foramen' from the alveolar rim of the upper molars does not vary much within the sample (sample range 6,5mm; SD 1,34), the measurements indicating that there is a gradual increase of the distance with increasing age. However, its position in relation to the maxillary teeth varies according to growth stage, being directly above the junction between the dp^4 and M^1 at early growth stage 2 (TM Nyasaland) and 'moving backwards' until it lies above the centre of the buccal part of the alveolar rim of the M^2 at growth stage 6.

8.2 Measurements of the premaxilla

1. Length of the nasal process of the premaxilla (Fig. 50 H¹; 7.2.2.1 Appendix V Table IV pp. 67-68) (mm)

(Max. = 55,5; Min. = 29,0; $\bar{X}$ = 41,97; SD = 5,51; N = 26)

This parameter has nowhere been defined in the available literature nor is it apparent from the published measurements what reference points have been used to define the limits of the parameter. The nasal process of the premaxilla is poorly differentiated from the remainder of the premaxilla and hence the present author has measured the length of the nasal process along the naso-premaxillary suture although other users of the parameter may have measured the length along the suture with the maxillary.

A great deal of growth occurs between growth stages 2 and 3 (a difference of more than 10,0mm between the means) but relatively little between growth stages 3 and 4 and 4 and 5. There is a slight acceleration of growth between stages 5 and 6, a pattern which was frequently encountered in the general cranial characters. The sample range (26,5mm) and sample SD (5,51) are moderately high.

2. Breadth of nasal process of premaxillary at fronto-premaxillary suture (Fig. 50 I¹; 7.2.2.2; Appendix V Table IV pp.67-68) (mm)

(Max. = 8,1; Min. = 1,0; $\bar{X}$ = 4,38; SD = 1,84; N = 24)

Most users of the character 'breadth of nasal process of premaxilla' fail to define a position along the length of the process at which the measurement should be taken, one exception being Corbet and Jones (1964, see 3) below). As a second measure of the width of this process, the breadth was measured at its posterior extremity, i.e. across the fronto-premaxillary suture. The length of this suture proved somewhat variable (sample range 7,1mm) and no trend towards either an increase or a decrease in its length was apparent from the examination of the mean measurements which appeared to be random. The longest sutures were encountered at growth stages 3 and 4; after these stages it may be that adjacent parts of the cranium are expanding at the expense of posterior portion of the nasal process, thus decreasing its width. The mean measurements also imply that the shape of the posterior portion of this bone is highly variable, from truncate to sharply pointed.

3. Breadth of nasal process of premaxilla midway between the maxillo-frontal suture and the masseteric ridge Fig. 50 J¹; 7.2.2.3; Appendix V Table IV pp. 68-69) (mm)

(Max. = 14,8; Min. = 7,0; $\bar{X}$ = 9,96; SD = 1,96; N = 25)

Unlike the posterior portion of the nasal process, growth towards the middle portion shows a definite gradual trend to increasing expansion with advancing age, with most growth occurring between g/s 2 and 3 followed by stages 5 and 6. The sample range (7,8mm) and sample SD are a little higher than for 1).

4. Median sutural length of premaxilla ventrally (Fig. 48 T; 7.2.2.4; Appendix V Table IV pp.67-68) (mm)

(Max. = 28,3; Min. = 16,0; $\bar{X}$ = 23,01; SD = 3,48; N = 26)

An examination of the mean measurement for this parameter for each growth stage shows that there is an increase from $\bar{X}$ = 16,57 at g/s 2 to $\bar{X}$ = 26,48 at g/s 6, with most growth taking place between stages 2 and 3. The rate of growth then slows, with least growth taking place between stages 4 and 5, after which another spurt of growth takes place. The sample range is 12,3mm.

5. Sutural length of the premaxilla anterior to the foramina incisiva (Fig. 48 U; 7.2.2.5; Appendix V Table IV pp. 67-68) (mm)

This parameter was not encountered in the taxonomic literature but has been included because the distance it defines is more frequently found intact in both recent and fossil specimens than is the previous parameter in which the area posterior to the foramen incisiva is often absent.

The mean sutural length anterior to the foramen increases with age, with the biggest growth increments occurring between stages 3 and 4 and 5 and 6. The sample range is 12,4mm.

6. The posterior extent of the premaxillary process (Figs. 46, 49; 7.2.2.6)

The posterior extent of the nasal process of the premaxillary (= premaxillary process of some authors) was visually examined for the entire sample using the anterior margin of the lachrymal as a reference point. In no instance did the premaxillary extend posterior to the anterior margin of the lachrymal; in most instances it terminated approximately 3-5mm short of the lachrymal margin, although in a few cases the distance was less.

7. Shape of terminal part of premaxillary process (Fig. 49; 7.2.2.7)

The measurements recorded under 8.2.2. (length of fronto-premaxillary suture) imply that the shape of the posterior portion of the premaxillary process must be somewhat variable; visual checking confirmed this. Narrowly truncate (i.e. narrow rectangular), spatulate, tapering triangular and pointed terminations were found. Table IV column B p.67 of the Appendix volume indicates the breadth of the terminal portion of the premaxillary process and should provide an insight into the shapes encountered.

8.3 Analysis of measurements of the nasal used as diagnostic criteria

1. Length of nasals (Fig. 46 I; 7.2.3.1; Appendix V Table V pp.69-70) (mm)

(Max. = 89,3; Min. = 40,5; $\bar{X}$ = 68,78; SD = 12,05; N = 23)

The measurements of the length of the nasals indicate that they undergo a growth pattern which is common to most of the cranial parameters considered above, with most growth occurring between stages 2 and 3 with a second period of increased growth between stages 5 and 6. The sample range is high (48,8mm) indicating that considerable expansion occurs in this region of the skull with age.

2. Length of nasal suture (Fig. 46 J; 7.2.3.2; Appendix V Table V Col. B pp. 69-70) (mm)

(Max. = 84,5; Min. = 39,5; $\bar{X}$ = 66,33; SD = 11,20; N = 23)

The high sample range of 45,0mm indicates that considerable growth occurs in this region of the skull. The nasal suture is slightly shorter than the total length of the nasal bone, and the same pattern of growth occurs. The sample SDs of 11,20 and 12,05 respectively are comparable.

3. Maximum width of nasals; width of nasals at posterior end of nasopremaxillary process (Fig. 46 K, L; 7.2.3.3; 7.2.3.5; Appendix V Table V Col. C pp. 69-70) (mm)

(Max. = 41,4; Min. = 19,9; $\bar{X}$ = 29,48; SD = 4,85; N = 23)

The sample range of 11,5mm indicates that less growth takes place in the width of the nasal bone than occurs in either the length of the

bone or its mesial suture. Maximum growth is between stages 2 and 3 and, to a lesser extent, between stages 5 and 6. The sample SD is lower than those of the previous two parameters which concern nasal length.

4. Width of nasals at anterior end of the naso-premaxillary process
(Fig. 46 K; 7.2.3.4; Appendix V Table V Col. d pp.69-70) (mm)

(Max. = 24,0; Min. = 12,7; $\bar{X}$ = 17,86; SD = 2,94; N = 24)

The sample range is 11,3mm indicating that a similar degree of expansion occurs posteriorly on the nasal as occurs anteriorly. The nasal is nevertheless far wider posteriorly than it is anteriorly.

5. Posterior extent of nasals behind fronto-premaxillary suture;
posterior extent of nasal in relation to lachrymal and orbit
(Fig. 46 N; 7.2.3.6-8; Appendix V Table V Col. E pp. 69-70) (mm)

(Max. = 27,9; Min. = 5,8; $\bar{X}$ = 17,40; SD = 5,80; N = 24)

It is obvious from the data available that expansion of the posterior part of the nasal forces its posterior margin progressively further behind the fronto-Premaxillary suture - the mean distance of the posterior margin of the nasal behind the latter suture being only 7,03mm. at growth stage 3 but 22,90mm at growth stage 6. In most mature growth stage 5 and 6 specimens this means that the nasal terminates level with, or very slightly posterior to, the posterior boundary of the lachrymal bone, whereas in younger specimens it terminates anterior to this point. In mature specimens the nasals extend back to a level in line with the anterior border of the orbit or very slightly beyond (see TM 6066) but in younger specimens they stop short of this.

6. Shape of posterior margin of nasals (7.2.3.9)

In H. africae australis the posterior termination of the nasals is broadly convex (see Fig. 46) in most specimens.

7. Size and shape of nasal orifice (Fig. 51)

This varied considerably within the sample. The breadth of the choanae has been discussed in section 8.1.3.

8.4 The analysis of frontal and parietal characters used as
diagnostic criteria in the description of new species of
porcupine

1. Length of frontal suture (Fig. 46 O; 7.2.4.1; Appendix V Table V
Col. A pp. 71-73) (mm)

(Max. = 53,0; Min. = 27,5; $\bar{X}$ = 42,38; SD = 6,20; N = 23)

The sample range of 25,5mm is considerably lower than those of either of the two length measurements of the nasal (48,8 and 45,0mm), suggesting that greater expansion takes place in the anterior portion of the cranium than in the central and rear portions. The sample SD is likewise lower. The usual growth pattern occurs, with the greatest increments between stages 2 and 3 followed by stages 5 and 6. The frontal is far shorter than the nasal (g/s 6 mean length of frontal = 44,21; g/s 6 mean length of nasal = 78,77).

2. Fronto-occipital distance (Fig. 46 Q; 7.2.5.2; Appendix V Table VI Col. C pp. 71-73) (mm)

(Max. = 37,0; Min. = 24,3; $\bar{X}$ = 30,08; SD = 3,43; N = 20)

The term 'fronto-occipital distance' was introduced by the present author to refer to the distance between the fronto-parietal suture and the posteriormost point reached by the top of the median occipital crest on the dorsal midline. The median sutural length of the parietal is usually impossible to measure on account of an early and thorough fusion with the occipital bone posteriorly.

The sample range of 12,7mm is still less than that for the parameter 'length of frontal suture', which stresses the point that most expansion of the cranium occurs anteriorly.

8.5 The analysis of occipital characters used as diagnostic criteria

1. Distance between the upper edge of the foramen magnum and occipital crest along midline (Fig. 54 S¹; 7.2.6.1; Appendix V Table VIII Col. A pp. 76-78) (mm)

(Max. = 32,0; Min. = 23,7; $\bar{X}$ = 25,77; SD = 3,08; N = 20)

The outline of the upper margin of the foramen proved to be very variable indeed. The low sample range of 8,3mm indicates that little growth occurs in the height of the occiput above the foramen magnum. The pattern of growth is unusual in that the occipital height at growth stage 5 is lower than that at growth stage 4. Examination of the material showed that this was due to the upper margin of the foramen magnum (one reference point) approaching closer to the transverse occipital crest,

rather than to an actual decrease in occipital height. Because the upper margin of the foramen magnum is so variable in its approach to the top of the occipital crest, it appears that it is unreliable to use it as a reference point.

2. Distance between the lower edge of the foramen magnum and occipital crest along midline (Fig. 54 T¹; 7.2.6.2; Appendix V Table VIII Col. B pp. 76-78) (mm)

(Max. = 42,8; Min. = 32,5; $\bar{X}$ = 39,69; SD = 2,95; N = 19)

The outline of the lower margin of the foramen magnum is much less variable than the upper. The growth pattern indicated by the measurements of this parameter is one of gradual increase with age. The occiput almost reaches its maximum height by growth stage 4 after which little growth occurs. It appears to be more reliable to measure the occipital height using the lower margin of the foramen magnum as a reference point rather than the upper. The sample range of 10,3mm suggests that relatively little growth occurs in this part of the cranium.

3. Greatest occipital breadth at paroccipital processes (Fig. 54 W¹; 7.2.6.4; Appendix V Table VIII Col. C pp. 76-78) (mm)

(Max. = 45,4; Min. = 42,2; $\bar{X}$ = 49,22; SD = 3,43; N = 18)

The mean measurements of this parameter for each growth stage show an increase of the occipital breadth with age, with most growth occurring between stages 2 and 4 and 5 and 6. Between stages 4 and 5 growth slows. The sample range is 11,8mm indicating that the occiput expands slightly more in width than it does in height over the growing period.

4. Length of paroccipital processes (Fig. 54 X¹; 7.2.6.5; Appendix V Table VIII Col. D pp. 76-78) (mm)

(Max. = 13,7; Min. = 6,4; $\bar{X}$ = 9,70; SD = 1,74; N = 19)

The mean measurements for this parameter at each growth stage show an unusual tendency for the length of the paroccipital processes to decrease with increasing age. The paroccipital processes probably act as a brace for the head and the decrease in their length may be due to wear produced by normal head movements over a long period of time. The sample range is 7,3mm.

5. Distance between paroccipital processes (Fig. 54 Y¹; 7.2.6.6;
Appendix V Table VIII Col. E pp. 76-78) (mm)

(Max. = 43,5; Min. = 31,7; $\bar{X}$ = 39,01; SD = 3,13; N = 18)

There appears to be a tendency for the distance between the paroccipital processes to increase with age but the measurements for growth stage 5 are unusual in that they are lower than those for any other growth stage. There seems to be no obvious functional explanation for this. The sample range is relatively low (12,8mm).

6. Maximum width of occipital condyles between external edges (Fig. 54 Z¹; 7.2.6.7; Appendix V Table VIII Col. F pp. 76-78) (mm)

(Max. = 37,0; Min. = 27,6; $\bar{X}$ = 31,43; SD = 2,26; N = 18)

The maximum width of the occipital condyles increases gradually with increasing age. The growth stage 4 mean appears to be unusually low but this may be because only one growth stage 2 and no growth stage 3 measurements are available.

7. Orientation of the long axis of the occipital condyle (7.2.6.8)

The long axis of the occipital condyle is oblique, angled approximately at 45° from the horizontal in most mature specimens. The lower extremities of the two condyles are closer together than the uppers. However, the orientation of the axis is highly variable within the sample, ranging from almost vertical to almost horizontal. Juvenile specimens tend to have more nearly vertical condyle axes than do adult individuals, where the axis is often 45° or less from the horizontal.

8.6 The analysis of palatal characters used as diagnostic criteria

1. Upper diastemic length (Fig. 48 V; 7.2.7.1; Appendix V Table VI
Col. D pp. 71-73) (mm)

(Max. = 59,0; Min. = 31,0; $\bar{X}$ = 47,73; SD = 6,77; N = 27)

The palatal diastemic length increases with increasing age from $\bar{X}$ = 34,67 at growth stage 2 to $\bar{X}$ = 52,59 at growth stage 6. Maximum growth occurs between stages 2 and 3 and between stages 5 and 6. Least growth occurs between stages 4 and 5. The sample range of 28,0mm indicates that considerable expansion occurs in this region.

2. Median sutural length of palate (Fig. 48 W; 7.2.7.2; Appendix V Table VI Col. E pp.72-74) (mm)

(Max. = 90,0; Min. = 52,8; $\bar{X}$ = 75,66; SD = 9,38; N = 27)

The difference in measurement between the smallest (and youngest) and largest and most mature specimens is 47,2mm which suggests that considerable lengthwise expansion of the palate occurs with increasing age. Examination of the mean values for each growth stage shows that there is a steady increase from growth stage 2 to 6, with most growth occurring between stages 2 and 3.

3. Median sutural length of maxillary (Fig. 48 X; 7.2.7.3; Appendix V Table VI Col. F pp.72-74) (mm)

(Max. = 54,0; Min. = 33,8; $\bar{X}$ = 46,06; SD = 5,48; N = 27)

The sample range of 20,2mm is slightly less than that for the diastemic length (8.6.1; 28,0mm). There is a gradual increase in the length of the maxillary with increasing age, from $\bar{X}$ = 35,47 at growth stage 2 to $\bar{X}$ = 50,46 at growth stage 6. This expansion suffices to accommodate the mature tooth row of 4 teeth which has an average length of 28,09mm.

4. Width of palate between dp^4 or P^4 , M^1 , M^2 and M^3 (Fig.48 Y,Z,A¹,B¹) 7.2.7.4-7; Appendix V Table VII pp.74-75)

	<u>Max.</u>	<u>Min.</u>	<u>$\bar{X}$</u>	<u>SD</u>	<u>N</u>	<u>Sample Range</u>
Inter- P^4 distance	15,0	8,0	10,81	2,04	27	7,0
Inter- M^1 distance	16,8	6,2	9,59	2,30	26	10,6
Inter- M^2 distance	17,1	6,0	10,37	2,43	24	11,1
Inter- M^3 distance	15,1	9,0	11,58	1,76	19	6,1

The palatal width between the maxillary, deciduous and permanent pre-molars and third molars has also been discussed in the introductory section to Chapter 10. Examination of the measurements taken showed that the palatal width between opposite teeth in the maxillary tooth rows tended to increase gradually and very slightly with increasing age. The standard deviations and sample ranges are fairly low, indicating that relatively little growth in width occurs in this part of the cranium - compare with the sample ranges of 47,2mm and 20,2mm for the sutural length of the palate and maxillary respectively.

5. Shape of the palate behind (Fig. 48; 7.2.7.8)

In H. africae australis the palatal notch is basically paraboloid-shaped or inverted 'u'-shaped. The acuteness of the apex of the inverted 'u' or the steepness of the parabola was found to vary within the sample, some individuals having broader, shallower palatal notches than others. In some specimens a small bony projection of left and right palatine bones was present at the midline, at the apex of the notch.

6. Anterior extent of palatal incision (Fig. 48; 7.2.7.9)

In H. africae australis the anterior extremity of the palatal notch does not extend anterior to the mesial border of the last tooth in the maxillary tooth row, and usually reaches only as far as the lingual enamel fold. In a few specimens the palatal notch terminates behind the posterior-most maxillary tooth.

7. Length, breadth, shape and position of the foramina incisiva (Fig. 48; 7.2.7.10; Appendix V Table VI Col. G pp. 71-73) (mm)

(Length: Max. = 8,5; Min. = 3,5; $\bar{X}$ = 6,60; SD = 1,20; N = 27)

(Breadth: Max. = 7,5; Min. = 4,0; $\bar{X}$ = 5,52; SD = 0,96; N = 27)

The measurements of the length of the foramina incisiva showed a trend towards increase in length up to the end of growth stage 4, after which there appeared to be a gradual decrease in length. The sample range is low (5,0mm). The measurements for the breadth of the foramina show that there is a gradual increase from growth stage 2 to 6, with the maximum value at the latter growth stage. The foramina incisiva often has the shape of an elongate oval, or may be tear-shaped, with the broad end of the tear towards the posterior. The pair of foramina are slightly angled, diverging from front to back, with their anterior extremities almost touching (Fig. 48).

The position of the foramina incisiva is very constant, the pair being situated on the midline in the anterior third of the diastema, just anterior to the intersection of the premaxillary-maxillary suture. The posterior extremities of the foramina are frequently in contact with the latter suture.

The sample standard deviations for both length and breadth are low.

8.7 Analysis of zygomatic characters used as diagnostic criteria

1. Least vertical diameter of lower anterior zygomatic root (Fig. 50 K¹ 7.2.8.1; Appendix V Table IX Col. I pp. 79-81) (mm)

(Max. = 4,0; Min. = 1,0; $\bar{X}$ = 2,21; SD = 0,63; N = 26)

The measurements for the minimum vertical diameter of the lower anterior zygomatic root showed that this parameter varies very little throughout the sample and the sample range (3,0mm) and sample SD (0,63) are predictably low. No tendency towards higher minimum vertical diameters with increasing age could be detected, as high and low values occurred randomly throughout the growth series. There is therefore probably a specific functional requirement for a slender anterior zygomatic root, and the character therefore may prove to be of diagnostic value.

2. Jugal height of maxillo-jugal suture (Fig. 50 L¹; 7.2.8.2; Appendix V Table IX Col. B pp. 79-81) (mm)

(Max. = 23,5; Min. = 15,3; $\bar{X}$ = 19,42; SD = 2,21; N = 24)

The measurements show that there is a tendency for the length of this suture to elongate with increasing age. The value for growth stage 3 is unusually high. The sample range of 8,2mm is fairly low. The difference in measurement between the youngest and oldest specimens is only 3,4mm indicating that relatively little growth occurs in this region.

3. Jugal height at jugo-squamosal suture (Fig. 50 M¹; 7.2.8.3; Appendix V Table IX Col. C pp. 79-81) (mm)

(Max. = 9,3; Min. = 4,1; $\bar{X}$ = 6,62; SD = 1,59; N = 22)

The measurements show a somewhat uncertain trend towards an increase in length of the suture with increasing age up to growth stage 5, after which the suture appears to decrease in length. A difference of only 4,1mm between one of the youngest, smallest specimens (TM 5662) and one of the largest most mature specimens (TM 6066) indicates that little growth occurs in the height of the jugal at this point, and slightly less than at the maxillo-jugal suture.

4. Length of jugal along orbital rim (Fig. 50 N¹; 7.2.8.4; Appendix V Table IX Col. D pp. 79-81) (mm)

(Max. = 25,2; Min. = 16,0; $\bar{X}$ = 19,65; SD = 5,34; N = 23)

The measurements indicate a gradual increase in the length of the jugal with increasing age although the mean figure for growth stage 5 is somewhat low. A difference of 9,2mm between the smallest, youngest specimen and the oldest, most mature demonstrates that more growth takes place in the length of the jugal than the height (see above).

8.8 Analysis of characters of the lachrymal used as diagnostic criteria

1. Distance of the lachrymal from the zygomatic suture (Fig. 50 0¹; 7.2.9.1; Appendix V Table IX Col. E pp.79-81) (mm)

(Max. = 8,8; Min. = 1,6; $\bar{X}$ = 4,88; SD = 1,73; N = 25)

The distance between the lachrymal and the maxillo-jugal suture tends to increase with age up to and including g/s 5, after which it apparently decreases. The decrease could be due to the posterior expansion of the lachrymal or to encroachment by the jugal in an anterior direction. Examination of the specimens suggests that the latter is predominantly the case.

2. Extent of facial surface of the lachrymal (Fig. 49)

Examination of the growth series showed that the facial portion of the lachrymal usually occupied just under half of the width of the vertical zygomatic process, bringing the anterior limit of the facial portion of the lachrymal level with or just anterior to the maxillo-jugal suture. This proved to be true of juvenile as well as adult individuals and hence the character appears to have potential taxonomic value.

8.9 The analysis of cranial relationships used as diagnostic criteria and of the molar-tympanic distance

1. Molar-tympanic distance (Fig. 48 D¹; 7.2.10.1; Appendix V Table IX Col. F pp. 79-81) (mm)

(Max. = 35,7; Min. = 20,8; $\bar{X}$ = 29,21; SD = 3,67; N = 19)

The measurements show that there is an increase in the distance between the posteriormost molar and the tympanic bone with increasing age, with most rapid growth occurring during and between the older growth stages, i.e. stages 5 and 6. However, a difference of only 3,6mm between the measurements of the youngest and most mature specimens indicates that

little expansion occurs in this region of the cranium.

The length of the measurement obtained for this parameter depends largely on the state of eruption of the posteriormost molar - if this is in position but not yet erupted or incompletely erupted, the measurement will be taken from the distal surface of the molar in front, and an unusually high measurement will be obtained. This accounts for the high readings (followed by lower, more 'normal' readings) at the interface between successive growth stages e.g for TM Nyasaland (beginning of g/s 2) and PPM 116 (beginning of g/s 4) and TM 12165 (beginning of g/s 5).

2. Length of nasal bones as a proportion of the occipitonasal skull

length (Fig. 46 I:B; 7.2.11.1; Appendix V Table X p. 82) (ratio %)

(Max. = 60%; Min. = 43%; $\bar{X}$ = 52%; SD = 4,44; N = 18)

The proportion of the occipitonasal skull length occupied by the nasal increases with increasing age, with most rapid growth occurring between stages 2 and 4. By growth stage 4 the nasal occupies half or more of the occipitonasal length, increasing to $\bar{X}$ = 55,60% by growth stage 6 at the expense, one suspects, of the development of the frontal bone which lies immediately posterior to the nasal (see below).

3. Frontal length as a percentage of nasal length (Fig. 46 O:I; 7.2.11.2; Appendix V Table XI p.83) (ratio %)

(Max. = 84%; Min. = 53%; $\bar{X}$ = 62%; SD = 10,48; N = 21)

As can be expected from the results of 2), the frontal length as a percentage of the nasal length decreases steadily with age, from $\bar{X}$ = 71,33% at growth stage 2 to $\bar{X}$ = 56,14% at growth stage 6, i.e. the frontal is approximately three-quarters the length of the nasal at growth stage 2 diminishing to just over half the nasal length at growth stage 6. From the relatively high standard deviation it appears that the former character (1) is more reliable.

4. Relative width of nasals; greatest width : greatest length

Fig. 46 K:I; 7.2.11.3; Appendix V Table XII p.84) (ratio %)

(Max. = 51,85; Min. = 37,40; $\bar{X}$ = 42,43; SD = 3,77; N = 22)

No clear growth trend was observed from the measurements; instead it appears as if the ratio greatest width : greatest length remains fairly constant, regardless of age. The sample mean of 42% indicates that

the greatest width is more than a third but less than half the length of the nasal. The relatively low standard deviation indicates that the ratio is more constant than either of the two preceding ratios.

5. Width of nasals anteriorly : width of nasals posteriorly, i.e. narrowing shape (Fig. 46 M:K; 7.2.11.4; Appendix V Table XIII p.85) (ratio %)

(Max. = 77,39%; Min. = 48,59%; $\bar{X}$ = 61,42%; SD = 6,67; N = 23)

There appears to be a slight but definite trend towards reduction in the value of this ratio with increasing age. Since it reflects the proportion of the anterior nasal width to the posterior width, this signifies that the nasal is expanding posteriorly with age.

6. Width of nasal process of premaxilla in relation to the greatest width of the nasal (Fig. 50 J¹: Fig. 46 K; 7.2.11.5; Appendix V Table XIV p.86) (ratio %)

(Max. = 46,73%; Min. = 24,02%; $\bar{X}$ = 34,37%; SD = 5,48; N = 23)

This tended to decrease slightly with age up to the end of growth stage 3, after which the mean value for each growth stage remained approximately the same. This suggests that initially, the width of the nasals may increase somewhat at the expense of the development of the nasal process of the premaxilla; however, taken as a whole the ratio appears to be fairly age-independent, and the relatively low sample standard deviation suggests that it may be a better ratio to use than any of the preceding, with the possible exception of ratio no. 4), relative nasal width.

7. Maximum width of occiput : maximum height of occiput measured a) from the upper and b) from the lower margin of the foramen magnum (Fig. 54 U¹:S¹; Fig. 54 U¹:T¹; 7.2.11.6; Appendix V Table XV p.87)

(ratio %)	<u>Max.</u>	<u>Min.</u>	<u>$\bar{X}$</u>	<u>SD</u>	<u>N</u>
a) from upper margin of foramen magnum	237,55	176,17	199,63	17,44	20
b) from lower margin of foramen magnum	142,14	120,79	129,84	6,82	19

An examination of Table XV showed that the ratios using the measurement taken from the upper margin of the foramen magnum centred around 200%, indicating an occiput approximately twice as broad as high. The

mean ratios computed by using the measurement from the lower margin of the foramen magnum were much lower, indicating a higher, more compact occiput.

The mean measurements (ratios) for both (a) and (b) show no definite trend towards either an increase or decrease in occipital height with age. The ratio thus appears to be growth independent and relatively constant despite the very high sample standard deviation for (a). The sample SD for (b) is far lower, this being accounted for by the fact that the shape of the upper boundary of the foramen magnum is far more variable than that of the lower. It would thus appear that it is more reliable to compute the relative occipital height using the lower occipital margin as a reference point.

8. Maximum width of occiput : maximum width of condyli (Fig. 54 U¹ : Z¹; 7.2.11.7; Appendix V Table XVI p. 88) (ratio %)

(Max. = 183,69; Min. = 148,39; $\bar{X}$ = 165,50; SD = 8,12; N = 18)

Unfortunately, no proper data is available for growth stages 2 and 3. The mean measurements for the remaining growth stages do not show any trend towards increase or reduction in the value of the ratio, but instead are constant at approximately 166%. This means that the condylar width is accommodated in the total occipital width almost exactly one and two-third times.

9. Height of skull as a percentage of basal length (Fig. 50 E¹ as a percentage of Fig. 48 S; 7.2.11.8; Appendix V Table XVII p. 89) (ratio %)

(Max. = 50,65; Min. = 42,55; $\bar{X}$ = 46,29; SD = 2,16; N = 18)

The mean ratios for each growth stage showed a tendency to increase, albeit slightly, with increasing age, indicating that the cranium becomes relatively high and globular with age. The relatively low standard deviation is lower than any of the sample standard deviations of the cranial indices considered hitherto.

10. Zygomatic breadth : basal length (Fig. 46 C: Fig. 48 S; 7.2.11.9 Appendix V Table XVIII p.90) (ratio %)

(Max. = 65,53; Min. = 55,38; $\bar{X}$ = 61,29; SD = 2,68; N = 17)

The mean ratios for each growth stage show no definite trend towards increase or reduction with increasing age, indicating that the width: length ratio and hence skull shape is age-independent. This is also reflected in the low sample standard deviation.

11. Length of molar series : molar tympanic distance (Fig. 48 C¹:D¹; 7.2.11.10; Appendix V Table XIX p.91) (ratio %)

(Max. = 155,44; Min. = 77,87; $\bar{X}$ = 110,26; SD = 23,77; N = 19)

The excessively high sample and individual growth stage standard deviations suggest that the ratio is a very unreliable one to use taxonomically. No trend towards increase or reduction with increasing age could be discerned and the high standard deviations are in all probability due to the fluctuating value of the molar-tympanic distance, discussed in section 8.9.1.

9 THE MANDIBULAR MORPHOLOGY OF HYSTRIX AFRICAEAUSTRALIS

The external morphology and muscle insertions of the mandible of H. africaeaustralis are illustrated in Figs. 55a and b and are thus not discussed here. The parameters measured are shown in Fig. 56 and defined in section 7.2.12.

9.1 The analysis of mandibular characters used as diagnostic criteria

1. Greatest length of mandible (Fig. 56 B², 7.2.12.1; Appendix VI Table I pp.94-96) (mm)

(Max. = 115,6; Min. = 59,9; $\bar{X}$ = 95,38; SD = 13,20; N = 28)

The greatest mandibular length increases progressively with increasing age from $\bar{X}$ = 71,63 at growth stage 2 to $\bar{X}$ = 106,87 at growth stage 6. The sample range is 55,7. Most rapid growth occurs between growth stages 2 and 3 (difference between means = 17,21mm) and growth stages 3 and 4 (difference between means = 9,52mm). Growth slows during growth stage 4 so that the difference between the g/s 4 and g/s 5 is only 3,81mm. During growth stage 5, the rate of growth again accelerates somewhat, giving a difference between the g/s 5 and 6 means of 4,90mm. The standard deviation at any one growth stage and particularly for the sample (13,20) is high, indicating a high degree of variation.

2. Length of mandible from posterior border of incisor alveolus to tip of angular process (Fig. 56 C², 7.2.12.2; Appendix VI Table I pp. 94-96) (mm)

(Max. = 114,5; Min. = 56,5; $\bar{X}$ = 93,50; SD = 13,60; N = 26)

Growth occurs in the same manner as for the greatest mandibular length, increasing from $\bar{X}$ = 69,70 at growth stage 2 to $\bar{X}$ = 107,32 at growth stage 6. The sample range is 58,0. Most rapid growth occurs between g/s 2 and 3, and least at growth stage 4. As with 1), the standard deviation for any one growth stage and particularly the sample is high, as is to be expected in a character which changes markedly with increasing age.

3. Height of mandibula (Fig. 56 D², 7.2.12.3; Appendix VI Table I pp.94-96) (mm)

(Max. = 45,3; Min. = 21,0; $\bar{X}$ = 35,95; SD = 5,58; N = 26)

As with characters 1) and 2), the height of the mandibula increases with increasing age, with most rapid growth between growth stages 2 and

3, and least between stages 4 and 5. However, in absolute terms, less growth occurs in this region than in either 1) or 2) as indicated by the lower sample range (24,3mm as opposed to 55,7 and 58,0) and lower standard deviation (5,58). The standard deviation for any single growth stage is moderately low.

4. Depth of ramus below P_4 , M_1 and M_2 (Fig E^2 , F^2 , G^2 ; 7.2.12. 4-6;

Appendix VI Table I pp.94-96) (mm)

	<u>Max.</u>	<u>Min.</u>	<u>$\bar{X}$</u>	<u>SD</u>	<u>N</u>	<u>Sample range</u>
Depth below P_4	27,7	16,4	23,63	2,55	30	11,2
Depth below M_1	26,5	15,7	22,31	2,48	24	10,8
Depth below M_2	24,6	15,0	21,0	2,65	26	9,6

As with characters 1) to 3), the depth of the ramus below the P_4 , M_1 and M_2 increases with age, although less growth occurs in this region than occurs in the height of the mandibula and particularly in the length of the mandible, as can be seen by the lower sample ranges and standard deviations. The greatest growth increment takes place between growth stages 2 and 3 and the least between stages 4 and 5. The depth of the ramus appears to be a potentially more reliable character than any of the three discussed above.

5. The distance from the alveolus of P_4 to the foramen mentale; position of foramen mentale (Fig. 56 H^2 ; 7.2.12.7-8; Appendix VI Table II pp.97, 98) (mm)

(Max. = 12,5; Min. = 7,0; $\bar{X}$ = 9,57; SD = 1,58; N = 30)

The distance between the alveolus of the P_4 (or dp_4) and the foramen mentale increases gradually with age, with the most substantial growth increment between growth stages 2 and 3. However, the amount of growth in this region is small, as suggested by the low sample range (5,5mm) and sample SD (1,58).

The position of the foramen mentale is also fairly constant, usually being situated below and slightly anterior to the mesial alveolar rim of the dp_4 or P_4 , on the lateral surface of the mandible. The diameters of the foramina mentale would appear to be somewhat variable.

6. Length of diastema (Fig. 56 I²; 7.2.12.9; Appendix VI Table II pp. 97, 98) (mm)

(Max. = 39,6; Min. = 18,5; $\bar{X}$ = 28,15; SD = 4,97; N = 30)

The length of the diastema increases gradually with age from $\bar{X}$ = 21,08 at g/s 2 to $\bar{X}$ = 32,91 at g/s 6. No significant acceleration of growth is observable at or between any growth stages. The sample standard deviation is moderate, and the sample range is 11,1mm.

7. Curvature of diastema (Fig. 108; 7.2.12.10; Appendix VI Table II pp.97, 98) (%)

(Max. = 40,8; Min. = 27,7; $\bar{X}$ = 28,58; SD = 3,74; N = 30)

The degree of curvature of the diastema remains fairly constant regardless of age, with no trend towards a straighter or more strongly curved diastema with age being apparent. The SD for the sample is moderate (3,74) as it is for any particular growth stage. The sample range is 13,1. The character appears to be less variable than the diastemic length.

8. Presence or absence of a dorsally thickened crest on coronoid process (7.2.12.11)

In H. africae australis the prominence and thickness of the ridge or 'crest' along the dorsal surface of the coronoid process appears to be controlled by the development and strength of the m. temporalis which has its attachment in this region (see Fig. 55b). Older specimens thus tend to have well-marked dorsally-thickened coronoid crests while in young specimens the crest is absent, with a gradation of conditions in between. No significance can thus be attached to the presence or absence of such a crest, unless in some species it is consistently apparent in immature specimens.

9. Position of ascending ramus in relation to alveolar plane of molars (Fig. 56 J; 7.2.12.12; Appendix VI Table II pp. 97, 98) (mm)

(Max. = 25,0; Min. = 7,5; $\bar{X}$ = 13,54; SD = 4,55; N = 27)

The distance between the alveolar plane of the mandibular tooth row and the top of the ascending ramus tends to increase gradually with age, from $\bar{X}$ = 10,13 at g/s 2 to a maximum of $\bar{X}$ = 17,33 at g/s 5, after which the height of the ascending ramus decreases again to $\bar{X}$ = 17,00 at g/s 6. The sample range is 17,5 and the sample SD is moderate (4,55).

10. Position of top of mesial symphysis in relation to alveolar plane of the molars (Fig. 56 K²; 7.2.12.13; Appendix VI; Table II pp. 97, 98) (mm)

(Max. = 8,0; Min. = 0,0; $\bar{X}$ = 3,67; SD = 2,43; N = 30)

As with character 9), the distance from the alveolar plane of the mandibular molars to the top of the mesial symphysis tends to increase gradually but very slightly with age, with the greatest growth increment again occurring between stages 2 and 3. The sample range is low (8,0mm), as is the sample SD (2,43). The character thus appears to be under fairly rigid functional and/or genetic control, and is thus potentially a good diagnostic character.

11. The extent of the development of and position of muscle attachments (Fig. 55b; 7.2.12.14)

As mentioned for character 8, the degree of development of muscle attachments appears to be age-related, with older specimens sometimes having very well-marked muscle attachments indeed. Immature specimens usually have very obscure muscle attachments, particularly those of the ascending ramus, but the pit-like depression marking the attachment of m. temporalis is always obvious and its location is invariable in H. africae australis, being approximately 1cm below the junction of the buccal alveolar rims of the P_4 and M_1 . In some specimens it may occur as far back as + 1cm below the centre of the buccal alveolar rim of the M_1 , but never anterior or posterior to these two points mentioned. Little importance can thus be attached to the degree of development of muscle attachments, but the position of muscle attachments appears to be rigidly functionally controlled.

The data available suggests the following order of potential reliability of the mandibular characters used in specific diagnoses:

1. Distance of foramen mentale from the alveolus of P_4
2. Height of mesial symphysis above the alveolar plane of the mandibular molars
3. Depth of ramus below P_4 , M_1 and M_2 respectively
4. Curvature of diastema
5. Height of ascending ramus above alveolar plane
6. Diastemic length

7. Mandibular height
8. Greatest mandibular length
9. Length of mandible from incisor alveolus to angular process

The dorsal thickening of the coronoid process to form a crest and the development of muscle attachments both appear to be enhanced with increasing age.

10. THE DENTAL MORPHOLOGY OF HYSTRIX AFRICAEAUSTRALIS AND ITS
ADAPTATIONS TO THE DEMANDS OF FUNCTION

All the structural peculiarities of the Hystrix dental apparatus (and of rodents in general) become explicable in terms of adaptation to the gnawing habit - the incisors, cheek teeth, mandible, maxilla and musculature are all structurally adapted to the function of gnawing and the grinding of a tough, fibrous vegetable diet. The adaptations of the masticatory apparatus have been discussed where relevant.

An adult Hystrix (growth stage 5 or 6) has 20 teeth: 2 incisors, 2 premolars and 6 molars in both the upper and lower jaw, i.e.

$$\frac{1}{1}I ; \frac{1}{1}P ; \frac{3}{3}M$$

In Hystrix only the fourth premolar is present (P^4 and P_4) but in more advanced rodents the entire premolar series is lost.

The most striking features of the Hystrix dentition are the long, broad, strongly-curved, tusk-like central incisors (Fig. 112) which are highly specialized to the gnawing habit (see below).

Behind the incisors, the absence of the outer incisors, canines and most of the premolar series gives rise to a wide toothless gap or diastema which separates the incisors from the cheek teeth. The absence of the above-mentioned teeth is probably due to the excessive development of the intra-alveolar portion of the incisors. During gnawing, thick pads of cheek fold inwards behind the incisors into this gap, dividing the mouth chamber into two parts. The chips strike against the folds and fall out without ever injuring the soft membrane of the posterior part of the cavity.

The premolars and molars are almost identical in form and structure, but the premolars (which are 'molarized') are notably larger than any of the molars (Figs. 113, 114), often at the expense of the adjacent first molars, which may become antero-posteriorly compressed. The maxillary cheek tooth rows of many genera of rodents diverge somewhat from front to back but this phenomenon is not at all well-marked in Hystrix, where the tooth rows appear to be almost parallel or even divergent from back to front (see below). The mandibular tooth rows, however, almost invariably diverge from front to back (see below). The palate of H. africaeaustralis is invariably wider than any of the cheek teeth.

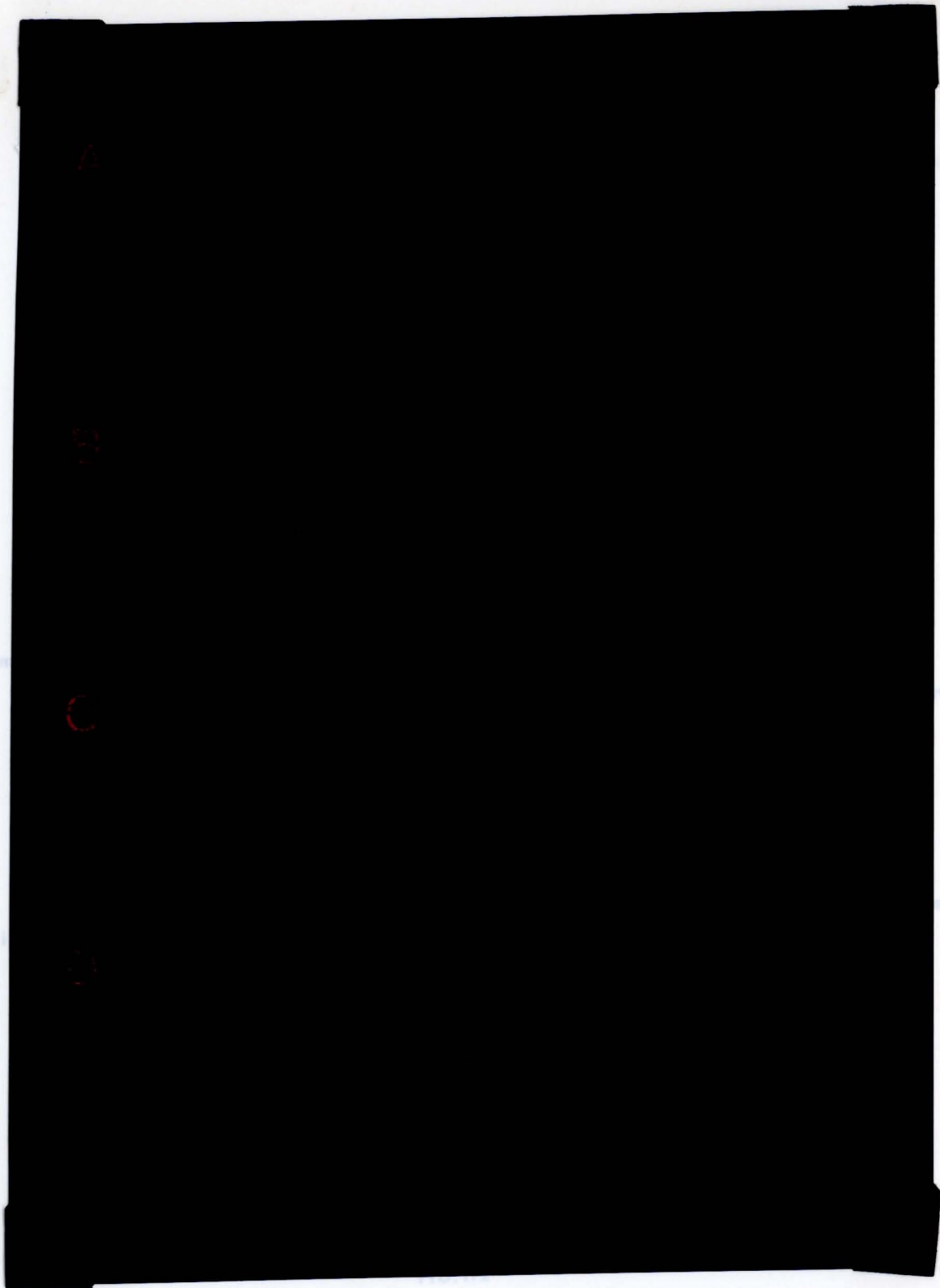
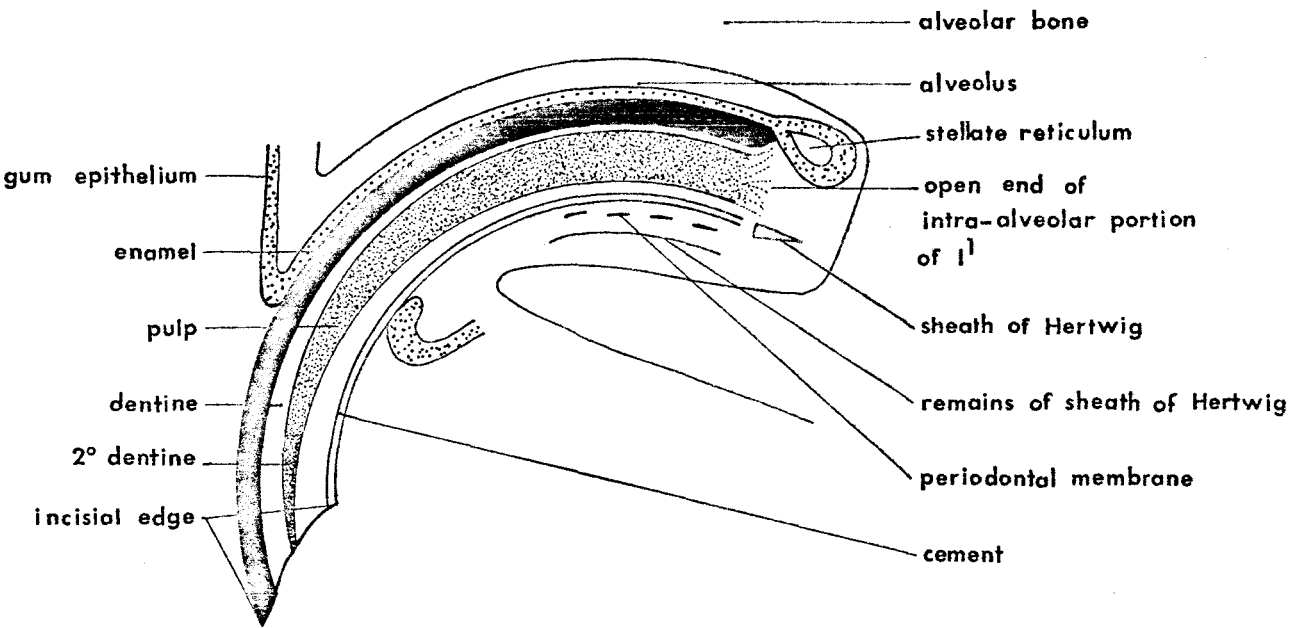
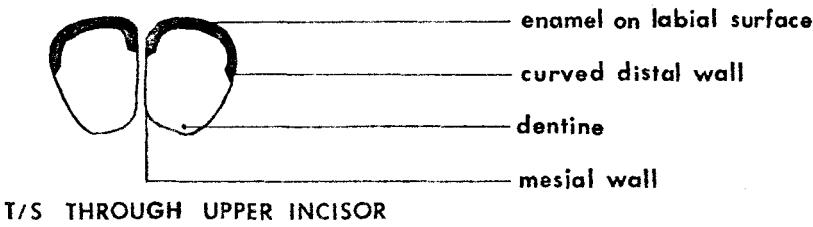


Fig 111

X-ray radiographs of a series of left mandibles of Hystrix africae-australis Peters 1852 at different stages of growth, showing tooth structure, eruption and replacement and root development with increasing age. Note position of root end of incisor A: early growth stage 3; B: late growth stage 3; C: early growth stage 4; D: late growth stage 4.



L/S THROUGH UPPER INCISOR
(after Scott & Symons, fig.219)

FIG.112

Fig. 113a

The external morphology, root structure and alveolar root patterns of the permanent upper premolar and molars. Left hand row shows distal views of maxillary teeth, right hand row shows patterns of roots visible in empty alveoli.

Note that the permanent premolar (P^4) is by far the largest tooth. Note also the differing crown heights of the four teeth indicating differing degrees of exposure to wear - the M^1 as the oldest tooth has been exposed to most wear, followed by the M^2 , M^3 and finally the P^4 . The root development is also an indication of age, hence the M^1 has the best developed and most divergent rootlets, although these are still not well developed and papillate. The M^3 and P^4 have poorly developed rootlets. There is also a tendency to develop accessory rootlets with increasing age as indicated by the root impressions of the M^1 . Curvature is characteristic of newly erupted maxillary molar teeth, hence the M^3 and P^4 are the most strongly curved. Note the unequal planes of wear on the occlusal surfaces of all four teeth.

d-b-r - distobuccal root
m-b-r - mesiobuccal root
l-r - lingual root.

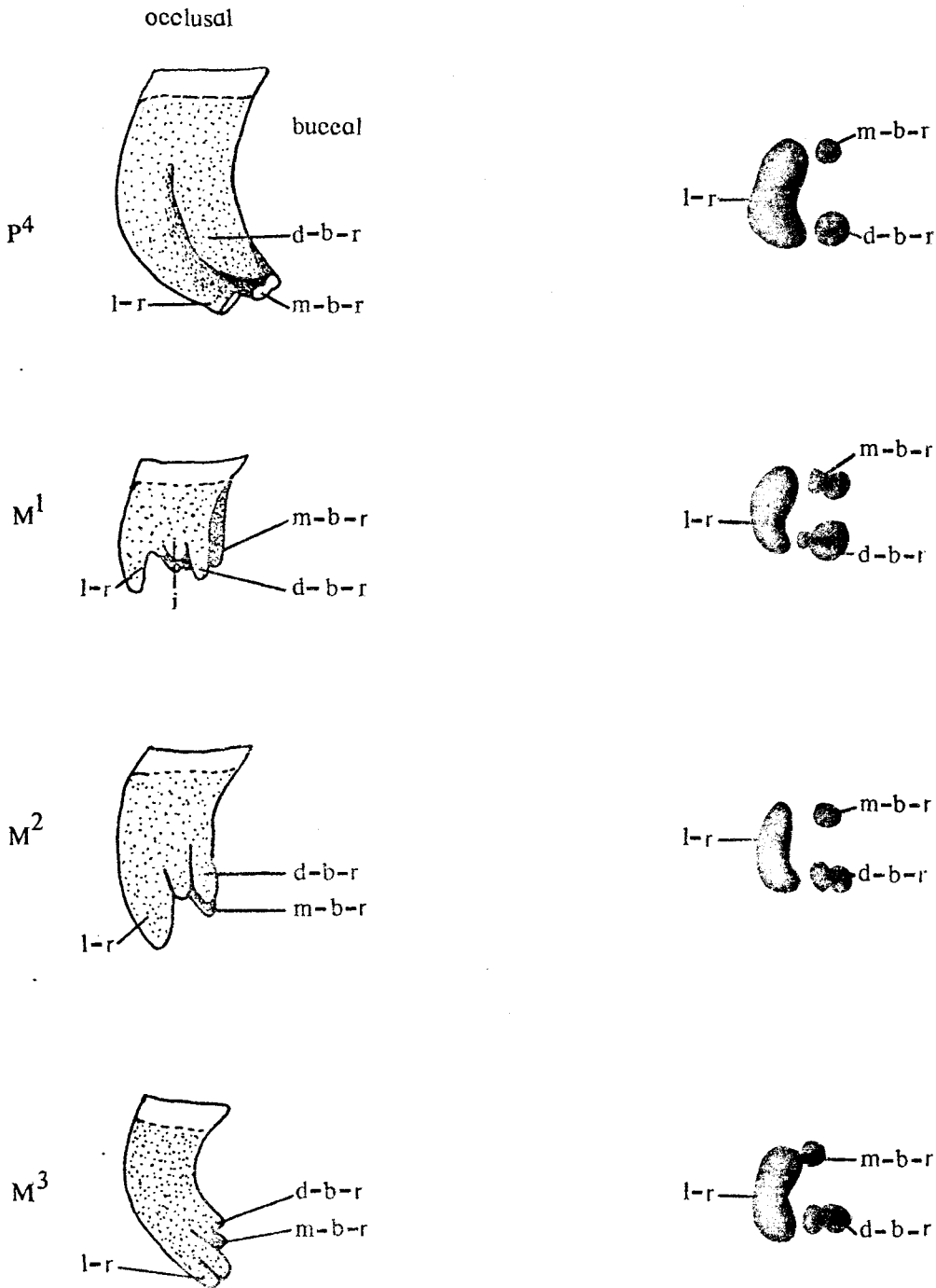


FIG. 113 a

Fig 113b

The morphology and root systems of the maxillary and mandibular deciduous premolars

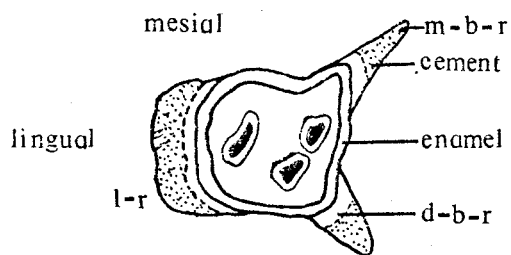
- 1 = Left deciduous maxillary premolar, occlusal view
- 2 = Left deciduous maxillary premolar, distal view
- 3 = Alveolar root patterns of deciduous maxillary premolar,
occlusal view
- 4 = Left deciduous mandibular premolar, occlusal view
- 5 = Left deciduous mandibular premolar, lingual view
- 6 = Alveolar root patterns of deciduous mandibular premolar,
occlusal view

```
m-b-r = mesio-buccal root )  
      )  
d-b-r = disto-buccal root ) maxillary dentition  
      )  
l-r   = lingual root     )
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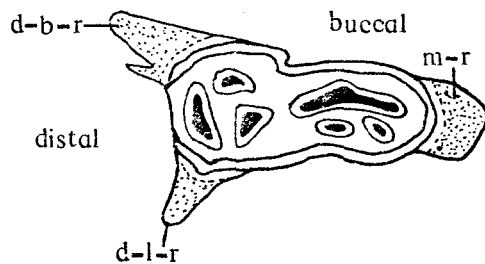
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m-r      = mesial root      )
          )
d-b-r    = disto-buccal root )
          )
d-l-r    = disto-lingual root )  mandibular dentition
          )
i         = large accessory root )
          )
ii        = smaller accessory root )
          )
iii       = smallest accessory root )

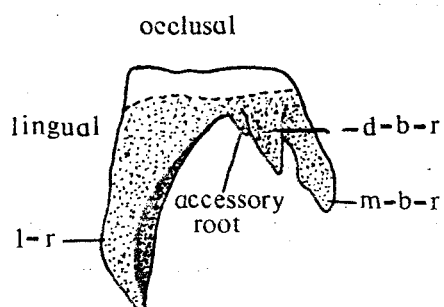
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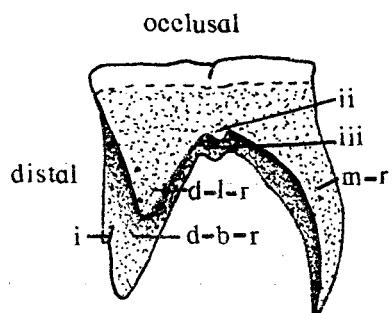
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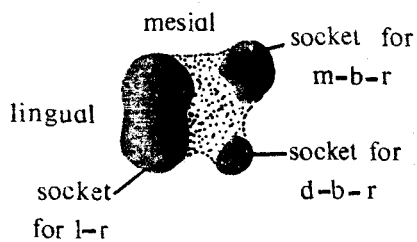
4.



2.

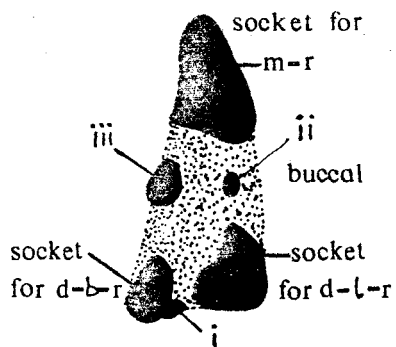


5.



3.

DP⁴



6.

DP⁴

FIG. 113b

Fig 114

The external morphology, root structure and alveolar root impressions of the mandibular teeth. Lingual views of mandibular teeth left column, root impressions, right column, with mesial surfaces of teeth towards right hand side in both cases.

Note that the mandibular teeth are much straighter than those of the maxillary and that the roots are more strongly developed. Those of the M_1 , the first tooth to erupt and hence the oldest tooth in the jaw, are better developed than those of any other tooth, followed by the M_2 and the M_3 and P_4 . The same irregular wear is apparent on the occlusal surface as is apparent on the occlusal surfaces of the maxillary teeth. The P_4 is the largest of the four teeth. All teeth illustrated are from the left mandible of TM 623 at growth stage 6.

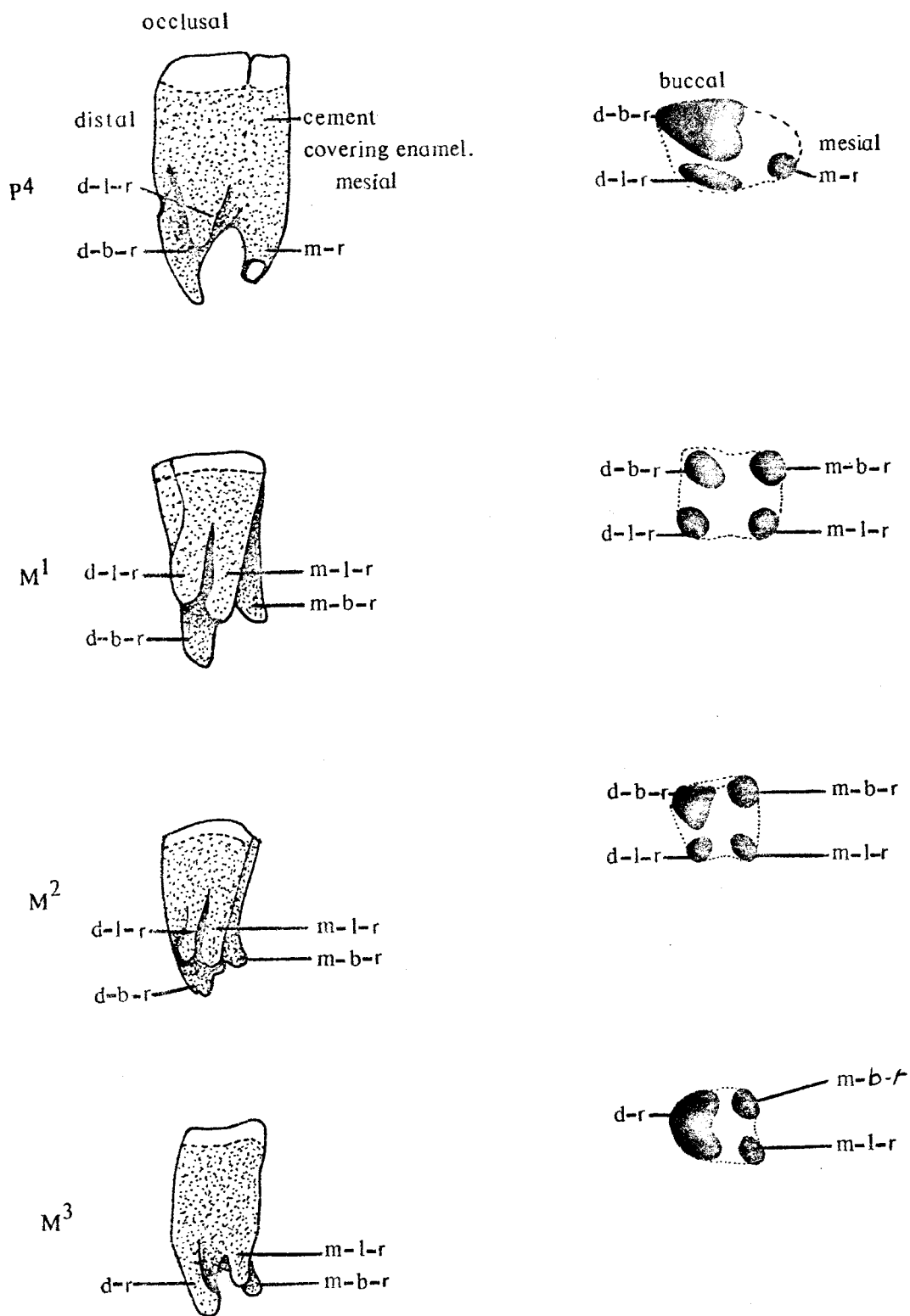


FIG.114

The main features of the porcupine dentition can be seen in Figs. 57 and 112-114; dental terminology has been discussed in section 7.1 (Figs. 58-62), and the sequence of tooth replacement in section 7.1.4 (Figs. 63-73). The method of measurement has been detailed in section 7.2.13 (Figs. 108-110) and the crown enamel patterns illustrated in Figs. 74-107. The measurements of all dental characters are tabled in Appendix VII.

The analysis of general dental parameters used as diagnostic criteria

1. Degree of divergence from the parallel of the maxillary tooth row
(Appendix VII, Table I pp.102-104, 7.2.13.1)

(Max = 132%; Min = 64%; $\bar{X}$ = 101%; SD = 15,26; N = 27)

Very variable (100% = parallel-sided dentition, 100+% = divergent from back to front). There is no evidence to suggest that the maxillary tooth rows increase or decrease their divergence with age. High and low percentages occur randomly throughout the sample, but most specimens would appear to have tooth rows which diverge from back to front. Apparently an unreliable diagnostic criterion.

2. Degree of divergence from the parallel of the mandibular tooth row
(Appendix VII Table I pp.102-104, 7.2.13.2)

(Max = 104%; Min = 79%; $\bar{X}$ = 88%; SD = 9,37; N = 6)

Less variable than the divergence of the maxillary tooth rows. Again, there is no evidence to suggest that the divergence increases or decreases with age. The mandibular tooth rows almost invariably diverge from front to back. Potentially a better diagnostic criterion than no. 1.

3. Distance between left and right maxillary premolars lingually (mm)
(Appendix VII Table I pp.102-104, 7.2.7.4)

(Max = 15,0; Min = 8,0; $\bar{X}$ = 10,81; SD = 2,04; N = 27)

Not very variable for any one growth stage. The mean increases from 8,43 at g/s 3 to a maximum of 12,18 at g/s 5, decreasing to 11,75 at g/s 6. The reason for the maximum palatal width at g/s 5 is that the permanent premolars have just erupted, increasing eruption during the g/s 6 having the effect of narrowing the palate. Potentially a good diagnostic criterion.

4. Distance between left and right M^3 's lingually (mm)

(Appendix VII. Table I pp.102-104, 7.2.7.7)

(Max = 15,1; Min = 6,9; $\bar{X}$ = 10,81; SD = 2,15; N = 27)

The mean inter- P^4 distance increases gradually from g/s 3 (7,97) to g/s 6 (11,98). Not very variable for any one g/s and hence a potentially good diagnostic criterion.

5. Distance between left and right mandibular premolars lingually (mm)

(Appendix VII, Table I pp. 102-104, 7.2.13.3)

(Max = 22,0; Min = 13,5; $\bar{X}$ = 16,10; SD = 3,15; N = 6)

Very little data available because left and right rami are seldom found in articulation. There is apparently a gradual increase in the inter- P^4 distance from g/s 3 to 6. Insufficient data available to judge its potential as a diagnostic character.

6. Distance between left and right M_3 's lingually (mm)

(Appendix VII, Table I pp. 102-104, 7.2.13.4)

Max = 27,0; Min = 13,0; $\bar{X}$ = 18,52; SD = 4,80; N = 6)

For discussion see No. 5

Before examining the detailed tooth morphology, the possible effects of sexual dimorphism on the dentition were investigated. This was not easy because in the comparative collection the sex of only three specimens (two females and one male) has been recorded, so that there was no basis for the comparison of male and female dentitions.

The local Africans at Morea Estate, Klaserie, the collection locality of PPM114 (a female) and PPM115 (a male), were able to sex the specimens on the basis of their differing quill cover. However, when the cleaned skulls only were presented, they were unable to determine by the dentition or by any other cranial feature which was male and which female. Laboratory examination of the two skulls and their dentitions showed no differences between the two which could be attributed solely to sex.

10.1 The detailed morphology of the incisors

The upper and lower incisors are structurally identical, differing only in their curvature: the upper incisor has its root apex in front of the

maxillary tooth row immediately anterior to the P⁴ whilst the root end of the lower incisor lies above and posterior to the mandibular tooth row (see X-ray, Fig. 111). In both jaws these teeth take the form of markedly curved deeply-implanted 'tusks'. The curvature and mode of implantation of the incisor within the socket (there is cement only on its lingual surface) is such that the considerable pressures, jars and jolts generated by gnawing are imparted to the front walls of the socket and are dissipated along the curve of the root, so that the soft persistent pulp at the socket base is protected from injury. The curvature thus relieves the pulp from any pressure, hence the root of the incisor never closes but remains open throughout life, enabling the tooth to grow from a persistent pulp. In this way, the considerable wear resulting from continuous gnawing is compensated for.

The detailed structure of a Hystrix upper incisor is shown in Fig. 112.

Enamel, the hardest of the materials constituting the tooth, is disposed in a single layer only on the convex labial surface and extends from the incisive edge to the growing apex. The enamel adjacent to the growing point has a finely fissured and pitted matt surface, unlike the smooth glossy appearance of the anterior enamel. Adjacent to the enamel layer lingually is a thicker layer of dentine, which is a softer material than enamel. However, the dentine which is in contact with the labial enamel is harder than that towards the lingual surface of the tooth. Cement, which is softer still than dentine, covers only the lingual surface of the incisor, leaving the enamel-covered surface of the tooth free of any attachment to the anterior wall of the socket. The latter arrangement probably serves a shock-absorbing function.

The ingestion of food depends entirely upon functionally efficient incisors. The sharpness of the incisial edge of the incisor, upon which the life of the animal depends, is maintained by the differential rates of wear of the above mentioned materials. In porcupines (and most other rodents), the continuously growing incisors must be kept to a definite length and sharpness by attrition. In Hystrix even the woody and fibrous vegetable diet may not provide resistant enough materials to ensure this attrition, explaining the necessity for the compulsive bone-collecting and gnawing behaviour of porcupines. With

a decrease in the degree of attritional gnawing the incisors may grow to extreme size, e.g.

The teeth of a beaver living in the Zoological Gardens, London, grew to such an extent that the animal could no longer open its mouth and was dying of starvation. One inch was excised, much to the animal's comfort. Overgrowth of teeth in rodents in Zoos is often due to the normal function of gnawing being in abeyance.

(Colyer 1936 p.574) i)

The process of attrition would in time expose the front end of the pulp cavity, but the formation and deposition of a laminated granular mass of secondary dentine within the anterior end of the pulp cavity continues throughout life so that exposure of the pulp seldom takes place.

In natural conditions, the incisive edge is being continuously worn away, the loss of tooth material in this region being compensated for by the formation of new tooth substance at the persistent pulp. Continuous eruption thus keeps the incisors in contact with their opposing pair. The normal length, the incisive edge and occlusal relationships are thus maintained by a delicate correlation of tooth formation, rate of eruption and rate of attrition.

Seen in transverse section (Figs. 112 and 132) the incisor is roughly triangular in shape with flattened mesial walls, enabling adjacent incisors to fit well together. The distal surface is curved.

Analysis of characteristics of the incisors used for diagnostic purposes

1. Colour of the enamel on upper and lower incisors (7.2.13.8)

Variable. The enamel in almost all cases is darker than the dentine and ranges from brownish and yellowish-orange to almost white. Some incisor enamel may be only blotched with colour. Older specimens do not have more intensely coloured enamel than juvenile individuals, in fact, some of the g/s 6 specimens had the lightest enamel. A subjective and unreliable diagnostic character.

2. The presence or absence of grooves on incisors (7.2.13.8)

Grooves of any kind were absent from all the incisors examined,

i) Colyer, Sir F. (1936). Variations and diseases of the teeth of animals
London: John Bale, Sons & Danielson Ltd. 1-750

3. Upper incisor 'width': lower incisor 'width' (%) (Appendix VII, Table VII pp.111-112, 7.2.13.9)

(Max = 115%; Min = 100%; $\bar{X}$ = 105%; SD = 4,37; N = 17)

All upper incisors proved to be broader than the lower incisors, although by a small margin. The difference in the 'widths' of the two pairs of teeth does not increase with age. Potentially a 'good' diagnostic character, except that opposing upper and lower incisors are seldom found in association in the fossil state.

4. Curvature of the upper and lower incisors (mm = r) (Appendix VII, Table VIII p.113, 7.2.13.10)

Uppers:

(Max = 22,5; Min = 12,5; $\bar{X}$ = 19,44; SD = 3,49; N = 9)

Lower:

(Max = 62,5; Min = 37,5; $\bar{X}$ = 51,36; SD = 6,92; N = 11)

The curvature of both upper and lower incisors increases gradually with age, and would appear relatively constant for any one growth stage. Note the markedly differing curvature readings for upper and lower incisors. Potentially a good diagnostic feature, especially as sections of incisor teeth are frequently encountered in the fossil record.

10.2 The detailed morphology of the premolars and molars

The detailed morphology of the premolars and molars has been discussed in broad terms in section 7.1.3 and illustrated in Fig. 60.

The premolars, having undergone a considerable degree of molari-zation, are similar in form and structure to the molar teeth except in respect of size, root system and the order of closure of the enamel folds.

As with the incisors, the cheek teeth are adapted to grinding a fibrous vegetable diet. Unlike the brachydont cheek teeth of the more primitive members of the Hystricidae (the genera Trichys, Atherurus and Thecurus, which are mainly tropical forest forms - see maps figs. 38-41 - and therefore probably have access to a softer diet), the cheek teeth of the living and some fossil forms of Hystrix and Acanthion have become high-crowned or hypsodont, probably in response to the harder

diet available in the savanna and semi-desert habitats which these more advanced members of the family occupy. As dental adaptations have ecological implications, they have been discussed in some detail below, in order that the fossil porcupine dentitions can be ecologically assessed. The adaptation to grinding a hard diet is shown in the following ways:

1. The maxillary teeth, particularly in the early stages of their functional life, are strongly curved buccally (Fig. 113 A) so that the pressures generated by grinding are dissipated along the curve of the tooth and the pulp is thus protected from direct pressure. The roots therefore remain open for a long time after eruption, enabling the considerable loss of tooth material at the grinding surface to be compensated for by continuous growth from the persistent pulps. With continued eruption, the protective effect of tooth curvature becomes lost (Figs. 113A and 133) and the papillate roots eventually close, although they never become well-differentiated from the crown or divergent. Once the roots have closed, active eruption ceases and tooth attrition proceeds uncompensated. In H. africae australis complete closure of the roots of all the maxillary teeth is not accomplished until late in growth stage 6 (the M³ and P⁴ maintain open roots for the longest period), at which stage skeletal growth has ceased, and the demand on food supplies becomes less intense. The roots of the various teeth close at different growth stages, and there is some evidence that the roots of the mandibular teeth close sooner than those of their counterparts in the upper jaw (see Table V).
2. The mandibular teeth are far less curved than the upper cheek teeth (cf. Figs. 114 and 113) but their pulps are nevertheless protected because the rootlets themselves are curved, and they thus grow from persistent pulps for a considerable period after they first cut the gums. In accordance with the lesser degree of curvature, the mandibular teeth have better developed, straighter roots which also accounts for their slightly shorter period of persistent growth.
3. In both mandibular and maxillary cheek teeth, the tooth enamel of the premolars and molars folds deeply inwards from the sides of the teeth (Figs. 61 and 62) as a form of protection - the harder the diet, the deeper, more numerous and more complex the enamel folds.

TABLE V

The order of closure of the roots of the maxillary and mandibular premolars and molars

Tooth Growth stage	Max. Premolar	Mand. Premolar	Max. M ¹	Mand. M ₁	Max. M ²	Mand. M ₂	Max. M ³	Mand. M ₃
Growth stage								
1	Open	Open	-	-	-	-	-	-
Growth stage								
2	Open- Closed	Closed?	Open	Open	-	-	-	-
Growth stage								
3	Closed	Closed	Open?	Open- Closed	Open	Open	-	-
Growth stage								
4	Closed	Closed	Closed	Closed	Open	Open	Open	Open
Growth stage								
5	Open	Closed	Closed	Closed	Open	Open	Open	Open
Growth stage								
6	Open- Closed	Closed	Closed	Closed	Closed	Closed	Open- Closed	Closed

This feature is very evident on the teeth of rodents such as the Beaver and Capybara, the former being capable of felling trees.

4. The unequal rates of wear of the enamel, dentine and cement provides a rough occlusal surface which is essential for the mastication of a fibrous vegetable diet.
5. Full dental maturity is delayed as the deciduous premolar is only replaced by the permanent premolar in adulthood.

The structure of the maxillary and mandibular teeth is adequately illustrated in Fig. 60.

The arrangement of the rootlets anchoring the maxillary and mandibular cheek teeth was examined by extracting teeth and by examining the root impressions of the alveoli of extracted or absent teeth. An evaluation of root development and arrangement frequently occurs in taxonomic discussions of the Hystricidae, but for H. africae australis at least, it would appear that root development and arrangement is variable. However, the following pattern is apparent (see Figs. 113a, b and 114):

Only the maxillary and mandibular deciduous premolars have well-developed divergent roots, although these would seem to be at least partially enamel ensheathed. The former has three main rootlets, the largest by far being the lingual rootlet which appears to be formed by the fusion of a larger mesio-lingual with a smaller disto-lingual rootlet. The smaller mesio-buccal and disto-buccal rootlets are much the same size although the latter is frequently smaller. A minor rootlet lingually placed to the disto-buccal root sometimes occurs. These roots are all fairly well developed and divergent (Fig. 113b).

The mandibular deciduous premolar also has three main divergent roots: the mesial or anterior root, the disto-buccal and disto-lingual roots. Of these, the first is the largest and the last the smallest. The large anterior root has a well-marked groove down its inner surface probably representing the area of fusion between anterior buccal and lingual rootlets. The anterior root often curves forward beyond the anterior rim of the occlusal surface. There are often two, and sometimes three small accessory rootlets, the largest of these being a lingually placed branch rootlet of the disto-lingual root. The other two are sometimes found between the mesial and disto-buccal and mesial and disto-lingual roots (see Fig. 113b).

The roots of the permanent premolars and molars, both maxillary and mandibular, are very different from those of the deciduous premolars in that they remain papillate and poorly differentiated from the crown even at an advanced stage of tooth maturity. Rather than being divergent, the roots of the permanent teeth, particularly those of the upper jaw, curl inwards towards one another, those of the maxillary dentition buccally and those of the mandible lingually.

The roots of the permanent maxillary dentition are far less developed than those of the lower jaw, being insignificant papillate structures, of which there are basically three for each tooth: a large lingual root which seems to represent fused mesio-lingual and disto-lingual rootlets, and approximately equal-sized smaller mesio-buccal and disto-buccal rootlets. All the maxillary cheek teeth have this root arrangement although there may be small 'accessory' rootlets on the M^1 and M^2 . Tooth structure and root systems are shown in Fig. 113a, b.

The permanent mandibular premolar has three roots: a large disto-buccal root which is conspicuously larger than the mesial or anterior root and the disto-lingual root. The latter is the smallest and is closely adjacent to the large disto-buccal root. There is a tendency towards fusion of the latter two roots.

The mandibular molars have a basic pattern of four rather than three rootlets. Once the deciduous premolar has been shed, the M_1 takes its place as the oldest tooth in the cheek tooth series, and the four roots of this tooth become the best-developed of the three molars. The largest is the disto-buccal rootlet, the other three (mesio-buccal, mesio-lingual and disto-lingual) being approximately equal in length and thickness, with a tendency for the latter to be the smallest; it also tends to fuse with the large disto-buccal root.

The rootlets of the M_2 are much less well developed, with the tendency towards fusion of the disto-buccal and disto-lingual rootlets being more marked; these roots are often contiguous along their entire inner margins. In the M_3 this fusion becomes complete so that there appear to be only three very poorly developed rootlets. In some cases the two mesial roots fuse or partially fuse. The structure and root arrangement of the mandibular teeth is shown in Figs. 114 and 133.

10.2.1 The analysis of maxillary dental parameters used as diagnostic criteria

1. Length of maxillary tooth row measured at a) the occlusal surface and b) the alveolar rim (7.2.13.6, 7; Appendix VII, T.III, IV pp.107,108) (mm)

(a) Max = 36,2; Min = 16,3; $\bar{X}$ = 28,09; SD = 6,17; N = 26)

(b) Max = 36,4; Min = 17,0; $\bar{X}$ = 30,48; SD = 6,00; N = 27)

In both cases there is a gradual increase of the tooth row length from growth stage 2 to growth stage 6, the measurements being fairly constant for any one growth stage. Unfortunately complete tooth rows or complete alveolar rows are rare in the fossil record; otherwise both characters are potentially good diagnostic criteria if growth stage is considered.

2. The 'height' of the maxillary teeth; hypsodonty or brachydonty (7.2.13.11, Appendix VII, Table IX pp.114, 115) (mm)

	<u>Max</u>	<u>Min</u>	<u>$\bar{X}$</u>	<u>SD</u>	<u>N</u>
p ⁴	17,5	5,8	10,55	5,57	11
M ¹	19,5	9,0	13,94	3,43	8
M ²	19,0	12,3	15,45	2,26	6
M ³	17,4	12,0	14,58	2,01	5

Insufficient data on crown height is available because in situ teeth could not be removed for measurement without damage to the specimens. However, from the analysis of Table IX it would appear that crown height is a very variable character for all the cheek teeth. This is to be expected on account of the considerable loss of tooth material from the occlusal surface. There is a general decrease in crown height with increasing age. For example the M¹, M² and M³ are all longer in the earlier growth stages than they are at g/s 6, the M¹ particularly suffering height loss - from $\bar{X}$ = 17,25mm at g/s 2 to $\bar{X}$ = 9,20mm at g/s 6. Growth stage should therefore be carefully considered when using this character.

3. The development and divergence of roots; number and situation of the roots of the maxillary teeth

This has already been discussed in the section dealing with the general morphology of the premolars and molars (10.2) and noted as being variable, although conforming to a basic pattern (see Fig. 113a,b).

4. The mesio-distal diameters or lengths of the maxillary teeth (including incisors) measured a) at the occlusal surface and b) at the alveolar rim (7.2.13.17, 21, 22; Appendix VII, Table XI A-D, H pp.118-121; Table XVII pp.138, 139)

The basic data (maxima, minima, etc.) is analysed on pp.119 and 121 (measurements taken at the occlusal surface) and p.139 (measurements taken at the alveolar rim) of the Appendix volume. Using the measurements taken at the occlusal surface (Table XIH), the incisors can be seen to increase gradually in mesiodistal diameter from $\bar{X} = 3,97\text{mm}$ at g/s 2 to $\bar{X} = 6,44\text{mm}$ at g/s 6. The deciduous premolar gradually decreases in length from $\bar{X} = 9,20\text{mm}$ at g/s 2 to $\bar{X} = 8,18\text{mm}$ at g/s 4 after which it is replaced by P^4 which measures $\bar{X} = 8,30\text{mm}$ at g/s 5, increasing to $\bar{X} = 9,56\text{mm}$ at g/s 6. The M^1 gradually increases in mean length from g/s 2 to 4, after which the expanding permanent premolar causes antero-posterior compression and it decreases in length from $\bar{X} = 8,61\text{mm}$ at g/s 4 to $\bar{X} = 7,74$ at g/s 6. The M^2 follows a similar trend, also reaching its maximum mesiodistal diameter at g/s 4. The M^3 , which erupts only at g/s 4, gradually increases to its maximum length at g/s 6, and does not experience compression by the P^4 .

The measurements taken at the alveolar rim suggest similar trends, but the compressive effect of the permanent P^4 is not as obvious as at the occlusal surface.

The mesiodistal diameter of any of the maxillary teeth thus varies considerably according to growth stage, and unless the latter is carefully considered, the character may not be a very good diagnostic criterion.

5. The bucco-lingual diameters of the maxillary teeth (including incisors) measured at a) the occlusal surface and b) the alveolar rim (7.2.13.18, 23, 24; Appendix VII, Table XI A, E-H pp.118,120,121; Table XVII pp.138, 139) (mm)

The basic data is analysed on pp.119 and 121(for a)) and on p.139(for b)) of the Appendix volume.

Using the measurements taken at the occlusal surface (Table XI H p.121) the incisors can be seen to increase gradually in labiolingual (= bucco-lingual) diameter from $\bar{X} = 4,83\text{mm}$ at g/s 2 to $\bar{X} = 6,44\text{mm}$ at g/s 6, with the most rapid growth taking place between g/s 2 and 3. The buccolingual diameter of the dp^4 follows the same trend as its MD diameter, increasing

gradually at to g/s 4, after which it is replaced by the permanent premolar, which increases rapidly in width from $\bar{X} = 5,20\text{mm}$ at g/s 5 to $\bar{X} = 8,48\text{mm}$ at g/s 6. The M^1 increases gradually up to g/s 5 when, compressed by the rapidly expanding permanent premolar in front of it, the BL diameter increases abruptly to its maximum at g/s 6. At this stage, the BL (width) of the M^1 usually exceeds the MD (length). The compressive effect of the P^4 is not usually detectable at the occlusal surfaces of the M^2 and M^3 , both these teeth tending to increase in width with age.

The measurements taken at the alveolar rim suggest similar trends, except that the compressive effect of the P^4 can be noticed on the alveolar rim of the M^2 as well as on that of the M^1 ; the 'width' of the alveolus of the former tooth exceeds its 'length', indicating anteroposterior compression.

As with the mesiodistal diameters, the buccolingual tooth diameters are rather variable with age and width of tooth may therefore not be a very reliable diagnostic criterion unless growth stage is considered.

6. The crown occlusal areas of the incisors and maxillary teeth, and the area enclosed by their alveolar rims (7.2.13.19,25,26; Appendix VII, Table XII A-E pp.122-124 and Table XVIII pp.140-141)(sq.mm)

By combining the measurements length and breadth measured at the occlusal surface it was hoped that the effects of tooth compression would be allowed for; in addition, crown occlusal areas were computed in order to obtain some idea of the grinding area provided by each tooth.

However, both the crown occlusal and alveolar rim areas proved more variable than any of the basic length or breadth measurements, as can be seen by the high standard deviations. The measurements do demonstrate the changing importance of the various cheek teeth at each successive growth stage. For example, at growth stages 2 and 3 the dp^4 is the dominant tooth, followed by the M^1 and M^2 . At growth stage 4, prior to its replacement by the permanent premolar at g/s 5, the dp^4 has diminished in size, the M^1 replacing it as the dominant tooth. The M^2 follows the M^1 in size, whilst the newly-erupted M^3 is the smallest tooth in the series. At growth stage 5, pressure from the erupting permanent premolar compresses the M^1 and the M^2 becomes the largest tooth in the row. At full dental maturity (g/s 6) the permanent premolar has become the dominant tooth ($\bar{X} = 81,29$ sq.mm), followed by the M^2 ($\bar{X} = 73,52$ sq.mm) and the M^3 ($\bar{X} = 68,56$ sq.mm). The

much compressed M^1 ($\bar{X} = 67,72$ sq.mm) is the smallest tooth in the row. The picture obtained from the analysis of the alveolar rim areas shows similar trends but is not as clear, probably on account of the asymmetrical barrel-like shape of the maxillary teeth.

From the above it can be seen that crown occlusal area and alveolar rim areas are highly variable characters, and should be distrusted as diagnostic criteria, even if growth stage is considered.

7. The crown shape indices of the maxillary teeth measured at a) the occlusal surface and b) at the alveolar rim (7.2.13.27,28; Appendix VII Table XIII A-E pp.125-127; Table XIX pp.142-143) (ratio)

The crown shape index (the ratio of tooth breadth to tooth length x 100) was computed in order to provide an alternative measurement to mesiodistal and buccolingual diameter measurements, both of which proved to vary with growth stage and be influenced by the compressive effect of the large permanent premolar. The index also provides a numerical expression of the tooth shape of the various teeth in the maxillary series - ratios approaching 100 indicating square teeth and low ratios indicating long, narrow teeth. Tooth shape is a frequently used diagnostic criterion.

The crown shape index measurements proved to be more variable than either the length or breadth measurements, with standard deviations in excess of 5,98. They did, however, provide an excellent picture of tooth shape. The incisors (from the measurements taken at the occlusal surface) invariably give readings in excess of 100 - that is, their buccolingual diameter (width) exceeds their mesiodistal diameter (length, or the 'width' of most authors). The only other case where this occurs is in the M^1 at g/s 6. With all the other teeth (see Volume II p.127) and the M^1 from g/s 2 to 5, there is a gradual trend towards sub-equal tooth diameter, which results in a cylindrical rather than rectangular tooth outline in the later growth stages. Sub-equal MD and BL diameters and cylindrical tooth outline, both frequently cited as diagnostic criteria, would therefore appear to be a function of dental maturity.

Both ratios are apparently rather variable and therefore of limited use as diagnostic criteria, unless growth stage information is also available.

10.2.2 The analysis of characters of the mandibular premolar and molar series used as diagnostic criteria

1. The length of the mandibular cheek tooth series measured at a) the occlusal surface and b) at the alveolar rim (7.2.13.6,7; Appendix VII Table V p.109, Table VI p.110) (mm)

(a) Max = 37,40mm; Min = 32,50mm; $\bar{X}$ = 34,93mm; SD = 1,51; N = 10)

(b) Max = 39,30mm; Min = 16,50mm; $\bar{X}$ = 32,57mm; SD = 6,62; N = 30)

In the case of the tooth row length measured at the occlusal surface (available for growth stages 5 and 6 only) the length appeared to be fairly constant, not increasing or decreasing significantly with age. Measured at the alveolar rim, the tooth row length could be seen to increase gradually up to its maximum length in the early part of g/s 6, after which there was a slight decrease, due to shrinkage caused by bone resorption after the abscission of one or more teeth.

Complete tooth or alveolar rows are rare in the fossil record, otherwise both characters are potentially reasonable diagnostic criteria, if growth stage is considered.

2. The 'height' of the mandibular teeth; hypsodonty or brachydonty (7.2.13.11; Appendix VII Table X pp.116-117) (mm)

Insufficient data on the crown heights of the mandibular teeth is available, because in situ teeth could not be removed for measurement without damage to the specimens. However, from the analysis of Table X (p.117, Appendix volume) it would appear that crown height is very variable, tending to decrease with age, on account of the ever increasing degree of wear. The mandibular molars are all shorter at g/s 6 than they are at g/s 2 or 3. The deciduous premolar decreases in height from $\bar{X}$ = 7,36mm at g/s 3 to $\bar{X}$ = 4,70mm at g/s 4, after which it is shed. The replacement premolar decreases from $\bar{X}$ = 17,40mm at g/s 5 to $\bar{X}$ = 14,50mm at g/s 6. Growth stage should therefore be carefully considered when using this rather variable character.

3. The development and divergence of roots; number and situation of roots of the mandibular teeth

This has already been discussed in the section dealing with the general morphology of the premolars and molars (10.2) and noted as being variable, especially in respect of root fusion and the position of accessory rootlets, although the root system does conform to a basic pattern in each tooth.

4. The mesiodistal diameters or length of the individual teeth of the mandibular dentition measured at a) the occlusal surface and b) at the alveolar rim (7.2.13.17,29,30; Appendix VII Table XIV A-D,H pp.128-131; Table XX pp.144,145)

The basic data is analysed on pp.129 and 131 for a) and on p.145 for b) of the Appendix volume.

Similar trends to the ones encountered in the maxillary dentition were found in the mandibular teeth. Using the measurements taken at the occlusal surface (Table XIVH p.131) the incisors are shown to increase in MD from $\bar{X} = 3,83\text{mm}$ at g/s 2 to $\bar{X} = 5,98\text{mm}$ at g/s 6. The deciduous premolars decrease in size from $\bar{X} = 9,55\text{mm}$ at g/s 2 to $\bar{X} = 8,91\text{mm}$ at g/s 4. At g/s 5 they are replaced by the permanent premolar with a mean MD of only 7,75mm; this rapidly increases to the maximum mean of 9,70mm at g/s 6. The M_1 , as in the case of the maxillary first molar, first increases in length (up to g/s 4) after which the expanding permanent premolar causes antero-posterior compression and the MD decreases again to reach its minimum at g/s 6. The M_2 increases in MD diameter up to g/s 4, suffers some effects of compression at g/s 5 which is overcome by continued growth by the time g/s 6 is reached. The M_3 gradually increases in length.

The measurements taken at the alveolar rim show similar trends, but not so clearly, and the compressive effect of the P_4 is more noticeable on the M_2 .

The mesiodistal diameter of any of the mandibular teeth thus varies with age, and if it is to be used as a diagnostic criterion growth stage must be taken into consideration.

5. The buccolingual diameters of the mandibular teeth (including the incisors) measured at a) the occlusal surface and b) at the alveolar rim (7.2.13.18,31,32; Appendix VII Table XIV A,E-H,pp.128,130,131; Table XX pp.144,145)

- Using the measurements taken at the occlusal surface (Table XIV H p.131) the EL diameters of all the mandibular teeth can be seen to increase gradually with age. The compressive effect of the P_4 is not as marked as in the maxillary dentition, and in no case does the mean BL (width) exceed the mean MD (length) as it does in the maxillary dentition. The measurements for any one growth stage are not excessively variable, and if growth stage is considered, both characters may make reasonable diagnostic criteria.

6. The crown occlusal areas of the incisors and mandibular teeth, and the area enclosed by their alveolar rims (7.2.13.19,33,34; Appendix VII Table XV A-E pp.132-134; Table XXI pp.146, 147)

As in the case of the maxillary dentition, crown occlusal areas were calculated in order to provide an alternative measurement for mesiodistal diameter (length) and buccolingual diameter, which, taken in isolation, seemed to be rather variable, particularly the former. By combining length and breadth, it was hoped that the compressive effect of the P_4 on the M_1 and M_2 would be allowed for. Furthermore, crown area provides a useful means of assessing the relative importance of the various teeth as grinders at each growth stage.

However, both the crown occlusal area and alveolar rim area computations proved more variable than either the MD or BL measurements, as can be seen by comparing the standard deviations. The measurements do, however, demonstrate the changing importance of the occlusal surfaces of the various mandibular teeth with increasing age, for example (using Table XVE p.134):

Growth stage 2: dp_4 dominant, newly-erupted M_1 the only other cheek tooth present

Growth stage 3: M_1 dominant, although the dp_4 has increased in size. The newly-erupted M_3 has the smallest occlusal area

Growth stage 4: M_1 and M_2 approximately equal in occlusal area at this growth stage with that of the latter being slightly larger. The area of the dp_4 has diminished from what it was at growth stage 3, as this tooth has become excessively worn and is about to be shed. The newly-erupted M_3 has the smallest occlusal area.

Growth stage 5: The occlusal area of the newly-erupted permanent premolar is the least significant. However, the side walls of this, the largest tooth in the series, causes compression to the adjacent M_1 with eruption (actually causing loss of tooth material in the mandibular dentition) so that the occlusal area of the latter decreases dramatically from what it was at the previous growth stage, leaving M_2 as the dominant tooth. Apart from the premolar, the M_3 has the smallest occlusal surface.

Growth stage 6: The expanding permanent premolar rapidly acquires the largest grinding surface, followed by the M_2 and M_3 . The much-compressed M_1 has the smallest surface.

The measurements taken at the alveolar surface show similar trends although not as clearly.

Crown occlusal area and alveolar area are both highly variable characters, and should be distrusted as diagnostic criteria, even if growth stage is considered.

7. The crown shape indices of the mandibular teeth measured at a) the occlusal surface and b) at the alveolar rim (7.2.13.20,35,36,; Appendix VII Table XVI pp.135-137; Table XXII pp.148, 149)

With all the mandibular teeth, the crown shape index was seen to increase with increasing age (indices of 100 indicating mesiodistal and buccolingual diameters of equal length). Cylindrical tooth shape and subequal tooth diameters, two characters frequently cited in the description of new species, is demonstrably only the effect of age and prolonged wear.

10.3 The crown enamel patterns of the maxillary and mandibular teeth

Apart from basic tooth measurements (length, breadth and height), the configuration of the crown enamel pattern is the most frequently-used character in the description of new species of porcupines, particularly fossil forms. However, it is apparent from the literature available that there is no clarity on the diagnostic significance of the crown enamel pattern, i.e. whether species can legitimately be separated by means of their crown enamel patterns or not.

For this reason an attempt has been made to examine the variability of the crown enamel pattern in H. africae australis to establish whether any definable pattern exists, and by comparing the range of patterns occurring with those of H. cristata and H. indica, to determine whether the crown enamel pattern has diagnostic validity or not. The result of this investigation is reported in section 12.4, while the C.E.P. of H. africae australis is described below.

If porcupine dentitions were freely available the easiest manner of studying the C.E.P. would be to embed and serially section individual

teeth in a simulation of natural wear. Professor T. Jones of the University of the Witwatersrand Dental School agreed to arrange for the sectioning of a series of teeth on the author's behalf, but it was found (in the case of all five specimens submitted) that the teeth disintegrated in the course of the preparation procedure (a vacuum-impregnation, dyeing and plastic embedding technique). This method, even if successful, would have had several disadvantages, the most disadvantageous being the loss of tooth material due to the thickness and vibration of the sectioning blade. This would mean that successive sections would represent too great an interval of 'wear' and the developmental history of the enamel folds would be difficult to follow. Furthermore, natural wear at the occlusal surface does not occur strictly at right angles to the long axis of the tooth; it is frequently oblique, the degree and direction of obliquity varying from specimen to specimen. Wear may occur irregularly over the surface of any one tooth, for example as on the occlusal surfaces shown in the distal views of the maxillary teeth, Figure 113 A. The angle at which wear proceeds also differs from tooth to tooth. It would be difficult if not impossible to set a sectioning blade to simulate natural wear and thus to obtain naturally-occurring C.E.P.s. The method was thus not pursued.

Destructive serial grinding was not considered because of the scarcity and difficulty of obtaining material.

Instead, the comparative material was arranged in order of increasing dental maturity, and the crown enamel patterns of each tooth type examined in sequence. To make examination easier, each tooth row (left and right) was photographed and printed to a magnification of x 4. Right tooth rows were printed as lefts to facilitate comparison. For each tooth type the photographs were arranged in order of increasing crown pattern maturity, the order being slightly different for each tooth type, and a series of pattern tracings made. This procedure was followed for both maxillary and mandibular teeth and the results are shown in Figs. 74 to 107.

In this way the maturation and variability of the C.E.P. with increasing amounts of natural wear was studied, and is discussed for each tooth below.

10.3.1 The crown enamel patterns of the maxillary teeth
(Figs. 74 to 90)

As mentioned in section 7.1.3 which deals with dental nomenclature, the basic pattern of enamel folds in the maxillary teeth is a single deep centrally-placed lingual fold or hypoflexus and three to four (usually four) external or buccal enamel folds - the para-, meso-, meta- and entoflexi. The conformation and order of closure of these flexi differs according to tooth type, hence the basic pattern, order of closure and range of variation for each tooth has been discussed separately below:

1. The dp⁴ (Figs. 74, 75, 76A, 76B)ⁱ⁾

Basic pattern of one lingual and four buccal folds, no mesial or distal folds. Order of closure of folds and the resultant C.E.P. is highly variable.

C.E.P. at growth stage 2 (Fig. 74)

Typical pattern Fig. 74 tooth 2. Five basic folds apparent, with entoflexus (d) tending to close first (tooth 4) followed by the paraflexus (a) and hypoflexus (e). Hypoflexus and paraflexus confluent in very early stage of wear (tooth 1); mesoflexus (b), metaflexus (c) and entoflexus (d) confluent internally almost throughout this growth stage, the latter having a deep posteriorly orientated loop which embraces the actual or incipient entofossette (D) (tooth 4).

C.E.P. at growth stage 3 (Fig. 75)

Pattern highly variable, most typical is Fig. 75 tooth 3. In the early stages the meso-(b), meta-(c) and hypoflexi (e) may still be apparent as folds (teeth 1-3) but the ento- and paraflexi are almost always closed to form the entofossette (D) and parafossette (A) respectively. The meso- and metaflexi (b and c) are usually confluent internally. The entofossette (D) becomes smaller (tooth 1 through 4) and may not be present at all (teeth 5 to 7). Excessively worn growth stage 3 premolars (unusual at this growth stage and probably due to very 'hard' diet) may show only three fossettes; a parafossette (A), hypofossette (E) and a large fossette probably representing the fused

i) The explanations to the abbreviations (a), (b) etc. can be found in the captions to Figs. 75 and 92 and in the Glossary, Appendix XII.

mesofossette (B, anterior portion) and metafossette (C, posterior portion). The entofossette (D) is absent (teeth 6 and 7).

C.E.P. at growth stage 4 (Figs. 76 A and B)

Typical pattern Fig. 76A tooth 6. The mature g/s 4 enamel pattern (i.e. prior to shedding) consists of four fossettes, para-(A), meso-(B), meta-(C) and hypofossettes (E) (Fig. 76A tooth 6 and Fig. 76B teeth 1-6). Some patterns at early g/s 4 are similar to those at g/s 3.

2. The P⁴ (Figs. 77 and 78)

C.E.P. at growth stage 5 (Fig. 77)

The newly-erupted permanent premolar has a basic pattern of one internal (hypoflexus (e)) and three external enamel folds, the para-(a), meso-(b) and metaflexi (c). The fourth fold (the entoflexus) appears to be 'closed' externally, i.e. buccally, even in the unworn state (D). Typical pattern Fig. 77 tooth 3.

C.E.P. at growth stage 6 (Fig. 78)

Typical mature crown enamel pattern of five (Fig. 78 tooth 5) or six (tooth 8) fossettes: para-, meso-, meta-(sometimes divided into two) and entofossettes buccally (A-D) and hypofossette lingually. Mature C.E.P. very variable - see teeth nos. 9-12.

3. The M¹ (Figs. 79-83)

The M¹ has a basic pattern of one internal (lingual) and four external (buccal) enamel folds, but the order of closure of these folds and the resultant patterns on worn teeth are highly variable.

C.E.P. at growth stage 2 (Fig. 79)

Basic pattern of five folds clearly visible, i.e. para-(a), meso-(b), meta-(c), ento-(d) and hypoflexids (e) all confluent internally. Para-flexus (a) closes earlier than the other flexi to form parafossette (A) (Fig. 79 teeth nos. 2, 5), followed by the entoflexus (d) to form entofossette (D) (tooth 5). Tooth 4 has typical g/s 2 crown enamel pattern.

C.E.P. at growth stage 3 (Fig. 80)

Typical C.E.P.s of this growth stage are seen in Fig. 80 (teeth nos. 5, 6 and 8). Although the wear patterns are highly variable their derivation from the five basic enamel folds apparent at the previous growth stage is obvious. During the course of this g/s, the incipient parafossette (A), mesoflexus (b) and hypoflexus (e), although

remaining confluent with each other internally, become separated from the meta-(c) and incipient entofossette (D) (teeth nos. 4 and 5). At a later stage, the internal connection between the mesoflexus (b) and the incipient parafofsette (A) and hypoflexus (e) is severed, separating the former from the two latter (tooth 6 onwards). The mesoflexus then becomes internally contiguous with the metaflexus and incipient entofossette. At a still later stage, the internal connection between the incipient parafofsette and hypoflexus is lost, leaving the parafofsette (A) completely isolated (teeth nos. 7 and 8). Tooth no. 9 is unusual in that the metaflexus has already closed while the hypoflexus and incipient parafofsette are still confluent, probably due to an unusually excessive amount of wear along the buccal part of the occlusal surface.

C.E.P. at growth stages 4 and 5 (Figs. 81, 82)

Some of the crown enamel patterns shown at early g/s 4 (Fig. 81 teeth 1-4) might more appropriately belong in g/s 3; however, the state of tooth eruption of the specimens concerned dictates that they be considered as growth stage 4. The C.E.P.s of growth stages 4 and 5 are indistinguishable. The next event in the developmental history of the C.E.P. from g/s 3 is that the entofossette (D) becomes completely isolated (Fig. 81 tooth 5). The internal connection between mesoflexus and metaflexus is then severed (tooth 6) after which these two folds close externally to form mesofossette and metafofsette respectively (tooth 8); evidence available suggests that the mesoflexus closes before the metaflexus (tooth 10). The hypoflexus closes shortly afterwards (tooth 10 Fig. 81 is an exception). The mature g/s 4 or 5 tooth thus shows a pattern of five fossettes, derived from five enamel folds visible on a g/s 2 M¹ (Fig. 81 tooth 10, Fig. 82 tooth 5).

C.E.P. at growth stage 6 (Fig. 83)

During this growth stage the entofossette (D) is lost (Fig. 83 tooth 1) and the metafofsette (C) splits into two (teeth nos. 2 and 3). The parafofsette (A) may also divide (teeth nos. 4, 8), one of the pair becoming lost. Typical C.E.P.s are teeth nos. 2, 4 and 5.

4. The M² (Figs. 84-87)

As in the M¹, there is a basic pattern of one lingual and four buccal enamel folds.

The C.E.P. at growth stage 3 (Fig. 84)

This is very similar to that of newly-erupted M^1 at g/s 2. Basic pattern of five folds clearly visible, all flexi (or incipient fossettes) confluent internally. The paraflexus is the first to close externally (buccally) to form an incipient parafossette, followed by the entoflexus. Typical patterns are teeth nos. 3 and 7.

The C.E.P. at growth stages 4 and 5 (Figs. 85A, 85B and 86)

The C.E.P.s at growth stages 4 and 5 are frequently indistinguishable. During the course of this growth stage the incipient parafossette (A), the mesoflexus (b) and the hypoflexus (e), although remaining confluent with one another, become separated from the metaflexus (c) and incipient entofossette (D), which in turn are confluent with one another (Fig. 85A tooth 2). The connection between the mesoflexus (b) and the incipient parafossette (A) and hypoflexus (e) is then severed, the latter two remaining confluent (Fig. 85A tooth 3). The incipient parafossette (A) then becomes separated from the hypoflexus (e) and the mesoflexus (b) may re-establish a connection with the meta- and entoflexi (Fig. 85A tooth 4). This connection is later lost (Fig. 85A tooth 6, Fig 85B tooth 2 onwards). The mesoflexus then closes to form the mesofossette (B) (Fig. 85B tooth 5 onwards). The incipient entofossette (D) then loses its internal connection with the metaflexus (c) and becomes isolated (Fig. 85B tooth 7). Finally, the metaflexus closes (Fig. 86 tooth 5). Tooth 6, Fig. 86 is aberrant in that the externally closed meso-, meta- and entofossettes are confluent internally.

The C.E.P. at growth stage 6 (Fig. 87)

The typical mature crown enamel pattern of the M^2 consists of five fossettes, derived from the five enamel folds apparent at growth stage 3 (Fig. 87 tooth 3). The metafossette may divide into two, giving a pattern of six fossettes, as in tooth 2. The entofossette (D) is lost during the course of this growth stage (teeth nos. 4, 6 and 7), leaving four fossettes. The parafossette may also divide to form two separate fossettes (tooth 6).

5. The M^3 (Figs. 88, 89 and 90)

As in M^1 and M^2 , there is a basic pattern of one internal and four external (buccal) enamel folds. The same crown enamel patterns and

process of closure occurring in the M^1 and M^2 occurs also with the M^3 but at different growth stages. Some growth stage 3 C.E.P.s show the basic pattern of four folds, e.g. Fig. 88 tooth 5, but the entoflexus (d) followed by the paraflexus (a) tend to close externally to form incipient ento- and parafossettes respectively (Fig. 88 teeth nos. 6 and 7). The order of closure of the folds is the same as in the M^1 and M^2 and is thus not repeated here. A typical mature M^3 C.E.P. consists of five or six (if the metafossette (C) divides into two) fossettes (Fig. 90 teeth nos. 4 and 5). As in the M^1 and M^2 , the entofossette (D) is lost, and the parafossette (A) may or may not divide. The mature pattern is, however, highly variable with regard to the various permutations of internal connections between the fossettes (Fig. 90, teeth nos. 7-10).

10.3.2 The crown enamel patterns of the mandibular teeth (Figs. 91 to 107)

There is a basic pattern of one approximately centrally-placed and posteriorly orientated buccal (external) enamel fold or hypoflexid and three or four evenly spaced lingual (internal) enamel folds or flexids. The anteriormost of the lingual flexids (the paraflexid, a,) may sometimes arise from the mesial surface, leaving three lingual flexids, the mesoflexid (b), the metaflexid (c) and the entoflexid (d). It is not actually apparent from the material available whether the fold that is responsible for the parafossettids (labelled A in all the diagrams) is a rapidly closing mesial flexid, (as suggested by the C.E.P. of teeth nos. 3 and 5, Fig. 91) or whether the fossettids marked A and designated 'parafossettids' are actually derived from an anterior part of the mesoflexid (b), as suggested by tooth no. 3, Fig. 96, in which case they should be labelled 'B' and be considered as one of two mesofossettids. The study of a larger sample may resolve this problem.

The paraflexid, if such exists, is directed posteriorly (Fig. 91 tooth no. 3), while the mesoflexid is directed inwards, crossing the tooth transversely (Fig. 91 tooth no. 5). If the paraflexid (a) is absent, the mesoflexid (b) takes an anterior direction (Fig. 96 tooth no. 3). The metaflexid (c) is the deepest enamel fold, running first transversely and then anteriorly (Fig. 98A tooth no. 9). The

entoflexid (d) is transversely or slightly posteriorly orientated (Fig. 91 tooth no. 5) while the hypoflexid (e) has a decidedly posterior trend (Fig. 92 tooth no. 5).

1. The crown enamel pattern of the dp_4 (Figs. 91 to 93)

There appears to be a basic pattern of one external and at least three internal enamel folds, the hypo-, meso-, meta- and entoflexids respectively (Fig. 91 tooth no. 5). It is not clear whether the paraflexid (a) is absent, the parafosettids (A) being derived from an anteriorly projecting loop of the mesoflexid (b) and thus in reality a second mesofossettids, or whether a mesially placed paraflexus, as suggested by Fig. 91 tooth no. 3, is present, its closure giving rise to the parafosettids (A). The paraflexid (a) and mesoflexid (b) are the first of the flexids to become closed externally, the latter rapidly forming an isolated mesofossettids (Fig. 91 tooth no. 4). The incipient parafosettids (A) may be connected with the anterior loop of the metaflexid (c), which in turn is internally contiguous with the ento- (d) and hypoflexids (e) (Fig. 91 tooth no. 4).

The parafosettids (A) then becomes isolated, the anteriorly-orientated loop of the metaflexid (c) also becomes isolated to form a metafosettids (C), and the internal connections between the mesoflexid, hypoflexid and entoflexid are lost. The entofossettids (D) closes externally, leaving the hypoflexid (e) and transverse section of the metaflexid (c) as the only enamel folds still open to the exterior (Fig. 92 teeth nos. 1 and 2).

The metaflexid and finally the hypoflexid close to form fossettids (Fig. 92 teeth nos. 3 and 4). The mesofossettids (B) followed by the parafosettids (A) are then lost, leaving a mature crown enamel pattern of four fossettids - two metafosettids (C), an entofossettids (D) and a hypofossettids (E) (Fig. 92 tooth no. 6). The two metafosettids may again become confluent (Fig. 92 tooth no. 7). Of these fossettids the hypofossettids (E) is the largest and most persistent (Fig. 93 tooth no. 10). Typical g/s 2 C.E.P. = Fig. 91 tooth no. 5; typical g/s 3 C.E.P. = Fig. 92 tooth no. 3; typical g/s 4 C.E.P. = Fig. 93 tooth no. 7.

2. The crown enamel pattern of the P_4

The same basic pattern of enamel folds occurring in the deciduous premolars is apparent in the newly-erupted growth stage 5 permanent

premolars. The order of closure of folds also appears to be similar. Typical mature crown enamel patterns are Fig. 95 teeth nos. 2 and 5.

3. The crown enamel pattern of the M_1 (Figs. 96 to 100)

The slightly worn growth stage 2 first molar shows a crown enamel pattern of one centrally placed external (buccal) enamel flexid (hypoflexid) and three more or less evenly spaced lingual flexids, the meso-, meta- and entoflexids (b, c and d respectively). It is not clear whether the parafoissettid (A of Fig. 96 tooth no. 3) has been derived from a rapidly-closing paraflexid entering the tooth from the mesial surface or whether it is derived from an anterior portion of the mesoflexid (b).

The order of closure of these folds and hence the crown enamel patterns resulting is highly variable, as can be seen from an examination of Figs. 97 to 100. The most common sequence of events seems to be as follows:

The C.E.P. at growth stages 2, 3 and 4

(Figs. 96, 97, 98A and 98B)

The incipient parafoissettid (A), the mesoflexid (b), metaflexid (c), entoflexid (d) and hypoflexid (e) are all initially confluent internally (Fig. 96 teeth nos. 3, 4, Fig. 97 tooth no. 1). The incipient parafoissettid (A) may then become completely isolated (Fig. 97 teeth nos. 2, 4-7) and the mesoflexid and entoflexid close lingually (i.e. externally, Fig. 97 teeth nos. 2, 3). The incipient mesofossettid (B) and entofossettid (D) thus formed may be confluent with the anterior loop of the metaflexid (c) (Fig. 97 tooth no. 3) and with the hypoflexid (e) (Fig. 97 tooth no. 2) respectively. The connection between the contiguous incipient entoflexid and hypoflexid and the remaining folds and fossettids may be lost (Fig. 97 teeth nos. 2, 3, 5-6), but this is highly variable; the hypoflexid and transverse portion of the metaflexid are frequently connected (Fig. 97 teeth nos. 4, 7; Fig. 98A teeth 1-5).

The anteriorly directed portion of the metaflexid then becomes separated from the transverse loop, although the anterior loop may still be confluent with the incipient mesofossettid (B) (Fig. 97 tooth 5). The incipient entofossettid eventually loses its connection with the hypoflexid and becomes completely isolated (Fig. 97 tooth no. 6). The para- and mesofossettids (A and B) and less frequently

the anterior and transverse mesofossettids, may again establish contact (Fig. 98A teeth nos. 7, 8 and 9). The hypoflexid (e) is the last to close (Fig. 98B tooth no. 5).

A mature growth stage 4 C.E.P. therefore consists of five or six fossettids: a parafosettoid and mesofossettoid, anterior and transverse metafosettoids, an entofossettoid and a hypofossettoid (as in tooth 4, Fig. 98B). The para- and mesofossettids may be combined (as in tooth 5, Fig. 98B), leaving five fossettids.

The C.E.P. at growth stages 5 and 6

(Figs. 99 and 100)

The mature C.E.P. is as in late growth stage 4 described above (see tooth 5 Fig. 99, which has a typical C.E.P.). During the course of g/s 6 the para- and mesofossettids (A and B) tend to separate again, and B, followed by A, tends to disappear (Fig. 100 teeth nos. 3 and 5). Very old first molars therefore have only four fossettids - an anterior and transverse meta-fossettoid, an ento- and a hypofossettoid, (Fig. 100 tooth no. 5).

4. The crown enamel pattern of the M_2 (Figs. 101 to 104)

The basic pattern of enamel folds visible on the occlusal surface of a slightly worn growth stage 3 second molar are identical to those of the growth stage 2 first molars described above - compare Fig. 101 tooth 4 (g/s 3 M_2) with Fig. 96 tooth 3 (g/s 2 M_1).

As is the case with the M_1 , the order of closure of the folds and hence the resultant C.E.P.s is highly variable, and very similar to that of the M_1 and proceeds as follows:

The C.E.P. at growth stages 3, 4 and 5

(Figs. 101, 102 and 103)

Growth stage 3 second molars show the basic pattern of enamel folds, of which only the paraflexid has closed externally (mesially) to form an incipient parafosettoid (A). All folds confluent internally. Typical tooth pattern Fig. 101 tooth 4.

During growth stage 4 the entoflexid (d) followed by the mesoflexid (b) close externally (i.e. buccally) to form an incipient entofossettoid (D) and mesofossettoid (B) respectively (Fig. 102 teeth nos. 3 and 5). At this stage the incipient fossettids and remaining open flexids are still all confluent internally (tooth 5).

The anterior part of the metaflexid (c) then becomes separated from the transverse loop to form the anterior metafossettid (C), the transverse portion of the metaflexid (c) remaining confluent with the incipient para-(A) and mesofossettids (B) (Fig. 102 tooth 6). The incipient entofossettid becomes separated from the posterior-projecting hypoflexid, and the connection between the latter and the transverse loop of the metaflexid is lost (tooth 6). The transverse loop then separates from the still confluent incipient para- and mesofossettids (Fig. 102 tooth 7). This and Fig. 103 tooth no. 6 show the mature crown enamel pattern.

The C.E.P. at growth stage 6 (Fig. 104)

During the course of growth stage 6 the incipient para- and mesofossettids separate (Fig. 104 teeth nos. 2 and 3), although they may remain confluent (tooth 4), and the metaflexid, followed by the hypoflexid, close. The anterior metafossettid (C) becomes confluent with the mesofossettid (B) (tooth 5) and the parafossettid (A) may be lost (tooth 6).

5. The crown enamel pattern of the M_3 (Figs. 105, 106 and 107)

The basic pattern of folds and order of closure is similar to that occurring in the M_2 . The mature C.E.P. of the M_3 (Fig. 107 teeth nos. 4 and 5) is identical to that of the M_2 (Fig. 104 teeth nos. 4, 5).

11. SUMMARY - THE VARIABILITY OF THE CRANIAL, MANDIBULAR AND DENTAL CHARACTERS OF HYSTRIX AFRICAFAUSTRALIS

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is
imp
yes

Low sample standard deviations are taken to indicate a low degree of variability, and parameters giving such low sample standard deviations are, on the whole, also considered as being more likely to prove 'good' diagnostic criteria for the separation of species. However, the number of observations (N) was seen to affect the SD value in some cases, low N numbers sometimes being responsible for low SD values, particularly if the observations were made on specimens at the same stage of growth. On the other hand, a low number of observations made on specimens at different stages of growth sometimes produced a high SD, particularly if the magnitude of the parameter measured was dependent on age and development. There appears to be no simple means of directly comparing the SD values of different parameters with different N numbers without involving the use of mathematical procedures. As this is beyond the scope of the present work the characters have simply been listed in order of ascending SD value, with this and the N number indicated in brackets following each character. Parameters marked with an asterisk are those which have low SD values for measurements taken at any particular growth stage although the sample SD may be high.

Taking into consideration all cranial, mandibular and dental parameters measured, the basic measurements of the dentition, that is, mesiodistal (length) and buccolingual (breadth) diameters proved to be the characters with the lowest sample standard deviations and hence the lowest degree of variability. With the exception of the buccolingual diameters of the M^1 , M^2 and M^3 measured at the occlusal surface and the mesiodistal diameters of the dp^4/P^4 measured at the occlusal surface and alveolar rim, all the sample SD values for the basic tooth measurements, (i.e. for 35 of the 40 basic values computed) fall between 0,05 and 0,99. The five exceptions fall between 1,03 and 1,22.

The explanation for the slightly higher variability of the buccolingual measurements of the maxillary molars lies in the compression of these teeth by the large expanding premolar, which has the effect of increasing the BL diameter quite markedly with increasing age. The compressive effect of the premolar as evidenced by the BL diameters

is not as apparent at the alveolar rim. The occlusal MD diameters, on the other hand are apparently not affected to the same degree as the occlusal BL diameters, and may even decrease with increasing age on account of the deeply-incised mesial and distal pressure facets which develop. The adult occlusal MD dimensions hence compare favourably with those of juvenile individuals which would explain the lower variability and correspondingly lower sample SD values.

The relatively high sample SD values for the occlusal and alveolar rim mesiodistal diameters of the maxillary premolars are explicable in terms of the considerably different shape and size of the deciduous and permanent premolars.

On the whole, the measurements taken at the alveolar rim did not prove either markedly less or more variable than those taken at the occlusal surface.

The only other parameters with sample SD values of less than 0,99 were a) the least vertical diameter of the lower zygomatic root (0,63) and b) the breadth of the foramina incisiva (0,96). All other cranial, mandibular and dental criteria had sample SDs of between 1,03 and 30,06.

In sum, the variability trends were as follows: amongst cranial and mandibular parameters, those concerning length proved more variable than those dealing with height or breadth, those belonging to the latter category, on the whole, proving amongst the most reliable. Of the cranial parameters, those dealing with the anterior portion of the cranium were more variable than those concerning the posterior regions. The above facts suggest that the cranium and mandible grow relatively more in length than they do in height or breadth, and that the region that undergoes most growth (in both length and breadth) is the anterior portion of the cranium (and mandible). The various ratios (% proportions of combinations of parameters) or other combinations such as MD x BL diameter† (tooth area) usually showed higher standard deviations than those for straightforward single parameters. Finally, many parameters, especially those whose high variability and SD values were attributable to growth, showed very low SD values for the measurements taken at any particular growth stage. Such parameters have been marked with an asterisk in the lists below.

To obtain some idea of relative reliability, the parameters are listed in order of increasing sample SD below:

Characters with sample standard deviations of between 0,05 and 0,99

- *ⁱ⁾ 1. All basic mesiodistal and buccolingual tooth diameters measured at both the occlusal surface and at the alveolar rim with the exception of the occlusal BL diameters of M^1 , M^2 and M^3 and the MD diameters of P^4 measured at the occlusal surface and alveolar rim (see below). Standard deviation values between 0,05 and 0,99; N values between 11 and 28.
- 2. Least vertical diameter of lower zygomatic bar (SD = 0,63; N = 26)
- * 3. Breadth of foramina incisiva (SD = 0,96; N = 27)

Characters with sample standard deviations of between 1,00 and 2,00

- * 1. The occlusal BL diameters of M^1 , M^2 and M^3 (SD values between 1,07 and 1,12; N values between 11 and 23)
- * 2. MD of P^4 measured at a) the occlusal surface and b) at the alveolar rim (SD values 1,03 and 1,22 and N values 20 and 25 respectively)
- * 3. Length of foramina incisiva (SD = 1,20; N = 27)
- * 4. Distance of sphenopalatine foramen from alveolar rim (SD = 1,34; N = 28)
- 5. Mandibular tooth row length measured at the occlusal surface (SD = 1,51; N = 10)
- * 6. The distance from the alveolar rim of the dp_4 or P_4 to the foramen mentale (SD = 1,58; N = 30)
- * 7. Vertical height of zygoma at jugo-squamosal suture (SD = 1,59; N = 22)
- * 8. Distance of lachrymal from maxillo-jugal suture (SD = 1,73; N = 25)
- * 9. Length of paroccipital processes (SD = 1,74; N = 19)
- 10. Inter- M^3 distance (SD = 1,76; N = 19)
- 11. Crown height of M_3 (SD = 1,83; N = 6)

i) low SD for individual growth stages, i.e. at least two of the growth stage SDs less than 1,50.

- * 12. Length of fronto-premaxillary suture; breadth of nasal process of premaxilla at fronto-premaxillary suture (SD = 1,84; N = 24)
- * 13. Breadth of nasal process of premaxilla half-way between fronto-premaxillary suture and masseteric crest (SD = 1,84; N = 24)

Characters with sample standard deviations between 2,01 and 3,00

- 1. Crown height of M^3 (SD = 2,01; N = 5)
- * 2. Inter- P^4 distance (SD = 2,04; N = 27)
- * 3. Least breadth of vertical bar separating orbit and foramen infra-orbitale (SD = 2,06; N = 23)
- 4. Inter M^3 distance (SD = 2,15; N = 27)
- * 5. Height of skull as a percentage of basal length (SD = 2,16; N = 18)
- * 6. Vertical height of zygoma at maxillo-jugal suture (SD = 2,21; N = 24)
- * 7. Maximum width of occipital condyles (SD = 2,26; N = 18)
- 8. Crown height of M^2 (SD = 2,26; N = 6)
- * 9. Inter M^1 distance (SD = 2,30; N = 26)
- 10. Crown height of M_1 (SD = 2,42; N = 6)
- 11. Inter M^2 distance (SD = 2,43; N = 24)
- * 12. Top of mesial symphysis above alveolar plane of mandibular molars (SD = 2,43; N = 30)
- * 13. Depth of ramus below M_1 (SD = 2,48; N = 29)
- * 14. Depth of ramus below P_4 (SD = 2,55; N = 30)
- 15. Depth of ramus below M_2 (SD = 2,65; N = 26)
- 16. Crown height of M_2 (SD = 2,49; N = 6)
- 17. Zygomatic breadth as a percentage of basal length (SD = 2,68; N = 17)
- 18. Width of nasals anteriorly (SD = 2,94; N = 24)
- 19. Height of occiput from lower edge of foramen magnum to top of occipital crest (SD = 2,95; N = 19)

Characters with sample standard deviations of between 3,01 and 4,00

- * 1. Median sutural length of premaxilla anterior to foramina incisiva (SD = 3,06; N = 26)
- * 2. Height of occiput from upper margin of foramen magnum to top of occipital crest (SD = 3,08; N = 20)

3. Distance between paroccipital processes (SD = 3,13; N = 18)
4. Inter P_4 distance (SD = 3,15; N = 6)
- * 5. Smallest postorbital skull width (SD = 3,43; N = 20)
6. Crown height of M^1 (SD = 3,43; N = 8)
7. Fronto-occipital distance (= frontal 'length') (SD = 3,43; N = 20)
8. Breadth of occiput at paroccipital processes (SD = 3,43; N = 18)
- * 9. Median sutural length of premaxilla ventrally (SD = 3,48; N = 26)
10. Radius of curvature of upper incisors (SD = 3,49; N = 9)
11. Molar-tympanic distance (SD = 3,67; N = 19)
12. Curvature of diastema
13. Greatest skull width : greatest skull length (SD = 3,77; N = 22)
14. Length of sagittal crest (SD = 3,80; N = 15)

Characters with sample standard deviations of between 4,01 and 5,00

1. Upper incisor width : lower incisor width (SD = 4,37; N = 17)
2. Length of nasal : occipitonasal skull length (SD = 4,44; N = 18)
3. Breadth of choanae (SD = 4,50; N = 25)
4. Height of top of ascending ramus of mandible above alveolar plane of molars (SD = 4,55; N = 27)
5. Inter- M_3 distance (SD = 4,80; N = 6)
- * 6. Maximum width of nasals (= maximum width of nasals posteriorly) (SD = 4,85; N = 23)
7. Length of mandibular diastema (SD = 4,97; N = 30)
- * 8. Skull width between outer margins of occipital condyle (SD = 4,98; N = 18)
9. Crown height of P_4 (SD = 5,00; N = 7)

Characters with sample standard deviations of between 5,01 and 6,00

- * 1. Length of jugal along orbit (SD = 5,34; N = 23)
2. Length of nasal process of premaxilla (SD = 5,51; N = 26)
3. Median sutural length of maxilla (SD = 5,48; N = 27)
4. Width of nasal process of premaxilla : greatest width of nasal (SD = 5,48; N = 23)
5. Crown height of P^4 (SD = 5,57; N = 11)
6. Height of mandibula (SD = 5,58; N = 26)
7. Posterior extent of nasal behind fronto-premaxillary suture (SD = 5,80; N = 24)

8. Crown shape index $\left(\frac{BL}{MD} \times 100\right)$ of M^3 measured at the alveolar rim (SD = 5,98; N = 14)
9. Length of maxillary tooth row measured at the alveolar rim (SD = 6,00; N = 27)

Characters with sample standard deviations of between 6,01 and 7,00

1. Length of maxillary tooth row measured at the occlusal surface (SD = 6,17; N = 26)
2. Length of frontal suture (SD = 6,20; N = 23)
- * 3. Length of mandibular tooth row measured at the alveolar rim (SD = 6,62; N = 30)
4. Width of nasal anteriorly : width of nasal posteriorly (SD = 6,67; N = 23)
5. Palatal diastemic length (SD = 6,77; N = 27)
6. Maximum width of occiput : maximum height (B, from lower margin of foramen magnum) (SD = 6,82; N = 19)
7. Radius of curvature of lower incisors (SD = 6,92; N = 11)

Characters with sample standard deviations of between 7,01 and 8,00

1. Crown shape index of I_1 measured at the alveolar rim (SD = 7,24; N = 24)
2. Skull width at rudimentary post-orbital process (SD 7,33; N = 21)
3. Crown area M_1 measured at the alveolar rim (SD = 7,73; N = 28)
4. Crown shape index P_4 measured at the alveolar rim (SD = 7,76; N = 26)
5. Crown area M^3 measured at the alveolar rim (SD = 7,78; N = 14)
6. Crown shape index of M^3 measured at the occlusal surface (SD = 7,80; N = 11)
7. Skull width at border of lachrymal (SD = 7,80; N = 18)

Characters with sample standard deviations of between 8,01 and 9,00

1. Maximum width of occiput : maximum width of occipital condyles
(SD = 8,12; N = 18)
2. Crown shape index M_3 measured at the alveolar rim (SD = 8,16; N = 18)
3. Crown shape index I_1^1 measured at the alveolar rim (SD = 8,17; N = 20)
4. Height of skull from maxillo-palatine suture to posterior end of
nasals (SD = 8,20; N = 25)
5. Crown shape area M_2 measured at the alveolar rim (SD = 8,27; N = 23)
6. Crown shape area M_3 measured at the alveolar rim (SD = 8,46; N = 18)
7. Crown shape index M_2 measured at the occlusal surface (SD = 8,46;
N = 22)
8. Crown occlusal area M_1 measured at the occlusal surface
(SD = 8,55; N = 27)
9. Height of mandibula
10. Height of skull from palate between M^1 to median suture between
nasals (SD = 8,68; N = 21)
11. Crown area I_1 measured at the occlusal surface (SD = 8,70; N = 25)
12. Crown area I_1 measured at the alveolar rim (SD = 8,87; N = 24)
13. Crown area M_3 measured at the occlusal surface (SD = 8,94; N = 13)

Characters with sample standard deviations of between 9,01 and 10,00

1. Crown shape index of M_2 measured at the
(SD = 9,03; N = 23)
2. Divergence of mandibular tooth rows (SD = 9,37; N = 6)
3. Median sutural length of palate (SD = 9,38; N = 27)
4. Greatest width of skull above (SD = 9,47; N = 18)
5. Crown occlusal area of M^2 measured at the alveolar rim
(SD = 9,69; N = 22)

Characters with sample standard deviations of between 10,01 and 11,00

1. Crown area M^1 measured at the occlusal surface (SD = 10,05; N = 23)
2. Crown shape index P_4 measured at the occlusal surface (SD = 10,20; N = 24)
3. Crown shape index M_1 measured at the occlusal surface (SD = 10,46; N = 27)
4. Frontal length % nasal length (SD = 10,48; N = 21)
5. Crown shape index M_1 measured at the alveolar rim (SD = 10,60; N = 28)
6. Crown area I^1 measured at the alveolar rim (SD = 10,91; N = 20)
7. Crown shape index P^4 measured at the occlusal surface (SD = 10,98; N = 20)

Characters with sample standard deviations of between 11,01 and 12,00

1. Crown area I^1 measured at the occlusal surface (SD = 11,02; N = 19)
2. Length of nasal suture (SD = 11,20; M = 23)
3. Condylolincisive length (SD = 11,27; N = 18)
4. Crown shape index M^2 measured at the occlusal surface (SD = 11,36; N = 19)
5. Crown area of M^1 measured at the alveolar rim (SD = 11,82; N = 26)

Characters with sample standard deviations of between 12,01 and 13,00

1. Length of nasal's (SD = 12,05; N = 23)
2. Crown area M_2 measured at the occlusal surface (SD = 12,05; N = 22)
3. Crown area P_4 measured at the occlusal surface (SD = 12,27; N = 24)
4. Crown area M_3 measured at the occlusal surface (SD = 12,49; N = 19)

Characters with sample standard deviations of between 13,01 and 14,00

1. Length of mandible measured to back of ascending ramus
(SD = 13,20; N = 28)
2. Basilar length of skull (SD = 13,29; N = 19)
3. Crown area M^3 measured at the occlusal surface (SD = 13,60; N = 11)
4. Length of mandible measured to end of angular process (SD = 13,60; N = 26)

Characters with sample standard deviations of between 14,01 and 15,00

1. Crown area P^4 measured at the occlusal surface (SD = 14,17; N = 20)
2. Crown shape index M^2 measured at the alveolar rim (SD = 14,48; N = 22)
3. Crown shape index P^4 measured at the alveolar rim (SD = 14,92; N = 25)

Characters with sample standard deviations of between 15,01 and 16,00

1. Crown area of P^4 measured at the alveolar rim (SD = 15,10; N = 25)
2. Crown area of P_4 measured at the alveolar rim (SD = 15,12; N = 26)
3. Degree of divergence of the maxillary tooth rows (SD = 15,26; N = 27)
4. Crown shape index I^1 measured at the occlusal surface (SD = 15,63; N = 19)
5. Crown shape index M^1 measured at the occlusal surface (SD = 15,68; N = 23)

Characters with sample standard deviations in excess of 16,00

1. Greatest length of skull above (SD = 16,03; N = 20)
2. Occipitonasal skull length (SD = 16,19; N = 19)
3. Crown shape index of M^1 measured at the alveolar rim (SD = 17,59; N = 26)
4. Average width of palate : average width of maxillary teeth
(SD = 21,78; N = 23)

5. Maximum width occiput : maximum height (B = from upper margin of foramen magnum (SD = 17,44; N = 20)
6. Length of molar series : molar-tympanic distance (SD = 23,77; N = 19)
7. Crown shape index of I_1 measured at the occlusal surface (SD = 26,23; N = 25)
8. Crown shape index of M_3 measured at the occlusal surface (SD = 30,06; N = 13)

12. THE RELIABILITY OF VARIOUS MORPHOLOGICAL CHARACTERS USED AS DIAGNOSTIC CRITERIA

12.1 Method

The literature dealing with the taxonomy of the genus Hystrix was first investigated to establish which morphological characters had been considered of diagnostic significance, and a list of these was compiled - see Chapter 6. During the course of this investigation it was noted that there was no standard terminology to describe many morphological structures and that many of the parameters taken as being diagnostic were undefined or so poorly defined that different authors were using different terminal points for their measurement. For this reason, all the structures involved in this investigation (Chapter 7, section 7.1) and all parameters measured (section 7.2) were first defined. The variability of each of the characters listed in Chapter 6 was then tested within a sample of 34 modern H. africaeaustralis specimens of all ages - Chapters 8, 9 and 10. The aim of the present chapter is to see to what degree the range of measurements available for H. cristata and H. indica overlap (or otherwise) with those obtained for H. africaeaustralis, entirely or largely overlapping ranges indicating poor diagnostic reliability.

33
Unfortunately no sample of H. indica specimens and only one H. cristata specimen was available, so that ranges of measurements for these two species had to be compiled from published data and illustrations. For this reason information on several parameters was not available for all three species; but on the whole sufficient published data was available to determine the diagnostic reliability of most parameters.

12.2 Cranial characters

12.2.1 General cranial characters

The ranges and means of all the general cranial parameters measured for H. indica, H. cristata and H. africaeaustralis are shown in Table VI. The measurements for H. indica and H. cristata, with the exception of those for a single H. cristata cranium, have been compiled from published metrical data. Because of this it has been impossible in many

The ranges and means of the general cranial characters measured for *H. indica*, *H. cristata* and *H. africae australis* (mm)ⁱ⁾

SPECIES	H. indica ^{vii)}			H. cristata			H. africae australis		
	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
CHARACTER									
Greatest length of skull above ⁱⁱ⁾	58-150,4	134,4	30	101,6-156,5	138,4	6	101,8-158,5	139,4	20
Occipitonasal skull length ⁱⁱⁱ⁾	55-162	130,2	27	118 -176	144,6	5	94,5-150,3	130,9	19
Condylolncisive length	-	-	-	138 -149	142,3	3	113,8-159,0	143,2	18
Basilar length (= basial length)	46,5-156,7	119,4	30	105,9-149	131,4	10	98,7-147,1	131,8	19
Greatest width of skull above ^{iv)}	30-83	72,1	21	73 -84	78,1	4	60,3- 96,4	80,7	18
Smallest postorbital breadth ^{v)}	29,5-53	44,6	26	46,5-48,5	47,8	3	39,1- 50,7	45,5	20
Skull width at condyles	25,4-31,8	29,3	5	25,4-29,7	27,5	2	25,8- 48,6	30,8	18
Interorbital distance at lachrymal edge	-	-	-	62,3-73,0	67,6	2	49,7- 80,8	67,5	18
Interorbital distance at rudimentary postorbital process ^{vi)}	24-63	54,2	24	58 -68,5	63,3	6	49,9- 78,0	65,4	21
Height of skull from palate to posterior end of nasals	53,0-59,0	56,0	2	65	65	1	42,0- 74,5	59,9	25
Height of skull from palate between M ¹	52,8-65,5	58,7	4	68,0-77,0	74,7	5	52,0- 73,0	59,6	21
Least breadth of vertical zygomatic process of premaxillary	5 -14	?	?	6 -16	?	?	11,2- 19,6	16,1	23
Breadth of choanae	-	-	-	33	33	1	20,5- 37,4	29,9	25
Length of sagittal crest	17,0-23,0	18,3	11	17,0	17,0	1	9 -20,1	14,2	15
Position of sphenopalatine foramen	-	-	-	10	10	1	6,5-13,0	8,9	28

i) The other two cranial characters considered, prominence and breadth of sagittal crest and prominence of lamboid or occipital crest are discussed in the text.

ii),iii),iv),v),vi) have been taken as being the same distances as referred to by Müller (1911,1919,1920) as 'Totallänge', 'Scheitellänge', 'Jochbogenbreite', 'Kleinste Breite des Hinterhauptes hinter dem Jochbogen' and 'Breite der Frontalia am rudim. Processus postorbitalis' respectively.

vii) Many of the very low values for some of the ranges listed under *H. indica* were apparently obtained from a newborn individual preserved in alcohol (Jericho pullus, 12252, Müller 1911 pp.123,124). The exclusion of this specimen from the calculations will have the effect of decreasing the range by raising the lower limit and increasing the mean.

35 | instances to determine whether or not the collated data for any one parameter has been obtained by using the same reference points as those used by the present author. However, it seems unlikely that very different points would have been used as many of the characters are descriptive in their definition, and their reference points may be guessed at or assumed. The conclusions derived from the collated data are thus considered to be valid.

36 | Amongst the data for H. indica are several unusually low measurements for a newborn alcohol-preserved specimen "Jericho pullus. 12252" (Müller 1911 pp.123, 124). The inclusion of the measurements for this specimen, although deemed reasonable by Müller, may not be advisable because shrinkage due to preservation may have caused distortion. Its exclusion would have the effect of decreasing the sample range for H. indica by raising its lower limit, and of increasing the mean. This would mean that the ranges for the three species would overlap even more substantially than is indicated by Table VI.

37 | No attention has been paid to growth stage because no information on this aspect was available with any of the published metrical data. The collated information presented is thus probably representative of both juvenile and adult specimens, while that presented for H. africae-australis includes measurements of individuals from growth stages 2 to 6.

1) Greatest length of skull above (= 'Totallänge' of Müller 1911, 1919, 1920) If the single measurement of 58mm for Jericho pullus 12252 is excluded the lower limit of the sample range for H. indica will be increased to 101 so that the ranges for the three species practically coincide (see Table VI). The mean for H. indica will also be increased to 137,2 so that the greatest difference between the three means will be only 2,2mm between the means of the latter species and H. africae-australis. It is therefore not possible to differentiate these species by means of greatest skull length and the character thus has no diagnostic significance. Source of collated metrical data: Gray 1847; Müller 1911, 1919, 1920; Hooijer 1946.

2) Occipitonasal skull length (?= 'Scheitellänge' of Müller op.cit.) If the low measurement of 55mm for Jericho pullus 12252 is excluded, the sample range for H. indica will revert to 105-162mm and the mean to 133,13mm. The area of range overlap is so large that the character

cannot be considered as diagnostically significant. However, from the means it is apparent that H. cristata does tend to have a slightly longer cranium than either H. indica or H. africaeaustralis. Source of collated metrical data: Müller 1911, 1919, 1920; Corbet and Jones 1964.

3) Condylolncisive length

No data is available for H. indica but, from the measurements for H. cristata and H. africaeaustralis which overlap closely, and considering the above two characters, it appears highly improbable that the condylolncisive length will prove of diagnostic significance. Source of collated metrical data: Lönnberg 1912.

4) Basilar length or basial length

The sample ranges for both H. cristata and H. africaeaustralis are contained within the range for H. indica, even if the unusually low measurement of 46,5mm for the Jericho pullus 12252 H. indica skull is excluded. The range for the latter species would then fall between 86 and 156,7mm and the mean would increase to 121,9mm. The area of range overlap is so extensive and the means so close that basilar length can not be regarded as a diagnostically significant character. Source of collated metrical data: Müller 1910, 1911, 1919, 1920; Lönnberg 1912; Hooijer 1946.

5) Greatest width of skull above, greatest width of skull below
(= 'Jochbogenbreite' of Müller op. cit.)

If the very low measurement of 30mm for the Jericho H. indica specimen is excluded, the sample range for the latter species will be 50,5-83mm and the mean 74,20mm. This means that the sample ranges for all three species overlap very closely and that their means too are very close, only 7,3mm separating the highest and lowest. From the ranges and means it appears that H. africaeaustralis crania tend to be wider than those of H. indica and H. cristata but in the latter case this may be due to sample size. The character is not taxonomically significant. Source of collated metrical data: Müller 1910, 1911, 1919, 1920; Hooijer 1946.

6) Smallest postorbital breadth (?='Kleinste Breite des Hinterhauptes hinter dem Jochbogen' of Müller op. cit.)

With the exclusion of the low measurement of 29,5mm for the Jericho H. indica cranium, the sample range and mean for the latter species

become 39,5-53mm and 45,2mm respectively. Table VI shows the closeness of the range overlap and of the means of the three species, thus the smallest postorbital breadth is not diagnostic. Source of collated metrical data: Müller 1911, 1919, 1920.

7) Skull width at condyles

The sample ranges for the three species coincide almost exactly, the upper limit of that for H. africae australis exceeding the others slightly, probably on account of larger sample size. The character is apparently not diagnostic. Source of collated metrical data: Gray 1847.

8) Skull width at lachrymal edge, interorbital distance at lachrymal edge

No data is available for H. indica but the data for H. cristata and H. africae australis suggests that the character is not diagnostically significant, the sample range for the former species being entirely contained within that for H. africae australis. Source of collated metrical data: Müller 1910.

9) Interorbital distance at rudimentary postorbital process (?= 'Breite der Frontalia am rudim. Processus postorbitalis' of Müller op. cit.)

With the exclusion of the low measurement of 24mm for the aberrant Jericho 12252 cranium, the sample range available for H. indica is 42-63mm. From Table VI it can be seen that the sample ranges for the three species overlap very substantially, that for H. cristata (58-68mm) being entirely contained in that for H. africae australis (49,5-78,0mm), and the means for the two species differ by only 2,1mm. The mean for H. indica is somewhat lower than that for the other two species, indicating that H. indica tends to have a slightly narrower cranium. On its own the character would not appear to be diagnostic, but taken in conjunction with other criteria, may serve to separate H. indica from H. cristata and H. africae australis. Source of collated metrical data: Müller 1910, 1911, 1919, 1920; Lönnberg 1912.

10) Height of skull from maxillo-palatine suture to naso-frontal suture

The information available for H. indica and H. cristata is somewhat

limited, and the sample ranges for these two species are contained in that obtained for H. africaeaustralis. The character would thus not appear to be diagnostically critical, but larger sample ranges for the first mentioned species may prove to the contrary. Source of collated metrical data: Hooijer 1946.

11) Height of skull from palate between M¹ to median nasal suture

The sample ranges for H. indica and H. africaeaustralis are very similar but that for H. cristata is remarkable in its rather high values. The lower limit of the sample range for the latter species exceeds the value for the upper limit of that for H. indica and is near the upper limit of the H. africaeaustralis range. The upper limit for H. cristata exceeds that for the H. africaeaustralis range and the mean for H. cristata is almost 10mm higher than that for the other two species. This character in conjunction with others may thus prove useful in the separation of H. cristata from H. indica, and possibly even from H. africaeaustralis. Source of collated metrical data: Gray 1847; Müller 1910; Lönnberg 1912.

12) Least breadth of bridge between orbit and foramen infraorbitale

The data available is inconclusive, the ranges for the three species that are available overlap considerably. It appears unlikely that the character will prove taxonomically significant. Source of collated metrical data: Corbet and Jones 1964; Lönnberg 1912.

13) Breadth of choanae

No information is available for H. indica and only one measurement, which falls within the range for H. africaeaustralis, is available for H. cristata. The data is thus inconclusive.

14) Length of sagittal crest

Examination of the sagittal crest within the sample of 32 H. africaeaustralis criteria showed that it is an age-dependent character, being present only from growth stage 4 onwards. Even amongst those individuals possessing a crest, it proved highly variable, being either broad and flat or high and blade-like (see section 8.1.14). The breadth of the crest proved particularly variable. The length measurements for the sagittal crest available for the three species shown in Table VI indicate

that the character is unlikely to prove of diagnostic significance. Source of collated metrical data: Frenkel 1970.

15) Position of sphenopalatine foramen

No data is available for H. indica and only one measurement which falls within the range obtained for H. africae australis is available for H. cristata. The data is thus inconclusive, but it appears unlikely that the character will prove taxonomically significant.

16) Prominence of lambdoid or transverse occipital crest

No difference in the prominence of the transverse occipital crest could be detected between H. indica, H. cristata and H. africae australis.

To summarize, the only general cranial characters which may prove of use diagnostically are the interorbital breadth at rudimentary post-orbital process, which may separate H. indica from H. cristata and H. africae australis and the height of the skull from the palate between the M^1 , which may separate H. cristata from H. indica and H. africae australis. In H. cristata the accentuated height of the cranium above the palate between the M^1 is especially apparent when the skulls of the three species are examined in profile: H. cristata has a comparatively strongly convex 'inflated' nasal so that there is a 'notch' in the generally convex profile of the skull at the junction between the nasal and frontal; in H. africae australis the nasals are not nearly as inflated and convex and the 'notch' in the somewhat less convex cranial profile is not as well marked, if apparent at all, whereas in H. indica the nasals are almost flat and the skull profile almost flat (see Müller 1911 Fig. 2 p.125).

12.2.2 Premaxillary, nasal and frontal characters (Table VII)

1) Length of nasal process of premaxilla

No data is available for H. indica and only one observation (42mm) is available for H. cristata. This just falls beyond the upper limit of the range for H. africae australis (41,9mm). The data is insufficient to assess the reliability of this character.

2) Breadth of nasal process of premaxilla at fronto-premaxillary suture;
length of fronto-premaxillary suture

The data is insufficient to assess the diagnostic validity of the characters, the single measurement available for H. cristata falling within

TABLE VII

The ranges and means of some premaxillary, nasal, frontal and parietal parameters of H. indica, H. cristata and H. africae australis (mm)ⁱ⁾

SPECIES	H. indica			H. cristata			H. africae australis		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Length of nasal process of premaxilla	-	-	-	42,0	42,0	1	29-55,5	41,9	26
Breadth of nasal process at fronto-premaxillary suture	-	-	-	3,5	3,5	1	1-8	4,4	24
Breadth of nasal process between fronto-premaxillary suture and masseteric ridge	-	-	-	10,7-20,0	16,4	3	7-14,8	9,9	25
Sutural length of premaxilla ventrally	-	-	-	25,7-29	27,3	2	16-28,3	23,0	26
Sutural length of premaxilla anterior to foramina incisiva	-	-	-	18,0	18,0	1	11,6-24,0	17,4	26
Length of nasals	64-81	72,5	2	85	85	1	40,5-89,3	67,8	23
Length of nasal suture	42,5-76,2	61,99	28	44,5-101	83,08	14	39,5-84,5	66,3	23
Maximum width of nasals ⁱⁱ⁾	8-25,5	18,95	28	27,5-42,5	33,0	11	19,9-41,4	29,4	23
Width of nasals anteriorly	-	-	-	17,25-20,5	18,60	5	12,7-24,0	17,8	24
Posterior extent of nasals behind fronto-premaxillary suture	-	-	-	31,0	31,0	1	5,8-27,9	17,4	24
Length of frontal suture	17-47	40,25	26	24-49	30,64	11	27,5-53,0	42,3	23
Length of fronto-premaxillary suture	-	-	-	3,5	3,5	1	1,0-8,0	4,3	24
Fronto-occipital distance	-	-	-	31-39	33,6	5	24,3-37,0	30,8	20

i) Premaxillary, nasal and frontal characters not dealt with in the Table are discussed in the text.

ii) Assumed to be equivalent to 'Hintere Breite der Nasalia' by Müller 1911, 1919, 1920. The data for H. africae australis refers to the posterior or maximum width of only one of the pair of nasals. From the published data for H. cristata it appears as if other authors have used the combined widths of the pair of nasals. For this reason the data in this table has been calculated on half of each published measurement.

the sample range obtained for H. africaeaustralis.

3) Breadth of nasal process of premaxilla halfway between fronto-premaxillary suture and the masseteric ridge

The data available is unsatisfactory in that there are no measurements for H. indica. The measurements for H. cristata overlap considerably with those for H. africaeaustralis but it would appear that the nasal process of the premaxilla of H. cristata tends to be wider (and longer - see above) than those of H. africaeaustralis. Taxonomic importance indeterminate. Source of collated metrical data: Lönnberg 1912.

4) Sutural length of premaxilla ventrally

As with the above three characters, the diagnostic validity of this character cannot be assessed because no data is available for H. indica. However, the sample ranges for H. africaeaustralis and H. cristata overlap very closely and it appears that these two species at least cannot be separated by this character. Source of collated metrical data: Müller 1910.

5) Sutural length of premaxilla anterior to foramina incisiva

No data is available for H. indica. The single measurement for H. cristata falls within the H. africaeaustralis sample range. The diagnostic validity of the character is thus uncertain, but it cannot be used to differentiate between the latter two species.

6) Length of nasals

This character is understood to imply the total length of the nasal, from the median naso-frontal suture to the anteriormost point reached by the nasal, which usually extends some distance beyond the anterior termination of the median suture. The data available is inconclusive on account of the very small sample size for H. indica and H. cristata, the measurements for these species falling well within the sample range obtained for H. africaeaustralis. Source of collated metrical data: Hooijer 1946.

7) Length of nasal suture ('Länge des Nasalnaht' of Müller 1911, 1919, 1920)

Although the ranges for the three species overlap to a great extent, the mean for H. cristata (83,08mm) considerably exceeds those for H. indica (61,99mm) and H. africaeaustralis (66,3mm), and it appears that the character, if used in conjunction with a second (e.g. frontal length) has

diagnostic significance. The upper limit of the range for H. cristata (101mm) is considerably higher than the upper range limit for H. africaeaustralis (84,5mm) which in turn is higher than that for H. indica (76,2mm). Because the nasal increases its length at the expense of the frontal, any relationship or ratio between these two bones should accentuate the differences between H. cristata and the other two species, and would be more reliable diagnostically in that on its own, there is still a substantial area of overlap between the ranges of the three species. Source of collated data: Gray 1847; Müller 1910, 1911, 1919, 1920; Lönnberg 1912.

8) Maximum width of nasals (?=Hintere breite der Nasalia of Müller op.cit.)

It is unfortunately not always clear from the published data whether the measurements given refer to the combined width of a pair of nasals or to a single nasal. In some instances, particularly with measurements for H. cristata (because they are so high) it is obvious that a pair of nasals has been referred to. In such cases the measurement was halved as were measurements for this character for other species appearing in the same publication. This was done to enable comparison with the present author's measurements for H. africaeaustralis, where a single nasal has been measured. In other cases, it has not been possible to determine which distance has been measured, but if an author has in a previous publication been found to have measured across both nasals, it has been assumed that he has done so again, and the measurements for this character have been halved. In some cases an illustration has aided a decision on the matter.

A second source of confusion is that the characters "greatest width of nasals" and "posterior width of nasals" are so poorly defined in existing publications; is this distance measured from the intersection of the naso-frontal suture with the median suture to the point of intersection of the naso-premaxillary, naso-frontal and fronto-premaxillary sutures, or is it the perpendicular distance from this latter point to the midline? It is not possible to tell from the published measurements. The present author has measured the "greatest width of nasals" using the latter reference points (where the nasal achieves its greatest width) and has also considered this to be equivalent to "posterior width of nasals", although some authors may have used the first pair of reference points given.

From the above it is clear that the information available may not be altogether reliable. However, the data prepared for Table VI indicates that H. cristata tends to have wider nasals than either H. indica or H. africaeaustralis. Although there is a substantial area of overlap between the ranges for H. africaeaustralis and H. cristata, the sample ranges available for the latter species and H. indica do not overlap at all. This character (used in conjunction with others) may thus be diagnostically significant. Source of collated metrical data: Müller 1910, 1911, 1919, 1920; Lönnberg 1912; Frenkel 1970.

9) Width of nasals anteriorly

The data is incomplete and thus no decision as to the validity of the character can be made. The sample range available for H. cristata overlaps entirely with that of H. africaeaustralis so that it appears unlikely that for these two species at least the character has taxonomic significance on its own. Source of collated metrical data: Müller 1910; Lönnberg 1912.

10) Posterior extent of nasals behind fronto-premaxillary suture

The numerical data is incomplete so that no judgement on the validity of the character can be made. It appears that H. cristata tends to have nasals which extend further posterior to the fronto-premaxillary suture than do those of H. africaeaustralis, and from published illustrations, than do those of H. indica. The character may well be diagnostically significant and warrants further investigation.

11) Length of frontal suture (= 'Länge des Frontalnaht' of Müller 1911, 1919, 1920)

Again there are substantial areas of overlap between the three sample ranges, and the means for H. indica and H. africaeaustralis are close. Judging by the means H. cristata tends to have shorter frontals than either of the other two species, probably on account of the very long posteriorly-expanded nasals. Used in combination with other characters, the length of the frontal suture may well have diagnostic significance. Source of collated metrical data: Müller 1910, 1911, 1919, 1920; Lönnberg 1912; Hooijer 1946; Frenkel 1970.

12) Length of fronto-premaxillary suture

The data available is incomplete but for H. cristata and H. africae-australis at least, the character appears to be of no significance. However, illustrations of H. indica indicate that this species may have a significantly longer fronto-premaxillary suture than the other two species, so that the character warrants further investigation.

13) Fronto-occipital distance

The suture between the parietal and occipital is completely obliterated (in H. africae-australis) by late growth stage 3 and there appears to be no reason not to assume a similar early and thorough fusion of the suture in the other two species. In any case, in both H. indica and H. cristata it is obliterated by growth stage 6, and hence the 'length of parietal suture' would be impossible to measure. It is apparent from measurements of 'parietal length' taken from specimens at this growth stage that what has been measured is the distance from fronto-parietal suture at the midline to the posterior-most tip of the transverse occipital crest on the midline.

The data for this character is incomplete but from the measurements available it does not appear to be diagnostically significant. Source of collated metrical data: Müller 1910; Lönnberg 1912.

14) Posterior extent of the nasal process of the premaxillary

Illustrations of H. indica suggest that the process of the premaxillaries extends back as far as the anteriormost part of the facial margin of the lachrymal, whereas in H. cristata and H. africae-australis it approaches but does not quite reach this level. The character may thus prove useful in separating H. indica from the remaining two species.

15) Shape of terminal part of nasal process of premaxillary

This was found to vary considerably within the H. africae-australis sample, from sharply tapering and point-like to spatulate and occasionally truncate. There appears to be no difference in the shape of the posterior termination of this process between this species and H. cristata, but illustrations of H. indica indicate that the process is much broader and abruptly truncate at its posterior termination.

The character may thus be significant in that it would serve to separate the latter species from H. cristata and H. africae australis.

16) Posterior extent of nasals in relation to lachrymals and orbits

It has already been intimated (this section, no. 6) that the posterior extent of the nasals is likely to prove of diagnostic significance. There is evidence that the nasals in mature specimens of H. cristata extend further back than do those of mature specimens of the other two species, i.e. as far as the posterior margin of the lachrymal or even posterior to this, or halfway along the length of the orbit. In H. africae australis the nasal extends backwards only to a level about half to threequarters of the length of the lachrymal (working backwards) or as far as the anterior border of the orbit, while the published illustrations of H. indica indicate that the nasals terminate slightly short of the anterior border of the orbit. The character appears to be diagnostically significant.

17) Shape of posterior margin of nasals

In H. cristata the posterior margins of the combined pair of nasals are broadly rounded; in H. indica their shape is sub-truncate to truncate while in H. africae australis an intermediate situation exists, and the combined posterior margins of the nasals have a subtruncately rounded to sub-truncate shape. The shape of the posterior margins of the nasals therefore does appear to have diagnostic significance.

18) Size and shape of nasal orifice

Insufficient data was available and no judgement on the diagnostic validity of this character could be made.

Several characteristics of the premaxilla, nasal and frontal thus appear to be of actual or potential diagnostic significance. Of these the length of nasal suture, maximum width of nasals (width of nasals posteriorly), posterior extent of nasals behind fronto-premaxillary suture, length of fronto-premaxillary suture, posterior extent of the nasal process of the premaxillary, posterior extent of the nasals in relation to lachrymals and orbits and shape of posterior margin of the nasals are the most important. Several other premaxillary, nasal and

frontal characters require further investigation before judgement can be made on their validity.

12.2.3 The diagnostic reliability of some palatal characters

(Table VIII)

1) Palatal diastemic length

The sample ranges for all three species overlap very closely and the mean values are all very close, although H. indica does tend to have a slightly shorter palatal diastema than the other two species. The character does not appear to be diagnostic. Source of published metrical data: Müller 1911, 1919, 1920; Hooijer 1946.

2) Median sutural length of palate (= 'Palatilarlänge of Müller op.cit.)

The sample ranges of the three species overlap very closely, but from the means it appears as if H. indica has a shorter palate than either H. cristata or H. africae australis, which have almost identical means. If the very low measurement of 25mm for the Jericho pullus skull mentioned in section 12.1 is excluded the range for H. indica is reduced to 49-82,6mm, so that the sample ranges of the three species coincide even more closely. It appears unlikely that the character has any diagnostic significance. Source of published metrical data: Gray 1847; Müller 1910, 1911, 1919, 1920.

3) Median sutural length of maxillary

No data is available for H. indica and the single measurement for H. cristata falls within the range for H. africae australis. Insufficient data is available for assessment of the taxonomic validity but the indications are that the character is not diagnostic.

4) Length and breadth of foramina incisiva.

No data for either the length or the breadth of this foramen are available for H. indica and the single measurement available for H. cristata falls within the range for H. africae australis. Although the data is incomplete the indications are that the character is not diagnostic. There is no difference in the location of the foramina between the three species.

TABLE VIII

THE RANGES AND MEANS OF SOME PALATAL CHARACTERS OF *H. INDICA*, *H. CRISTATA* AND *H. AFRICAEAUSTRALIS* (mm)ⁱ⁾

SPECIES	<u><i>H. indica</i></u>			<u><i>H. cristata</i></u>			<u><i>H. africaeaustralis</i></u>		
	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Palatal diastemic length	28,5-47,0	40,0	25	42-52	45,3	3	31,0-59,0	47,7	27
Median sutural length of palate	25 -82,6	65,12	29	55,1-86,5	74,5	8	52,8-90,0	75,6	27
Median sutural length of maxillary	-	-	-	53	53	1	33,8-54,0	46,0	27
Length of foramina incisiva	-	-	-	6,0	6,0	1	3,5-8,5	6,6	27
Breadth of foramina incisiva	-	-	-	7,0	7,0	1	4,0-7,5	5,5	27
Inter-P ⁴ distance	7,5-11,0	9,4	17	12,5	12,5	1	8,0-15,0	10,8	27
Inter-M ¹ distance	-	-	-	12,0	12,0	1	6,2-16,8	9,6	26
Inter-M ² distance	-	-	-	11,0	11,0	1	6,0-11,1	10,4	24
Inter-M ³ distance	11,5-15,2	12,9	17	10,5	10,5	1	9,0-15,1	11,6	19

i) Palatal characters not listed in the table are discussed in the text.

5) Inter P^4 , M^1 , M^2 and M^3 distance

The information available for these four characters is incomplete in that only a single measurement is available in each case for H. cristata and none for the inter- M^1 and M^2 distance for H. indica. The data available indicates that used in isolation all four of the characters are undiagnostic. However, considering only the inter- P^4 and inter- M^3 data, H. indica appears to have maxillary tooth rows which diverge from front to back while in the other two species this feature is less noticeable. Used together, therefore, the inter P^4 and M^1 data may enable the separation of H. indica from the other two species. Source of published metrical data: Frenkel 1970.

6) Shape of palate behind

This character deserves investigation, as from the H. cristata and H. africae australis material available it appears that the 'palatal notch' of the two species are markedly different in shape, that in H. cristata being much wider and broadly 'u' shaped or horseshoe shaped, while that in H. africae australis is narrowly 'u' or even 'v' shaped. The apex of the notch in H. cristata is smooth and broad whereas in H. africae australis the palatine bones project very slightly at the midline into the apex, forming a 'bump'. No information on the palatal notch of H. indica was available.

7) Anterior extent of palatal incision

Information on this character is insufficient to debate its taxonomic validity. In H. africae australis, the anterior extremity of the palatal notch was found to vary from just posterior to the distal margin of the alveolus of the last tooth to just posterior to its mesial border (section 8.6.6), with the most common terminal point being opposite the lingual enamel fold. Only one specimen of H. cristata was available with the palatal notch terminating just posterior to the distal margin of the M^3 . The situation in H. indica is unknown. The diagnostic potential of this character deserves investigation.

Of the palatal characters, the relationship between the inter- P^4 and inter- M^1 distance, the shape of the palatal notch and the anterior extent of the palatal notch are the only three which are potentially

of diagnostic value.

12.2.4 The diagnostic reliability of some occipital and zygomatic characters

The ranges and means for various characters investigated are shown in Table IX.

1) Upper edge of foramen magnum to top of median occipital crest

The ranges of the three species overlap very closely and the means for H. indica and H. cristata are fairly close. H. africae australis appears to have a slightly lower mean than the other two species (indicating a flatter occiput) although an increased sample size for H. cristata would probably reduce the mean. The character does not appear to be significant. The unreliability of using the upper margin of the foramen magnum as a reference point has been discussed in sections 8.5.1 and 8.5.2. Source of published metrical data: Gray 1847; Müller 1910, 1911, 1919, 1920; Frenkel 1970.

2) Lower edge of the foramen magnum to top of median occipital crest

The sample ranges for the three species overlap so substantially and the means are so close that it appears unlikely that this character has diagnostic significance. Source of published metrical data: Müller 1911, 1919, 1920.

3) The means for this character for all three species are practically identical so that it appears to have no diagnostic significance. Source of published metrical data: Müller, op. cit.

4) Length of paroccipital processes

The data available is incomplete in that no measurements are available for H. indica while the single measurement for H. cristata falls within the sample range for H. africae australis. For the latter two species at least, the character is not diagnostic, but judgement on the taxonomic validity will have to await a series of measurements for H. indica.

5) Distance between paroccipital processes

An identical situation to that described above (4) exists.

TABLE IX

The ranges and means of some occipital and zygomatic characters of H. indica, H. cristata and H. africaeausustralis (mm)ⁱ⁾

SPECIES	H. indica			H. cristata			H. africaeausustralis		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Upper edge of foramen magnum to top of median occipital crest	12-42,4	30,3	24	25,0-44,3	36,1	3	23,7-32,0	25,7	20
Lower edge of foramen magnum to top of median occipital crest	18,5-41	35,0	16	42,0	42,0	1	32,5-42,8	39,7	19
Breadth at paroccipital processes	27-55,5	49,7	23	49,5	49,5	2	42,2-54,0	49,2	18
Length of paroccipital processes	-	-	-	12,5	12,5	1	6,4-13,7	9,7	19
Distance between paroccipital processes	-	-	-	36,5	36,5	1	31,7-43,5	39,0	18
Maximum width of occipital condyles	25,4-30,0	27,9	4	30,7-31,7	31,3	3	27,6-37,0	31,4	18
Minimum vertical height of lower bar of foramen infraorbitale	-	-	-	2,0	2,0	1	1,0-4,0	2,7	26
Vertical height of zygoma at maxillo-jugal suture	10,5-21,5	17,7	15	24,0	24,0	1	15,3-23,5	19,4	24
Vertical height of zygoma at jugo-squamosal suture	-	-	-	6,7	6,7	1	4,1-9,3	6,6	22
Length of jugal along orbital rim	-	-	-	20,0	20,0	1	16,0-25,2	19,6	23
Distance of lachrymal from maxillo-jugal suture	-	-	-	2,5	2,5	1	1,6-8,8	4,8	25
Molar tympanic distance	-	-	-	32,0	32,0	1	20,8-35,7	29,2	19

i) Occipital and zygomatic characters not mentioned in this Table are discussed in the text.

6) Maximum width of occipital condyles

The data given in Table IX indicates that the character has no diagnostic significance. Source of published metrical data: Frenkel 1970.

7) Minimum vertical height of lower bar of foramen infraorbitale

The lower bar of the foramen infraorbitale appears to be very slender in all three species of Hystrix, the range for H. africae australis being 1-4mm. The single measurement for H. cristata falls within this range, and although there are no measurements for H. indica, illustrations of this species suggest that the measurements for this character will fall within the range for H. africae australis. The character thus apparently has no diagnostic status.

8) Vertical height of zygoma at maxillo-jugal suture

Although the sample ranges for this character overlap substantially between the three species, the means indicate that H. indica has a slightly narrower jugal (= zygoma) than H. africae australis, which in turn has a more slender jugal than H. cristata. The difference between H. indica and H. cristata is quite well marked, and used in conjunction with one or more other characters, the zygomatic height at the maxillo-jugal suture may prove useful in separating these two species. Source of published metrical data: Müller op. cit.

9) Vertical height of zygoma at jugo-squamosal suture

The data is inconclusive as no measurements are available for H. indica. The character apparently does not serve to distinguish H. cristata from H. africae australis.

10, 11), 12) Length of jugal along orbital rim, distance of lachrymal from maxillo-jugal suture and molar-tympanic distance

For all three of these characters, the data available is incomplete in that no measurements are available for H. indica and the single measurements for H. cristata fall within the range for H. africae australis. It thus appears unlikely that any of these characters will serve to separate H. cristata from H. africae australis, but any one of them may be diagnostic for H. indica. An assessment of their diagnostic validity can thus not be undertaken.

13) Orientation of the long axis of the occipital condyle

Within H. africaeaustralis alone, the orientation of the axis of the condyle was from almost horizontal to almost vertical (see section 8.5.7) so that character can have no diagnostic validity at all.

14) Extent of facial surface of lachrymal

From illustrations it appears that H. cristata and H. africaeaustralis have larger facial areas of the lachrymal than does H. indica. The character thus warrants further investigation as it does appear to be potentially significant.

The taxonomic validity of the characters length of jugal along orbital rim, distance between the lachrymal and maxillo-jugal suture at orbital rim and molar-tympanic distance could not be assessed on account of the lack of information for both H. indica and H. cristata. No measurements for the length of the paroccipital processes and the inter-paroccipital distance were available for H. indica, but those available for H. cristata and H. africaeaustralis indicate that these characters are not diagnostic for the latter species. The characters vertical height of zygoma at maxillo-jugal suture and vertical height of zygoma at jugo-squamosal suture may prove useful in separating H. indica from H. cristata and H. africaeaustralis and it is apparent that there are various differences in the jugal region between the latter two species as well, particularly in the vicinity of the maxillo-jugal suture. The extent of the facial surface of the lachrymal appears to differ between the three species and may thus prove a diagnostically significant character.

12.2.5 The taxonomic validity of some cranial relationships and ratios used as diagnostic criteria

The sample ranges and means for the cranial relationships investigated are listed for H. indica, H. cristata and H. africaeaustralis in Table X.

1) Length of nasal : occipitonasal skull length (%)

Although the ranges for the three species overlap substantially it is apparent from both these and the three means that H. cristata has the longest nasals followed by H. africaeaustralis, whilst H. indica has the shortest nasals. It is probable that if growth stage could be considered the differences between the species would be more apparent. However, if

TABLE X

The ranges and means of some cranial relationships used as diagnostic criteria for H. indica, H. cristata and H. africaeaustralis (mm)ⁱ⁾

SPECIES	H. indica			H. cristata			H. africaeaustralis		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Length of nasal : occipitonasal skull length (%)	38-61	50,4	33	44-68	54,5	4	43-60	52	18
Frontal length : nasal length (%)	33-94	68	25	23-38	32	10	53-84	62	21
Greatest width : greatest length nasals (%) ⁱⁱ⁾	16-36	30,1	26	21,5-42	34,5	11	37-52	42	22
Width nasals anteriorly : width nasals posteriorly (%)	71	71	1	53-78	63,8	6	49-77	61	23
Width nasal process of premaxilla : greatest width nasals (%)	44	44	1	19-36	?	?	24-47	34	23
Maximum width : maximum height occiput (A) (%) ⁱⁱⁱ⁾	162-256	218	14	119-126	122	2	176-238	199	20
Maximum width : maximum height occiput (B) (%) ^{iv)}	123-155	142	14	119-126	122	2	121-142	130	19
Maximum width occiput : maximum width condyli (%)	171-200	185	?	160-165	162,5	2	148-184	166	18
Height of skull % basal length	37-50	45,5	4	41-55	49	4	43-51	46	18
Zygomatic breadth % basal length	58-67	62,2	24	60-62	60,8	5	55-66	61	17
Length molar series : molar tympanic distance (%)	-	-	-	113	113	1	78-151	110	19

i) To the nearest %

ii) Calculated as the greatest width of a single nasal. Many of the published measurements for greatest width of nasals posteriorly have been halved - see text

iii) From the top of the foramen magnum

iv) From the bottom of the foramen magnum

growth stage is not considered, it is apparently not possible to separate the three species by means of this ratio alone, except that specimens with ratios of less than 43% are likely to belong to H.indica

2) Frontal length : nasal length (%)

The range for this ratio for H. cristata does not overlap at all with that for H. africae australis and overlaps only slightly with that for H. indica. The mean for H. cristata (32%) is less than half that for H. indica (68%) and only slightly more than half that for H. africae australis (62%). This indicates that H. cristata has longer nasals and shorter frontals than either H. africae australis or H. indica, and that the latter species has the shortest nasals and hence the longest frontals. The ratio is diagnostically significant in that H. cristata can readily be distinguished from the other two species, although it may not be possible to differentiate H. indica from H. africae australis whose ranges overlap substantially and whose means are close.

3) Greatest width : greatest length of nasals (%)

As mentioned in section 12.2.2.8 (maximum width of nasals) it is frequently not clear from published data whether the measurements given for the maximum width of the nasals posteriorly refer to the combined width of a pair of nasals or to a single nasal, and the reference points used for measuring this parameter are also in doubt; see section 12.2.2.8. The data given therefore cannot be regarded as being altogether reliable, and the taxonomic validity of the ratio thus remains debateable.

From the data presented in Table X it appears that H. indica can be separated from H. africae australis because the ranges of the two species do not overlap, although this is probably on account of the small sample sizes. It is also apparent that H. africae australis has the highest width : length nasal ratio, followed by H. cristata (the ratio in the latter species is lower because the nasals are longer than in H. africae australis, although in absolute terms H. cristata may actually have wider nasals than this species), while H. indica has nasals which are relatively narrow and long in comparison with H. cristata and H. africae australis. The ratio appears to be potentially significant and warrants further investigation.

4) Width of nasals anteriorly : width posteriorly

The same considerations concerning the posterior width of the nasals as outlined above (no. 3) apply in this case, and the data presented for this character for H. indica and H. cristata in Table X must be regarded as suspect. However, it appears that H. indica has the least tapering, 'straightest' nasals with little difference between the anterior and posterior widths whilst H. africae australis is at the other extreme with nasals that are much-expanded posteriorly, H. cristata occupying an intermediate position. Examination of illustrations of the nasals of H. cristata show them to be extremely expanded posteriorly and narrow anteriorly; the intermediate position indicated by the table for this species may be due only to small sample size. The sample sizes for H. indica and H. cristata are so low that no judgement can be made on the diagnostic significance of this character.

5) Width of nasal process of premaxilla : greatest width of nasals (%)

The data is unsatisfactory in that only one observation is available for H. indica and the sample size for H. cristata is unknown. It appears that the measurements available for both these species fall within the sample range for H. africae australis (24-47%) with the exception of the lower range limit for H. cristata (19%). However, it is apparent from illustrations that H. indica has very much wider premaxillary nasal processes than either H. cristata or H. africae australis, the latter species apparently having the narrowest. No judgement on the validity of this character is possible, but it appears to have potential and is worth further investigation.

6) Maximum width : maximum height of occiput, measured from the upper margin of the foramen magnum

It is not positively known whether the data compiled for H. cristata (range = 119-126, $\bar{X}$ = 122, N = 2) was measured from the upper or the lower margin of the foramen magnum. It is highly improbable that it was measured from the former margin as the range for this species is so much lower than those for the other two species (which overlap substantially) whereas illustrations of the occipital regions of the three species indicate no such marked difference. Judging by the

ranges for H. indica and H. africaeaustralis it appears unlikely that the character is diagnostic for these two species although their means differ somewhat, that for H. indica (218%) indicating a broader, flatter supra-foramen occipital region than occurs in H. africaeaustralis. The taxonomic validity of this character must be regarded as uncertain but the indications are that it is not diagnostic.

7) Maximum width : maximum height of occiput measured from the lower margin of the foramen magnum

The sample ranges for H. indica and H. africaeaustralis overlap fairly closely, the upper range limit for the former exceeding that of the latter by 13mm. The sample range for H. cristata does not overlap as substantially with those of the other two species probably on account of the low sample size (2). The means for the three species are fairly widely separated, that for H. indica (42%) being the highest and exceeding those for H. africaeaustralis and H. cristata by 12 and 20% respectively. The means thus suggest that H. indica has the broadest and flattest occiput whilst H. cristata has the tallest and narrowest. H. africaeaustralis occupies a somewhat intermediate position but tends towards the H. cristata condition. On its own the character does not appear to be diagnostic for H. indica and H. africaeaustralis and an increased sample size for H. cristata would probably show that the character is not diagnostic at all.

8) Maximum width of occiput : maximum width of condyli

The data available is unsatisfactory because only two observations are available for H. cristata, while the sample size for H. indica is unknown. The sample range for H. cristata does not overlap at all with that for H. indica, although this may be due purely to sample size. The ranges for the latter species and H. africaeaustralis overlap considerably, but the means differ by more than 20mm. The means indicate that H. indica has a relatively broad occiput and narrower condylar region than H. africaeaustralis or H. cristata. The character requires further investigation before its diagnostic reliability can be adequately assessed, but superficially it appears not to be significant.

9) Height of skull as a percentage of basal length

The skull height measurement used in the calculation of this ratio (by numerous authors and hence also by the present author) is the distance from the maxillo-palatine suture to the naso-frontal suture above, although as is pointed out below, this parameter is not the best one to use to indicate differences in relative skull height and cranial inflation between the species. Using this parameter, the sample ranges of the three species are seen to overlap substantially despite the small sample sizes for H. indica and H. cristata, and the means for the three species are also very close. This character would thus not appear to have any diagnostic significance.

If, however, the height parameter selected to assess relative height to length ratio were the distance from the palate between the first molars to the median nasal suture vertically above, differences between the species are more likely to emerge. This is because H. cristata has an excessively dorsally vaulted nasal, but this is only anterior to the naso-frontal suture, reaching its maximum height at a point vertically above the palate between the first molars. H. africaeaustralis has much less vaulted nasals in this region while the nasals of H. indica are practically flat anterior to the naso-frontal suture.

However, as it stands, the ratio does not appear to be diagnostic.

10) Zygomatic breadth as a percentage of basal length

The ranges of the three species overlap substantially and the means are also very close and the ratio is thus not diagnostic.

11) Length of molar series : molar-tympanic distance

No data is available for H. indica and only one measurement for H. cristata (falling well within the range for H. africaeaustralis) so the diagnostic validity of this ratio cannot be judged. It does not appear to be diagnostic for H. cristata and H. africaeaustralis.

Of the cranial relationships examined, only the ratio frontal length: nasal length and the ratio width of nasal process of premaxilla : greatest width of nasals appear to be of definite taxonomic value, while the ratios greatest width : greatest length of nasal and width of nasals anteriorly : width posteriorly appear to have potential diagnostic value, but require further investigation. The validity of the ratio length molar series : molar-tympanic distance could not be assessed.

12.3 The diagnostic reliability of mandibular characters and relationships

The ranges and means for some of the mandibular characters and relationships investigated for the three valid species of the sub-genus Hystrix are shown in Table XI. Particular attention was paid to the assessment of the validity of the mandibular characters as diagnostic criteria because mandibles or portions of mandibles are frequently encountered as fossils, as they are robustly constructed.

1) Greatest mandibular length

The sample ranges for this character for H. indica and H. cristata are practically identical; both are encompassed by the H. africaeaustralis sample range. The three means are very close, the largest difference between the three being only 3,8mm. The character thus appears to have no diagnostic significance. Source of published metrical data: Gray 1847.

2) Length of mandible from incisor alveolus to angular process

As is the case with the above character, the H. indica and H. cristata sample ranges are encompassed by that for H. africaeaustralis. However, the mean for H. indica is almost 20mm less than those for the other two species. The character thus may prove useful in diagnosing H. indica, if used in conjunction with other characters; on the other hand, the mean may be lower on account of the inclusion of a disproportionately high number of juvenile individuals. Source of metrical data: Müller 1911, 1919, 1920.

3) Height of mandibula

Once again, the sample ranges for the three species overlap very closely. The means for H. cristata and H. africaeaustralis are similar, but the mean for H. indica indicates a tendency towards a slightly higher mandibula. This is to be expected in view of the shorter length from incisor alveolus to angular process discussed above (2): presumably since the greatest mandibular lengths(measured to the back of the coronoid) of the three species are similar, the mandibula of H. indica has to slope anteriorly to a greater degree in H. indica than in the

TABLE XI

The ranges and means of some mandibular characters used as diagnostic criteria for H. indica, H. cristata and H. africae australis (mm)ⁱ⁾

SPECIES	H. indica			H. cristata			H. africae australis		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Greatest length	74,2-106,9	94,8	4	74,2-103,0	91,5	3	59,9-115,6	95,3	28
Length from incisor alveolus to angular process	62-102,5	76,5	19	95,0-101,0	47,0	3	56,5-114,5	93,5	26
Height of mandibula	37,0-46,5	43,0	18	36,5-39,0	37,7	2	21,0-45,3	35,9	26
Depth ramus below P ₄	-	-	-	25,7	25,7	1	16,4-27,7	23,6	30
Depth ramus below M ₁	22,0-26,5	23,8	23	24,5-25,0	24,7	2	15,7-26,5	22,3	29
Depth ramus below M ₂	20,0-23,2	21,4	22	22,5-24,0	23,2	2	15,0-24,5	21,1	26
Alveole P ₄ to mental foramen	11,0-13,0	12,2	10	10,5-11,2	10,8	2	7,0-12,5	9,5	30
Length of diastema	-	-	-	35,0	35,0	1	18,5-39,6	28,1	30
Curvature of diastema	-	-	-	-	-	-	22,7-40,8	28,5	30
Height of ascending ramus above alveolar plane	-	-	-	19,0	19,0	1	7,0-25,0	13,5	27
Height of mesial symphysis above alveolar plane	-	-	-	8,0		1	0,0-8,0	3,6	30

i) Mandibula characters not mentioned in the table are discussed in the text.

other two species, to account for lower alveolar-angular process distance and greater mandibula measurements. Used in conjunction with others, this character thus may prove successful in separating H. indica from H. cristata and H. africae australis. Source of published metrical data: Frenkel 1970.

4), 5), 6) Depth of mandibular ramus below P_4 , M_1 and M_2

From the data presented in Table XI, none of these three characters appears to be of diagnostic significance. Source of published metrical data: Frenkel 1970.

7) Alveolus of P_4 to edge of foramen mentale

The sample ranges for H. indica and H. cristata are both encompassed by that for H. africae australis and the means for the three species (12,2; 10,8 and 9,5mm respectively) are very close. The character thus appears to have no diagnostic significance. Source of published metrical data: Frenkel 1970.

8), 9), 10), 11) Length of diastema, curvature of diastema, height of ramus above alveolar plane, height of mesial symphysis above alveolar plane

No assessment of the taxonomic reliability of these four characters could be made in view of the total absence of any measurements for H. indica. The single measurement available for H. cristata for each of the characters except 'curvature of diastema' all fall within the sample ranges obtained for H. africae australis; it would thus appear that for these two species at least, none of these characters has diagnostic significance. Source of published metrical data: Nil.

12) Position of foramen mentale

This was found to vary somewhat within the sample of H. africae australis but no significant difference in its location was found between the three species.

13) Presence of dorsally thickened crest on dorsal surface of coronoid process

See section 9.1.8. This character appears to be controlled by the degree

of muscle development and tends to be more pronounced in older (and possibly in male) specimens.

14) Prominence and development of muscle attachments

See section 9.1.11. This character like 13) appears to be controlled by the degree of muscle development and age, and thus does not appear to be taxonomically significant.

The validity of the characters length and curvature of diastema, and height above the alveolar plane of the molars of the ascending ramus and of the mesial symphysis remains undetermined. Of the remaining mandibular characters commonly used in diagnoses, only the length of the mandible from the incisor alveolus to the angular process and the height of the mandibula appear to be potentially significant, if used in conjunction with other characters.

12.4 The diagnostic reliability of dental characters and relationships

Particular care was taken with the investigation of the diagnostic validity of these characters because teeth, especially isolated teeth, are the most commonly preserved skeletal element of fossil porcupines, often occurring to the exclusion of all else. The ranges and means for the various dental characters and ratios used as diagnostic criteria are shown in Tables XII and XVI.

1) Degree of divergence from the parallel of the maxillary rows (%) (Table XII)

The divergence from the parallel of the maxillary tooth rows was found to be highly variable within the sample of H. africaeaustralis studied, with some specimens having tooth rows which were divergent from front to back, whereas in others the reverse was true. Specimens with parallel-sided tooth rows were also present. From the ranges and means available for the three species it appears that H. indica has tooth rows which tend to be fairly strongly divergent from front to back whereas H. africaeaustralis tends to have practically parallel tooth rows. Only one measurement is available for H. cristata, this occupying an intermediate position. However, the sample ranges for the three species overlap considerably and it is unlikely that on its own the character will prove valid in separating them. The character is unlikely to be of use in fossil taxonomy because the pair of maxillary tooth rows is seldom preserved intact. Source of collated data: Frenkel 1970.

2) Degree of divergence from the parallel of the mandibular rows (%) (Table XII)

Investigation of the H. africaeaustralis sample indicated that this is a less variable character than the above, the mandibular tooth rows almost invariably diverging from front to back. Its diagnostic significance cannot be assessed because of the absence of any data for H. indica, but judging from the range for H. africaeaustralis and the single measurement for H. cristata (which falls within it) the character would appear not to be valid. As left and right rami are seldom preserved in association, the character would not be much use in fossil taxonomy.

TABLE XII

The ranges and means of some dental characters and ratios apart from basic MD and BL measurements, tooth areas and crown shape indices, used as diagnostic criteria for H. indica, H. cristata and H. africae australis (mm)ⁱ⁾

SPECIES	H. indica			H. cristata			H. africae australis		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Degree of divergence of upper tooth rows (%)	58-80	70	17	80	80	1	64-132	101	27
Degree of divergence of lower tooth rows (%)	-	-	-	104	104	1	79-104	88	6
Width of palate in relation to width of maxillary teeth (%)	-	-	-	150	150	1	118-138	131	5
Length of maxillary tooth row measured at occlusal surface	29-34,7	31,8	18	29,2-36,1	34	7	16,3-36,2	28	26
Length of maxillary tooth row measured at alveolar rim	31,0-34,7	32,9	22	34,5-37,0	35,7	2	17,0-36,4	30	27
Length of mandibular tooth row measured at occlusal surface	29-36,5	33,6	18	35,0	35,0	1	32,5-37,4	34,9	10
Length of mandibular tooth row measured at alveolar rim	32,0-36,3	34,2	23	35,2-36,5	35,8	2	16,5-39,3	32,6	30
Upper : lower incisor width	-	-	-	100	100	1	100-115	105	17
Radius of curvature of upper incisors	-	-	-	-	-	-	12,5-22,5	19,4	9
Radius of curvature of lower incisors	-	-	-	-	-	-	37,5-62,5	51,4	11

i) Characters not mentioned in any of Tables XII to XVI are discussed in the text.

3) Width of palate in relation to width of maxillary teeth (%) (Table XII)

The diagnostic validity of this character could not be evaluated because no data is available for H. indica and only one measurement for H. cristata, the latter falling above the range for H. africae australis. The character thus requires further investigation, but examination of illustrations of the palates of the three species suggests that no significant difference will be found between them.

4) Colour of the enamel on the upper and lower incisors

Section 10.1.1 discusses the subjective and unreliable nature of this character in view of the fact that the incisor enamel ranges in colour from just off-white to deep orange-brown within the sample of H. africae australis alone.

5) The presence or absence of grooves on the incisors

No grooves of any kind were found on either the upper or lower incisors of any of the three species. The enamel of the lower incisors is very smooth in all three species while that of the upper incisors may be slightly ridged, but never grooved.

6) Upper incisor width : lower incisor width (Table XII)

The upper incisors throughout the comparative sample of H. africae australis specimens invariably had incisors which were at least as wide as or, more commonly, slightly wider than the lowers. From the data available (no actual measurements are available for H. indica but illustrations were examined), it appears that the character is not significant in separating the three valid extant species of the subgenus Hystrix.

7), 8) Radius of curvature of the upper and lower incisors (Table XII)

No data for either of these characters was available for H. indica or H. cristata. However, because there appear to be no differences between the three species in either the upper diastemic length (12.2.3.1), mandibular length (12.3.1) or the length of the lower diastema (12.3.8), it appears unlikely that the radii of curvature of the upper and lower incisors will prove of diagnostic value.

9), 10), 11), 12) Length of maxillary and mandibular tooth rows measured both at the occlusal surface and at the alveolar rim (Table XII)

Examination of the data presented (particularly the means) indicates that

none of these characters will separate any of the three species involved. Source of collated data: Gray 1847; Miller 1911, 1919, 1920; Hooijer 1946; Frenkel 1970.

13), 14) The crown heights of the maxillary and mandibular teeth
(Tables XIII and XV)

No data for either H. indica or H. cristata is available. The diagnostic reliability of the character thus cannot be assessed. However, because there is considerable loss of tooth material from the occlusal surface with age (see 10.2.1.2 and 10.2.2.2), the amount depending on the hardness of the diet, it would appear to be an unreliable character to use diagnostically.

15), 16) The development and divergence of the roots of the maxillary (15) and mandibular (16) teeth (Figs. 113a, b)

This has been described for H. africae australis in sections 10.2. and 10.2.1.3 (maxillary dentition) and in section 10.2.2.3 (mandibular dentition) and found to be somewhat variable, although broadly conforming to a pattern of one lingual and two buccal (an anterior and posterior) roots in each of the maxillary teeth and a pattern of four rootlets, arranged to form a square, for the mandibular first and second molars. The mandibular premolar, both deciduous and permanent, has three roots, single anterior and two posterior roots, arranged to form a triangle, while the mandibular third molar has a pattern of two anterior and one posterior roots. The pattern of fusion between these 'basic' roots is often variable, as are the location and size of various 'accessory rootlets'. From an examination of published illustrations there do not appear to be grounds for considering this character as diagnostically significant.

17) The curvature of the maxillary teeth

Most of the teeth in the available Hystrix specimens were firmly fixed in their sockets and could thus not be extracted without damage. The significance of this character could thus not be studied.

18) Cross-sectional shape of incisors

There appears to be no significant difference between the three species of subgenus Hystrix in this feature. It is thus not diagnostic.

19) The nature of the crown enamel pattern (C.E.P.), the order of closure of the enamel folds and number of enamel islands

The nature of the crown enamel pattern is the character most frequently used in the description of new species of fossil Hystrix. As fossil teeth occur more frequently than any other cranial or skeletal element, considerable care was taken with the assessing of this particular character. The maturation of the C.E.P. of each maxillary and mandibular tooth has been investigated (sections 10.3.1 and 10.3.2 for the maxillary and mandibular crown enamel patterns respectively) and representative crown enamel patterns of each tooth at each growth stage were illustrated (maxillary Figs. 74 to 90; mandibular Figs. 91-107). In this way the basic pattern of enamel folds, the order of their closure and the maturation and final appearance of the crown enamel pattern could be studied. The following conclusions were drawn:

- a) There appears to be a definite basic pattern and number of enamel folds for each maxillary and mandibular tooth. These have been described in detail in the above-mentioned sections.
- b) The order of closure of these folds and the growth stage at which closure takes place is highly variable, depending on the angle of wear and the hardness of the diet.
- c) The number of enamel 'islands' in a mature crown enamel pattern is highly variable on account of 'subdivision' and 'fusion' of enamel fossettes and fossettids.
- d) The mature crown enamel pattern, although somewhat variable, conforms to the basic pattern of enamel folds that is apparent after the tooth first erupts.

The diagnostic validity of the crown enamel pattern was tested by comparing illustrations and actual crown enamel patterns of H. indica and H. cristata with the illustrations of those of H. africae australis. It appears that the basic pattern of enamel folds is the same for all three species, and hence it was not to be expected that the mature patterns would differ significantly. Bearing in mind the range of variation exhibited by the H. africae australis sample, no significant difference could be detected between the crown enamel patterns of this species and H. cristata. In H. indica, the posteriorly directed part of the metaflexus of the maxillary teeth fairly consistently opens at the distal surface, and the

fossette which results from the closure of this fold is strongly antero-posteriorly orientated rather than obliquely, as it is in the other two species. The fossettids of the mandibular teeth also show a stronger tendency toward subdivision than do those of H. cristata and H. africae-australis, but apart from these minor variations there appear to be no significant differences between the crown enamel patterns of the three species.

The differences in the crown enamel pattern thus appear to be too slight to be of use in the separation of the three valid species in the subgenus Hystrix. However, this study has not been in vain: if differences in the crown enamel patterns of fossil teeth are found from those described above, it can be said with some confidence that they do not belong to any one of these three species.

20) The downward extent of the external enamel fold on the mandibular teeth

Many of the teeth in the comparative sample of H. africae-australis were firmly embedded within their sockets and could not be removed for inspection without damage to the specimens. No measurements for this character were available for either H. indica or H. cristata and hence the diagnostic significance of this character could not be assessed.

21) The mesiodistal diameter ('length' measurements) of the maxillary and mandibular teeth measured at the occlusal surface (mm)
(Tables XIII and XV, graphs I and III)

It is obvious from the ranges and means shown in Tables XIII and XV and graphs I and III that the mesiodistal diameter measured at the occlusal surface is not a diagnostically significant character. Source of collated data: Sulimski 1960; Frenkel 1970.

22) The mesiodistal diameters of the maxillary and mandibular teeth measured at the alveolar rim (Tables XVII and XX, Appendix VII)

No data for the length measurements of either the maxillary or the mandibular teeth were available for H. indica and H. cristata. The diagnostic reliability of these measurements is thus uncertain but from the similarity of the measurements for H. africae-australis with those taken at the occlusal surface, it is highly improbable that the character is significant. It is in any case a poor character for use in fossil taxonomy

as so many teeth are completely isolated and the position of the alveolar rim is thus not apparent.

- 23) The buccolingual diameters ('breadth' measurement) of the maxillary and mandibular teeth measured at the occlusal surface (mm)
(Tables XIV and XVI, and graphs II and IV)

It is obvious from the ranges and means shown in Tables XIV and XVI and from graphs II and IV that the buccolingual diameter measured at the occlusal surface is not a diagnostically significant character. Source of collated metrical data: Sulimski 1960; Frenkel 1970.

- 24) The buccolingual diameters of the maxillary and mandibular teeth measured at the alveolar rim (Tables XVII and XX, Appendix VII)

See no. 22).

- 25) The crown occlusal areas of the maxillary and mandibular teeth measured at the occlusal surface (sq. mm) (Tables XII and XV, Appendix VII)

No data for this character is available for H. indica and H. cristata. From the similarity of the means and the sample range overlap of the basic measurements of the three species described under points 21) and 23) it appears highly improbable that the crown area will prove diagnostic.

- 26) The area enclosed by the alveolar rims of the maxillary and mandibular teeth (sq. mm) (Tables XVIII and XXI Appendix VII)

No data is available for H. indica and H. cristata. However, from the similarity of the basic length and breadth measurements taken at the alveolar rim to those taken at the occlusal surface and in view of the fact that neither occlusal length nor breadth measurements are diagnostic, it is highly improbable that the area enclosed by the alveolar rim (the product of the alveolar length and breadth measurements) will prove diagnostic.

- 27) The crown shape indices of the maxillary and mandibular teeth calculated at the occlusal surface (Tables XIII and XVI)

No data is available for H. indica and H. cristata. From the similarity of the means and the sample range overlap of the basic mesiodistal and buccolingual diameters for the three species it appears highly improbable that the crown shape indices will show any significant differences.

- 28) The crown shape indices of the maxillary and mandibular teeth calculated from the measurements taken at the alveolar rim (Tables XIX and XXII, Appendix VII)

The basic length and breadth measurements taken at the alveolar rim are very similar to those taken at the occlusal surface (cf. Tables XI, XIV, XVII and XX, Appendix VII). These basic measurements are of no diagnostic significance (see nos. 21) and 23)) and thus it is highly improbable that the crown shape index (the quotient of the breadth and length measurements measured at the alveolar rim) will prove to be of diagnostic significance.

None of the dental characters so commonly used in diagnoses of new species of fossil porcupine appear to have any real diagnostic validity. However, none of the above investigation has been in vain because the collated data serves an extremely useful comparative function: it is easy to tell, using this data as a basis for judgement, whether a fossil specimen belongs to one of the above three species or not; if any character assessed does show any significant degree of difference, it can be stated with confidence that the specimen concerned does not belong to either H. indica, H. cristata or H. africae australis.

TABLE XIII

The ranges and means of the crown heights and mesiodistal diameters of the maxillary teeth of *H. indica*, *H. cristata* and *H. africae australis* measured at the occlusal surface (mm)

SPECIES	<i>H. indica</i>			<i>H. cristata</i>			<i>H. africae australis</i>		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Crown height of dp^4/p^4	-	-	-	-	-	-	5,8-17,5	10,5	11
Crown height of M^1	-	-	-	-	-	-	9,0-19,5	13,9	8
Crown height of M^2	-	-	-	-	-	-	12,3-19,0	15,4	6
Crown height of M^3	-	-	-	-	-	-	12,0-17,4	14,5	5
MD diameter of I^1	5,0-6,0	5,6	10	6,5-8,0	7,2	3	3,3-7,3	5,5	19
MD diameter of dp^4/p^4	7,5-10,5=	9,0	15	7,5-10,5	9,7	4	6,4-10,7	8,8	20
MD diameter of M^1	5,7-8,0	7,3	16	7,2-8,0	7,8	4	7,0-9,2	8,1	23
MD diameter of M^2	7,0-9,0	8,0	16	7,4-9,0	8,5	4	7,3-9,8	8,6	19
MD diameter of M^3	6,2-8,3	7,2	15	6,6-8,5	8,0	4	6,8-9,5	7,9	11

TABLE XIV

The ranges and means of the buccolingual diameters of the maxillary teeth of *H. indica*, *H. cristata* and *H. africae australis* measured at the occlusal surface (mm)

SPECIES	<i>H. indica</i>			<i>H. cristata</i>			<i>H. africae australis</i>		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
BL diameter of I ¹	5,6-7,7	7,0	10	7,0-7,1	7,0	2	4,5-8,1	6,5	19
BL diameter of dp ⁴ /P ⁴	5,0-10,5	9,6	14	8,0-9,0	8,7	4	5,2 9,2	7,2	20
BL diameter of M ¹	6,1-8,5	7,3	16	7,0-9,0	8,2	4	4,6-9,3	7,4	23
BL diameter of M ²	6,8-8,4	7,4	16	7,0-9,0	8,4	4	5,1-9,1	7,3	19
BL diameter of M ³	5,1-6,6	6,1	15	6,0-8,0	7,0	4	5,2-8,4	6,9	11

TABLE XV

The ranges and means of the crown heights and mesiodistal diameters of the mandibular teeth of *H. indica*, *H. cristata* and *H. africaeaustralis* measured at the occlusal surface (mm)

SPECIES	<i>H. indica</i>			<i>H. cristata</i>			<i>H. africaeaustralis</i>		
	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
Crown height of dp_4/P_4	-	-	-	-	-	-	3,9-17,4	9,0	7
Crown height of M_1	-	-	-	-	-	-	10,3-17,5	13,6	6
Crown height of M_2	-	-	-	-	-	-	12,2-18,5	15,4	6
Crown height of M_3	-	-	-	-	-	-	13,0-18,0	14,8	6
MD diameter of I_1	4,9-6,5	5,4	20	6,5-7,5	7,0	4	3,1-6,8	5,2	26
MD diameter of dp_4/P_4	7,3-10,5	9,3	21	7,8-10,5	9,7	5	7,6-10,8	9,2	24
MD diameter of M_1	6,7-7,7	7,2	11	7,8-8,5	8,3	4	7,4-10,1	8,6	27
MD diameter of M_2	7,6-9,0	8,2	11	8,7-10,0	9,4	4	8,0-10,1	9,0	22
MD diameter of M_3	7,5-9,5	8,1	11	8,2-9,5	8,4	4	7,5-9,4	8,5	13

TABLE XVI

The ranges and means of the buccolingual diameters of the mandibular teeth of *H. indica*, *H. cristata* and *H. africae australis* measured at the occlusal surface (mm)

SPECIES	<i>H. indica</i>			<i>H. cristata</i>			<i>H. africae australis</i>		
CHARACTER	Range	$\bar{X}$	N	Range	$\bar{X}$	N	Range	$\bar{X}$	N
BL diameter of I_1	5,7-7,3	6,3	20	6,5	6,5	1	2,9-6,9	5,4	25
BL diameter of dp_4/P_4	5,5-9,0	6,7	21	7,0-8,0	7,7	5	4,1-8,3	6,4	24
BL diameter of M_1	6,2-7,3	6,8	11	7,0-8,0	7,4	4	5,0-8,0	7,0	27
BL diameter of M_2	6,6-7,5	7,0	11	7,7-9,5	8,3	4	5,8-8,9	7,2	22
BL diameter of M_3	5,5-7,4	6,4	11	7,5-9,0	8,0	4	5,7-7,8	6,7	13

12.5 Summary and a re-definition of *H. indica*, *H. cristata*
and *H. africae australis*

The degree of cranial inflation differs considerably between *H. indica*, *H. africae australis* and *H. cristata*, the first species having the least inflated cranium while the last is excessively inflated, *H. africae australis* occupying an intermediate position. It is thus not surprising that the cranial characters which appear to have the most diagnostic significance are, in the main, associated with those areas of the skull where this inflation is manifested, i.e. the premaxillary, nasal, frontal and zygomatic regions. Few of the many mandibular characters used in diagnoses proved to be of even potential taxonomic significance, while none of the dental characters appeared to be diagnostic. With so few (about 15) of the numerous (197) so-called 'diagnostic characters' proving to be of any significance, it is unfortunate that most of those that do appear to be of value are confined to delicate areas of the cranium which are seldom if ever preserved intact in the fossil state. Those characters that are of diagnostic value have been discussed at the end of each subsection in sections 12.2, 12,3 and 12,4 above and are summarized in Table XVII below: a written diagnosis of each species follows.

TABLE XVII

SUMMARY OF THE DIAGNOSTIC CHARACTERS OF THE THREE SPECIES IN THE SUBGENUS HYSTRIX

<u>Character</u>	<u>H. indica</u>	<u>H. cristata</u>	<u>H. africae australis</u>	<u>H. africae australis</u>
				<u>Growth stage 6</u>
1. Interorbital distance at rudimentary post-orbital process	24,0-63,0mm	58,0-68,5mm	49,9-78,0mm	68,0-78,0mm
2. Height of skull from palate between M ₁	52,8-65,5mm	68,0-77,0mm	52,0-73,0mm	57,0-73,0mm
3. Shape of cranial profile	almost flat	strongly convex	slightly convex	slightly convex
4. Presence of a 'notch' in skull profile at junction of nasal and frontal at midline	absent	present	absent	absent
5. Presence of a 'notch' in skull profile at junction of frontal and parietal at midline	absent	present	absent	absent
6. Breadth of nasal process of premaxillary at fronto-premaxillary suture ¹⁾	No measurements available but apparently in excess of 8,0mm	3,5mm	1,0-8,0mm	2,0-6,2mm
7. Breadth of nasal process of premaxillary between fronto-premaxillary suture and masseteric crest	No measurements available but apparently much wider than in other two species	10,7-20,0mm	7,0-14,8mm	8,0-14,8mm

TABLE XVII (continued)

Character	H. indica	H. cristata	H.africae- australis	H. africaeaustralis Growth stage 6
8. Shape of posterior termination of nasal process of premaxillary	broad and truncate	acute to narrowly spatulate	acute to narrowly spatulate	acute to narrowly spatulate
9. Length of nasal suture	42,5-76,2mm	44,5-101,0mm	39,5-84,5mm	63,3-84,5mm
10. Maximum width of nasal	8,0-25,5mm	27,5-42,5mm	19,9-41,4mm	28,0-41,4mm
11. Width of nasals anteriorly	No data available but apparently as wide or wider than posteriorly	17,2-20,5mm	12,7-24,0mm	16,5-24,0mm
12. Posterior extent of nasals behind fronto-premaxillary suture	7,0mm	31,0mm	5,8-27,9mm	18,4-27,9mm
13. Shape of posterior margins of nasals	sub-truncate to truncate	broadly rounded	sub-truncately rounded	sub-truncately rounded
14. Posterior extent of nasals in relation to lachrymals and orbit	terminate slightly short of or level with <u>anterior</u> border of orbit	terminate posterior to posterior margin of lachrymals i.e. towards <u>posterior</u> margin of orbit	terminate $\frac{1}{2}$ to $\frac{3}{4}$ of the length of the lachrymal, i.e. at or just posterior to anterior margin of orbit	as for general
15. Length of frontal suture	17-47mm	24-49mm	27,5-53,0mm	as for general
16. Shape of palatal notch	no information available	very broadly u-shaped	narrowly u-shaped	as for general
17. Anterior extent of palatal notch	no information available	as far as distal surface of last tooth	as far as lingual enamel fold	as for general
18. Vertical height of zygoma at maxillo-jugal suture ii)	apparently about 10mm or less	24,0	15,3-23,5	4,1-9,3

TABLE XVII (continued)

Character	<u>H. indica</u>	<u>H. cristata</u>	<u>H. africae- australis</u>	<u>H. africaeaustralis Growth stage 6</u>
19. Distance of lachrymal from maxillo-jugal suture iii)	apparently about 10mm or more	2,5mm	1,6-8,8mm	2,3-5,7
20. Length of nasals:occipitonasal length	38-61 %	44-68 %	43-60 %	48-60 %
21. Frontal length : nasal length	33-94 %	23-38 %	53-84 %	54-75 %
22. Greatest width : greatest length nasals	16-36 %	21,5-42 %	37-52 %	37-47 %
23. Width nasals anteriorly : width posteriorly	71 %	53-78 %	49-77 %	54-71 %
24. Width nasal proces of premaxilla : greatest width of nasals iv)	greater than 44%	19-36 %	24-47 %	24-41 %
25. Maximum width occiput : maximum width condyli	171-200 %	160-165 %	148-184 %	161-175 %
26. Hairs of crest v)	brown	white	white	white
27. Length of rattle quills (hollow part) vi)	less than 60mm	less than 60mm	greater than 50mm	-
28. Colour of rump	white	black or mottled	white	white

i), ii) Information for H. indica from Fig. 1 p.198, Müller 1920

iii) - vi) Information for H. indica from Corbet and Jones 1964 p.297

In the following descriptions numerical data is only given where it is of absolute diagnostic value in comparisons with the adjacent species (i.e. the data underlined in Table XVII) :

H. indica Kerr 1792

Characters: A medium-sized porcupine with a relatively low, moderately inflated cranium which has a very slightly convex, almost flat profile (height of skull from palate between M^1 less than 66mm) with no 'notch' at the junction of the nasal and frontal or at the junction of the frontal and parietal at the midline when viewed in profile; premaxillae wide (nasal process in excess of 8mm or more than 44% of nasal width), particularly at fronto-premaxillary suture but not inflated and expanded laterally, broad and truncate terminally; nasals short ($\bar{X} = 61,9\text{mm}$), parallel-sided and not expanded posteriorly (maximum posterior width less than 26mm) and broad anteriorly, extending as far as or just short of anterior border of orbit or only 7,0mm beyond the fronto-premaxillary suture, not convex but flat and not obviously inflated anterior to the naso-frontal suture, sub-truncate to truncate posteriorly; frontals long (frontal:nasal length $\bar{X} = 68\%$), not expanded in region of rudimentary post-orbital process; zygoma narrow at maxillo-jugal suture (approximately 10mm or less); lachrymal widely separated from maxillo-jugal suture; maximum width of occiput: maximum width of condyle between 171 and 200%; crest brown; rump white, rattle quills < 60mm.

H. cristata Linnaeus 1758

? Characters: A large to variable-sized porcupine with a relatively high, excessively inflated cranium which has a strongly convex profile (height of skull from palate between M^1 in excess of 68mm), when viewed in profile showing a readily evident notch at the junction of the nasal and frontal and also at the junction of the frontal and parietal at the midline; premaxilla narrow (nasal process $\pm 3,5\text{mm}$ or only 19-36% of nasal width) but much inflated and laterally expanded, acute to narrowly spatulate terminally; nasals long ($\bar{X} = 83,0\text{mm}$) tapering

anteriorly and much expanded posteriorly (maximum posterior width between 27,5 and 42,5mm) and hence of roughly triangular shape, extending to posterior margin of orbit or just posterior to posterior margin of lachrymal (31,0mm beyond fronto-premaxillary suture), much inflated and markedly convex immediately anterior to fronto-premaxillary suture, broadly rounded posteriorly; frontals short (frontal: nasal length $\bar{X} = 32\%$), much expanded due to inflation in region of rudimentary post-orbital process; zygoma wide at maxillo-jugal suture (24mm); lachrymal only just separate from maxillo-jugal suture (2,5mm); palatal notch broadly u-shaped, extending forwards only as far as posterior margin of last tooth; maximum width of occiput: maximum width of condyle between 160 and 165%; crest white; rump black or mottled; rattle quills < 60mm.

H. africae australis Peters 1852

Characters: A medium-sized porcupine with a moderately high, much inflated cranium which has a slightly convex profile (height of skull from palate between M^1 between 52 and 73mm) with no conspicuous 'notch' at the junction of frontal and parietal or at the junction of the frontal and parietal at the midline when viewed in profile; premaxilla narrow (nasal process 1-8mm or 24-47% of nasal width) not obviously inflated or laterally expanded, acute to narrowly spatulate terminally; nasals of intermediate length ($\bar{X} = 66,3\text{mm}$) tapering only slightly anteriorly and somewhat expanded posteriorly (maximum posterior width between 19,9 and 41,4mm), and hence of sub-rectangular shape, extending to anterior border of orbit or slightly beyond (5,8-27,9mm beyond fronto-premaxillary suture), only slightly convex and inflated immediately anterior to fronto-premaxillary suture, sub-truncately rounded posteriorly; frontals of medium length (frontal : nasal length $\bar{X} = 62\%$), not much expanded or inflated in region of post-orbital process; zygoma of intermediate height at maxillo-jugal suture (15,3-23,5mm); lachrymal separated from maxillo-jugal suture by between 1,6-8,8mm; palatal notch narrowly u-shaped, usually extending forwards as far as lingual

enamel fold; maximum width of occiput : maximum width of
condyle between 148 and 184%; crest quills white; rump white;
rattle quills < 50mm.

13. METHODS FOR DETERMINING THE POSITIONAL SOURCE OF ISOLATED AND SEMI-ISOLATED PORCUPINE TEETH, MODERN AND FOSSIL

This could not be devised until a thorough knowledge of the dental morphology of Hystrix had been acquired.

The identification of isolated teeth is essential for comparative and statistical purposes as well as for the assessment of the minimum numbers of individuals in a sample. Several of the identificatory criteria given below may have to be considered in conjunction with one another before the identity of an isolated tooth can be ascertained.

13.1 The identification of incisors

The upper and lower incisors are markedly different from the molar teeth, being long and strongly curved with an enamel covering on the anterior surface only.

13.1.1 The differentiation of upper incisors from lowers

Upper incisors can readily be distinguished from the lowers on account of their noticeably stronger curvature (Figs.132 a,b). The difference in curvature is visually apparent even in short sections of fragmentary incisor teeth. The marked difference in curvature is caused by the fact that the upper incisor originates in front of the upper tooth row which has an average length of $\pm 35\text{mm}$ in H. africaeaustralis, whereas the lower incisor originates in the condylar region, well behind the lower tooth row (see X-ray, Fig. 111). The radii of curvature of the upper and lower incisors of a sample of H. africaeaustralis and for the fossil material are provided in Appendices VII and VIII.

A further though less decisive differentiating feature is that the wedge-shaped occlusal surface of the upper incisors more frequently has the shape of an equilateral triangle, while that of the lowers often has the shape of an elongate isosceles triangle (Fig.132 f, g).

13.1.2 The differentiation of left incisors from right

The criteria used to distinguish left incisors from right are the same for both upper and lower teeth.

The mesial (inner) surfaces of the incisors of Hystrix africaeaustralis are flattened, while the distal surfaces are convex or rounded (Fig.132c) If any part of the incisal surface is preserved there should be no difficulty in distinguishing an incisor as either left or right.

If no part of the cutting edge has been preserved, the dimensions of the pulp cavity as seen on the two fractured 'cross-sections' on either end of the tooth fragment can be used. As mentioned in the section on tooth morphology (Chapter 10), the pulp cavity is larger (and the dentine and enamel thinner) at the root end of the incisors, tapering off and terminating at or near the incisal surface (see Fig.112 Chap. 10). The pulp cavity is usually not exposed on the occlusal surface where the dentine with its labial enamel sheath forms a continuous cutting wedge. In the vicinity of the incisal surface the pulp cavity (usually matrix-filled in fossil specimens) thus has a very narrow diameter and the dentine is considerably thicker (Fig.132 d, e) while at the root end the pulp cavity occupies most of the volume of the tooth and is enclosed in a thin layer of dentine.

A further means of orientating incisors is the presence of extremely fine fissures in the vicinity of tooth formation at the apical extremity of the incisors, if this has been preserved, (Fig.132 a, b). A final orientating clue is the fact that the incisor width and thickness decreases slightly from the incisal surface backwards (Fig.132 a, b).

13.2 The premolars and molars

Both upper and lower premolars and molars are very similar in appearance.

13.2.1 The separation of upper premolars and molars from lower premolars and molars

? The upper deciduous and temporary premolars and molars can usually be distinguished from the lowers by their well-marked curvature, especially in immature teeth. The curvature on the upper teeth is from the midline outwards, i.e. buccally, prolonged wear often having the apparent effect of reducing the curvature as illustrated in Fig.133b,c,d). In the latter situation, other criteria have to be used to separate the upper and lower teeth.

The upper teeth are more cylindrical in cross-section than the lower, which have a more rectangular outline, as can be observed from the occlusal surfaces of well-worn teeth. However, the latter feature is not a very satisfactory identificatory feature to use on its own, especially for immature teeth (Fig. 133e, f). *p. 136.*

The roots provide a reliable means of separating maxillary and mandibular dentitions. The roots of the mandibular teeth are always more

strongly developed than those of the curved upper premolars and molars, where the rootlets are poorly developed and papillate, so that the dentition of Hystrix is classed as 'semi-rooted'. However, in the giant fossil form Xenohystrix crassidens, the roots of both upper and lower premolars and molars are exceptionally well developed.

The maxillary deciduous and permanent premolars and molars have a single large broad lingual root, probably representing the fusion of mesio-lingual and disto-lingual rootlets and two smaller equal-sized buccal rootlets, termed the mesio-buccal and disto-buccal rootlets (Figs. 67, 68). The lingual root curves towards the two slightly divergent outer roots.

The mandibular premolars and third molars also have three roots, but these occupy different positions from those in the maxillary. The premolars have a large disto-buccal root, (i.e. posterior outer) and a smaller mesial rootlet. Their smallest rootlet is the disto-lingual rootlet (Fig.133 1,m). The lower third molars have a large distal root and smaller mesio-buccal and mesio-lingual rootlets. The four three-rooted mandibular teeth are thus easily separable from the upper teeth.

The lower first and second molars have four rootlets, equally developed and arranged in the form of a square: mesio-buccal, mesio-lingual, disto-buccal and disto-lingual (Fig.133 1,m). Any four-rooted tooth is therefore either a mandibular M_1 or M_2 .

Unfortunately the roots of fossil specimens are frequently missing.

Further points to which attention should be drawn in the separation of upper and lower teeth are: the upper molars have one internal (lingual) enamel fold which originates at the centre of the lingual surface of the tooth and extends obliquely forwards across the tooth, and three external enamel folds. The lower teeth have a single outer (buccal) enamel fold, which originates at the centre of the buccal surface and extends obliquely backwards across the tooth. In the mandibular dentition, the external enamel fold defines a larger segment of the tooth anteriorly, i.e. more of the tooth lies anterior to the fold than posteriorly. In the upper dentition, the anterior and posterior 'segments' of the tooth are sub-equal.

Furthermore, it should also be recorded that the upper and lower first and second molars have two proximate facets in the mature stage, one at the mesial and one at the distal contact points, while the upper and lower premolars and third molars only have one each.

From the above descriptions it should be possible to differentiate the upper and lower dentitions.

13.2.2 The separation of left maxillary premolars and molars from right

The internal enamel fold or hypoflexus, which is usually the last fold to become 'closed' or fused, is on the lingual surface of the tooth, originating near the centre of the lingual area of the circumference and extending obliquely forwards across the tooth. The hypoflexus is apparent on the lingual surface of the tooth as a groove or hypostria. Once this fold becomes 'closed' it appears as a hypofossette on the occlusal surface. The upper teeth have three or more external enamel folds. The enamel fossettes or islands representing the sealed-off folds form a series of staggered 'V's the open ends of which are towards the distal surface (Figs.69,133F). These features proved satisfactory in the separation of the left upper dentition from the right.

13.2.3 The separation of upper deciduous premolars and permanent premolars from the upper molars

The most diagnostic feature of the maxillary deciduous and permanent premolars is that they have only one pressure facet, situated on the distal surface of the tooth, being the anteriormost tooth in the row. The only other maxillary tooth which in a mature state has only one pressure facet is the M^3 , but this is on the mesial surface. The third molars can usually be differentiated from the cylindrical and fairly straight premolars by their more triangular outline and stronger buccal curvature. Should a M^3 be confused with a dp^4 or P^4 , it will appear back-to-front as the hypoflexus will slant from the middle of the lingual surface backwards instead of forwards. The 'V's formed by the flexuoses or fossettes will open anteriorly instead of posteriorly.

As tooth eruption occurs rotationally the upper first and second molars also have only one pressure facet in their early stages (distal) but these teeth can be distinguished from the premolars by the same means by which the M_3 can be differentiated.

Because it has no anterior adjacent tooth, the P^4 can expand unimpeded and is often conspicuously larger than any of the molars. For the same reason the anterior roots (mesio-buccal and mesio-lingual portion of the lingual root) extend further forward than those of the molars, anterior even to the mesial occlusal rim. Lastly, the roots of the dp^4 and P^4 are better developed than those of the M^3 , the dp^4 in particular having long and conspicuously divergent roots (Figs. 113b, 1 and 2)

13.2.4 The identification of upper first molars

The first molar, prior to the eruption of M^2 and the second molar prior to the eruption of M^3 have only one (mesial) pressure facet. As mentioned in 13.2.3, the M^3 at all stages of wear and development has one (mesial) pressure facet. There is therefore a danger of confusing newly-erupted unworn first, second and third molars. The latter, however, are fairly easily separable by their marked buccal curvature, poorly developed rootlets and roughly triangular shape; the first molars, and particularly the second molars have an approximately rectangular outline. However, newly-erupted upper first and second molars are frequently indistinguishable - possibly the M^2 might show a more marked buccal curvature and less well developed rootlets, but this is relative and can only be detected if an adjacent M^1 and M^2 are both present. If any doubt exists, measurements made on such teeth have been included under both M^1 and M^2 columns in the relevant tables, and marked with a double asterisk, denoting an uncertain identification.

The separation of worn upper first from worn upper second and third molars usually presents no difficulty. The M^3 can be separated by the three features mentioned above and by the fact that worn teeth have only an anterior pressure facet. Worn first molars rapidly become compressed due to pressure caused by the developing dp^4 or P^4 in front and by the M^2 behind; they thus rapidly attain a roughly circular or square occlusal surface with MD and BL diameters sub-equal or the latter even exceeding the former. The M^2 remains a more slender rectangular or elongate oval tooth and its breadth (BL) seldom exceeds its length (MD). Continued and increasing pressure from the P^4 progressively compresses the M^1 antero-posteriorly, until it becomes noticeably broader than long (Figs. 71, 133g). This pressure sometimes causes the tooth to decay, and the pressure facets of the M^1 are larger and more marked than those of any other tooth. In a mature dentition, the M^1 is the oldest tooth in the row (the dp^4 is replaced) and has better developed and more divergent roots. Longer exposure to wear causes the tooth to have a very simple crown enamel pattern and the least curved appearance (Figs. 73 and 133H).

13.2.5 The identification of upper second molars

The means of distinguishing upper second molars from other maxillary teeth have already been explained in 13.2.4.

13.2.6 The identification of M^3 's

See 13.2.3 and 13.2.4.

13.2.7 The separation of left mandibular teeth from right

The lower teeth have one external enamel fold (hypoflexid) and three or four inner enamel folds (the para-, meso-, meta- and entoflexids). The most prominent of the folds, the external hypoflexid, is usually the last to become 'closed' or fused, and extends obliquely backwards across the tooth, from its origin approximately halfway to two-thirds of the distance along the length of the buccal face of the tooth, working backwards. Once 'closed', the flexids form a series of enamel fossettids which form a pattern of 'V's, the apices of each 'V' facing disto-buccally and the open end of the 'V' facing forwards. These facts alone proved satisfactory in the separation of the left mandibular teeth from the right.

13.2.8 The separation of lower deciduous and permanent premolars from the lower molars

The main features whereby premolars may be separated from the remaining mandibular teeth are the single distal pressure facet, the presence of only three but markedly divergent roots, and the elongate-oval to roughly rectangular occlusal outline of the tooth. The other teeth which have only one pressure facet (the M_1 prior to the eruption of M_2 , the M_2 prior to the eruption of the M_3 and the M_3) have this on their mesial face; the M_1 and M_2 have four roots which are not markedly divergent and the two to four irregularly rooted M_3 generally has a more triangular occlusal outline. The roots of the latter tooth are neither as long nor as divergent as those of the P_4 . The dp_4 has particularly divergent roots, the mesial and disto-buccal being the largest, followed by the disto-lingual root. There are sometimes several other minor papillate roots. The permanent premolar has a well developed disto-buccal root which is the longest, followed by the mesial and disto-lingual roots. The P_4 is by far the largest tooth in the jaw (see Figs. 113b, 114).

13.2.9 The identification of the lower first molars

Newly-erupted and unworn lower first and second molars both have only an anterior pressure facet but acquire posterior pressure facets with the eruption of M_2 and M_3 at growth stages 3 and 4 respectively. In addition, up to late growth stage 5, both teeth have a similar oval or roughly rectangular occlusal outline, and four roots. Up to this stage, therefore, the

two teeth are very easily confused. If there is any doubt as to whether an isolated tooth is an M_1 or M_2 , the measurement has been listed under both columns in tables of measurement in Appendices and marked with a double asterisk to denote the uncertainty of the identification. The only possible distinction is that the M_2 is a slightly larger tooth than the M_1 and it would have a less mature crown enamel pattern for its size, since it would have suffered less attrition, having erupted after the M_1 .

From the onset of growth stage 5 and the eruption of the permanent premolar, the teeth can be distinguished by differences in the development of the pressure facets. The lower M_1 , instead of becoming markedly antero-posteriorly compressed as is the case in the maxillary dentition, has its mesial surface extensively faceted, to the extent that the dentine is exposed (Fig. 133 I). The tooth may be compressed until the occlusal outline is almost round and the MD and BL diameters subequal. Even before dentine is exposed on the mesial pressure facet, the facet acquires a concave curve which accommodates the posterior bulging surface of the large P_4 (Fig. 133 I). This curve becomes accentuated with increasing age. A concave mesial pressure facet only occurs on the M_1 ; the tooth has a rounded occlusal outline and is the smallest in the tooth row.

13.2.10 The separation of the lower second molars

See also 13.2.9. The M_2 has an approximately rounded-rectangular outline almost throughout its cycle of wear and except for the permanent premolar, is the largest tooth in the row. In old specimens (mid- to late growth stage 6) the rectangular outline becomes somewhat more rounded.

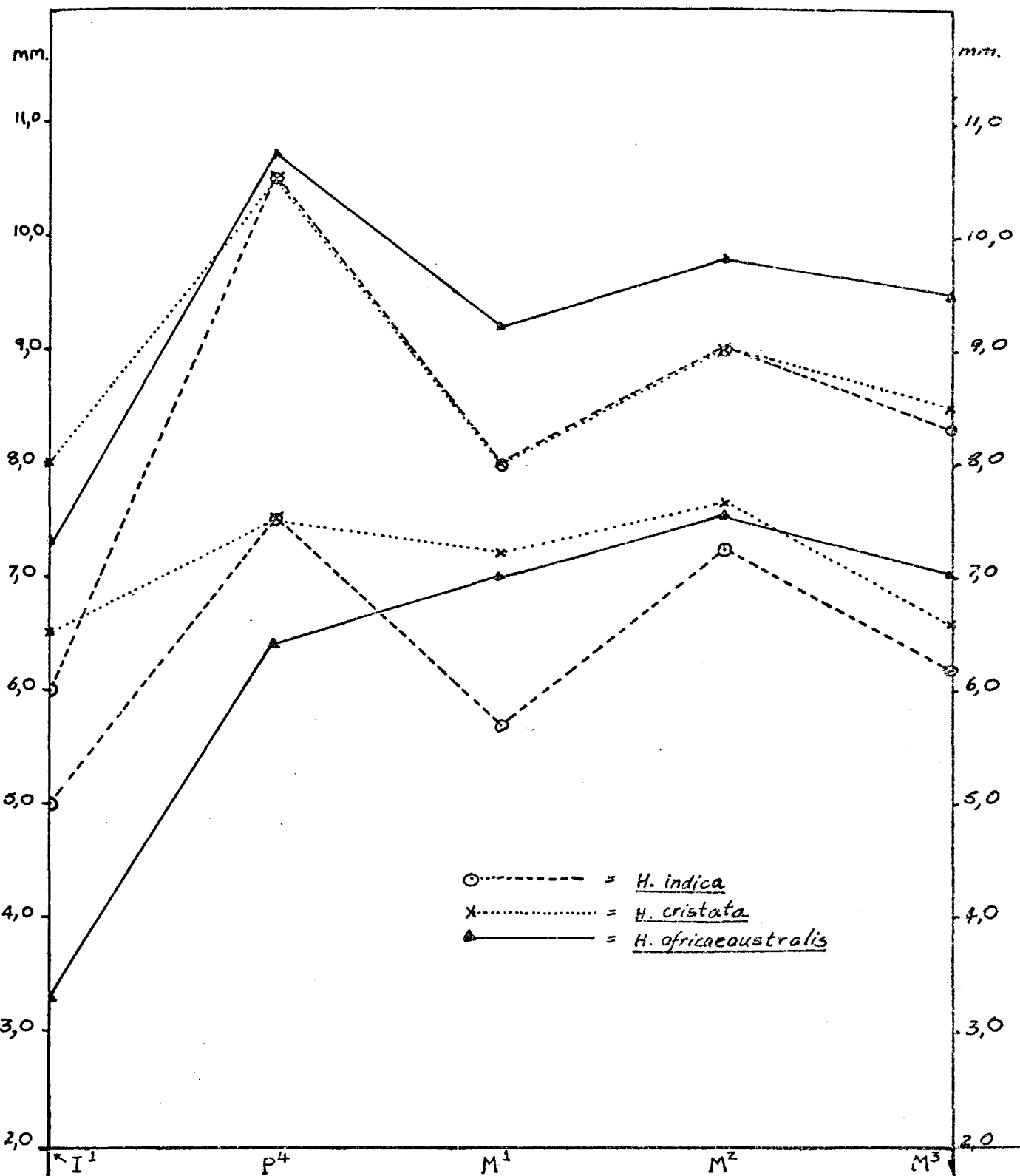
It is rare for the mesial pressure facet in M_2 to reach a stage where the dentine shows as in M_1 , nor is this facet ever as convex as in the latter. The mesial and distal pressure facets are equally well developed in M_2 whereas in the M_1 the mesial facet is noticeably larger from growth stage 5 onwards (see Fig. 133 I, J).

13.2.11 The separation of M_3 's

See also 13.2.8. The M_3 is the only tooth in a fully worn tooth row which has only an anterior pressure facet. Immature first and second lower molars also only have an anterior pressure facet but can be distinguished by the presence of four rootlets and a roughly rectangular shape. The M_3 has three roots, of which the distal root seems the largest and is probably the result of fusion of the distal rootlets. It is a much smaller tooth than the P_4 ,

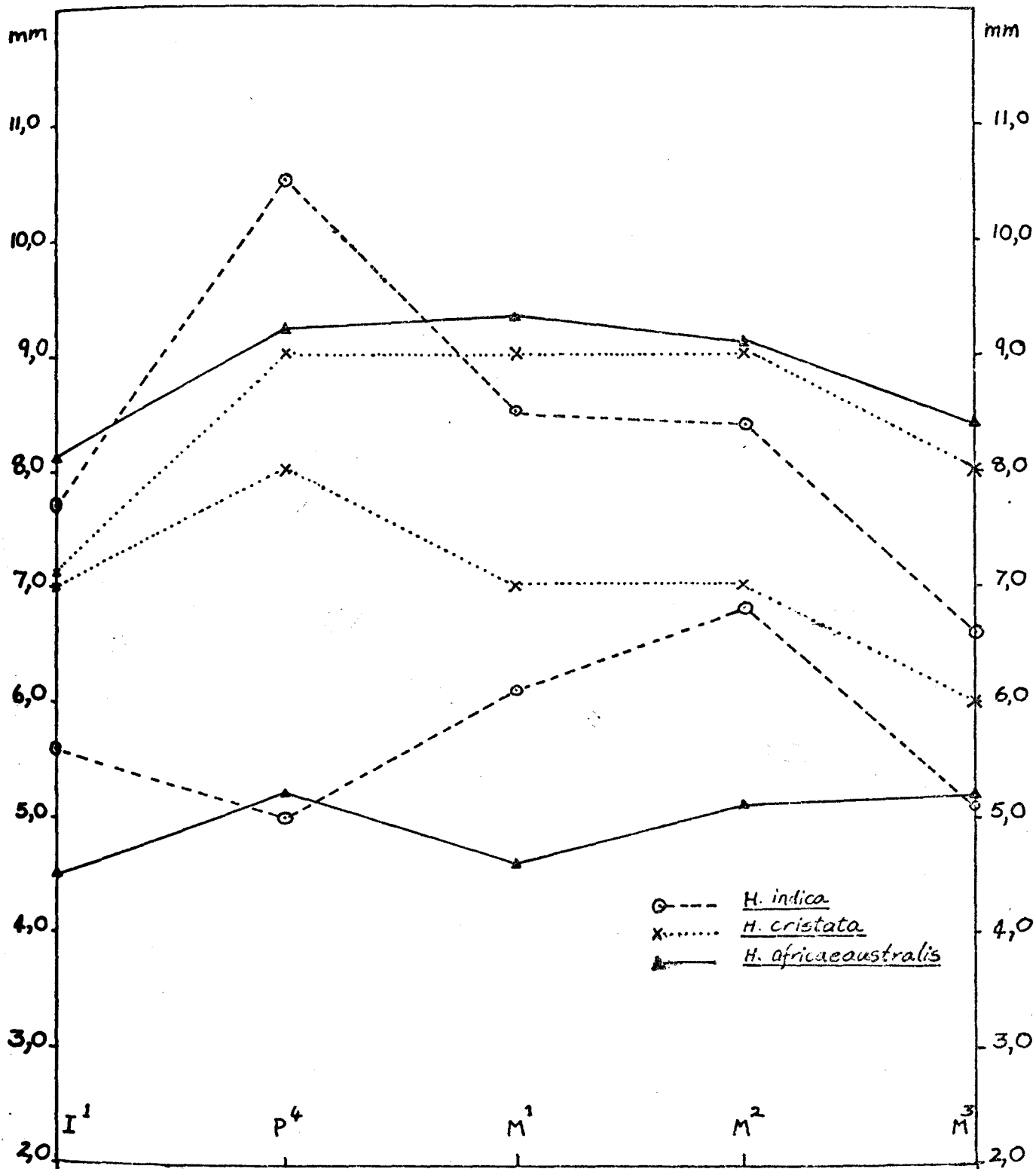
with which it might be confused. It has a roughly triangular outline.

The most easily-confused teeth are therefore the immature first and second molars of both jaws. Uncertain identifications of these teeth are noted in the tables of measurement.



Graph I

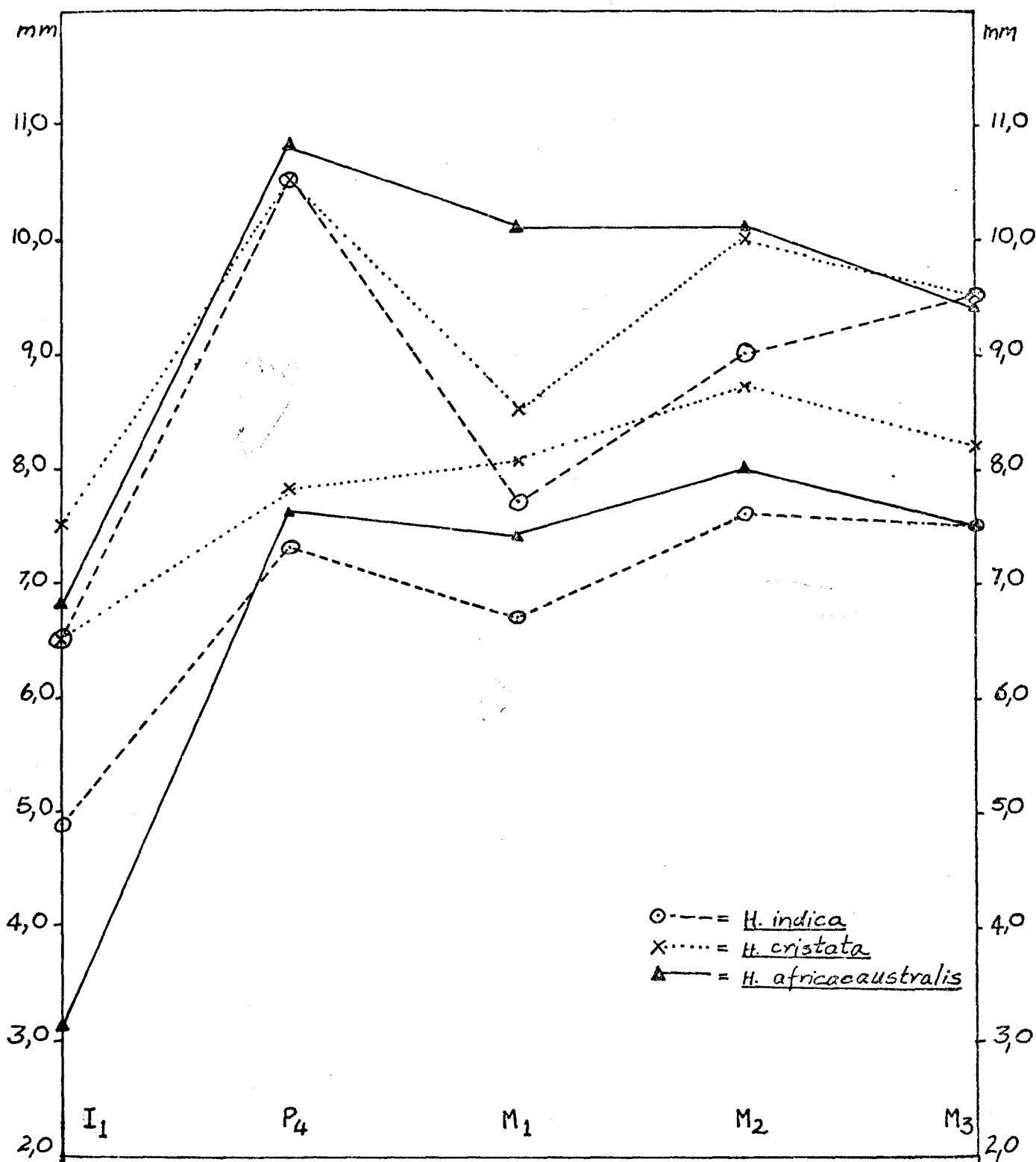
Graph showing the degree of overlap of the mesiodistal diameter measurements for the maxillary teeth of *H. indica*, *H. cristata* and *H. africaeustralis*. Lines represent upper and lower limits of sample ranges.



Graph II

Graph showing the degree of overlap of the buccolingual diameter measurements for the maxillary teeth of *H. indica*, *H. cristata* and *H. africae australis*

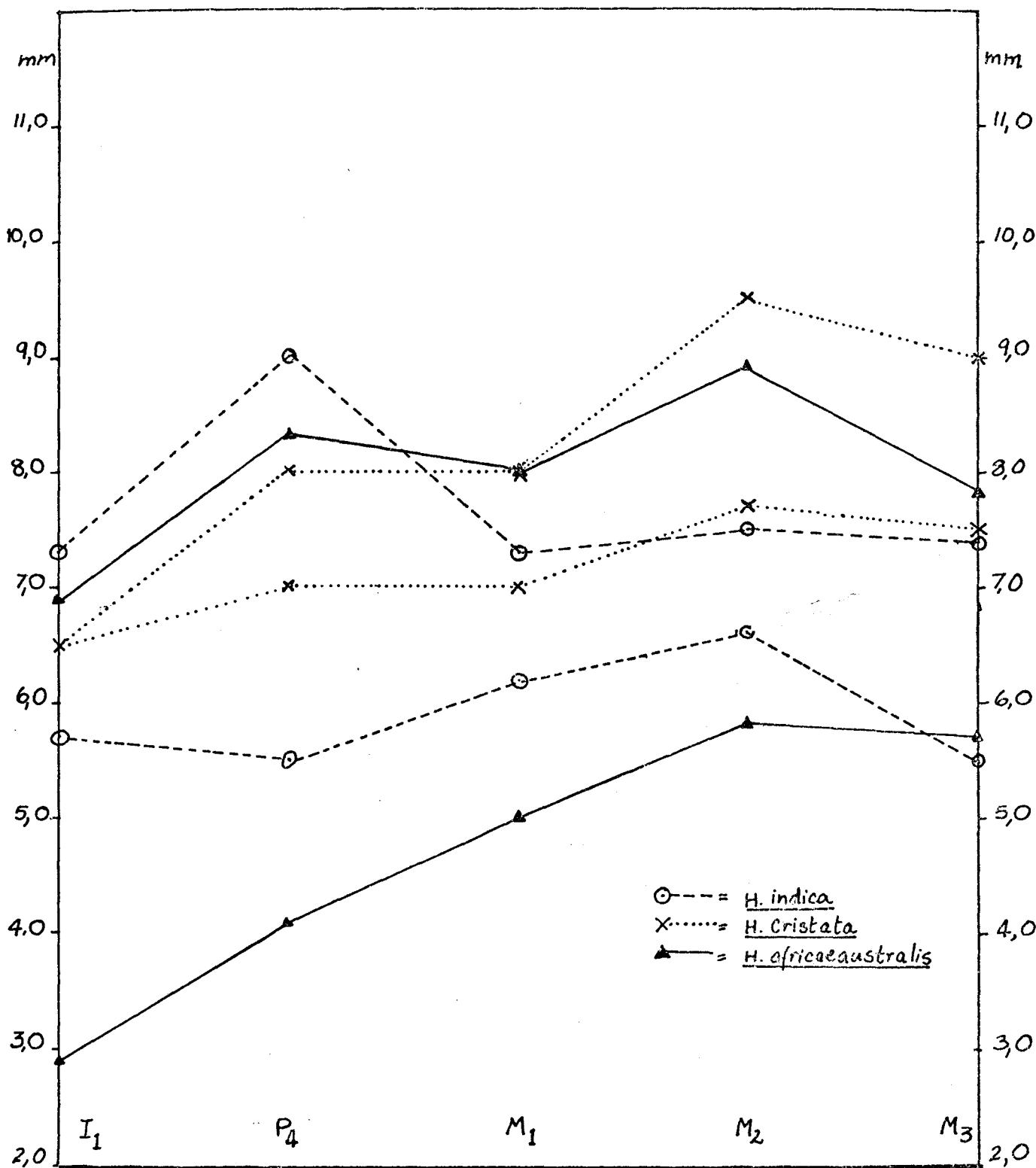
Lines represent upper and lower limits of sample ranges



Graph III

Graph showing the degree of overlap of the mesiodistal diameter measurements for the mandibular teeth of H. indica, H. cristata and H. africae australis

Lines represent upper and lower limits of sample ranges



Graph IV

Graph showing the degree of overlap of the buccolingual diameter measurements for the mandibular teeth of H. indica, H. cristata and H. africae australis
 Lines represent upper and lower limits of sample ranges

14. SYSTEMATIC PALAEOLOGY - THE TAXONOMIC STATUS AND DESCRIPTION OF THE SOUTH AFRICAN FOSSIL PORCUPINE MATERIAL

14.1 Taxonomic methods

The diagnostic reliability of the numerous characters used to define new species of porcupine was first investigated according to the method described in 12.1, with particular attention being paid to mandibular and dental characters as fragments of this type occur more frequently as fossils than do other cranial parts. The outcome of this investigation was to demonstrate that none of the mandibular and dental characters so frequently used to distinguish new species of fossil porcupine are of any use in the separation of the three modern valid species of Hystrix. The diagnostic characters are all associated with the degree of cranial inflation in the premaxillary, maxillary, nasal and frontal regions of the skull (seldom preserved in fossil form) while no significant differences in the dentitions or mandibles of the three species could be demonstrated. This discovery suggests that if significant differences in the mandibles and dentitions of two fossil forms can be demonstrated, it is very probable that they belong to different taxa.

A list of all described fossil Hystrix and closely related forms was then compiled and an attempt made at establishing which of these species are valid. The discussions on the validity of fossil forms are contained in the sections marked 'comments' of Appendix X Vol. II pp.198-344, and summarised in Table XVIII, this text. Descriptions, measurements and illustrations of all these forms were collated to facilitate validity assessments and comparison. Special note was taken of their geological age so that the South African fossil material could be compared with all contemporary fossil forms and evolutionary trends within the group commented upon.

This collated numerical data, the published data for the three South African fossil forms already described and the data compiled for H. africae australis was used as a basis of comparison for the undescribed fossil material. For example, the sample ranges for the mesio-distal and buccolingual diameters for each tooth of H. africae australis was plotted graphically against those for the sample of Xenohystrix crassidens described by Greenwood (1955), the ranges for the giant porcupine being decidedly higher than those of the first species with no area of overlap between (graphs 7 and 8). Suspected X. crassidens

specimens falling within or above the range for this species obtained from the measurements of Greenwood's referred sample could with confidence be referred to this species. In the case of suspected X. crassidens specimens with measurements falling in the area between the two ranges, characters other than size such as root development, basic enamel fold pattern, depth and curvature of diastema etc. were used to aid a decision. In this way, the lower limit of the X. crassidens sample range was lowered for some teeth. Similarly, suspected H. africae australis specimens falling within the range for the modern form were referred to this species after determining that their other characters also fell within the range for this species. Specimens falling just above the limits for H. africae australis were considered in the light of the considerable experience of all the dental characters of this species apart from size, and in most cases it was possible to make a confident decision as to whether they belonged to H. africae australis or not. In this way, the upper limit of the H. africae australis range was extended slightly for some teeth. Specimens still falling between the two ranges after these adjustments had been made were regarded as potential H. makapanensis specimens, this species being a large fossil form intermediate in size between H. africae australis and the giant X. crassidens.

A method was devised for identifying the positional source of isolated teeth (13.2) which are extremely similar in appearance, as well as a method for referring isolated teeth to a specific growth stage by means of their crown enamel pattern (7.1.5), to facilitate more significant comparisons.

Finally, the South African material was compared with all contemporaneous Old World fossil forms to determine whether or not any of it could be considered as synonymous with any of these earlier named species.

14.2 Statistical methods

The fossil samples available are far too small (usually of the order of 5 teeth or less of any one tooth class) for any simple statistical analyses to be undertaken. In any case, it was possible in most instances to assign a fossil specimen without difficulty to a specific taxon without recourse to mathematical procedures, only about 5 isolated teeth (mostly fragmentary incisors) proving problematic. However, all the

raw data (original observations, range, maximum, minimum, mean and SD) are presented in Appendices VIII and IX, Vol. II so that such computations can be done at a later stage if deemed necessary.

14.3 Description of the fossil material

The data on which all taxonomic decisions have been based is contained in Appendices VII, IX and X, Vol. II.

14.3.1 Hystrix africaeaustralis Peters 1852

- + ORDER: RODENTIA
- + SUBORDER: HYSTRICOMORPHA
- + SUPERFAMILY: HYSTRICOIDEA
- + FAMILY: HYSTRICIDAE
- + SUBFAMILY: HYSTRICINAE Lyon 1907 p.578

Note: Some authors, notably Ellerman (1940) and Mohr (1965) do not consider the subdivision of the family into two subfamilies, the Hystricinae (containing the genera Thecurus, Acanthion, Hystrix and presumably Sivacanthion and Xenohystrix) and the Atherurinae (containing the genera Trichys and Atherurus - see Table III) as necessary, arguing that there is an unbroken gradation from the least specialized genus Trichys to the genus (or subgenus) Hystrix, the most specialized of the Hystricine genera. The present author agrees with this point of view because the gap defined by Lyon (1907 p.592) when dividing the Hystricinae from the Atherurinae is to a large extent bridged by the fossil X. crassidens, which has teeth somewhat intermediate between the ultra-brachydont condition typical of the primitive Atherurinae and the hypsodont condition characteristic of the Hystricinae. The fossil is large (like the Hystricinae) but has a reconstructed skull outline and palate more typical of the Atherurinae (see reconstruction, Figs. 129,130 compared with the cranial illustrations of Trichys (Fig. 25) and Atherurus (fig. 27)). It is probable that in cranial inflation and quill cover X. crassidens was intermediate between the Atherurine and Hystricine conditions.

GENUS: HYSTRIX Linnaeus 1758

Generic diagnosis

Original diagnosis (Linn. 1758):

'Dentes primores II, oblique scissi, molares octo, corpus spinis tectum' (Linnaeus 1758 p.56)

Updated diagnosis (Ellerman 1940 pp.212-213):

Nasals even in primitive forms longer and broader than in Thecurus, extending about to lachrymal level in brachyurus group, ultimately approaching the level of the posterior zygomatic root (cristata group), usually longer than frontal. Prominent sagittal crest normally present in adult. Occiput thick, strongly ridged, prominent. Bullae relatively small; paroccipital processes not much lengthened. Palate broad, extending about to end of toothrows behind and straight, not depressed in front of toothrows; palatal foramina short and far in front of toothrow. Lachrymal moderately large. Mandible with hinder part flattened, angular portion powerfully ridged and distorted outwards. Coronoid process low. Externally very large (38" - 810mm). Body densely covered with well-developed protective spines; caudal rattling quills a well-developed hollow capsule (abbreviated).

SUBGENUS: HYSTRIX Linnaeus 1758 p.56 (Figs.33,34,35,36, this text)

Subgeneric diagnosis (Ellerman 1940 p.215)

'With highly specialized development of external characters, crest on nape and upper back long and fully developed, caudal rattling quills at maximum development, a profuse growth of very long many-ringed quills covering the short thick ones of Acanthion.'

SUBGENUS: ACANTHION Cuvier 1822 p. 425 (Figs.31a,31b,32, this text)

Subgeneric diagnosis (Ellerman 1940 p.213)

'Crest poorly developed, vestigial or absent; caudal quills moderately to poorly developed; body quills thick but without profuse mantle of many-ringed longer quills present and covering them. Quills with one ring only'

It has been noted (Chapter 5) that Lönnerberg (1922) concluded that no diagnosis could effectively distinguish the separate genera Hystrix and Acanthion, as they were prior to this date, and proceeded to use Acanthion in a subgeneric context. Ellerman (1940) upheld this view, but some authors (notably Mohr 1965) prefer to accord Acanthion full generic status. However, if the little-known form currently referred to as Hystrix (Acanthion) subcristatus proves to be an intermediate between Acanthion and Hystrix, the former name will have to be placed in synonymy under Hystrix.

SPECIES: Hystrix (Hystrix) africaeaustralis Peters 1852

Specific diagnosis

See chapter 12, section 12.5 which diagnoses all three valid species in this subgenus. As the description for H. africaeaustralis does not include the dentition, this has been discussed in some detail in the description of the fossil form below:

Referred specimens (see also Appendix VIII Table I pp.152-154 Vol. II)

Makapansgat Limeworks:

Grey breccia (Member 3): (Fig. 115)

M1000; M1001(?); M1016; M1806 (Fig.115); M1807;
M1817-M1823; M1825; M2527; M8291-8294(?)

Pink breccia (Member 4): (Fig. 116)

M8277

Phase II breccia (Member 5):

M8284, M8285

Sterkfontein: (Fig. 117)

Type site: STS 957a (Fig.117)-STS 957e; STS 1622; STS 2061;
STS 2078; STS 2095

Dump 1 : SFN 1-5

Dump 2 : SFN 6

Dump 8 : SFN 8-SFN 14; SFN 15?; SFN 16

Dump 10 : SFN 17?

Dump 13 : SFN 7

Swartkrans: (Fig. 118)

Member 1 : SK 2466a,b; SK 2875; SK 3082; SK 4315; SK 14237?

Member 2 : SK 2040; SK 2045; SK 2835; SK 3063 (Fig.118); SK 6945;
SK 7155; SK 14235; SK 14238

Kromdraai A: (Fig. 119)

Fine-grained breccia: KA 757 (Fig. 119); KA 1432; KA 1607; KA 1912?

Cave of Hearths (Graphs IX and X)

All 91 Cave of Hearths specimens (see Appendix II) have been referred to the recent southern African species, despite the somewhat large P_4 .

Description of fossil *Hystrix africaeaustralis* material

Cranium: Only two specimens (SK 2835 and SK 3082) were sufficiently

well preserved to show any cranial morphology at all, and the only characters for which measurements could be obtained were for the mesial sutural length of premaxilla ventrally (SK2835, 17,0mm), the palatal length of premaxilla medially in front of foramina incisiva (same specimen 10,7mm), the upper diastemic length (same specimen 40,3mm), the palatal width between M^2 and M^3 (SK3082, 15,0 and 15,7mm*) and the length and breadth of the foramina incisiva (SK2835 7,0 and 6,6mm). All of these measurements, with the exception of the palatal sutural length of the premaxilla anterior to the foramina incisiva which is somewhat shorter than in the modern sample, probably due to fracture, fall well within the range for the appropriate growth stage in the modern sample, see Table XX. The palate of SK3082 is sufficiently well preserved to indicate that the palatal notch is of the H. africae australis type rather than of the H. cristata type (see Table XVII), and in all other respects the fossil cranial remains suggest a cranium very similar to that of the modern southern African species.

Mandible: Nine specimens (M8277, STS957a; STS957e; STS2095; SK3063; SK6945; SK14235; KA757 and KA1432), ranging in maturity from growth stage 3 to 6 and several more fragmentary specimens give a fair picture of the appearance of the mandible of the fossil form - in all respects it appears to resemble that of the modern H. africae australis. The degree of similarity is demonstrated by Figures 116 and 117. Measurements for six mandibular characters - greatest length of mandible, depth of mandibular ramus below dp_4/P_4 , M_3 and M_2 , alveoli of P_4 to foramen mentale, diastemic length, diastemic curvature and the position of the top of the mesial symphysis in relation to the alveolar plane of the molars were measured (see Appendix VIII Vol. II pp.156-158) and with the exception of the measurements for the depth of the mandibular ramus below the M_1 and M_2 for SK3063 which fall above the range for the modern species, all the measurements of the fossil species fall within the ranges for the modern species, see Table XX. The reason for SK3063 falling beyond the modern range is probably error due to distortion - the lingual surface of this specimen is badly crushed and the lateral surface is cracked and distorted inwards.

* estimate due to fracture

Dental: The bulk of the material available is made up of entirely isolated teeth or small dentigerous fragments, and it was possible to obtain measurements for nine dental characters as well as the basic length and breadth measurements for individual maxillary and mandibular teeth - see Table XX. Measurements for the fossil mandibular teeth are shown plotted against the sample range for the modern form in Graphs 5 and 6, with measurements of contemporaneous fossil forms, where available, superimposed. The Table and the Graphs demonstrate the similarity of the dentitions of the fossil and modern forms. The measurements of only a single parameter on each of four different specimens (crown height of M1820 (M^2) and M1821 (M^3), MD diameter of M1001 (I^1) - which is in any case only tentatively referred to this species - and BL diameter of SK4315 (I^1) fell slightly beyond the range obtained for the modern sample, but with the exception of M1001, these specimens could confidently be included within H. africae australis because other parameters measured on them fell within the range for this species. Specimens M1820 and M1821 together with M1819 (all derived from the same individual) also differed in their stronger buccal curvature.

Root structure: Apparently poorly developed and semi-rooted particularly in the maxillary teeth, as in modern form. Number and arrangement as in modern form.

Crown enamel pattern (Fig. 120): Apparently the same number and arrangement of enamel folds as occurs in modern form (see sections 7.1.5 and 10.3). A comparison of Figure 120 with the series of crown enamel patterns of the modern form (Figs. 73-107) demonstrates the similarity.

Comparison with contemporaneous fossil forms

For practical purposes, the period spanned by australopithecine localities at which fossil H. africae australis is represented has been taken at 0,75m.y. (Kromdraai) to 3,7m.y. (Makapansgat Limeworks). Contemporaneous fossils (see Tables XVIII AND XIX) are therefore H. primigenia (Poussillon form) fossil H. indica, possibly H. bessarabica, ⁱ⁾H. etrusca, ⁱⁱ⁾H.cf. sub-cristata and H.(Acanthion) lagrelii.

i) and ii) see note at end of section

TABLE XVIII

TABLE SHOWING TYPE LOCALITY, GEOGRAPHICAL RANGE, POTENTIAL OR ACTUAL SYNONYMS AND GEOLOGICAL AGE OF ALL FOSSIL HYSTRIX DESCRIBED
 UP TO DECEMBER 1975

SPECIES i)	TYPE LOCALITY	OTHER LOCALITIES	SYNONYMS	GEOLOGICAL AGE ii)
<u>H. africae australis</u> Peters 1852	Makapansgat Limeworks Member 3	Makapansgat Limeworks Members 4 and 5, Sterkfontein Swartkrans Kromdraai Cave of Hearths Many S.A. Pleistocene and Holocene caves	<u>H. cf. africae australis</u> Greenwood 1955	Pliocene, approximately 3.5m.y.B.P. to Present
<u>H. angressi</u> Frenkel 1970	Geula(h) Cave, Mt. Carmel, Haifa, Israel	-	-	Upper Pleistocene, approx- imately 40,000 years B.P.
<u>H. astasobae</u> Bate 1951	Abu Hagar, nr. Singa Blue Nile, Sudan	-	synonym of <u>H. cristata</u> Linn. 1758	Middle or upper Pleisto- cene, thus younger than 700,000 years B.P.
<u>H. bessarabica</u> Rjabinin 1929	Taraklija Beds, Bessara- bia, Moldavian U.S.S.R	-	? synonym of <u>H. suevica</u> Schlosser 1884 ? synonym of <u>H. primigenia</u> (Wagner 1848)	Uncertain, probably Mio- cene, Meotian, 8-12m.y. B.P.
<u>H. crassidens</u> Lydekker 1886	Cathedral, Karnul Caves, Madras, India. Beds C and Cd	Beds Cc, Ce and Cf Karnul Caves	? synonym of <u>H. indica</u> Kerr 1792	Middle Pleistocene, Late Marbada Beds, approxima- tely 200,000 years B.P.
<u>H. etrusca</u> Bosco 1898	Upper Strata, Val d'Arno Italy	Val d'Agna, Italy Ghivizzano, Val d'Serchio Italy	? synonym of <u>H. refossa</u> Gervais 1852 ? synonym of <u>H. major</u> Gervais 1859 ? synonym of ' <u>H. primigenia</u> ' of Deperet 1890.	Plio-Pleistocene, Upper (Late) Villafranchian approximately 1.2m.y.B.P.
<u>H. greenwoodi</u> Bakr M.S.	Makapansgat Limeworks Member 3	-	synonym of <u>H. africae australis</u> Peters 1852	Pliocene, approximately 3.5m.y.B.P. to Present
<u>H. cf. indica</u> iii) Kerr 1792	-	Pliocene localities in Russian Caucasia Early-Upper Pleistocene loca- lities in Central Europe Pinjor Beds, Upper Siwaliks	<u>H. leucura</u> Sykes 1831 <u>H. hirsutirostris</u> Brandt 1835	Pliocene - Recent
<u>H. karnuliensis</u> (iv) (Lydekker 1886)	Bed cd Cathedral, Karnul Caves, Madras, India	-	synonym of <u>Atherura karnulien- sis</u> Lydekker 1886	Middle Pleistocene, Upper Marbada Beds, approxima- tely 200,000 years B.P.
<u>H. kiangsenensis</u> Wang 1931	Drachen-Maul-Höhle, Kiangsen, Chekiang, China	-	synonym of <u>H. (Acanthion)</u> <u>subcristata</u> Swinhoe 1870	Plio-Pleistocene or Samenian, approximately 1.8m.y.B.P.
<u>H. (Acanthion) lacrelli</u> Lanberg 1924	Mien-chih-hsien near Honan-Fu, Honan, Central China	Choukoutien, Localities 9 and 13	-	Late Lower Pleistocene approximately 700,000- 1,000,000 years B.P.
<u>H. lamandini</u> Filhol 1876	Phosphorites du Quercy, France	'Phosphorit von Bosc negre bei Lamandine (Tarn et Garonne) 'Phosphoriten von Escamps bei Lalbenque'	synonym within genus <u>Arctomys</u>	Upper Eocene
<u>H. cf. leucura</u> Sykes 1831	(see <u>H. cf. indica</u> Kerr 1792)	-	-	-
<u>H. major</u> Gervais 1859	Ratoneau Island near Marseille, France	-	synonym of <u>H. refossa</u> Gervais 1852	Probably Plio-Pleistocene or Villafranchian
<u>H. major</u> Greenwood 1955	Makapansgat Limeworks Member 3	Makapansgat Limeworks Member 4	synonym of <u>H. makapanensis</u> Greenwood 1955	Plio-Pleistocene, approx- imately 3.5m.y.B.P.
<u>H. makapanensis</u> Greenwood 1958	Makapansgat Limeworks, Member 3	Makapansgat Limeworks Member 4	<u>H. major</u> Greenwood 1955	Plio-Pleistocene, approx- imately 3.5m.y.B.P.
<u>H. minor</u> Malez 1963	Verternica-Höhle, near Zagreb, Hungary	-	? synonym of <u>H. cristata</u> Linn. 1758 ? synonym of <u>H. schaubi</u> Brünnner 1954	Middle Pleistocene, Riss Würm Interglacial, approx- imately 118,000-128,000 years B.P.
<u>H. primigenia</u> (Wagner 1848)	Pikermi, Greece	Several localities in Central and S.E. Europe v)	-	Miocene-Pliocene, Pontian Asian, approximately 5-9m.y.B.P.
<u>H. refossa</u> Gervais 1852	Puy de Dome, Issoire France	Perrier, Montpellier and Ratoneau Island, France	? actually <u>Hystrix</u> ? synonymous with part of <u>H. primigenia</u> (Wagner 1848)	Pliocene, Perrier-Villa- franchian, approximately 5m.y.B.P.

- i) Valid species marked with an asterisk
 ii) For geological timescale and correlation chart, see Table XIX
 iii) Often quoted as H. cf. hirsutirostris or H. cf. leucura
 iv) Originally described as Atherura karnuliensis and incorrectly assigned to Hystrix by Matthew (1929)
 v) See no. 18, Appendix VIII Vol. II pp. 282-283

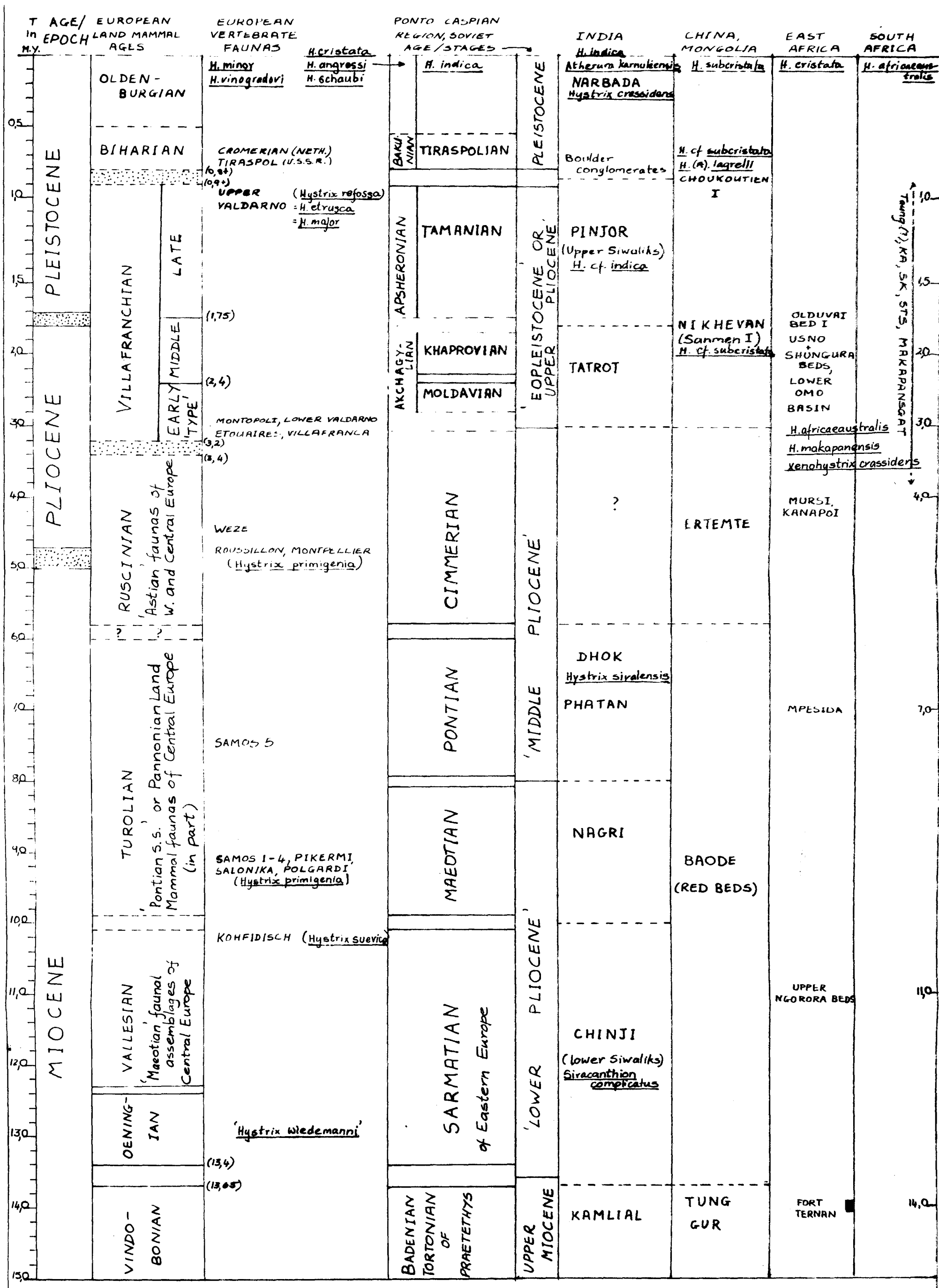
TABLE XVIII (continued)

SPECIES	TYPE LOCALITY	OTHER LOCALITIES	SYNONYMS	GEOLOGICAL AGE
<u>H. schaubi</u> Brunner 1954	Fuchsloch bei Siegmansbrunn, Oberfranken, Germany	-	? <u>H. minor</u> Malez 1963 ? synonym of <u>H. cristata</u> Linn. 1758	Middle-Upper Pleistocene Riss-Würm, approximately 118,000-128,000 years B.P.
* <u>H. sivalensis</u> Lydekker 1878	Asnot, Middle Siwaliks, India	-	-	Pliocene, Dhok Phatan stage of Siwalik Series, (Pontian-Plaisancian, approximately 6-8m.y.B.P.
<u>H. sivalensis sinhaleys</u> Deraniyapala 1958	Govak gaha deniya, Kuruvita, Sri Lanka	-	synonymous with <u>H. indica</u> Kerr 1792	Middle Pleistocene
* <u>H. (Acanthion) cf. sub-cristata</u> Swinhoe 1870	-	numerous lower and early Middle Pleistocene localities in China vi)	<u>H. kiangsenensis</u> Wang 1931	Lower to Middle Pleistocene to recent, from 1.5m.y.B.P. to Present
* <u>H. suevica</u> Schlosser 1884	Bohnerzen von Salmen- dingen, Hader bei Dinkelscherben, Germany	Reischenau and Dinotheriensande Swabia, Germany Kohfidisch Fissures, Burgen- land, Austria	-	Miocene to Lower Pliocene, Vindobonian to Late Pannonian, approximately 10-15m.y.B.P.
<u>H. venusta</u> Leidy 1869	Pliocene beds of Nebraska and Dakota	-	Not <u>Hystrix</u> because New World	Pliocene
* <u>H. vinogradovi</u> Argyropoulos 1941	Binagady near Baku, Moldavian U.S.S.R.	Apsheron, Transcaucasian U.S.S.R. Several localities in Germany, Austria, Hungary and Roumania vii)	? <u>H. schaubi</u> Brunner 1954 ? <u>H. minor</u> Malez 1963	Middle-Upper Pleistocene approximately 130,000 years B.P.
<u>H. wiedemanni</u> Rager 1885	Reischenau, Germany	Dinkelscherben, Dinotherien- sande and Pegensburg, Germany	Apparently not <u>Hystrix</u> but <u>Anchitheriomys</u> or <u>Amblycastor</u>	Upper Miocene, Vindobonian, approximately 13-15m.y.B.P.
* <u>Sivacanthion complicatus</u> Colbert 1933	Chinji Zone, Lower Siwalik Beds, Chinji, Punjab, India	-	-	Upper Miocene, approximately 12m.y.B.P.
* <u>Xenohystrix crassidens</u> Greenwood 1955	Makapansgat Limeworks, Member 3	Makapansgat Limeworks, Member 4	-	Plio-Pleistocene, approximately 3.5m.y.B.P.

vi) See no. 22 Appendix VIII Vol. 2 pp. 309-317

vii) See no. 25 Appendix VIII Vol. 2 pp. 325-328

GEOLOGICAL CORRELATION CHART AND TIMESCALE



Tungur, KA, SK, STS, MAKAPANEGAT

4.0

7.0

11.0

14.0

H. primigenia: The measurements collated for this species (no. 18 Appendix VIII pp.286 to 288, Vo.. II and graphs 5 and 6) indicate that H. primigenia is too large to be readily confused with fossil H. africae australis.

H. indica: The measurements available for the fossil form of this species overlap with those for fossil H. africae australis. Its geographical position and the present day distribution of H. indica and H. africae australis would preclude the southern African material from being placed in this species.

H. bessarabica: No measurements or illustrations are available for this species. The age of the Tarakliya beds which yielded this species is also uncertain and may be Miocene, in which case it would not be contemporaneous with the South African ape-man period. H. bessarabica apparently represents a somewhat less brachydont transitional form between the large and brachydont H. primigenia and the hypsodont H. cristata (see comment to No. 4 Appendix VIII) and is thus unlikely to be confused with H. africae australis which resembles the latter species. (see note at end of section)

H. etrusca: Too recent to be confused with any of the older South African material from Makapansgat Limeworks and Sterkfontein Type Site. The illustrations of H. etrusca indicate that it resembles H. cristata. However, it is larger in most respects than this species and is thus unlikely to be confused with the southern African H. africae australis, which is generally somewhat smaller than H. cristata. Its geographical position (Italy) would make it more likely to be confused with fossil H. cristata. (see note at end of section)

H.cf. subcristata: The diastema of this species is shorter and more strongly curved than in H. africae australis. The geographical distribution of fossil and present day H. subcristata would preclude the South African material from being confused with it.

H.(Acanthion) lagrelii: Far too small for fossil H. africae australis to be confused with it (see Figs. 12-14 Appendix VIII pp.255-257).

Discussion of doubtfully referred specimens

M 1001 - One measurement (MD diameter) falls beyond the range for the modern species. The other parameter (BL diameter) falls well

within the modern range. It thus appears logical to retain the specimen in H. africaeaustralis, but alternatively, it could be placed in H. makapanensis.

M 8294 - A very small strongly curved incisor of proportions not encountered in the modern H. africaeaustralis. It probably belonged to a newborn individual of this species or alternatively could belong to some other rodent genus altogether.

SFN 15 - A rather large and fragmentary mandibular P_4 , from which no diagnostic measurements could be obtained. The specimen could fall within the range for H. makapanensis but it is somewhat improbable that it belongs to this species.

SFN 17 - See comment for SFN 15.

SK 14237 - See comment for SFN 15. Although large, it is more likely to belong to H. africaeaustralis.

KA 1912 - The site from which this specimen was derived is problematic. The tooth (an M^3) is distinctly small for X. crassidens and almost too large for H. africaeaustralis. It could therefore belong to H. makapanensis.

General discussion:

Abu Bakr, in an unpublished manuscript (PhD dissertation, Harvard University Biology Department 1959) has referred much of the above material to Hystrix (Hystrix) greenwoodi, sp. nov., with M1806 as the type, the distinguishing characters being

...mandible shallower, wider, more robust (than H. africaeaustralis)
incisor alveolus forming a very prominent ridge on medial
surface ... p. 26 (brackets present author's)

The present author has noted that the shallowness and supposed greater width of the mandible as well as the 'very prominent ridge' on the medial surface are due to fossilizational distortion (the entire ramus of the type is deflected inwards) and apart from a certain degree of robustness (which in turn may be due to artifacts of preservation in this particular specimen) considers that there are insufficient grounds to distinguish this specimen from other H. (H) africaeaustralis. It should be noted that the damage to M1806 parallels that described for SK3063 almost exactly. Therefore the

TABLE XX

A comparison of the ranges of measureable cranial, mandibular and dental characters of the fossil H. africae australis material with those of a sample of modern H. africae australis (mm)

CHARACTERS	Fossil H. africae australis	N	Modern H. africae australis	N
<u>Cranial:</u>				
Mesial sutural length of premaxilla ventrally	17,0	1	16,0-28,3	26
Palatal length of premaxilla in front of foramina incisiva	10,7	1	11,6-24,0	26
Upper diastemic length	40,3	1	31,0-59,0	27
Palatal width between M ²	15,0	1	6,0-17,1	24
Palatal width between M ³	15,7	1	9,0-15,1	19
Length of foramina incisiva	7,0	1	3,5-8,5	27
Breadth of foramina incisiva	6,6	1	4,0-7,5	27
<u>Mandibular:</u>				
Greatest length	90,5-100,5	3	59,9-115,6	28
Depth of ramus below P ₄	20,0-26,5	9	16,4-27,7	30
Depth of ramus below M ₁	19,6-30,0	3	15,7-26,5	29
Depth of ramus below M ₂	17,3-29,0	2	15,0-24,6	26
Alveole P ₄ to foramen mentale	8,3-10,4	8	7,0-12,5	30
Diastemic length	19,4-35,0	3	18,5-39,6	30
Diastemic curvature	23,0-26,0%	3	22,7-40,8%	30
Top of mesial symphysis from alveolar plane of molars	0,0-1,5	3	0,0-8,0	30

TABLE XX (continued)ⁱ⁾

CHARACTERS	Fossil	N	Modern	N
	<i>H. africae australis</i>		<i>H. africae australis</i>	
<u>Dental:</u>				
Width of palate relative to teeth	185%	1	104-200%	23
Occlusal length of maxillary tooth row	30,4	1	16,3-36,2	26
Alveolar length of maxillary tooth row	31,5	1	17,0-36,4	27
Occlusal length of mandibular tooth row	28,1-37,3	5	32,5-37,4	10
Alveolar length of mandibular tooth row	30,3-40,0	5	16,5-39,3	30
Curvature of upper incisors	10,0-20,0	6	12,5-22,5	9
Curvature of lower incisors	52,5	2	37,5-62,5	11
Crown height of dp^4/P^4	22,6*	1	5,8-17,5	11
Crown height of M^1	9,6-14,8	2	9,0-19,5	8
Crown height of M^2	17,8-21,3	3	12,3-19,0	6
Crown height of M^3	11,8-21,2	8	12,0-17,4	5
Crown height of dp_4/P_4	14,0	1	3,9-17,4	7
Crown height of M_1	15,3	1	10,3-17,5	6
Crown height of M_2	12,7-15,3	4	12,2-18,5	6
Crown height of M_3	15,3	1	13,0-18,0	6
MD diameter of I^1	3,6-7,6	8	3,0-7,3	19
BL diameter of I^1	4,7-9,6	6	4,5-8,1	19
MD diameter of dp^4/P^4	8,7	1	5,4-10,7	20
BL diameter of dp^4/P^4	7,9	1	5,2-9,2	20
MD diameter of M^1	7,2-9,1	6	7,0-9,2	23
BL diameter of M^1	5,4-8,1	6	4,6-9,3	23

i) Measurements at alveolar rim not provided because the rim is impossible to locate on isolated teeth

* = estimate due to fracture or bad preservation

TABLE XX (continued)

CHARACTERS	Fossil	N	Modern	N
	<i>H. africae australis</i>		<i>H. africae australis</i>	
MD diameter of M ²	7,5-10,6	12	7,3-9,8	19
BL diameter of M ²	5,3-8,7	12	5,1-9,1	19
MD diameter of M ³	7,0-9,6	15	6,8-9,5	11
BL diameter of M ³	5,0-8,0	15	5,2-8,4	11

Fig 115.

Occlusal view of a left mandibular fragment (M1806, growth stage 5) of the fossil form of Hystrix africae australis Peters 1852 from the Makapansgat Limeworks grey breccia, showing crown enamel pattern. x 1.

Fig 116

Occlusal view of an almost complete right half-mandible (M8277, growth stage 6 above) of the fossil form of Hystrix africae australis Peters 1852 from the Makapansgat Limeworks pink or Upper Phase I breccia compared with modern H. africae australis mandible at the same growth stage. Note the great similarity of the crown enamel patterns. x 1



Fig 115



Fig 116

Fig 117

Occlusal view of left mandibular fragment of the fossil form of Hystrix africaeaustralis Peters 1852 (STS957a, growth stage 3, below) from the Sterkfontein Type Site, compared with modern H. africaeaustralis mandible at same growth stage. x 1

Fig 118

Occlusal view of almost complete left mandible of the fossil form of Hystrix africaeaustralis Peters 1852 (SK3063, early growth stage 6) from the Swartkrans brown breccia or Member 2. x 1

Fig 119

Occlusal view of left mandibular fragment of the fossil form of Hystrix africaeaustralis Peters 1852 (KA757, early growth stage 5) from the Kromdraai A faunal locality. x 1



Fig 117



Fig 118



Fig 119

Fig. 120

The crown enamel patterns of the mandibular dentitions of some of the Hystrix africaeaustralis specimens from the Transvaal australopithecine localities (x 4)

1, 2, 3	STS 957a	Sterkfontein Type Site Locality
4, 5, 10, 11	KA 757	Kromdraai A Locality
6, 7	SK 6945	Swartkrans Member 2
8, 9, 14, 15	SK 3063	Swartkrans Member 2
12, 17, 18	M 1806	Makapansgat Grey Breccia (Member 3)
13, 16, 21, 22	M 8277	Makapansgat Pink Breccia (Member 4)
19, 20	M 1807	Makapansgat Grey Breccia (Member 3)

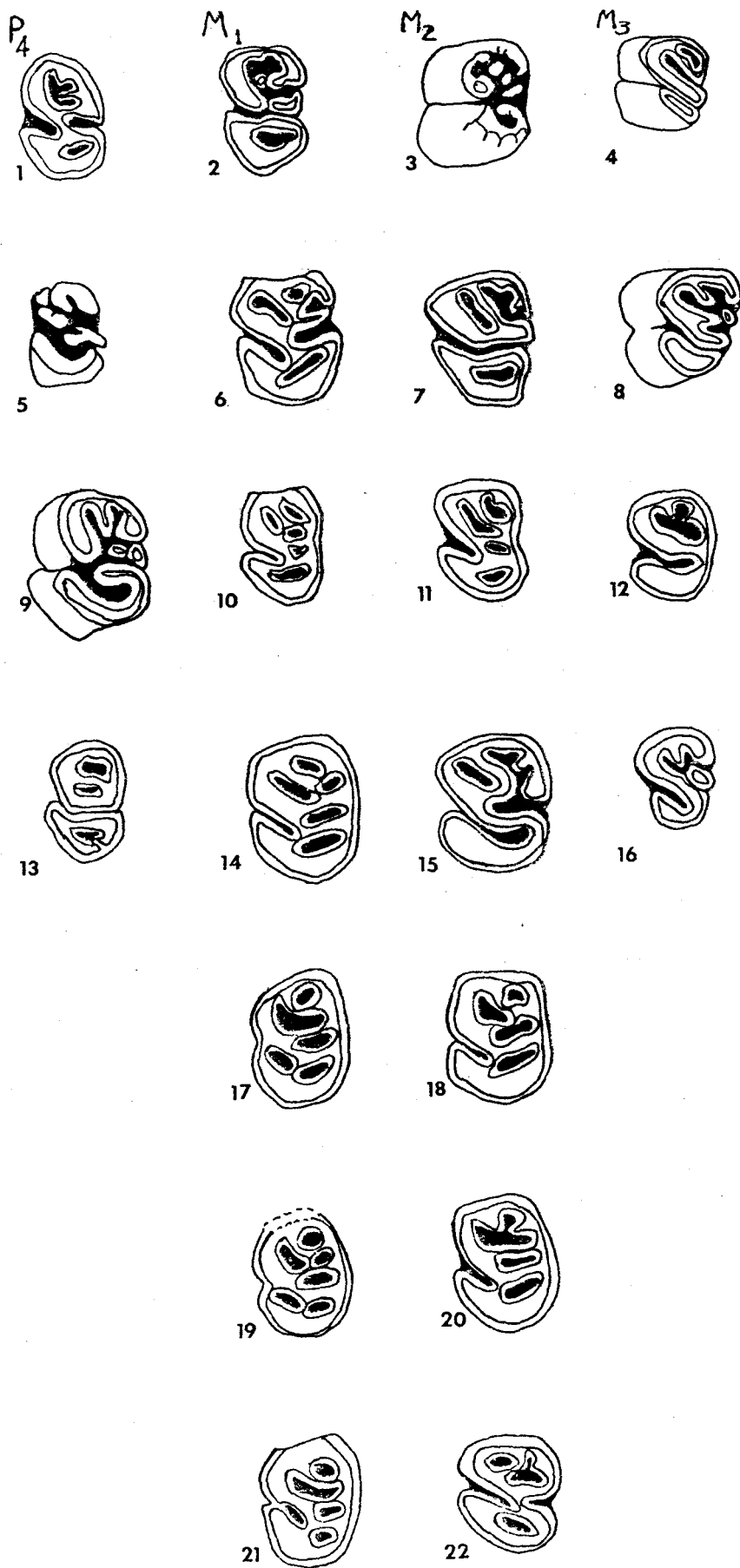


FIG. 120

characters used to separate H.(H) greenwoodi are not valid and the species is therefore a junior synonym of H.(H) africaeaeaustralis. Bakr himself noted that 'there is no difference from H. africaeaeaustralis in the cheek teeth, either in structure, size or degree of hypsodonty' (p.26).

14.3.2 Hystrix makapanensis (Greenwood 1958)

Hystrix major Greenwood 1955 p.78, Fig. 27, non Gervais 1859 p.511

Hystrix makapanensis Greenwood 1958 p.365

Type: M1002, a mandibular fragment with P_4 , part of M_1 diastema and incisor

Specific diagnosis

Greenwood 1955 p.78, as Hystrix major Greenwood sp. nov.

'An extinct Hystrix with cheek teeth approximately one third larger than H. africaeaeaustralis'

Revised specific diagnosis

'An extinct Hystrix with cheek teeth smaller than X. crassidens but approximately one third larger than H. africaeaeaustralis, the mandibular P_4 characterized in addition by the possession of a centrally placed lingual enamel fold or groove extending to the alveolar rim and persisting as long as the external enamel fold. With the latter, the lingual fold divides the tooth into two lobes of approximately equal size. Mandibular diastema neither as deep as nor as short and strongly curved as that of X. crassidens. The jaw of H. makapanensis is not as robust as that of X. crassidens but slightly more so than that of H. africaeaeaustralis (Figs. 121a and 121b)

Referred material: (see also Appendix VIII, Table I pp.152-154, Vol. II)

Makapansgat Lineworks:

Grey Breccia (Member 3): (Figs. 121a, 121b and 122)

M1001 (?); M1002 (Type, Figs. 121a,b); M1003 (?); M1811; M1812; M1815; M2516 (?); M2526; M8220 (?); M8326 (?)

Pink Breccia (Member 4):

M8278; M8282 (?)

Sterkfontein:

Dump 8:

SFN 15 (?)

Dump 10:

SFN 17 (?)

Swartkrans

Pink Breccia (Member 1):

SK 14237 (?)

Kromdraai A:

Fine-grained breccia

KA 1912 (?)

Description:

H. makapanensis (Greenwood 1958) is a very rare element in the Makapansgat Limeworks fossil fauna and the rarest of the three fossil porcupines present in the deposit - a total minimum number of only 5 or 6 as opposed to 14 and 9 for Xenohystrix crassidens and H. africae australis respectively. The species is so poorly represented that the present author initially suspected that there would be no real reason for maintaining this taxon and that the material referred to it could be included in H. africae australis, which it closely resembled. However, the type itself and some of the referred specimens differ sufficiently from H. africae australis to warrant separate specific status. However, only five of the 16 referred specimens listed above can with confidence be assigned to this species, the reason being that only two specimens were originally assigned to this species by Greenwood (M1002, the type and M1003, which, on investigation, proved to belong to X. crassidens). The type is a mandibular fragment with only one intact tooth, and in the absence of any further described mandibular material and no maxillary material, the species is thus very poorly defined. The maxillary teeth that have been referred to this species by the present author were so done mainly on the basis of their dimensions, which fall below the X. crassidens range and above the combined fossil and modern H. africae australis range (see graphs 7 and 8). It is interesting to note the synchronous presence of two such closely related species in the same deposit.

Cranium:

No cranial fragments are available, but drawing inferences from the mandible, it is unlikely that the H. makapanensis cranium could have differed much from that of the modern H. africae australis except in an enhanced degree of robustness and size.

Mandible:

The type specimen suggests a mandible which is somewhat more robustly built than that of H. africae australis, with longer and wider cheek teeth, but otherwise differing in no significant way from that of H. africae australis. The muscle attachments on the lateral jaw surface are similarly positioned to those of H. africae australis. There is an accessory mental foramen under the posterior end of P_4 but this is occasionally also encountered in H. africae australis.

Dentition:

The dentition is shown in Figs. 121a and 121b, while the crown enamel pattern is illustrated in Fig. 122. Measurements for the referred specimens are contained in Appendix VIII.

The teeth are intermediate in size between H. africae australis and X. crassidens. The mandibular P_4 is the only tooth which is well represented (M1002, M1811, M1815, M8290 and M8278). It is characterized by the possession of a particularly well-marked external enamel fold as well as a prominent centrally-placed and long persisting lingual enamel fold. When the tooth is young, these two folds meet internally, dividing the tooth into two lobes of approximately equal size, (M1811, M1815, M8290). The mature crown enamel pattern differs somewhat from that of a growth stage 6 H. africae australis - compare Figure 122 Nos. 4 and 5 with Figures 107, p. 281. Bakr (unpublished manuscript referred to above) states that "the above isolated teethshow a degree of hypsodonty comparable to that of modern Hystrix spp." (p.28), but the present author is of the opinion that the roots of the P_4 at least are better developed and more robust than those of H. africae australis. The species is thus intermediate in brachydonty between H. africae australis and Xenohystrix crassidens.

M1812 (left P_4) and M8220 (right P_4) are the only, albeit tentatively referred, maxillary teeth representing H. makapanensis. These

differ from those of H. africae australis in their superior size and somewhat better root development and from the corresponding teeth of X. crassidens in being smaller, more strongly curved and with less well-differentiated roots. In both specimens, the buccal (outer) anteriormost and centrally placed enamel folds are very prominent, the former being confluent with the deep internal enamel fold in the younger of the two specimens.

Comparisons with contemporaneous fossil forms

- H. primigenia - although in size the teeth of H. primigenia and H. makapanensis are practically identical, those of the former species are demonstrably more brachydont and the mandibular diastema is much flatter than that of H. makapanensis - compare Figures 24 (H. primigenia) and Figures 20A and B, Appendix X Vol. II, pp.294 and 277 respectively.
- H. bessarabica - Abu Bakr (unpublished MS 1959) has placed this species in the synonymy of H. primigenia.
- H. refossa - this species (with which the excellent H. etrusca material is considered synonymous) is based largely on cranial material and thus offers no grounds for comparison with the predominantly mandibular H. makapanensis material. The latter species and H. refossa are apparently very similar in appearance, degree of hypsodonty and size, and it is probable that H. makapanensis is the African equivalent to the European H. refossa.
- H. indica, H. cf. subcristata, H. (Acanthion) lagrelii - H. makapanensis has larger teeth and is more robustly constructed than any of these three species.

Discussion of doubtfully referred specimens

- M1001 - Undiagnostic small isolated upper incisor fragment of indeterminate growth stage which could equally well be referred to the fossil form of H. africae australis.
- M1003 - Excessively worn M₃. Referred by Greenwood 1955 to H. makapanensis but the present author is of the opinion that the specimen is too large and falls within the range for Xenohystrix crassidens.

- M1812 - There is no described maxillary material for H. makapanensis to form a basis of comparison for this specimen, a growth stage 6 P⁴. It is perhaps a particularly small X. crassidens P⁴, although the strong curvature and rather poorly-developed roots in view of its growth stage would suggest that H. makapanensis is a more correct designation. The measurements for tooth are beyond the size range for H. africae australis. The crown enamel pattern compares favourably with that of the latter species
- M2516 - A well worn M₃ at growth stage 6. The roots are not preserved, leaving its taxonomic affinities in some doubt; furthermore, its dimensions are somewhat small for X. crassidens, but too large for H. africae australis. Considering the thickness of the enamel and general robusticity, it appear more likely that the specimen is referable to X. crassidens.
- M2526 - Undiagnostic fragment of isolated upper incisor of indeterminate growth stage. Either juvenile H. makapanensis or large adult H. africae australis. The present author regards H. cf. makapanensis the most favourable designation. There are no described H. makapanensis upper incisors with which to compare the specimen.
- M8220 - See comment to M1812. Specimen is right P⁴
- M8362 - Could be a very large lower incisor of H. makapanensis but a more likely designation is juvenile X. crassidens.
- M8282 - See comment for this specimen under X. crassidens

General discussion

H. makapanensis appears to be very similar to H. africae australis and probably shared the ecological preference of this species. It differs from H. africae australis in its slightly more robust build, more brachydont dentition and in its notably larger teeth.

14.3.3 Xenohystrix crassidens Greenwood 1955

GENUS: XENOHYSTRIX Greenwood 1955 p.61

Generic diagnosis (original)

- ' A large extinct Hystricoid with rooted upper molars; transverse and anterior posterior diameter of the upper teeth subequal,

Fig 121A

Occlusal view of the type specimen (M1002, growth stage 6, above) of Hystrix makapanensis Greenwood 1958 compared with Xenohystrix crassidens Greenwood 1955 (M1803 at same growth stage. Both from the Makapansgat Limeworks grey breccia. x 1 (for lateral views of the same two specimens see Appendix 10, Fig. 20A)

Fig 121B

Occlusal view of the type specimen (M1002, growth stage 6, above) of Hystrix makapanensis Greenwood 1958 compared with modern H. africae australis Peters 1852 mandible of same growth stage. x 1 (for lateral views of same two specimens see Appendix 10, Fig. 20B)

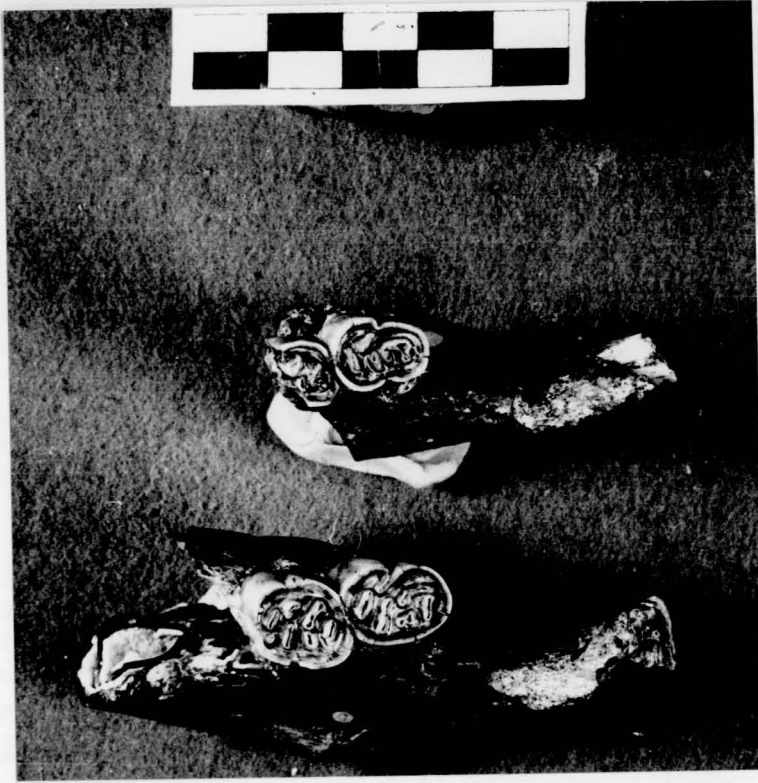


Fig 121 A



Fig 121 B

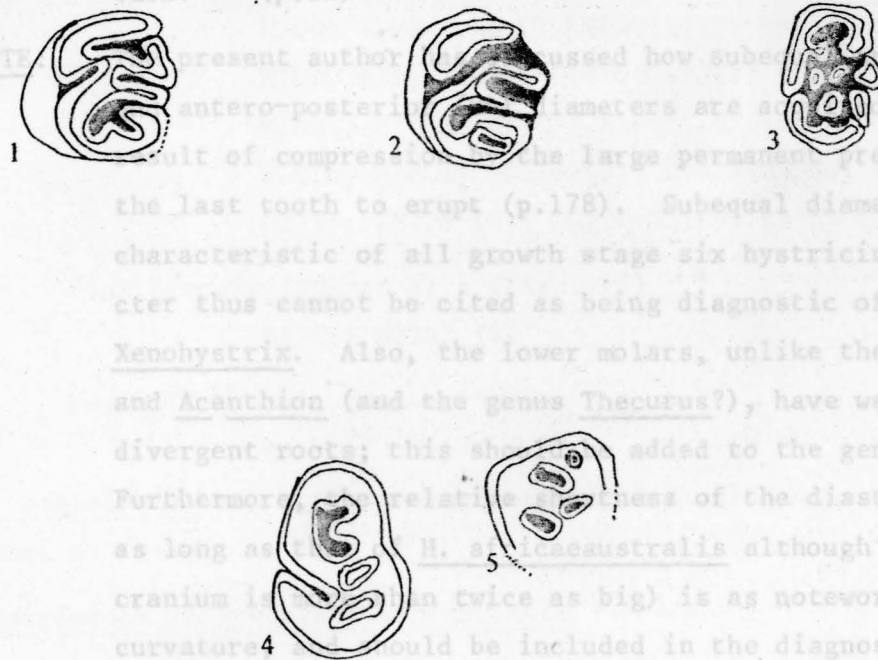
Fig. 122

The crown enamel patterns of some maxillary and mandibular tooth specimens referred to Hystrix makapanensis Greenwood 1958

(Approximately x 2)

1. M 8220 Upper right permanent premolar, drawn as left. Makapansgat Limeworks Grey Breccia (Member 3). The taxonomic affinity of this specimen is uncertain and alternatively it could belong to Xenohystrix crassidens Greenwood 1955. On the basis of the dimensions of the occlusal surface alone, however, the specimen compares most favourably with H. makapanensis.
2. M 1812 Upper left permanent premolar. Makapansgat Limeworks Grey Breccia (Member 3). As with specimen M8220, the taxonomic status of this specimen is also uncertain, the measurements taken at the occlusal surface indicating that it is somewhat large for H. africae australis and too small for Xenohystrix crassidens. The most likely assignation (mainly on the basis of size) is thus H. makapanensis. The problem is complicated by a total lack of comparative maxillary material which can unequivocally be referred to H. makapanensis.
3. KA 1912 Upper right third molar. Kromdraai A Faunal locality. The very tentative assignation of this specimen to H. makapanensis is based solely on the rather unsatisfactory criterion of size - if the tooth identification is correct, KA1912 is larger than one would expect for H. africae australis, particularly with regard to length, but smaller than Xenohystrix crassidens. It may, however, have belonged to a large Pleistocene form of H. africae australis.
4. M 1002 Mandibular left permanent premolar. Makapansgat Limeworks Grey Breccia (Member 3). From Type Specimen.
5. M 1002 Fragmentary anterior portion of mandibular first molar.

with occasionally the transverse diameter greater; distal portion of the premaxilla and the maxilla strongly arched and mandibular diastema with corresponding degree of curvature. (p.81)



the last tooth to erupt (p.178). Subequal diameters characteristic of all growth stage six hystricines, character thus cannot be cited as being diagnostic of the Xenohystrix. Also, the lower molars, unlike the subequal and Acanthion (and the genus Thecurus?), have well-developed divergent roots; this should be added to the generic diagnosis. Furthermore, the relative width of the diastema as long as that of H. australis although the cranium is twice as big) is as noteworthy a feature of curvature should be included in the diagnosis. A remarkable feature of Xenohystrix, apart from its proportions, is its short-snoutedness. Lastly, the abundant and robust diastema as opposed to the slender diastema noted in Hystrix, Acanthion and even Thecurus, should be noted.

A revised generic diagnosis for Xenohystrix is

Generic diagnosis (revised)

A gigantic extinct Hystricoid, larger than any living Hystricoid.

with occasionally the transverse diameter greater; diastemic portion of the premaxilla and the maxilla strongly arched, and mandibular diastema with corresponding degree of curvature. ' (p.81)

NOTE: The present author has discussed how subequal transverse (BL) and antero-posterior (MD) diameters are acquired with age, as a result of compression by the large permanent premolar, which is the last tooth to erupt (p.178). Subequal diameters are thus a characteristic of all growth stage six hystricines, and the character thus cannot be cited as being diagnostic of the genus Xenohystrix. Also, the lower molars, unlike the subgenera Hystrix and Acanthion (and the genus Thecurus?), have well-developed divergent roots; this should be added to the generic diagnosis. Furthermore, the relative shortness of the diastema (only about as long as that of H. africae australis although the Xenohystrix cranium is more than twice as big) is as noteworthy as its strong curvature, and should be included in the diagnosis. The most remarkable feature of Xenohystrix, apart from its gigantic proportions, is its short-snoutedness. Lastly, the abnormally deep and robust diastema as opposed to the slender diastemas encountered in Hystrix, Acanthion and even Thecurus, should be recognized.

A revised generic diagnosis for Xenohystrix is given below:

Generic diagnosis (revised)

'A gigantic extinct Hystricoid, larger than any living Hystricid genus or any fossil form yet described; maxillary and mandibular teeth both with well-developed divergent roots; diastemic portion of the premaxilla and maxilla relatively short ($\pm$ 58,0mm in growth stage 6 adults) but strongly arched, mandibular diastema correspondingly short ($\pm$ 29,0mm in growth stage 6 adults) and strongly curved; mandibular diastema deeper than in any living or fossil hystricid ($\pm$ 39,0mm below the P_4 in growth stage 6 adults).

SPECIES: CRASSIDENS Greenwood 1955 p.81

Specific diagnosis (original)

'Teeth of large size; overall length of P^4-M^3 series 40mm or more'

Referred specimens (see also Appendix VIII Table I pp.152-154 Vol II)

Makapansgat Limeworks:

Grey breccia (Member 3): (Figs. 123, 124, 126a-c, 127a, 127b, 128)
 M1003; M1004 (syn-type A); M1005 (syn-type B, Fig. 126b);
 M1006 (syn-type C); M1007 (syn-type D); M1008; M1009;
 M1010 (?); M1011; M1012; M1013; M1015; M1802; M1803;
 M1804; M1805; M1808; M1809; M1810; M1813; M1814;
 M1816; M1824; M2516 (?); M2517-M2523; M2525; M8220 (?);
 M8233; M8276 (?); M8286-M8289; M8362 (?); M8363; M8364;

Pink Breccia (Member 4) : (Fig. 125)

M8281; M8282 (?)

Phase II breccia (Member 5) :

--

X. crassidens has not been recovered from Sterkfontein, Swartkrans, Kromdraai or Taung.

Description of *Xenohystrix crassidens*

Cranium: A lateral (Fig. 129) and palatal (Fig. 130) view of the cranium of *Xenohystrix* has been reconstructed, based on specimens M1004, M1005, M1006 and M1804. From these it can be seen that *Xenohystrix* had a short snout (55-60mm) in relation to its total reconstructed cranial length (200mm). Even without the reconstruction, M1006 would demonstrate the short snout in that the upper diastema measures only 58,0mm which falls within the range obtained for *H. africae australis*, which has a total basilar skull length of only 131mm (the mean for 19 specimens). The lateral surface of the premaxilla preserved in M1006 does not give the impression of much cranial inflation, neither does the small foramina incisiva and the unruptured appearance of the median maxillary suture immediately behind it - in *H. cristata*, where cranial inflation is most strikingly developed, the median premaxillary suture in this region is usually interrupted by a gap caused by the expansion of the turbinal bones within the nasal cavity immediately above, which bulge palatally, forcing the left and right maxillae apart.

The spheno-palatine foramen is situated much where it is in *H. africae australis* (above the centre of the alveolar rim of M^2 at g/s 6) but it is between 15,0 and 18,2mm above this point as opposed to only $\bar{X} = 8,9$ mm in *H. africae australis*. The median sutural length of the palate is about 35,2mm at growth stage 6 as opposed to only $\bar{X} = 23,01$, $N = 26$ for

H. africaeaustralis. The sutural length of the premaxilla anterior to the foramina incisiva is $\pm 18,5\text{mm}$ which falls within the H. africaeaustralis range ($\bar{X} = 17,45\text{mm}$). The upper diastemic length is $58,0\text{mm}$, again falling within the range for the latter species. The median sutural length of the palate has been reconstructed as $\pm 105\text{mm}$; it is approximately $75,66\text{mm}$ in H. africaeaustralis. The palatal widths between P^4 , M^1 , M^2 and M^3 have been reconstructed as $13,0\text{mm}$, $12,5\text{mm}$, $16,0\text{mm}$ and $19,0\text{mm}$ respectively. The length and breadth of the foramina incisiva measure $15,0\text{mm}$ and $9,5\text{mm}$ respectively. No further information on the appearance of the cranium is available.

Mandible: The reconstruction of the lateral view of the right mandible (Fig. 131) indicates one that is hyper-robust and short, and rather similar to those found in Thecurus or Atherurus, except in its relatively short and sharply curving diastema. The estimated greatest length of mandible is $135,0\text{mm}$. The depth of the mandibular ramus below the P_4 ranged from $32,2\text{mm}$ to $39,2\text{mm}$ for g/s 5 and 6 specimens. This is well beyond the range for any Hystrix species and larger than any fossil hystricid yet known. The smallest distance between the alveolus of the P_4 and the foramen mentale is $12,0\text{mm}$. The diastema is between $29,0$ and $30,1\text{mm}$ for growth stage 5 and 6 individuals. The curvature of the diastema is between 30% and 32% for all growth stages; that for H. africaeaustralis averages 28%. The top of the mesial symphysis lies between an estimated $9,0\text{mm}$ and $12,0\text{mm}$ above the alveolar plane of the molars. No further information on the appearance of the mandible is available.

Dentition:

Incisors: The upper incisors, in conformity with the strongly curved premaxillary and maxillary diastema, are also strongly curved (the radius of curvature ranging from $17,5\text{mm}$ to $22,5\text{mm}$ in those specimens measured). The disposition of enamel and dentine is similar to that in H. africaeaustralis, with enamel covering only the anterior (labial) surface and parts of the mesial and distal surfaces of the tooth. Mesially, the enamel extends only about one quarter of the total distance from the labial to the lingual surface and distally about one third of the distance. The distal surface of the incisor is curved, and since the distal enamel bulges slightly beyond the curve of the dentine, there is a slight ridge at the junction of the two materials. Mesially, both enamel

and dentine are flattened on account of contact with the adjacent central incisor.

The upper incisors are very robustly built, with a mean labiolingual diameter of 12,0mm and a mean mesiodistal diameter of 10,8mm. The occlusal area is approximately 127,88mm and the occlusal shape index approximately 111,43mm, i.e. with LL diameter exceeding the BL diameter. Unlike H. africae australis which has a slender, elongate isosceles-triangle shaped incisial surface, the incisial surface of X. crassidens is almost equilateral triangle shaped and apparently much blunter. On the incisial surface fine striae are frequently visible, caused by gnawing and tooth sharpening activity. These striae run antero-posteriorly on the anterior third to half of the incisial surface and transversely on the posterior portion. The former probably owe their origin to feeding and gnawing activities while the latter are probably due to thegosis (tooth-sharpening).

The lower incisors are identical in structure to the uppers, differing only in their lesser degree of curvature ($r = 47,55,0\text{mm}$). The other dimensions are as follows: mesiodistal diameter 9,7mm-12,8mm; labiolingual diameter 10,6-11,5mm; area of incisial surface 111,3-147,20; crown shape index 89,83-111,49mm.

Both the upper and lower incisors widen slightly towards their root end.

Maxillary dentition: As in other hystricine genera there is a premolar (the only tooth which is replaced) and three molars. These teeth are all similar in structure. All have a single large lingual root, probably the result of fusion between a mesio-lingual and disto-lingual root, and single smaller mesio-buccal and distobuccal roots, which are approximately equal in size. These three roots are well developed and divergent, and as the enamel covering of the crown stops short at their point of divergence from the main body of the crown, they consist of cementum covered dentine. In this respect X. crassidens differs from all other Hystricinae. Those of the M^1 and P^4 are the best developed, followed by the M^2 and finally the M^3 , the roots of which are nevertheless well-developed and divergent in comparison with other hystricine porcupines. The crown enamel pattern is apparently very similar to if not identical to that of H. africae australis. The order of closure of the folds and the mature crown enamel pattern are very similar (compare Fig. 127A with

Figs. 78, 83, 87 and 90). As in the latter species, the permanent P^4 is the largest tooth, often compressing the adjacent M^1 (and sometimes the M^2) to the extent that its antero-posterior (MD) and transverse (BL) diameters become sub-equal, Figure 126B; in extreme cases the width (BL) may even exceed the length (MD). The M^3 acquires a roughly triangular occlusal outline with age, with the 'apex' facing posteriorly. The basic measurements for the individual teeth, their crown heights, crown occlusal areas and crown shape indices are given in Appendix VIII Vol.II. The total length of the maxillary tooth row measured at the occlusal surface has been estimated at 52,0mm from the reconstruction (Fig. 130). That for H. africae australis averages 28,0mm. The width of the palate in relation to the width of the teeth is %; that for H. africae australis averages 140%.

Mandibular dentition: The mandibular dentition consists of a premolar (the only mandibular tooth which is replaced) and three molars. No isolated deciduous premolars of X. crassidens are available, and the arrangement of roots on this tooth is unknown. The permanent premolar is the largest tooth in the row and has three well-developed divergent roots, very much better developed and more divergent than in Hystrix. The disto-buccal root is the largest and apparently the result of the fusion of distal and disto-buccal rootlets. The mesial root follows in size, and again probably represents fused mesio-buccal and mesio-lingual rootlets. The disto-lingual root is the smallest. This root arrangement is much as it is in H. africae australis, except that in Xenohystrix none of the roots are covered with enamel, which terminates at a point where the roots diverge from the main body of the tooth. The M_1 and M_2 each have four well-developed divergent roots of approximately equal length and thickness - mesio-buccal, mesio-lingual, disto-buccal and disto-lingual roots. As in the P_4 none of these are enamel-covered. The M_3 apparently has four rootlets of approximately equal size when newly erupted, these show an increasing tendency towards fusion with age. This fusion does not follow a fixed pattern; it may be the mesio-buccal and disto-buccal roots that fuse or partially fuse, or the disto-buccal with the disto-lingual root, so that in some specimens the M_3 appears to have only three roots. The mesio-lingual root is usually the least well developed.

The mandibular crown enamel pattern is apparently identical to that in H. africae australis, as is the order of closure of the folds and the

resulting mature crown enamel patterns (compare Fig. 127B with Figs. 95, 100, 104 and 107). The basic tooth measurements, their crown heights, occlusal surface areas and crown shape indices are given in Appendix VIII Vol. II and the mandibular measurements are plotted in graphs 7 and 8. The total length of the mandibular tooth row measured at the occlusal surface ranged between 48,0mm and 54,0mm for growth stage 5 specimens.

Comparison with contemporaneous fossil forms

The contemporaneous or approximately contemporaneous fossil forms are the following: H. primigenia, H. bessarabica (= H. primigenia), H. refossa, H. etrusca (= H. refossa), H. indica, H.(A) cf. subcristata and H. (Acanthion) lagrelii. Xenohystrix crassidens has longer maxillary and mandibular tooth rows and is more robust than any of the listed fossil forms, with which it is not easily confused.

Discussion of doubtfully referred specimens

- M1010 - This tooth (an extremely well-worn M_3 or P_4) as well as tooth numbers M1809 and M8276 are so large (see Graphs V, VI, VII and VIII) that a possibility exists that they may belong to a hystricid rodent still larger than Xenohystrix.
- M2516 - See comment for this specimen under H. makapanensis.
- M8220 - See comment for M1812 and M8220 under H. makapanensis.
- M8276 - See comment for M1010 above.
- M8362 - See comment for this specimen under H. makapanensis.
- M8282 - A badly-preserved juvenile specimen with teeth too large for its growth stage to belong to H. africae australis, but very similar in size to those of M8281, which has been referred to X. crassidens on account of the large teeth and deep, short and strongly curved diastema. The diastema of M8282 is not preserved, and the specimen can thus not be referred with certainty to X. crassidens, although its similarity to M8281 suggests that this is the correct designation. Alternatively, it could be a juvenile H. makapanensis.

General discussion

The taxonomic affinities and palaeoecology of X. crassidens have been discussed in the sections dealing with Hystricid phylogeny (section 16.3.1)

Fig 123

Lateral view of syn-type D (M1007, growth stage 5, above) of Xenohystrix crassidens Greenwood 1955, from the Makapansgat Limeworks grey breccia, compared with a modern Hystrix africae-australis mandible (PPM122, growth stage 6). x 1

Fig 124

Occlusal view of mandibular dentition of Xenohystrix crassidens Greenwood 1955 (M1802, growth stage 5), newly erupted P_4 on left. From the Makapansgat Limeworks grey breccia. x 2 (for natural size illustration of dentition see Appendix 10 Fig. 39)

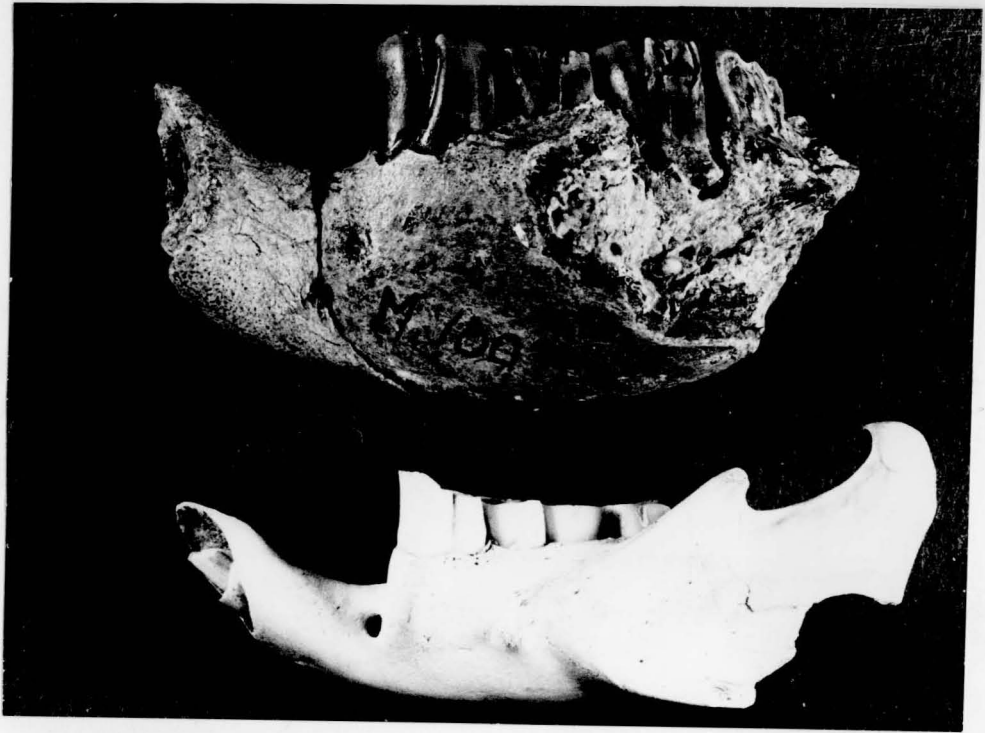


Fig 123



Fig 124

Fig 125

Lingual view of right mandible of juvenile Xenohystrix crassidens Greenwood 1955 (M8281, growth stage 2, above) from the Makapansgat Limeworks pink or Upper Phase I breccia, compared with modern Hystrix africaeaustralis mandible at same growth stage. x 1

Fig 126A, B, C

Occlusal views of the maxillary dentition of Xenohystrix crassidens Greenwood 1958; all specimens from the Makapansgat Limeworks grey breccia. A: growth stage 5, newly erupted P^4 , M^1 and M^2 ; B: growth stage 6, well-worn P^4 , M^1 and M^2 ; C: growth stage 6, empty alveolus for M^1 , M^2 and M^3 . x 1



Fig 125



A



B



C

Fig. 126

Fig. 127 A

The crown enamel patterns of the maxillary dentition of Xenohystrix crassidens Greenwood 1955 at growth stage 5 and 6. Approximately x 2. All crown enamel patterns drawn as lefts.

- | | | |
|----------|---------------|---|
| 1, 2, 3 | <u>M 1805</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| 4, 7 | <u>M 1804</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| 5, 8, 10 | <u>M 1005</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| | | Syn-type A |
| 6, 9 | <u>M 1004</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| | | Syn-type B |

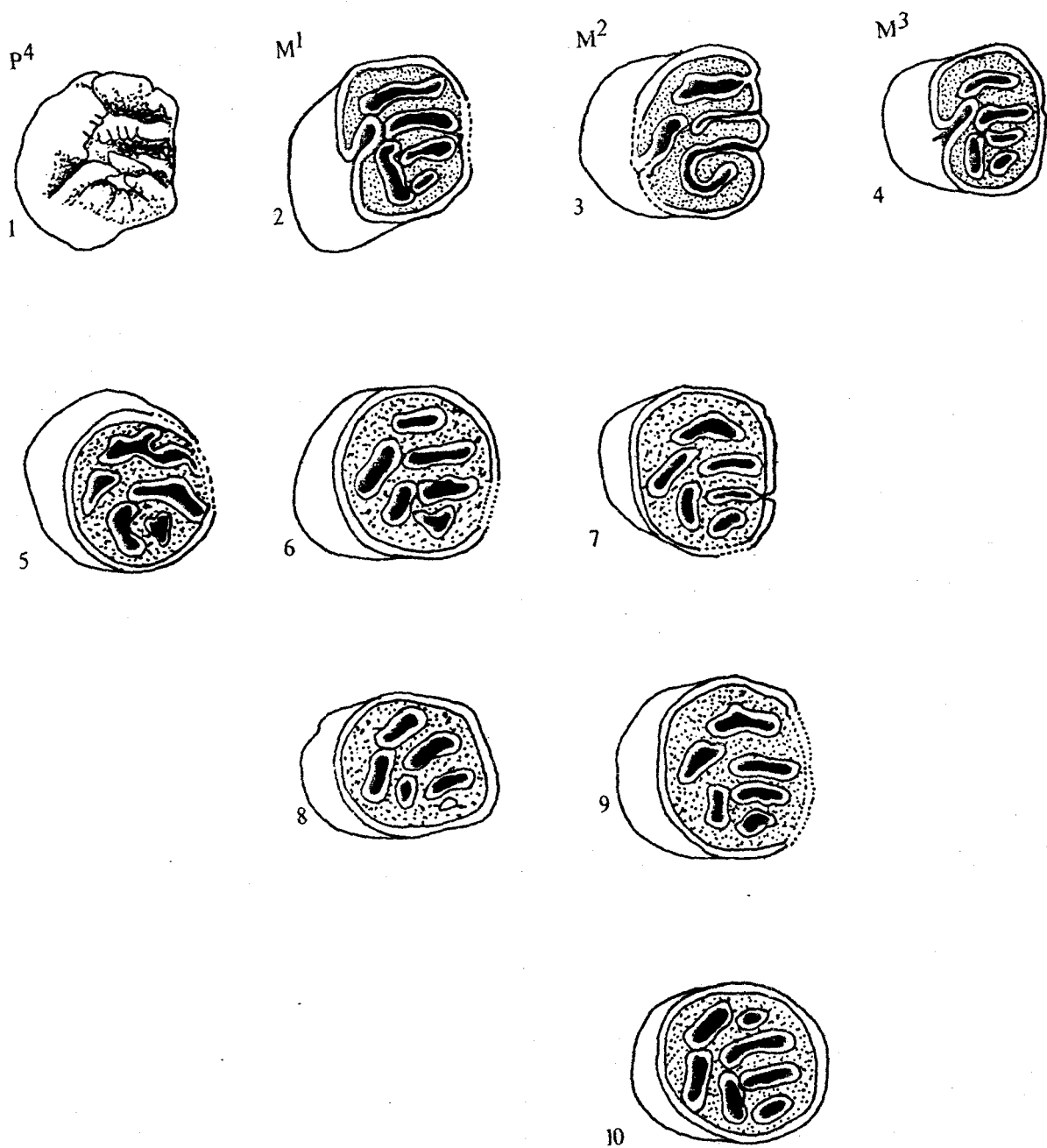


Fig.127A

Fig. 127 B

The crown enamel patterns of the mandibular dentition of
Xenohystrix crassidens Greenwood 1955 at growth stages 5 and 6.
Approximately x 2. All crown enamel patterns drawn as lefts.

- | | | |
|------------|---------------|---|
| 1, 2, 3, 4 | <u>M 1802</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| 5, 6, 7, 8 | <u>M 1007</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| 9, 10 | <u>M 1803</u> | Makapansgat Limeworks Grey Breccia (Member 3) |
| 11 | <u>M 8286</u> | Makapansgat Limeworks Grey Breccia (Member 3) |

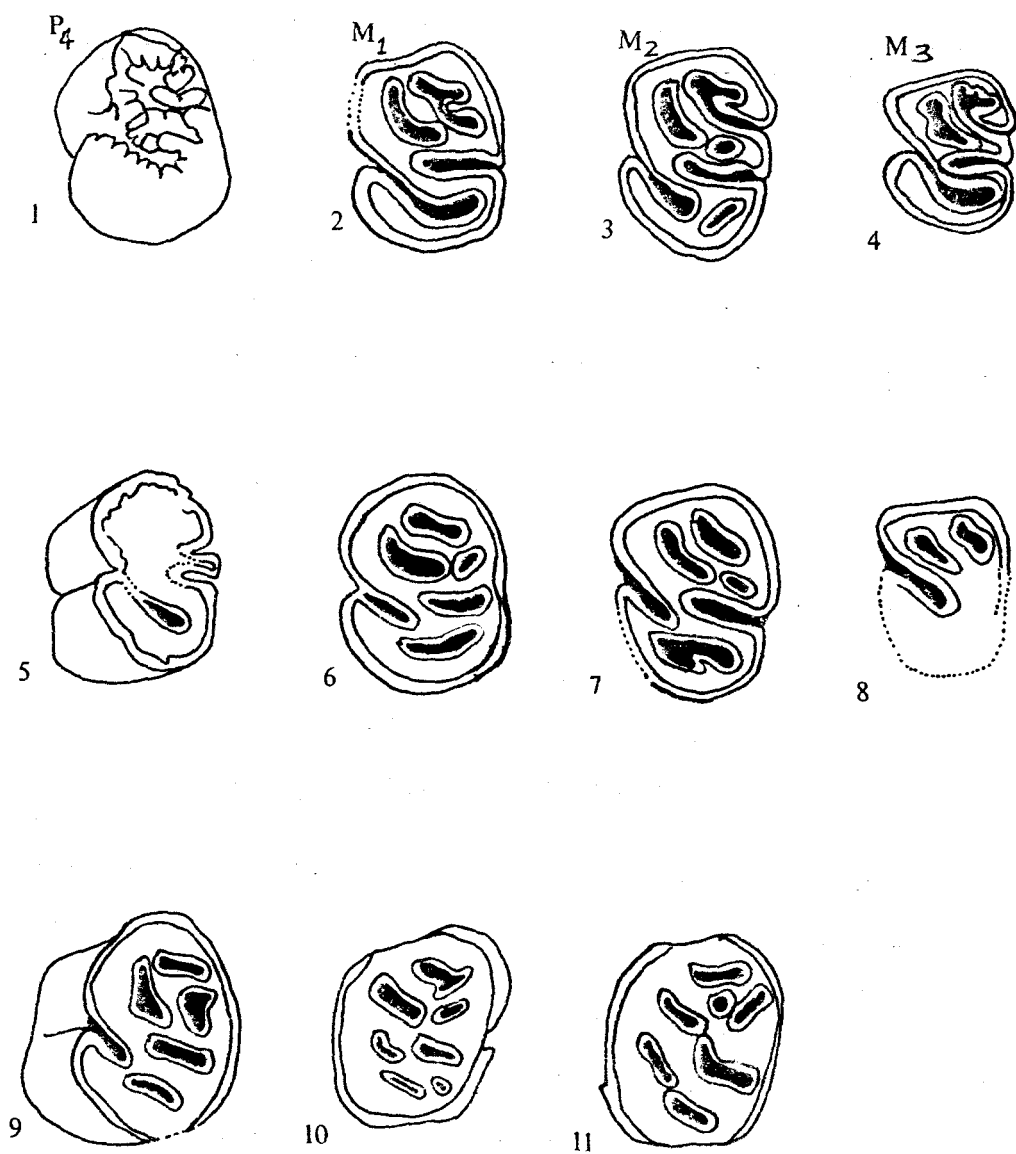
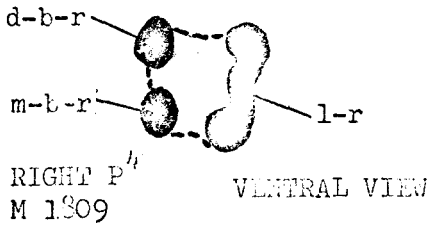
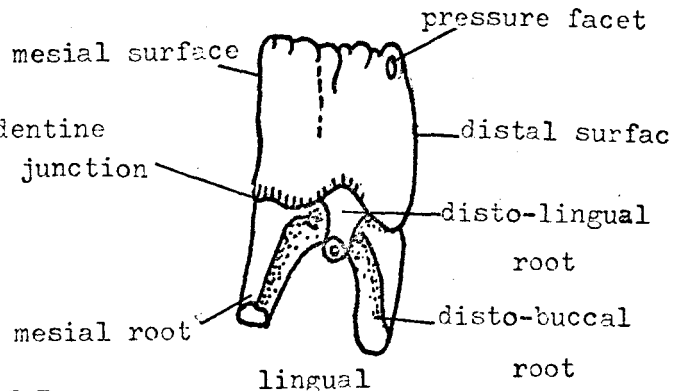
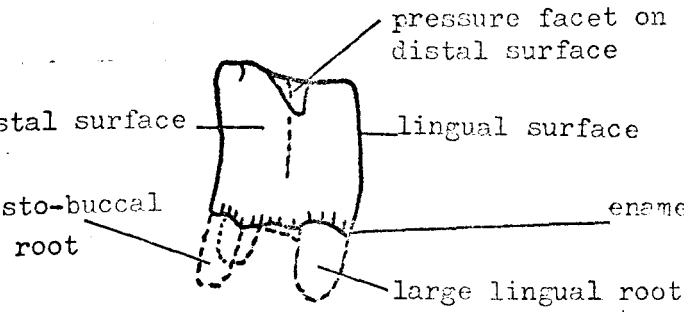


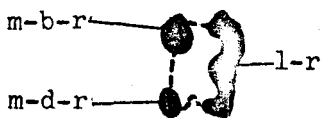
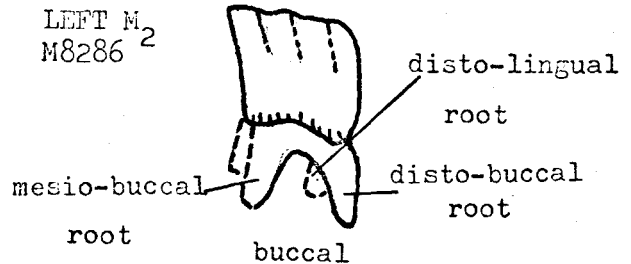
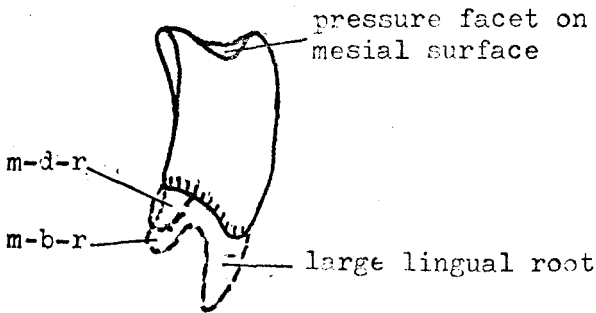
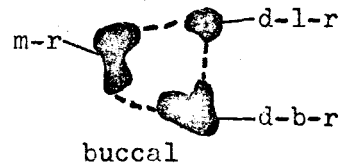
Fig. 127B

Fig. 128

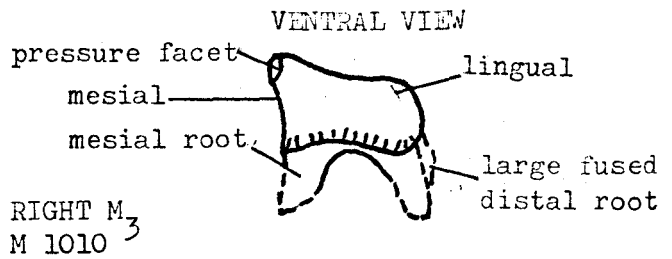
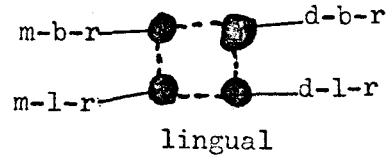
The root development of the maxillary (left column) and mandibular (right column) dentition of Xenohystrix crassidens Greenwood 1955.



RIGHT P₄
M 1808
VENTRAL VIEW



LEFT M₂
M2518



RIGHT M₃
M 1010



VENTRAL VIEW
MANDIBULAR DENTITION

Fig. 129

Reconstruction of the right lateral view of the cranium and mandible of Xenohystrix crassidens Greenwood 1955. Natural size.

Reconstruction based on specimens M1006, M1004, M1005, M1804 and cranium TM657 (Hystrix africaeaustralis) enlarged to coincide with tooth row length of Xenohystrix as suggested by the above specimens.

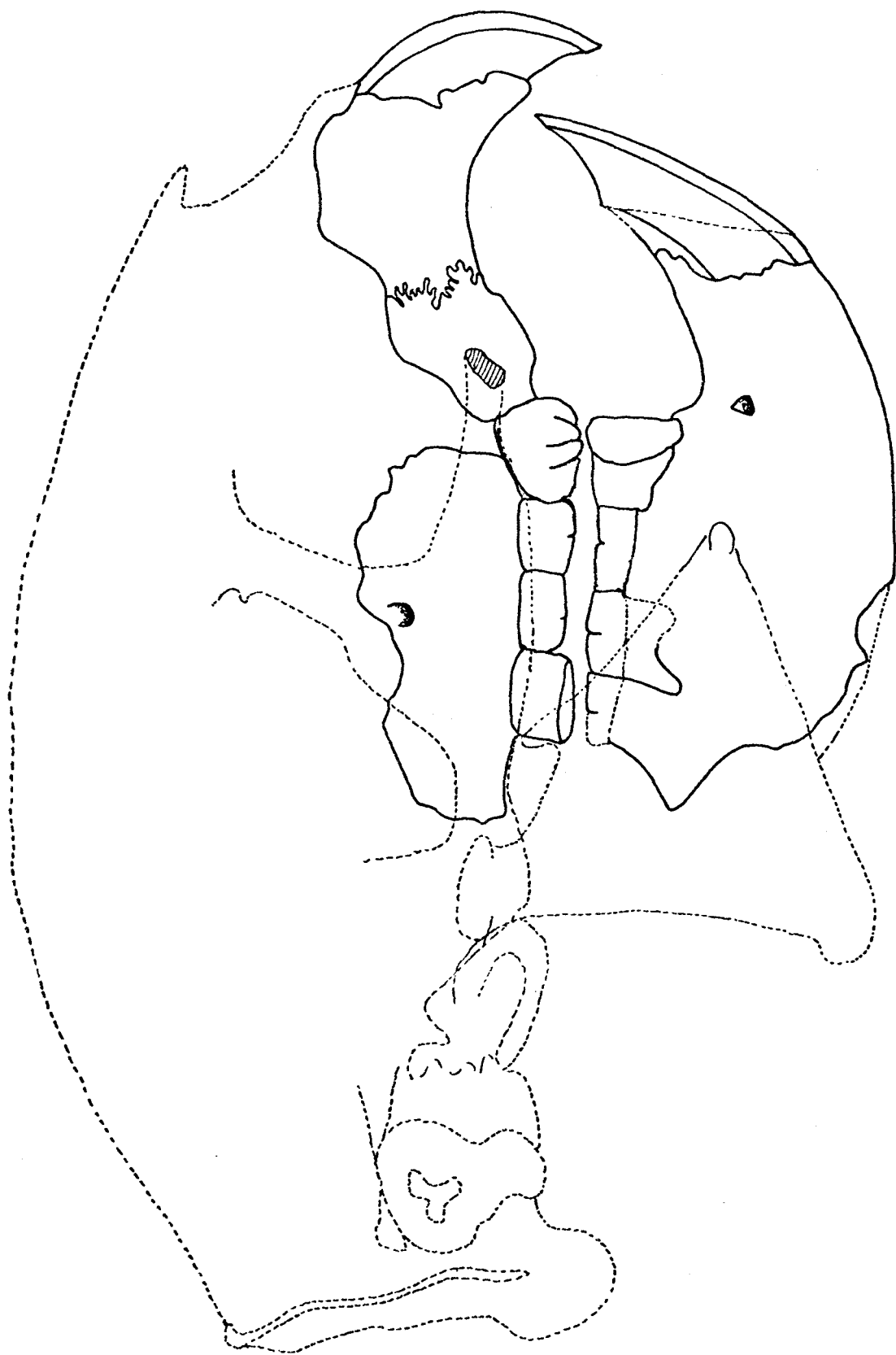


FIG. 129

Fig 130

Reconstruction of the palatal view of the cranium of Xenohystrix crassidens Greenwood 1955. Natural size.

Reconstruction based on specimens M1006, M1004, M1005, M1804 and cranium TM657 (Hystrix africaeaustralis) enlarged to coincide with tooth row length of Xenohystrix as suggested by the above specimens.

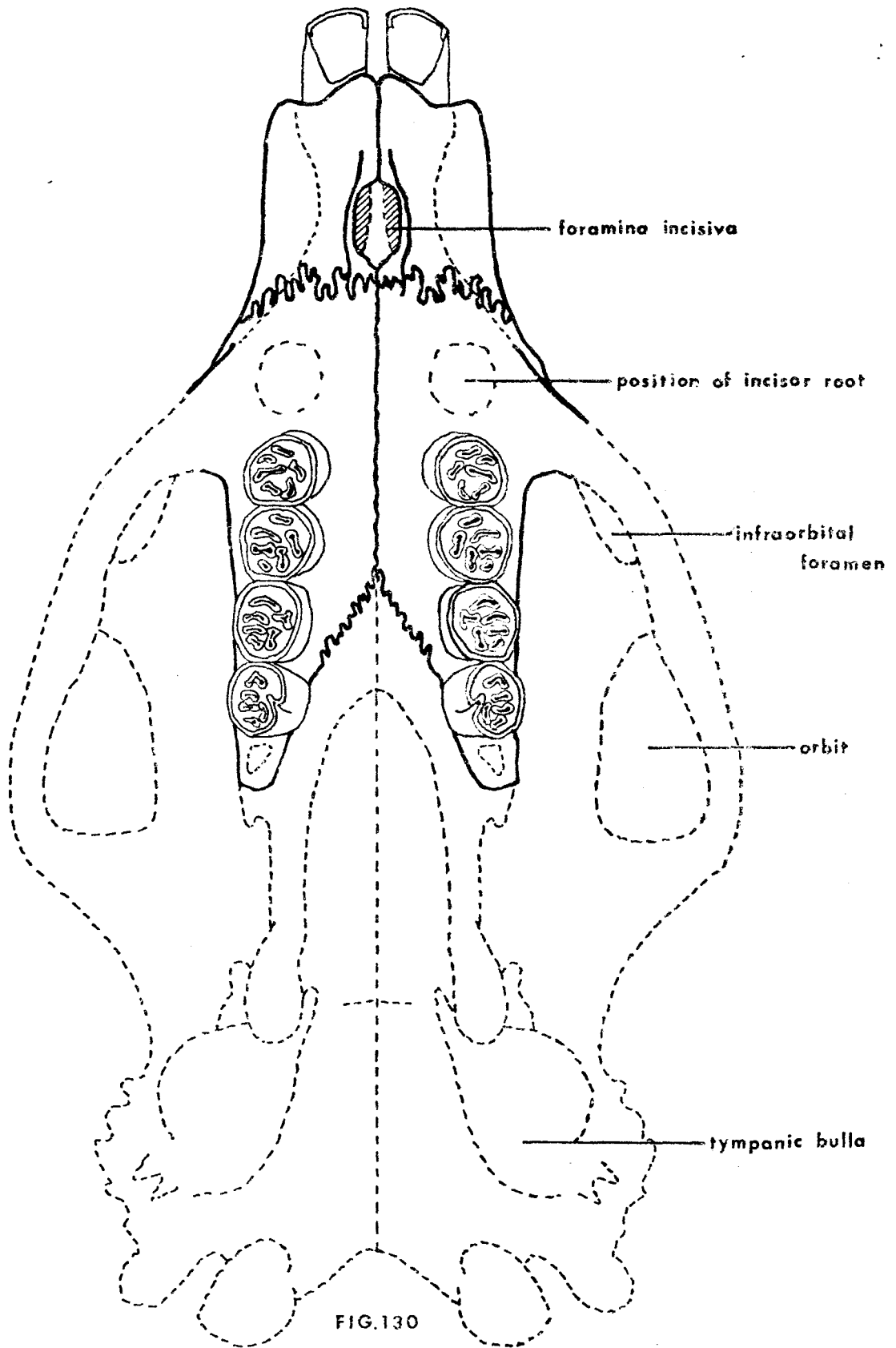


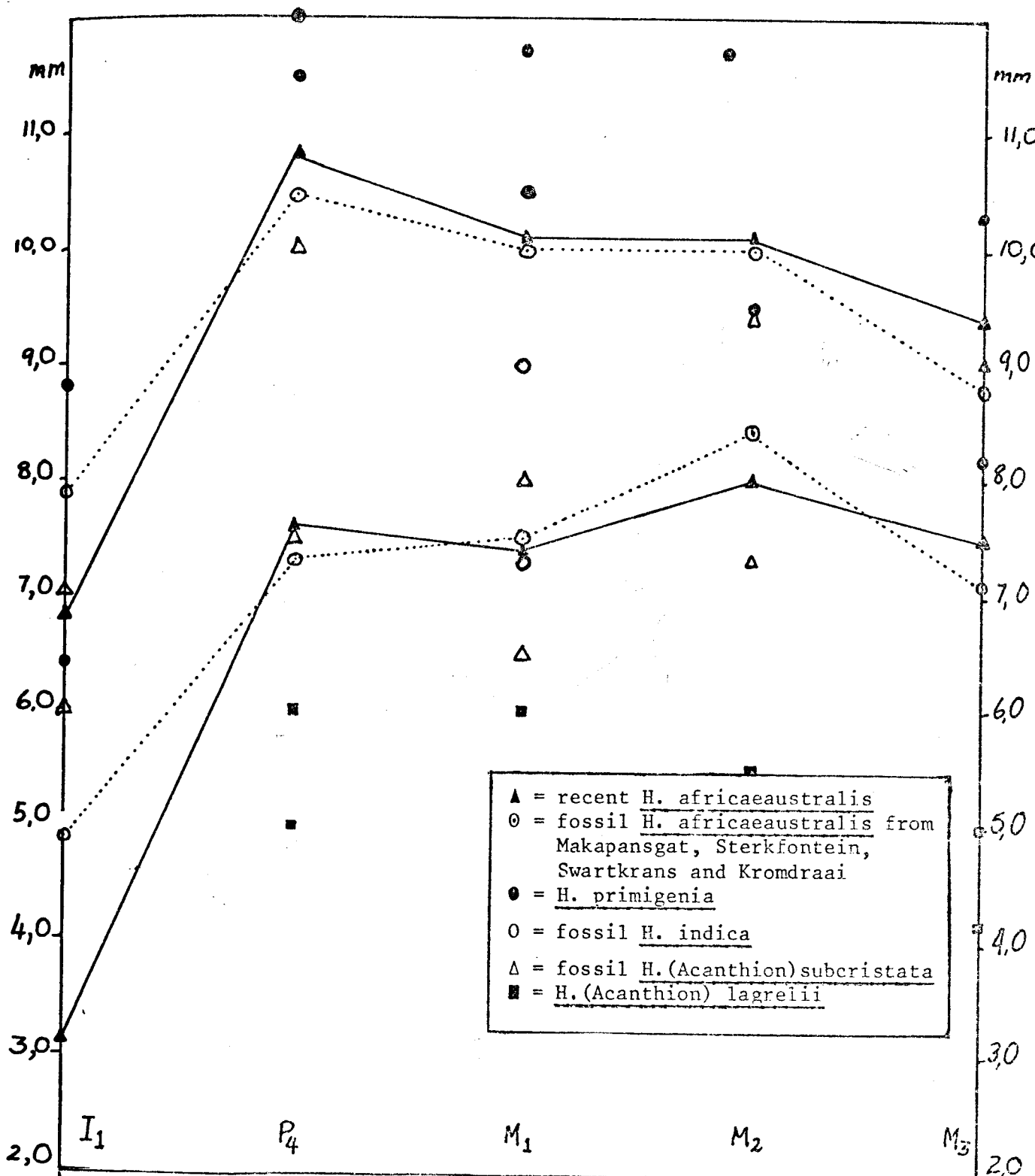
Fig 131

Reconstruction of a right half-mandible of Xenohystrix
crassidens Greenwood 1955, natural size.

Reconstruction based on specimens M1007, M1802, M1803 and
M8363.

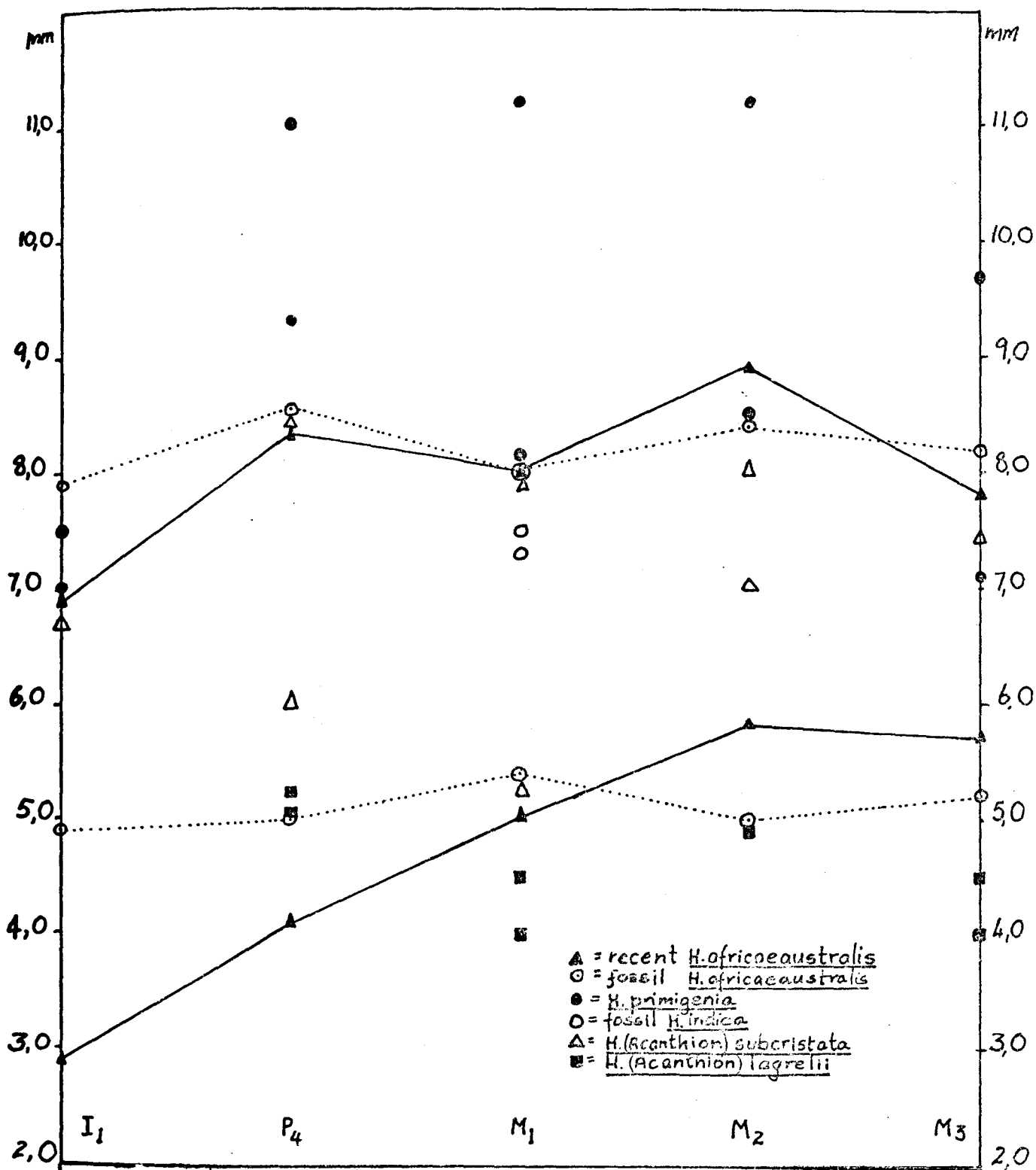


FIG. 131



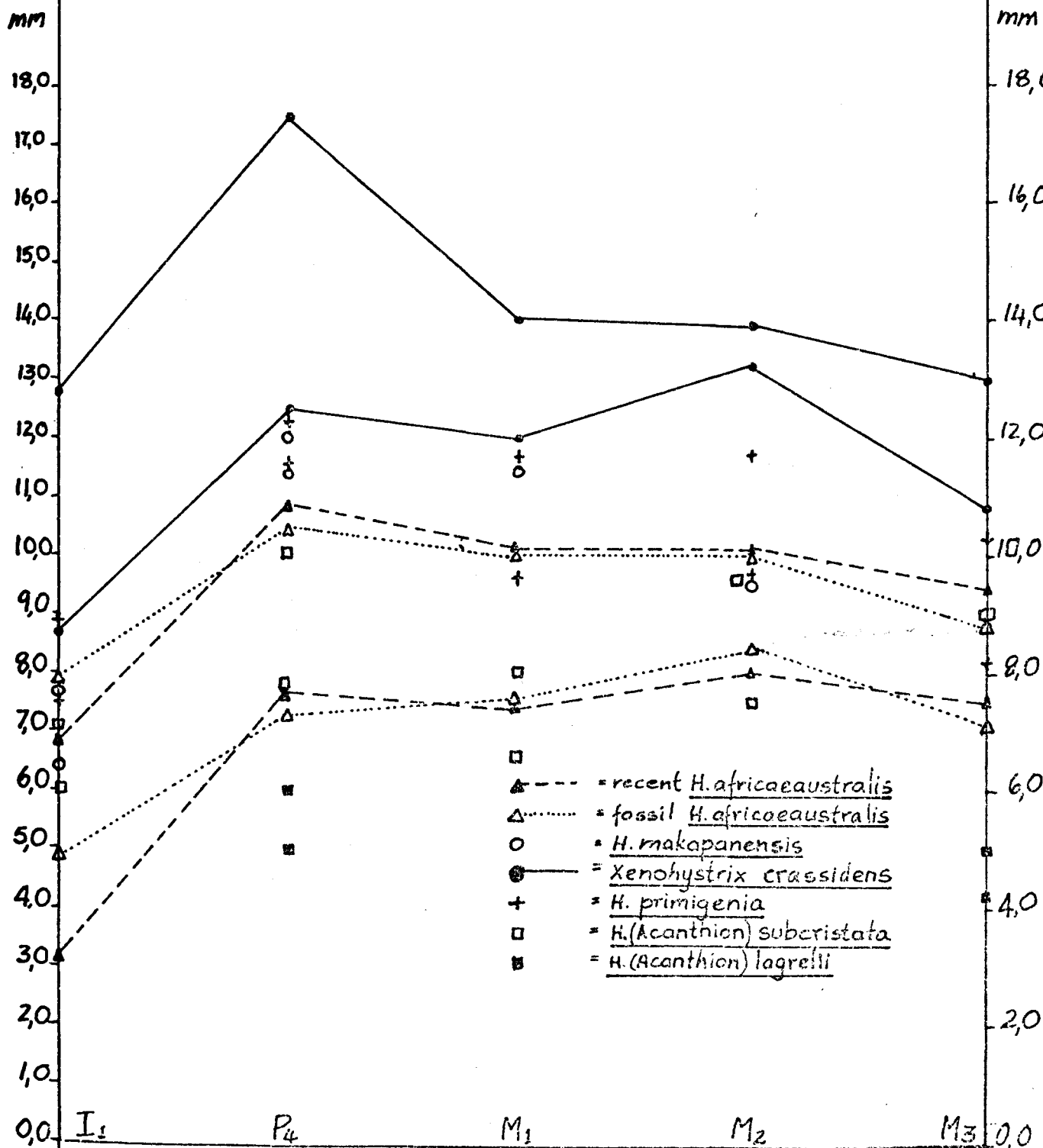
Graph V

The mesiodistal diameters of the mandibular teeth of fossil H. africae australis specimens plotted against the sample ranges of modern H. africae australis and including data of contemporaneous fossil forms



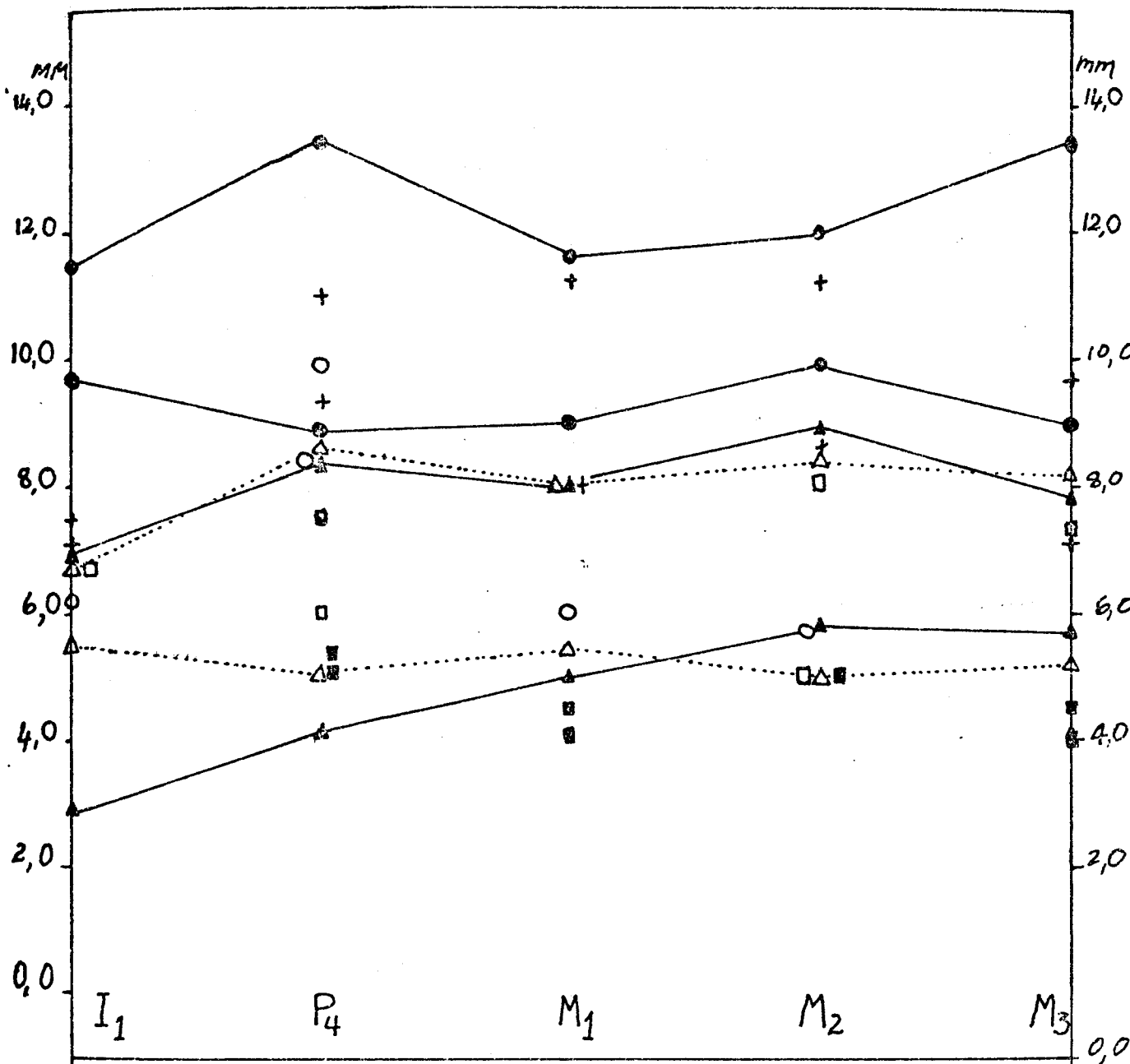
Graph VI

The buccolingual diameters of the mandibular teeth of fossil *H. africae australis* specimens plotted against the sample range of modern *H. africae australis* and including data of contemporaneous fossil forms



Graph VII

The sample ranges of the mesiodistal diameters of the mandibular teeth of modern and fossil H. africaeaustralis, of the giant Xenohystrix crassidens and of H. makapanensis with the data for contemporaneous fossil forms superimposed

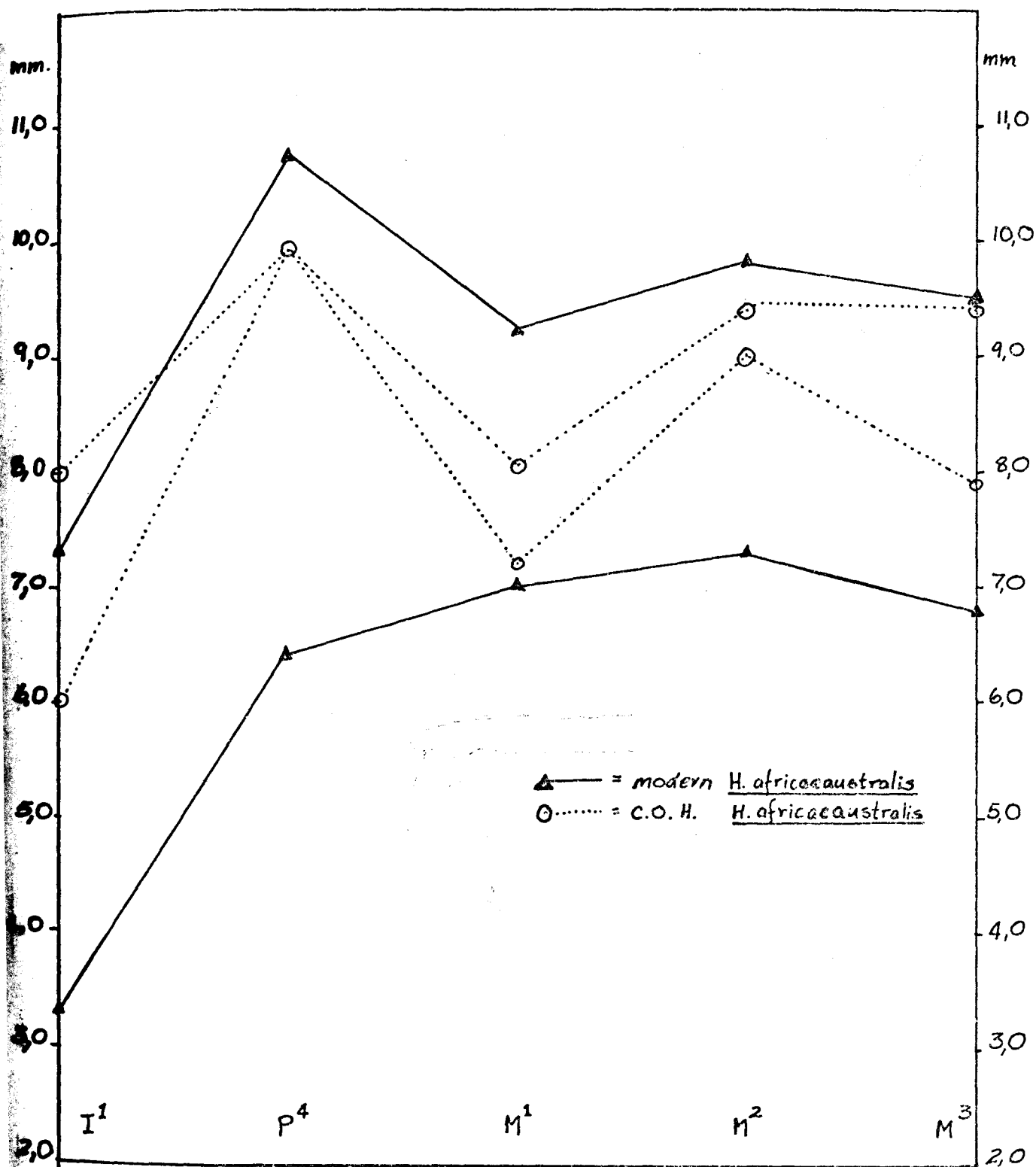


KEY

- ▲— = recent H. africae australis
- △..... = fossil H. africae australis
- = Xenohystrix crassidens
- = H. makapanensis
- + = H. primigenia
- = H. (Acanthion) subcristata
- = H. (Acanthion) lagrelii

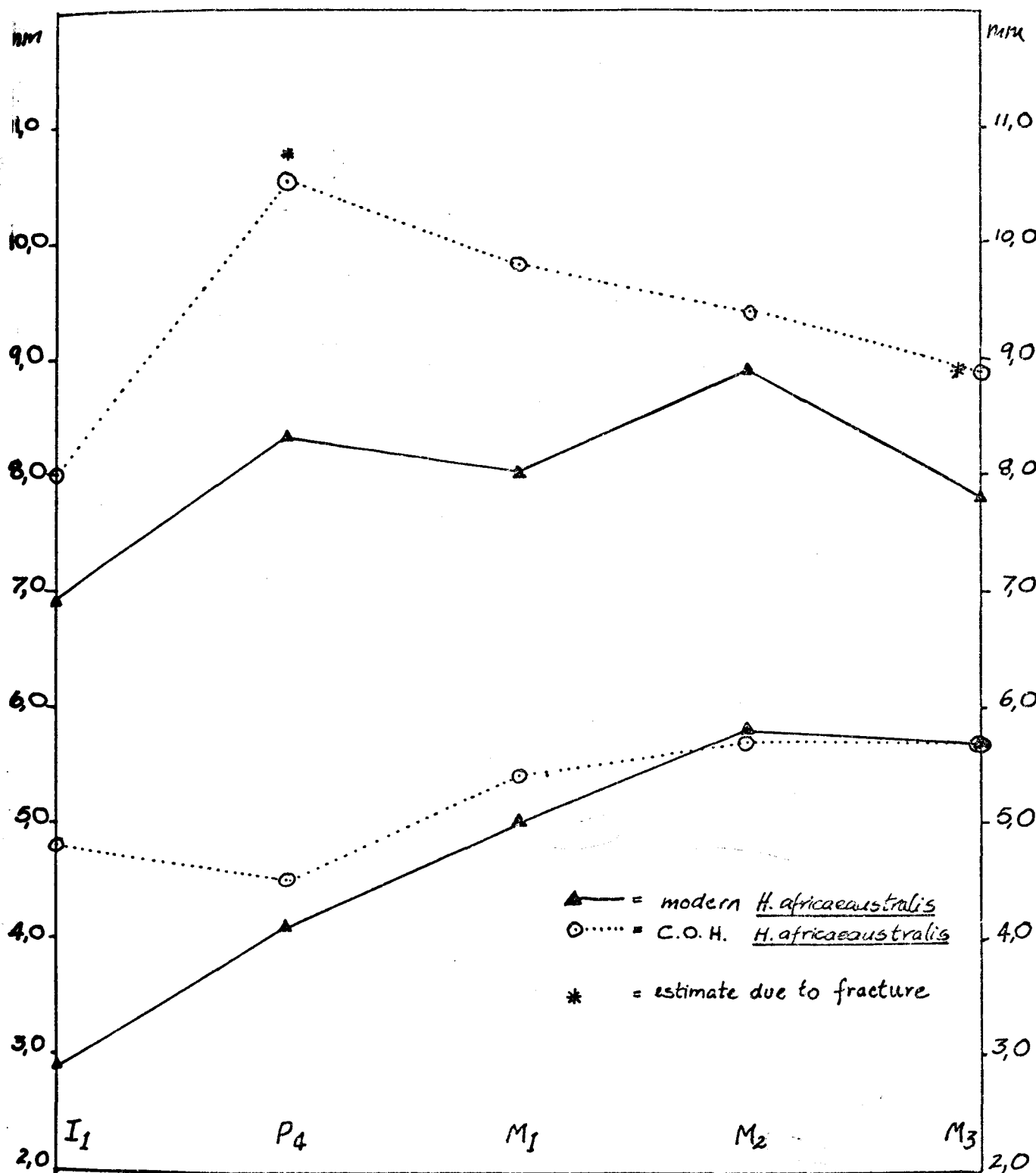
Graph VIII

The sample ranges of the buccolingual diameters of the mandibular teeth of modern and fossil H. africae australis, of the giant Xenohystrix crassidens and of H. makapanensis with contemporaneous fossil forms superimposed



Graph IX

Sample ranges for the MD diameters of the maxillary teeth of H. africanus remains from the Cave of Hearths compared with those for recent H. africanus



Graph X

Sample ranges for the BL diameters of the mandibular teeth of the *H. africae australis* remains from the Cave of Hearths compared with those for recent *H. africae australis*

and palaeoecological considerations (section 16.3.2) of the concluding chapter to Part I.

General note to section 14.3

Hystrix bessarabica Riabinin 1929 and H. etrusca Bosco 1898, both cited as fossil forms contemporaneous with fossil H. africae australis from the South African australopithecine localities, have been synonymized with H. primigenia (Wagner 1848) and H. refossa Gervais 1852 respectively by Bakr (MS 1959 pp.8 and 23).

14.4 The estimated minimum number of individuals of each species of fossil Hystricid present in each of the breccias of the four Transvaal australopithecine localities

After segregating the fossil material according to taxon, locality and breccia, the minimum number of individuals of each species present in any particular breccia was estimated in the following way:

1. Mandibular dentitions and isolated lower teeth were separated from upper dentitions and isolated upper teeth. The greatest number of any one tooth category present, e.g. lower left premolar (considering both in situ and isolated teeth) was noted, this being the minimum number of individuals present in the sample.
2. Any teeth of the tooth category used in step 1. but from the opposite side of the jaw, i.e. lower right premolars, were then compared with the premolars of each of the individuals obtained in step 1.; by 'matching' teeth and comparing the maturity of their C.E.P.s it could be established whether the right mandibular premolars represented any additional individuals, or not.
3. The remaining mandibular fragments and isolated teeth were then compared with the specimens representing the individuals decided upon in steps 1. and 2. By considering growth stage and C.E.P. it could be decided whether or not this material represented any additional individuals.
4. Finally, in the same way, the upper dentitions and isolated upper teeth were compared with the specimens representing the individuals obtained in steps 1.-3. The total number of individuals obtained is the estimated minimum number of individuals.

The results were as follows:

Makapansgat Limeworks

Xenohystrix crassidens Greenwood 1955

Basal Red Mud (Member 2): -

Grey Breccia (Member 3) : 13 individuals, 40 specimensⁱ⁾

i) This number includes specimens M1003, M2516 and M8362 which may belong to Hystrix makapanensis Greenwood 1958. Their exclusion from the Grey Breccia X. crassidens sample does not affect the estimated minimum number of individuals, neither does their inclusion in the Grey Breccia H. makapanensis sample affect the estimated number of individuals of this species.

Upper Phase I Breccia (Member 4): 1 individual, 1 specimenⁱ⁾

Phase II Breccia (Member 5) : -

Hystrix makapanensis Greenwood 1958

Basal Red Mud (Member 2): -

Grey Breccia (Member 3) : 4 individuals, 8 specimensⁱⁱ⁾

Upper Phase I Breccia (Member 4): 2 individuals, 2 specimensⁱⁱⁱ⁾

Phase II Breccia (Member 5): -

H. africae australis Peters 1852^{iv)}

Basal Red Mud (Member 2): -

Grey Breccia (Member 3) : 6 individuals, 17 specimens^{v)}

Upper Phase I Breccia (Member 4): 1 individual, 1 specimen

Phase 2 Breccia (Member 5) : 2 individuals 2 specimens

It is interesting to note that all 13 Xenohystrix crassidens individuals from the Grey Breccia are adult, i.e. at growth stages 5 and 6. The 4 Hystrix makapanensis individuals are likewise all adult. On the other hand, the H. africae australis remains (the smallest of the three fossil species) are predominantly those of juveniles (i.e. growth stages 2-4) although at least one adult individual is present.

In the overlying Upper Phase I Breccia, however, the single X. crassidens specimen present is that of a young juvenile at (small) growth stage 2, and of the two H. makapanensis specimens, one is juvenile (growth stage 3) and the other adult. The single H. africae australis specimen is adult (growth stage 6) whilst the two specimens of this species in the Phase II Breccia are both adult.

The absence of juvenile X. crassidens specimens from the grey breccia is interesting, particularly since there are more individuals of this species present than there are of the other two species combined.

i) If M8282 is H. makapanensis and not X. crassidens. Otherwise 2 individuals, 2 specimens

ii) Refer to note i), Grey Breccia, on previous page

iii) Specimen M8282 (see note i) included in this estimate. If it belongs to X. crassidens, then 1 individual, 1 specimen.

iv) Many specimens originally referred to H. cf. africae australis by Greenwood 1955.

v) M1001 is included in this number but may belong to

H. makapanensis. Its inclusion or exclusion from either sample does not affect the estimated number of individuals.

Sterkfontein

Xenohystrix crassidens Greenwood 1955

This species apparently does not occur at Sterkfontein.

Hystrix makapanensis Greenwood 1958

Apparently not present unless SFN15 (Dump 8) and SFN 17 (Dump 10) can be referred to this species, which seems rather unlikely.

H. africae australis Peters 1852

STS (Type Site Locality): 5 individuals, 5 specimens

Dump 1 : 3 individuals, 3 specimens

Dump 2 : 1 individual, 2 specimens

Dump 8 : 4 individuals, 8 specimens

Dump 10 : 1 individual, 1 specimen

Dump 13 : 1 individual, 1 specimen

No striking predominance of either juvenile or adult individuals was noted in any one site unit.

Swartkrans

Xenohystrix crassidens Greenwood 1955

Apparently not present

Hystrix makapanensis Greenwood 1958

Apparently not present unless SK14237 (Pink Breccia SKa or Member 1) can be referred to this species.

H. africae australis Peters 1852

Pink Breccia, SKa or Member 1 : 4 individuals, 7 specimens

Brown Breccia SKb or Member 2 : 4 individuals, 8 specimens

As was the case at Sterkfontein, no striking predominance of either juvenile or adult specimens was observed in either breccia.

Kromdraai A

Xenohystrix crassidens Greenwood 1955

Apparently not present

Hystrix makapanensis Greenwood 1958

Apparently absent unless KA1912 (the derivation of which is uncertain, see Appendix II p.26) can be referred to this species.

The exclusion of this specimen from the H. africaeaustralis sample does not affect the estimated minimum number of individuals.

H. africaeaustralis Peters 1852

Kromdraai A Breccia : 3 individuals, 4 specimens

14.5 The estimated minimum number of individuals of Hystrix africaeaustralis present in each Bed and in the Sinkhole of the Cave of Hearths

Only one species of porcupine, H. africaeaustralis, is present in the Cave of Hearths deposit. The material from each Bed and the Sinkhole was treated as a unit, and the same procedure as that described in section 11.4 was followed.

The results were as follows:

Bed 1	)	
Bed 2	)	1 individual, 1 specimen
Bed 3	)	
Bed 4		0
Bed 5		3 individuals, 4 specimens
Bed 6		2 individuals, 2 specimens
Bed 7		1 individual, 1 specimen
Bed 8		3 individuals, 4 specimens
Bed 9		3 individuals, 6 specimens
Bed 10		4 individuals, 7 specimens
Bed 11/12		3 individuals, 4 specimens (Iron Age)
Surface		1 individual, 1 specimen
Sinkhole		22 individuals, 57 specimens
Unknown		3 individuals, 4 specimens
Total	=	46 individuals, 90 specimens

15 RECONSTRUCTION OF THE CRANIUM AND MANDIBLE OF XENOHYSTRIX
 CRASSIDENS

Two views of the cranium (a palatal and a lateral) and one of the mandible (a lateral) were reconstructed.

In Chapter 5, where evolutionary trends with the family Hystricidae were discussed, it was demonstrated that the major skull changes which appear to have taken place in the evolution from the primitive to the advanced condition in the family Hystricidae have been concerned with increasing the 'pneumatization' of the cranium and the concomitant lengthening and broadening of the nasals and snout. The posterior half of the cranium has remained rather conservative in that the changes to effect improved 'pneumatization' have not involved this region of the skull.

It was therefore considered not unreasonable to use the posterior portions of scaled-up palatal and lateral outlines of the cranium of Hystrix africaeaustralis in the reconstruction of the cranium of Xenohystrix. These outlines were magnified on a "Goodkin Camera" until the teeth and palate fitted a natural size drawing (from a series of specimens) of the maxillary teeth and palate of Xenohystrix.

The anterior portion of the cranium of Xenohystrix is known to have differed from that of any species of Hystrix, as can be gauged from the relatively shorter, more strongly curved diastema - it is probable that the skull of Xenohystrix was short-snouted and blunt. Specimen M1006, an almost complete left premaxillary fragment was used to reconstruct the length of the snout. The palatal and lateral outlines obtained from the enlarged H. africaeaustralis cranium were adjusted to fit the shape suggested by this fragment.

The mandible was reconstructed by using the curvature of the lower incisor as a guide to its probable length, and assuming that as in H. africaeaustralis, the incisor has its origin above and posterior to the M_3 . There is evidence that this assumption is correct in that in specimen M1802 the incisor is seen to curve sharply upwards posterior to the M_3 . The length of the mandible was gauged by extending the curvature of the lower incisor to approximately this point. The length of the diastema was assessed from specimens M1803 and M1007 and the approximate outline of the coronoid process from M1803 and M1802.

The outline of the posterior portion of the mandible was dotted in, in a way which fitted most suitably to the more definite portions of the reconstruction. The reconstructed mandible was then compared with the reconstructed lateral view of the cranium to see if the maxillary and mandibular tooth rows and the mandibular condyle and glenoid fossa corresponded.

The results of the attempts at reconstruction are shown in Figures 129, 130 and 131, the speculative parts of the reconstruction being shown as dotted lines.

Fig 132

Diagrams illustrating means by which the upper and lower incisors may be identified and orientated.

- a = strongly curved upper incisor
- b = less strongly curved lower incisor
- c = flat mesial and curved distal incisor walls
- d = small diameter pulp cavity towards incisial edge
- e = large diameter pulp cavity towards root end
- f = equilateral triangle-shaped incisial surface of upper incisor
- g = elongate isosceles triangle-shaped incisial surface of lower incisor

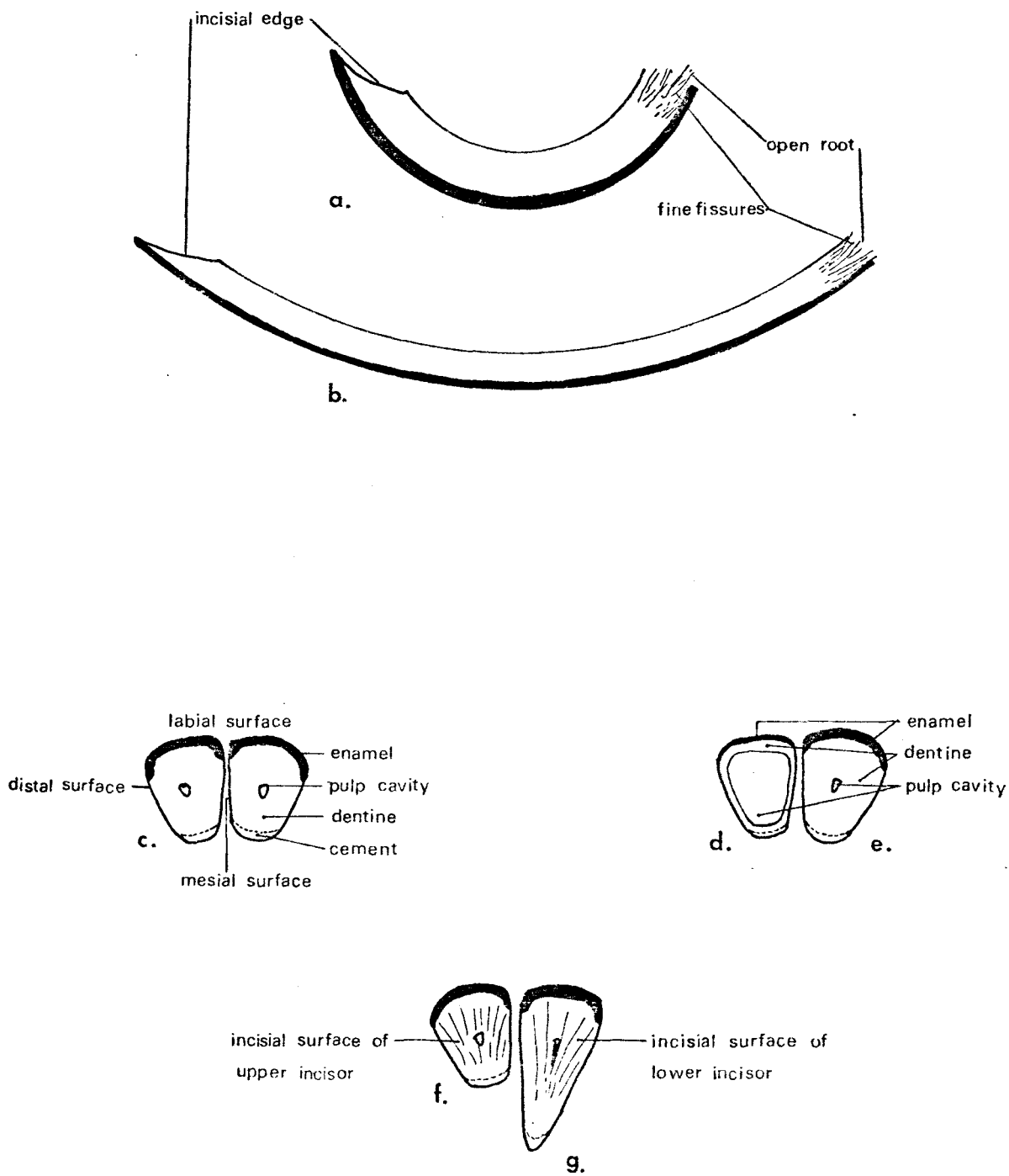


FIG.132

Fig. 133

Diagrams illustrating the means by which maxillary and mandibular teeth and individual maxillary and mandibular teeth of Hystrix africaeaustralis may be differentiated from one another.

- A - Diagrammatic mandibular molar. Note straight long axis and root development.
- B - Diagrammatic maxillary molar. Note marked curvature (from buccal to lingual surface) so that the root canals of the poorly developed papillate rootlets are almost perpendicular to the occlusal surface.
- C,D - Diagrams, which with B, demonstrate the apparent 'straightening' of the curvature of the maxillary teeth with increasing amounts of wear.
- E,F - Diagrams illustrating the shape of the occlusal surfaces of the mandibular and maxillary teeth respectively, E. being more 'rectangular' and F. being 'cylindrical'.
- G - Diagram illustrating the compression of the maxillary first molar by the developing P_4 so that the BL diameter ('width') exceeds the MD diameter ('length').
- H - Diagram illustrating the loss of crown height ('length' of some authors) due to prolonged wear. Tooth is M_1 at growth stage 6.
- I - Mandibular first molar showing well-marked concave mesial pressure facet which has exposed the dentine and less well marked distal pressure facet. The tooth has a more cylindrical outline than that of the M_2 (J).
- J - Mandibular second molar showing mesial and distal pressure facets. The tooth has a more rectangular outline than the M_1 (I) or the M_3 (K)
- K - Mandibular third molar showing roughly triangular occlusal outline. There is a mesial pressure facet only.
- L - Alveolar root impressions of a left mandibular tooth row $P_4 - M_3$. Note that the posterior roots of each tooth show a tendency towards fusion.
- M - Alveolar root impressions of a left mandibular tooth row $P_4 - M_3$. Note that in this case it is the outer or buccal roots of each tooth (with the exception of M_2) which show a tendency towards fusion. The M_1 shows a different pattern of fusion from that shown in L.

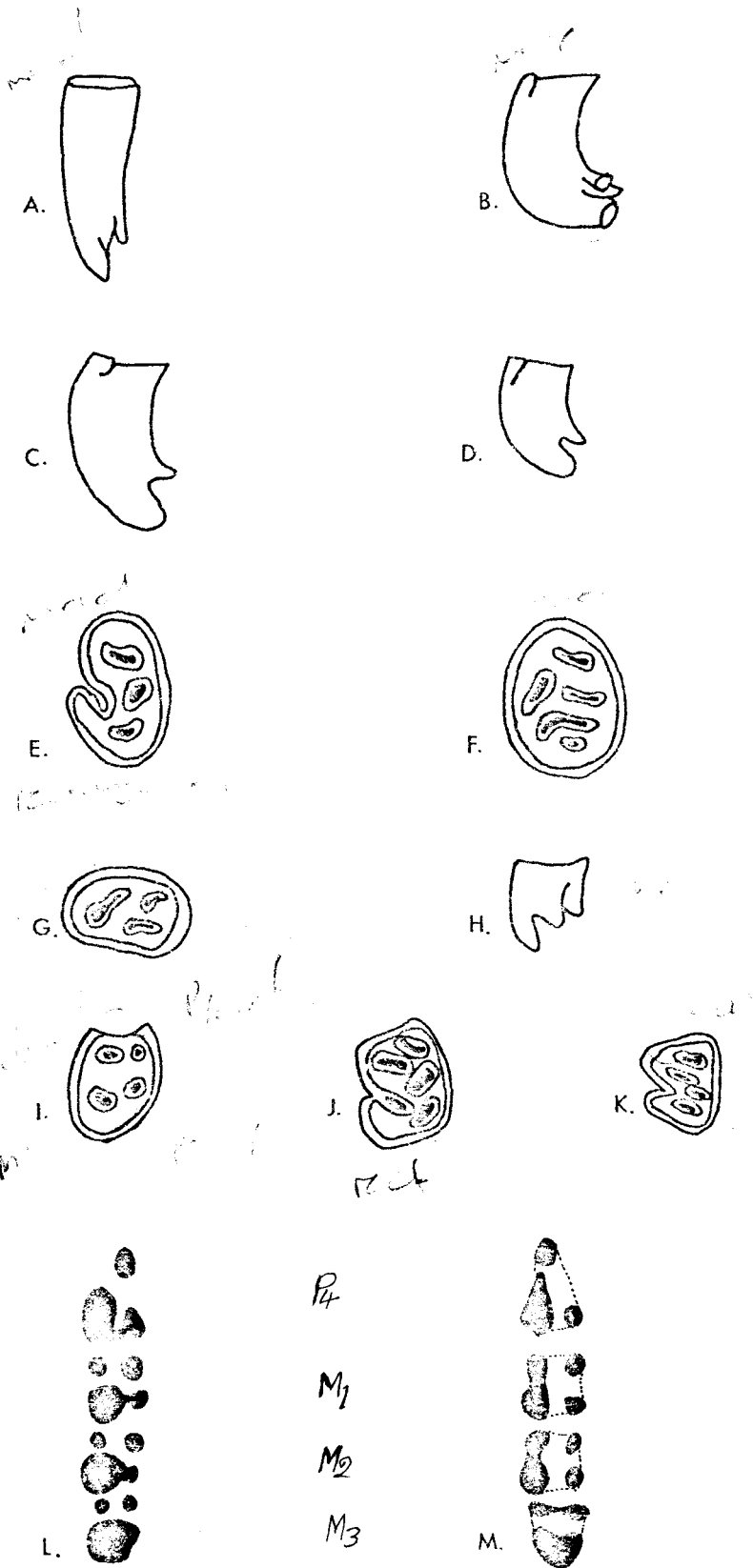


FIG. 133

16. SUMMARY, CONCLUSIONS AND DISCUSSION

16.1 Summary

1. The environmental setting, stratigraphy and age of the four Transvaal australopithecine cavern deposits and Cave of Hearths has been reviewed, with particular reference being paid to the information on age provided by the fossil Hystricidae.
2. The evolutionary and adaptive trends within the Hystricidae (Hystricinae and Atherurinae) have been investigated to enable the fossil Hystricidae to be 'placed' in an evolutionary sense.
3. Synonymy within the genus Hystrix has been investigated.
4. All cranial, mandibular and dental morphological characters that have been used in the diagnoses of new species of Hystrix have been listed, tested for variability within a sample of 32 recent Hystrix (Hystrix) africaeaustralis specimens, and then tested for diagnostic significance by comparison with the only two other valid species in the sub-genus Hystrix. The cranial, mandibular and dental morphology of Hystrix (H.) africaeaustralis has been discussed, and comprehensive sets of measurements provided.
5. A standard terminology for Hystrix morphology has been proposed, and the reference points to be used when measuring the above characters have been defined.
6. The sequence of tooth replacement in H. (H.) africaeaustralis has been discussed, and a method of segregating specimens into six proposed growth stages devised, using tooth replacement and/or the maturity of the crown enamel pattern. A method for positionally identifying isolated teeth has been devised.
7. The taxonomic status of 112 fossil Hystricid specimens from the four Transvaal australopithecine localities and 91 from the Cave of Hearths has been determined, and two genera and three species of fossil porcupine have been described. The distribution and minimum number of each has been discussed. All available South African fossil Hystricid material has been catalogued, and tables of measurements provided.
8. A reconstruction of the cranium and mandible of the giant porcupine Xenohystrix crassidens has been attempted.

9. A catalogue of all fossil Hystricidae (including the genera Hystrix, Acanthion, Xenohystrix, Lamprodon and Sivacanthion) has been compiled to facilitate comparison of contemporaneous fossil forms. Attention was paid to age and appearance. Synonymy and possible synonymy within the named fossil forms has been discussed.

16.2 Conclusions

1. Age of the australopithecine deposits

The fossil Hystricidae tell little about the potential ages of the Transvaal australopithecine deposits, mainly because the East African fossil forms, for many of which absolute dates are available (ranging from $\pm$ 5,4-0,25 m.y.B.P.) have as yet not been identified beyond generic level. It is thus not possible to correlate these with the forms occurring in the South African australopithecine deposits. Xenohystrix crassidens is of considerable potential in dating as it is easily recognizable as well as of limited temporal (stratigraphic) occurrence, being confined to Members 3 and 4 at Makapansgat Limeworks. However, its geographical distribution is unknown.

In Chapter 2.2 it was suggested that the Hystrix material from the Chemeron Formation, dated at $\pm$ 3,0m.y.B.P. and referred to cf. Xenohystrix crassidens, is suggestive of a date approximately 3,0m.y.B.P. or more for the breccias below the Phase II at Makapan Limeworks, which contain this species. However, a cast of the Chemeron porcupine has since been examined; this showed that the material is not referable to X. crassidens and there is thus no basis for the above age correlation. Until the dated East African material is identified, the porcupines will contribute little to the resolving of the South African dating problem. The evidence provided by the faunal correlations, cultural comparisons and geomorphological dating (see p. 73) do not appear to be in conflict with the limited evidence provided by even a world-wide consideration of fossil Hystricidae.

2. Evolutionary/adaptive trends within the Hystricidae

Investigation of the geographical distribution of the living genera of this family has shown that the 'primitive' or unspecialized genera (Trichys, Atherurus and Thecurus) are confined to high-rainfall tropical forest regions, mainly in South East Asia. The 'advanced' or highly specialized genera (Acanthion and Hystrix or subgenera Acanthion and Hystrix of genus Hystrix) occur over drier portions of the Asiatic mainland, the Middle East

and Africa, including parts of the Arabian, Sahara, Namib and Kalahari Deserts. The changes involved from the primitive to the advanced condition are concerned with adaptation to drier environments and include an increase in body size and in the effectiveness of quill cover, an increased development of the caudal rattle quills, increasing tooth hypsodonty and the improved efficiency of the sense of smell by increasing 'pneumatization' of the premaxillary, nasal and frontal sinuses. These specializations reach their peak in the subgenus Hystrix. The fossil history of the family is discussed in section 16.3 below.

3. Synonymy within the genus Hystrix

There are numerous extant species (77) listed under the genus Hystrix, mainly because the original generic definition was so wide that practically any hystricomorph rodent with spines was referred to it. A second reason is that many authors have ignored Cuvier's genus Acanthion (now with subgeneric status within Hystrix) so that the species that normally would have been referred to Acanthion have been included under Hystrix. In the subgenus Hystrix, only 3 species, Hystrix (Hystrix) cristata Linn. 1758, H. (H.) indica Kerr 1792 and H. (H.) africaeaeustralis Peters 1852 proved to be valid. Of these H. (H.) cristata is the most specialized (also occupying the driest environments) followed by H. (H.) africaeaeustralis while H. indica is closer to Acanthion. Abu Bakr (unpublished MS) has erected the subgenus 'Epicanthion' (of genus Acanthion) to house the latter species, as he considers H. indica to occupy an intermediate position between a genus Hystrix and Acanthion sensu stricto.

4. Variability and diagnostic significance of cranial, mandibular and dental characters used in diagnoses of new species of Hystrix

Taking into consideration all cranial, mandibular and dental characters investigated, the basic measurements of the dentition, that is, mesio-distal (length) and buccolingual (breadth) diameters proved to be the characters with the lowest sample standard deviation, and hence the least degree of variability. There was little difference in the variability between measurements taken at the alveolar rim or at the occlusal surface, the latter point being more convenient when measuring isolated fossil teeth. Amongst the cranial and mandibular characters tested for variability (within a sample of 32 recent H. (H.) africaeaeustralis specimens) those associated with height and particularly breadth measurements

proved to be far less variable than those associated with length measurements. Most characters were found to vary little within any particular growth stage.

However, despite the low variability shown by dental characters when examined within a single species, they proved to be of no diagnostic significance in separating the three valid species within subgenus Hystrix. The crown enamel pattern also proved to be undiagnostic. No mandibular characters proved to be of significance. Very few cranial characters proved to be diagnostic, those that are being associated with the differing degree of cranial inflation shown by the three species. Cranial inflation is manifested in the premaxillary, nasal, frontal and zygomatic regions of the skull, which are not frequently preserved in fossil form. The characters which are diagnostic are summarized in Table XVII of the main text.

5. Standard terminology

A standard terminology and definition of parameters was found to be necessary for purposes of comparison. Both have been proposed (Chapter 7).

6. Segregation of species into growth stages

Isolated premolars and molars can usually be referred to a particular growth stage by means of the maturity of their crown enamel pattern. Late growth stage 4 may be confused with growth stage 5 and occasionally late growth stage 5 with growth stage 6. This is because the harder diet available in some geographical regions may cause a greater and more rapid rate of wear, resulting in teeth having more mature crown enamel patterns for a particular growth stage than those of an individual at the same growth stage from an area where a softer diet was available. Growth stages segregation by means of crown enamel pattern coincides with that arrived at using tooth eruption.

7. The taxonomic status of the fossil material

Two genera and three species of fossil porcupine are represented in the South African australopithecine deposits: Xenohystrix crassidens Greenwood 1955, Hystrix makapanensis (Greenwood 1958) and Hystrix africae-australis Peters 1852. There appears to be no valid reason for erecting a distinct species to house the material initially referred by Greenwood (1955) to H. cf. africae-australis and it has thus been referred to the

recent southern African species. X. crassidens and H. makapanensis are confined to Members 3 and 4 at Makapansgat Limeworks although there are some large isolated teeth from Sterkfontein, Swartkrans and Kromdraai which may tentatively be referred to the latter species although it is more likely that they are large H. africae australis. The porcupine from Makapansgat Limeworks Member 5 and those from Sterkfontein, Swartkrans and Kromdraai are referred to H. africae australis. X. crassidens is the commonest form in the grey breccia (Member 3) at Makapansgat Limeworks (minimum number 13 individuals) followed by H. africae australis (minimum number 6 individuals) while H. makapanensis is rare (4 individuals). In the overlying pink breccia (Member 4), the three species are present in approximately equal numbers (1 X. crassidens, 2 H. makapanensis and 1 H. africae australis). The overlying Phase II breccia (Member 5) contains only H. africae australis (2 individuals). The grey breccia X. crassidens specimens are all adult (i.e. at g/s 5 or 6), as are those of H. makapanensis. The H. africae australis remains (the smallest form) are predominantly juvenile (i.e. g/s 2-4). In the overlying pink breccia the single X. crassidens specimen is a juvenile and of the two H. makapanensis individuals one is juvenile, one adult. The single specimen of H. africae australis is adult, as are both specimens of this species from the Phase II breccia. The absence of juvenile X. crassidens from the grey breccia, although there is a higher minimum number of individuals of this species than there are of the other two species combined, is interesting and has been discussed in section 16.3 below.

In Sterkfontein Type Site there is a minimum number of 5 H. africae australis individuals, with 3 in Dump 1, 1 in Dump 2, 4 in Dump 8, 1 in Dump 10 and 1 in Dump 13. At Swartkrans, the remains of a minimum number of 4 individuals have been recovered from SKa and an equal number from SKb. Kromdraai A has yielded a minimum number of 3 individuals of H. africae australis. At none of these sites is there a predominance of either juvenile or adult individuals.

The Cave of Hearths material, although it often shows a larger permanent premolar in both upper and lower jaws is referred to H.(H.) africae australis. There is a total minimum number of 46 individuals (90 specimens) from Beds 1 to 12. The distribution of these is discussed in section 14.5.

8. Reconstruction of Xenohystrix crassidens

The reconstruction of X. crassidens, particularly the palatal view of the

cranium (Figure 130) and the lateral view of the mandible (Figure 131) indicate that the genus Xenohystrix has more in common with the least specialized genus of the subfamily Hystricinae, Thecurus (Figure 29) or even with the Atherurine genus Atherurus (Figure 27). The distribution of these genera is confined to high-rainfall tropical forests (see distribution maps, Figures 39, 40 and 41). This is in keeping with the dentition of Xenohystrix, which is brachydont and suggestive of a soft diet, such as is available in forest habitats. It is probable (see discussion below) that X. crassidens in common with other fossil porcupines had a reduced quill cover (see Figures 28 and 30). It therefore to some extent bridges the gap between the Hystricinae and Atherurinae described by Lyon (1907).

9. Fossil Hystricidae

Investigation of the synonymy of fossil forms shows that of the approximately 33 named species, only about 14 are valid or potentially valid.

These are:

Synonyms

- | | |
|--|---|
| 1. <u>Hystrix (Hystrix) africaeaeaustralis</u> Peters 1852 | <u>H.cf.africaeaeaustralis</u>
Greenwood 1955 p.77
<u>H.cristatus</u> Broom 1946
p.82
<u>H.greenwoodi</u> Bakr MS.
p.25 |
| 2. <u>Hystrix (Hystrix) angressi</u> Frenkel 1970 | - |
| 3. <u>Hystrix (Hystrix) cristata</u> Linn. 1758 | <u>H.astasobae</u> Bate 1951
p.3
<u>H.cristata minor</u> Malez
1963 pp.1-198 Fig.5? |
| 4. <u>Hystrix (Hystrix) indica</u> Kerr 1792
or
<u>Acanthion (Epiacanthion) indicus</u> (Kerr)
(acc. Abu Bakr Ms. p.38) | <u>H.cristata indica</u> Kerr
1792 p.213
<u>H.leucura</u> Sykes 1831
p.103
<u>H.sivalensis</u> Lydekker
p.110 Fig. 5, <u>non</u> p.109
<u>H.hirsutirostris</u> Brandt
1835 p.375 |

Synonyms

H.hirsutirostris

Lydekker 1886 p.120

H.crassidens Lydekker
1886 p.37

H.cf.leucurus Matthew
1929 p.559

Acanthion sivalensis
sinhaleyus Deraniyagala
1951 p.122

Hystrix sivalensis sin-
haleyus Deraniyagala
1958 p.83

5. Hystrix (Acanthion) lagreltii Lönnerberg 1924

--

6. Hystrix (Hystrix) makapanensis (Greenwood 1958)

Hystrix major Greenwood
1955 pp.78,79

7. Hystrix primigenia (Wagner 1848)

or

Hystrix (Lamprodon) primigenia Wagner 1848
(acc. Abu Bakr MS p.8)

Lamprodon primigenia
Wagner 1848 p.347
Castor atticus Roth and
Wagner 1854 p.414
Hystrix primigenia
Gaudry and Lartet
1856 p.273
Wagner 1857 p.129
Gaudry 1862 p.122
H.bessarabica Rjabinin
1929 p.130

8. Hystrix refossa Gervais 1852

or

Hystrix (Lamprodon) refossa Gervais 1852
(acc. Abu Bakr MS. p.23)

Hystrix refossa
Gervais 1848-1852 p.6
Schlosser 1885 p.28
Vivet 1954 p.99
H.major Gervais 1859
p.511,1867-1869 p.76
H.etrusca Boser 1898
p.141

Synonyms

- | | |
|---|---|
| 9. <u>Hystrix (?) schaubi</u> Brunner 1954 | <u>Hystrix cristata minor</u>
Malez 1963 pp.1-198?
<u>H.vinogradovi</u> Argyro-
poulos 1941 pp.88-91? |
| 10. <u>Hystrix sivalensis</u> Lydekker 1878
or
<u>Hystrix (Epiacanthion) sivalensis</u> (Lydekker
(acc. Abu Bakr MS. p.23) 1868) | <u>Hystrix sivalensis</u>
Lydekker 1878 p.100 |
| 11. <u>Hystrix suevica</u> Schlosser 1885
or
<u>Hystrix (Lamprodon) suevica</u> Schlosser 1885 | <u>Hystrix</u> sp.Quenstedt
1885 p.58
<u>Hystrix suevica</u>
Schlosser 1885 p.28
non pl.3 fig.27 1902 |
| 12. <u>Hystrix (Acanthion) subcristata</u> | <u>Hystrix subcristata</u>
Swinhoe 1870 p.638
<u>H.cf.subcristata</u>
Young 1927 p.55,1934
p.109
Colbert and Hooijer
1953 p.41

<u>Hystrix</u> sp. Young 1932
<u>H.kiangsenensis</u> Wang
1931 p.47 |
| 13. <u>Atherurus karnuliensis</u> Lydekker 1886 | - |
| 14. <u>Sivacanthion complicatus</u> Colbert 1933 | - |
| 15. <u>Xenohystrix crassidens</u> Greenwood 1955 | - |

Hystrix wiedemanni Roger 1885 (= Anchitheriomys wiedemanni Roger 1900),
Hystrix lamandini Filhol 1876 and Hystrix venusta Leidy 1869 are no
longer considered as belonging to the genus Hystrix.

16.3 Discussion

The Phylogeny of the Family Hystricidae

As discussed in Chapter 5, the primitive or unspecialized Hystricidae
(the genera Trichys, Atherurus and Thecurus) are confined to the tropical

rain forest regions of southeast Asia, with the exception of Atherurus, some species of which occur in similar environments in Africa (see distribution maps Figs. 39, 40 and 41). There appears to be no reason to suppose that the ancestors of these primitive genera might have existed in other than tropical rain forest environments. Such environments are unfavourable for the preservation of fossils; it is for this reason that fossilized remains of any forest-dwelling animals, for example, forest primates, are rare. Fossil remains of the 'primitive' genera mentioned above are thus practically non-existent, and it is only from Pleistocene times onwards, when early man began to occupy cave sites and there discard the remains of the animals they hunted, that the fossilized remains of the forest-dwelling Hystricidae, for example Atherura karnuliensis from the Upper Pleistocene Karnul Caves near Madras, are encountered. From the outset, therefore, the absence of any fossil remains of the primitive genera poses a problem in evolutionary studies of the Hystricidae.

For this reason the available fossil history of the family, particularly prior to the Pleistocene period, is confined to the advanced or specialized genus Hystrix (which includes the subgenera Hystrix and Acanthion) members of which live in savanna or desert environments where conditions are more favourable for preservation. Even so, Hystrix remains are normally a rare component of fossil deposits and in addition are almost invariably highly fragmentary, frequently consisting only of isolated teeth. In many cases other authors have established new fossil species on the basis of one or two isolated teeth. The present study has demonstrated that dental characters are not satisfactory for diagnostic purposes, which leaves the taxonomic status of many of such fossil species in some doubt. This further complicates the establishment of a phylogeny.

Another consideration is that the apparent dominance of fossil Hystrix almost to the exclusion of other genera, may be due to the fact that early writers were unaware of the characteristics of related genera, and thus automatically referred any fossil Hystricid material to Hystrix, with which they were familiar. Until all the Old World fossil material can be re-examined in the light of this possibility, even the generic status of some fossil forms must remain in doubt.

Another problem which has hampered the phylogenetic study of the

Hystricidae has been the dating of such finds as have been made. The deposits from which the earlier described species were recorded are frequently undated, or very broadly dated, terms such as 'Miocene', 'Pliocene', 'Pleistocene' and 'Villafranchian' being used. Such terms are vague and the last, for example, is today known to span a period in excess of 2,00m.y. ($\pm 900,000 - 3,500,000$ years B.P.). The absolute or even geological ages ascribed to fossil-bearing beds have been (and are still being) frequently altered, while the temporal boundaries between the Epochs mentioned above are frequently being shifted. Finally, it has been difficult to cross-correlate the various local chronostratigraphic terms - e.g. European, Russian, African, Indian and Chinese. A rough attempt at this is shown in Table XIX.

For these reasons the compilation of a feasible or even plausible phylogenetic tree of Hystricidae is at present out of the question, since a viable phylogenetic hypothesis should explain at least a large segment of the available morphologies, stratigraphic and geographic data. However, study of the living members of the Hystricidae indicates that evolutionary changes, resulting in modern 'advanced' Hystrix, must have taken place along the following lines:

- (1) increase in body size
- (2) increase in density and defensive effectiveness of quill cover
- (3) improvement of the effectiveness of the rattle-quill signaling mechanism
- (4) increase in cranial 'pneumatization' or inflation, improving the olfactory sense
- (5) a change from the brachydont to the hypsodont dental condition

Evidence of only points (1), (4) and (5) will be preserved in fossil form. It has already been mentioned that crania are seldom preserved, while Abu Bakr (unpublished MS 1959) states, and the present author agrees, that:

Teeth, unfortunately, are of no help in determining the finer points of hystricine phylogeny, and mandibles, while suggestive, are not really decisive. Only with knowledge of the skull can one be reasonably sure.
(p.43)

The origin and early history of the family Hystricidae is obscure, a point also commented on by Wood (1975*). It would appear that South-

* Wood, A.E. (1975) The problem of the Hystricognathous Rodents
University of Michigan, Papers on Paleontology No. 12 pp.75-80.

East Asia was an important evolutionary centre, because living Hystricidae are best represented in this region (all five living genera occurring), whereas Africa is represented by only Hystrix and Atherura, and Europe by only Hystrix. Furthermore, fossils of 'primitive' genera (Sivacanthion, Atherura, Thecurus and Acanthion) are more frequent and occur earlier in this region than elsewhere.

With the referring of "Hystrix" lamandini Filhol (Upper Eocene) and "Hystrix wiedemanni Roger (Upper Miocene) to other genera, the history of the family begins in the Early Pliocene with the appearance of Sivacanthion complicatus Colbert from the Lower Siwaliks, Chinji, India. Modern authors might class the Lower Siwaliks as falling within the Miocene, see Table XIX. This species may represent a still small brachydont offshoot of the primitive Acanthion stock, worthy of generic rank, but Landry (1957 p.63) and the present author, believe it to be an Atherurine porcupine similar to, if not identical with, the genus Atherurus. The brachydont primitive subfamily Atherurinae is therefore found in the Early Pliocene (or Miocene - Chinji = Sarmatian), at which time, as far as can be told, the atherurines were essentially no different from living forms. They do not occur again in the fossil record until comparatively recent times, with the appearance of Atherura karnuliensis from the Middle Pleistocene. No fossil porcupine approaches in primitiveness the living genus Trichys, which to date appears to be without a fossil history.

The fossil history of the advanced, subfamily Hystricinae begins with the appearance in the late Miocene ('Vindobonian') of Europe of an advanced porcupine, Hystrix suevica Schlosser. The validity of this species is seemingly in some doubt (see Appendix X), but according to Abu Bakr (1959 p.23) this species is similar in brachydonty to H. primigenia (Wagner), differing from it only in its slightly smaller size. The latter species provides the earliest satisfactory fossil Hystrix material known. It differs from modern Hystrix in its larger size, more brachydont teeth and in its lesser degree of cranial inflation. It was probably ancestral to the Astian and Villafranchian H. refossa of Europe, which appears to be morphologically intermediate between H. primigenia and modern H. cristata. It is not known whether or not H. refossa is directly ancestral to the last-named species, but this is unlikely, since perfectly hypsodont H. indica and H. africae australis occur in the fossil record at approximately 4,0m.y.B.P. very shortly after the first

appearance of H. refossa, which persists until the beginning of the 'Villafranchian' at about 0,9m.y.B.P. H. suevica may be ancestral to (if not synonymous with) H. primigenia. The large and somewhat brachydont H. primigenia is paralleled in Africa by the roughly contemporaneous large but somewhat less brachydont undescribed Hystrix sp. from Langebaanweg, dated at between 4 and 7m.y.B.P. (Hooijer 1975 pers. comm.) and in India by the 6-7m.y. old H. sivalensis, which is also apparently slightly less brachydont than primigenia. Hypsodont procupines identical to the living forms (H. africae australis and H. indica respectively) are in evidence by about 4,0 m.y.B.P. in both regions. In Africa, a slightly larger and less hypsodont species, H. makapanensis, is also present. This may parallel the H. refossa 'stage' represented in Europe.

The affinities of Xenohystrix crassidens are uncertain, but on the basis of its brachydont, well-rooted teeth, its short snout and the reconstructed appearance of the cranium and mandible, these would appear to lie closer to Thecurus or even Atherurus than to Acanthion or Hystrix. As discussed under 16.2.8 above, this fossil to some extent bridges the gap between the subfamilies Hystricinae and Atherurinae.

Fossils referred to the subgenus Acanthion make their first appearance only in the Pleistocene, with Hystrix (Acanthion) cf. subcrissata (= H. kiangsenensis) at about 1,75 m.y.B.P. and H. (Acanthion) lagrelii at Choukoutien I - [±] 1,0 m.y.B.P. The genus Thecurus apparently does occur in fossil form (Mohr 1965 p.115), but no time indication for its occurrence is available.

The relationship of the Hystricinae to the Atherurinae is unknown, but their separation must have occurred during the early Miocene or even earlier.

2. Some palaeoecological considerations

The synchronous occurrence of three distinct species of porcupine in the grey and pink breccias at Makapansgat (Members 3 and 4 respectively) requires explanation in ecological terms. The largest of the three by far is the giant Xenohystrix crassidens. The rather brachydont well-rooted upper and lower teeth, the short strongly curved diastema and the somewhat blunt incisial surfaces of the incisor teeth suggest a much softer diet than that eaten by the other two species present, Hystrix makapanensis and H. africae australis. The reconstructed cranium and mandible of X. crassidens suggest that its affinities lie closer to

the forest-dwelling genera Atherurus and Thecurus than to the savanna and desert-adapted Hystrix. Taken together, these facts suggest that Xenohystrix crassidens was a forest form which was fairly common during grey breccia times (a minimum number of 13 individuals, 40 specimens) but becoming rare during the succeeding pink breccia period (1 individual, 1 specimen) after which it apparently became extinct, possibly on account of the shrinkage of its forest environment.

In the grey breccia Xenohystrix crassidens remains occur more than twice as frequently than do those of the other two porcupine species present combined. Furthermore, all the specimens are those of adults or mature adults, i.e. at growth stages 5 or 6. On the other hand, the H. africaeaustralis remains (the smallest form present) are predominantly those of juvenile individuals at growth stages 2-4. If a predator was responsible for the accumulation, it was capable of dispatching fully grown giant porcupines, probably weighing about 60kg or more, but only new-born or juvenile H. africaeaustralis specimens, full-grown adults of which weigh only about one-third as much. This suggests that X. crassidens was easy to kill and one possible explanation for this is that, in common with all other forest forms, its defensive quill cover was poorly developed and decidedly less effective than that of H. africaeaustralis.

In the overlying pink breccia (Member 4) the three species occur in approximately equal numbers, with no preponderance of either adult or juvenile individuals occurring in any of the three. The sample is too small to determine whether this indicates a change in predation pattern or not.

The fossil H. africaeaustralis occurring in Members 3, 4 and 5 at Makapansgat Limeworks is practically identical to the living form, and it is probable that it had identical ecological preferences. The living H. africaeaustralis is ecologically very tolerant, occurring in forest as well as desert conditions, but is more frequently encountered in bushveld and savanna environments.

The sample of H. makapanensis is too small to assess accurately its possible ecological preferences; the indications are that these were very similar to those of H. africaeaustralis, except that the slightly more brachydont teeth indicate a softer diet than that of the latter species.

PART II

AN ANALYSIS AND COMPARISON OF THE INTRODUCED CONTENTS
OF MODERN PORCUPINE LAIRS WITH THE BONE ACCUMULATION
FROM THE MAKAPANGAT LIMWORKS GREY BRECCIA

17 AIMS AND BACKGROUND

The aim of the second section of this thesis has been to investigate and define the characteristics of bone accumulations collected by porcupines, and to assess to what extent fossil porcupines may have been responsible for the accumulation of, and damage to, the masses of fossil bones present in the grey breccia at the Makapansgat Limeworks australopithecine site. The background to this project is as follows:

In 1926, after a consideration of the morphology of the Taung skull, its geographical and environmental setting and the associated faunal remains, Dart concluded that Australopithecus africanus was terrestrial, cursorial, troglodytic, omnivorous and an active hunter, and that the associated animal bones at Taung represented an australopithecine-accumulated 'kitchen midden'. Subsequently, he became convinced that an imperfectly-erect terrestrial omnivore could not have survived and hunted or scavenged in the hostile environment prevalent on the African savanna at that time without the aid of weapons of some sort. In an effort to find such weapons and the artefact type which might have been responsible for the characteristic depressed fractures present on the crania of numerous fossil baboons found in association with australopithecine remains at Taung, Sterkfontein and Makapansgat, Dart (1955, published 1957a, b) undertook an analysis of the entire bone sample then available from the grey breccia of the latter site. This was done because at that time stone tools had not been recovered from any A. africanus-bearing deposit, and Dart regarded the bones as a possible source of tools. The results of this analysis were published in the monograph 'The Osteodontokeratic Culture of Australopithecus prometheus' (1957a) which defined Dart's ideas on the cultural status and capabilities of the australopithecines. In this publication he restated his earlier conclusions and added, amongst others, the claim that A. africanus had practised a systematic bone, tooth and horn (osteodontokeratic) culture, and that the fragmentation of and damage to the bones in the deposit was explicable in terms of australopithecine feeding and tool-making activities. The disproportionate representation of certain skeletal elements he explained in terms of selection on the part of Australopithecus - those skeletal parts likely to prove useful as weapons and tools such as horns, teeth

and long limb bones with hooves attached were specially sought out while other skeletal elements were disregarded and not brought back to the cave. The preponderance of cranial remains was thus interpreted as being indicative of head-hunting. The almost total lack of vertebrae (with the exception of atlas and axis) and particularly of caudal vertebrae was attributed to the fact that:

.....the disappearance of tails was probably due to their use as signals and whips in hunting outside the cavern. Caudal and other vertebrae may also have disappeared because of the potential value of their bodies as projectiles and of their processes (when present) as levers and points.
(op. cit. p.84)

As with his earlier claims concerning the hominid status and evolutionary significance of Australopithecus, Dart's new conclusions concerning the australopithecine mode of life were in turn rejected. Leakey (1953) and Coon (1963) opposed the idea that Australopithecus was cave-dwelling, while the proposed predaceous habit was criticised by Leakey (op.cit.) and Washburn (1957, 1960). The proposition that the australopithecines themselves accumulated the bones found in association with their remains at Makapansgat and Taung, was rejected by Broom et al. (1946) Von Koenigswald (1953), Leakey (op.cit.), Oakley (1953a,b), Washburn (1959) and more recently, by Klein (1975). These authors generally concluded that Australopithecus, rather than being a hunter, instead constituted the prey of carnivores, and that his remains as well as the associated accumulations of bone were either the products of predation and feeding habits of such carnivores as hyenas, leopards or sabre-toothed cats which used the australopithecine caverns or their environs as lairs, or due to the bone-accumulating activities of porcupines. The origin of the carnivore idea was probably a publication by Buckland (1822) in which hyenas were cited as the primary agents responsible for bone deposits in caves. Without further investigation the idea became established, and was later extended to the other large carnivora until it became a basic postulate of archaeological and anthropological thought. Dart's explanations for the disproportionate representation of skeletal parts have been questioned by Brain (1967c, 1969b, 1970a).

The osteodontokeratic tools described by Dart were either rejected outright or otherwise attributed to the bone-damaging activities of

carnivores or to porcupine gnawing (Singer 1956, 1959); at most, they were regarded merely as the discarded residue of australopithecine meals.

Dart has argued strongly in favour of an australopithecine origin for the bone accumulation at Makapansgat and has proposed that the australopithecines there practised a bone, tooth and horn culture, which, in his opinion, would explain both the skeletal part representations and the fragmentation of the bone. The controversial nature of these claims and the counter-arguments put forward, has stimulated much further research into the means by which bones became accumulated in caves, and into the behaviour, predation patterns, bone-accumulating potential and food remains of the carnivores implicated. The survival potential of various skeletal elements has also been investigated. Despite this research, the origin of the Makapansgat grey breccia bone accumulation and the question whether the australopithecines did or did not have an 'Osteodontokeratic Culture' remain controversial subjects. For this reason, the conclusions reached on the above topics of research are of significance to the present project; a list of the various ways in which bones may become incorporated in cavern deposits is given below, with summaries of the research done and conclusions reached on each:

1. Voluntary entering of caves by animals

- a) Sick, wounded and dying animals may seek out caves as a last refuge - the Congo Caves are reputed to have been discovered by following a wounded buck into them. If animals die inside, their bones may become incorporated in the deposit, and eventually fossilize. The present author found the partially-mummified complete skeleton of a dog deep within the furthestmost recesses of a cave, it appeared to have died from natural causes. As far as is known, no published studies on the incidence of this refuge-seeking exist.
- b) In dolomitic areas, animals may enter caves in search of the water which often stands at their lower levels, particularly if water is not available at the surface. Gow (1973) describes the behaviour of a troop of baboons which not only negotiated the precipitous entrance to an underground cavern system in search of the water which occurred within, but also habitually sheltered there, even overnight. This cave is reported to have contained several baboon skeletons, all of

which seemed to indicate that the animals had died from natural causes. Wells (1973) reports a similar situation in a dolomitic cave near Koster, Transvaal, and in both cases it appears as if the animals entered voluntarily. As far as is known, no collation of records or study of the types of animals which are known to do this exists.

- c) Carnivores such as hyenas, leopards and possibly extinct forms of lion and sabre-toothed cats may have intermittently used caves or their environs as lairs while raising kittens, pups or cubs. Abandoned young may die within the cave or its catchment area, and their bones become incorporated in the cave deposit. Alternatively, a few bones may be brought to such a lair by the adults for the young to 'practise' on; when the young are grown, the family moves on and the 'practise bones' may be abandoned (see also no. 7)

With the exception of the latter part of c), all the resultant skeletal material will be complete or almost complete, provided it is not scavenged upon. Many bones in the fossilized state will be found in articulation with one another and the rest closely associated with one another. The individual bones should show very little damage.

2. Accidental entrance

Fissures, shafts, sinkholes and precipitous entrances to caves may act as natural death traps for animals, which may fall in and die at or near the point of entry. Brain (1956) witnessed a brown hyena falling down a shaft and the present author has frequently observed numerous bones, in some cases amounting to a pile, below the vertical shaft or 'bottle-neck' entrances to dolomitic caves on the Highveld.

In such instances, as in the case of voluntary entry, the skeleton tends to be complete or nearly so, with some bones still in articulation, but unlike 1. many individual bones are broken or shattered. As far as is known, no published study of such bone accumulations or record of the types of animals liable to such a fate exists.

3. Hillwash

Various writers have stated that water can be responsible for transporting bones into underground caves. Bones lying on the open hillside near a cavern entrance or in a catchment area (see Chapter 2.1 and Fig. 21) may

be washed or funnelled into a subterranean cavern by the action of running water. For instance Partridge (1975 in prep.) has proposed that this is the mechanism which has operated in the accumulation of the bones in the grey breccia at Makapansgat, although the means by which these bones have become as concentrated as they are (see Fig. 9) without any associated hillside gravel or detritus is unknown. Alternatively, in karst country, if an animal is killed in a stream bed that then leads underground, the bones may be washed into the cave.

Apart from Behrensmayer's work (1975), which is not strictly applicable to the South African australopithecine cavern situation, little is known of the velocities and water volumes required to shift bones of various weights, shapes and sizes under differing conditions such as slope.

Bones accumulated by running water are likely to be associated with waterworn stones or gravel. Bones washed or rolled into caverns can be expected to show signs of abrasion and wear depending on the distance travelled and the time taken; they may also show varying degrees of sun-cracking, on account of exposure to the elements prior to their arrival in the cavern environment, the degree depending on the duration of their exposure. Such bones may also show chemical weathering. Water-transported bones are likely to be broken and skeletal elements or even the bones of individual animals are unlikely to be found in association.

4. Owls

Owl pellets, regurgitated by owls using the cavern or its entrance shafts as a perch will on disintegration contribute their micromammalian (rodent and insectivore) and small reptile (lizard and gecko) content to the cave fill. At Makapansgat, almost all the micromammalian remains come from distinct 'rodent breccias' which are completely separate from the grey breccia. The grey breccia has yielded few, if any, mammals of the micromammalian category, the smallest recovered ('cave rat' and 'golden mole') being somewhat beyond the size range of the prey hunted by modern owls. It is thus very unlikely that owls contributed significantly to the grey breccia bone accumulation.

5. Fossil 'lion' and other unidentified fossil felids

Although modern lions are not known to use caves and are generally creatures of more open country, extinct lions dating from the glacial periods in Europe are known to have occupied caves, presumably to shelter

from the cold. Fossil lions should therefore be regarded as potential bone accumulators, although the behaviour of modern lions (Schaller 1972) would suggest that this is unlikely. Lions, in any case, do not occur amongst the grey breccia fossil fauna.

The palaeoecology and bone accumulating potential of the other unidentified fossil felids present is unknown and unstudied.

6. Sabre-toothed 'cats' (Homotherium, Dinofelis and Megantereon)

All three genera are present in the grey breccia at Makapansgat (Collings 1974) but their palaeoecology is still largely a matter of speculation. However, the dentition of all three genera is adapted for slicing meat and not for crushing bone, so it is probable that the sabre-toothed cats did little damage to the skeletons of their prey. Thus, if they frequented caverns or their environs as lairs, they should be considered as potential bone-accumulators, although it is as likely that a co-existing suite of scavengers (hyaenids and jackals) would have dealt with the remains of any carcasses abandoned, if given the chance.

The living cheetahs (Acionyx jubatus) have similar dental adaptations to sabre-teeths and Brain's (1970b and in prep.) studies on the food remains of this species are likely to throw some light on what the food remains (although not the prey species) of the sabre-teeths may have looked like.

7. Hyenas

From the time of Buckland's (op. cit.) publication onwards, it has been almost universally accepted that hyenas are the primary agents responsible for bone accumulations in caves. Hughes (1954a,b and 1958) in order to confirm or disprove Buckland's theory, and stimulated by the criticisms of Dart's work, undertook field studies on the behaviour and lair contents of both brown and spotted hyenas, and failing to find a single bone-containing hyena lair was able to conclude that:

...the hyena, whether striped, spotted or brown, may be confidently eliminated as an agent for the collection of bone in lairs and caves;... (1958 p.113)

Sutcliffe, however, working on spotted hyenas in East Africa, found evidence to the contrary:

A burrow in the Ngorongoro Crater was found to contain great quantities of gnawed mammalian bones within its mouth.....

...A spotted hyaena lair, believed to contain young animals, two miles from Kajiado Hospital cemetery, was found to contain a great quantity of mammalian bones within its mouth, including some human remains which had been carried there by adult animals.....Excavation of two spotted hyaena burrowsin the Queen Elizabeth Park, Uganda showed that these contained, in their entrance tunnel, substantial quantities of bones of baby hippopotamus, warthog, buffalo, gazelle and even a bone of a baby elephant.....East African hyaena lairs....commonly contain great quantities of bone within their mouths. These have been brought there by adult hyaenas and carried underground by juveniles. Such remains are mostly of herbivores, with only a small proportion of hyaena bones. They may show both splintering by adults and gnawing by juveniles. Hyaena droppings are often common on the surface around the entrances of lairs, but are rare within them....(1969 p.3)

In a second paper (1970) elaborating upon these findings, Sutcliffe concluded that:

present investigations suggest that there may be regional differences in the behaviour of spotted hyaenas, those in East Africa having a greater tendency to carry bones to their lairs than those of South Africa, although the reason for this is probably merely the proximity of the food supply
(p.1112)

Sutcliffe's work on the spotted hyena (Crocuta crocuta) would therefore seem to conflict with the conclusion reached by Hughes on bone accumulation by this species.

Kruuk, perhaps the greatest authority on the behaviour of the spotted hyena, has informed the present author that the bone-collecting propensity of these hyenas varies from clan to clan (pers. comm.1973). He also states (1972 pp.114-116) that the bones available after a kill has been made vary; the number of bones lying about in the field is an indication of hyena density in relation to food supply. If there are few hyenas and an abundance of ungulates, numerous bones and often whole skeletons may be left, but if hyena density is high, such bones will be demolished completely. This availability factor will naturally affect the incidence of bone accumulation. Together these two factors may help to explain why Hughes did not find any bone accumulations made by hyenas.

Because of Kruuk's tremendous knowledge of the species, and because of its relevance to the present study, it is not inappropriate to quote,

even if at some length, his observations on bone accumulation by Crocuta from his monograph (1972);

Hyenas also do not carry any substantial amount of food to their cubs; they may occasionally take a bone or a head along, but this seems comparable to taking it to their lying-up place, where they can chew it in peace. Cubs may chew these bits, but only after the original owner has finished with them. Older cubs are more likely to carry bones to their dens than adults; they sometimes take them down their holes, but more usually these are left in front of the den, or in the entrance. Some dens accumulate quite a collection of bones around the entrance, contrary to the belief expressed, for example, by Hughes (1954a, b 1958, 1961) but this does not often happen; it may be more common among brown hyenas (Pienaar 1969). It is possible that porcupines are in some cases responsible for the bone collection, as asserted by Hughes (1961); however, I have several times actually observed spotted hyenas carrying bones to their holes. This means, therefore, that they could well be responsible for the fossil bone accumulations which are sometimes held to be made by prehistoric man (Dart 1949, 1957; Ardrey 1961). Moreover, bones splintered by hyenas or regurgitated bone slivers have a remarkable semblance to those bone pieces that are considered to be artifacts by these same authors (Thenius 1966b; Sutcliffe 1970) (1972 p.244)

Goodall (1970 p.196) has observed similar behaviour by this species. Pienaar (1969) and Mills (1973, and in prep.) have described similar bone accumulating behaviour by the brown hyena (Hyaena brunnea) in the Kruger National Park and Kalahari Gemsbok National Park respectively.

From the above it is apparent that there is no 'typical' hyena behaviour, feeding habits, food remains or lair contents. Nevertheless, it appears that both spotted and brown hyenas will have to be considered as potential bone accumulating agents at Makapansgat, especially as both Sutcliffe (op. cit.) and Kruuk (op. cit) have observed that the same burrows are used as lairs by successive generations of hyenas - although the contribution of each set of occupants may be small, given enough time substantial accumulations of bone will build up. However, to date, Hyaena hyaena makapani, (striped hyena) and H. brevirostris are the only hyaenids which have been recovered from the grey breccia. Little is known about the bone-collecting habits of modern striped hyenas.

At this stage it is relevant to draw attention to the fact that Sutcliffe, Kruuk and Goodall (op. cit.) invariably describe hyena bone accumulations as occurring at the burrow mouths or tunnel entrances

and not deep within the main part of the lair. The manner in which the grey breccia bones have become concentrated in the low-lying rearmost regions of the Makapansgat cavern needs to be explained. Furthermore, the damage on the Crocota-accumulated bones described by Sutcliffe (1969, 1970) (caused by gnawing activities of the cubs) would appear to be absent, or largely absent from the grey breccia bones; the actual damage and fracturing of these hyena-accumulated bones has never been adequately studied, but from published photographs, it would appear that in most cases, it is unlike that found at Makapansgat.

Hyena remains are a relatively common component of the grey breccia fossil fauna at Makapansgat Limeworks.

8. Leopards

Brain (1968, 1969a, 1970b) has argued strongly in favour of leopards being the primary agent responsible for the bone accumulation at Swartkrans, albeit indirectly. He has observed that leopards under pressure from scavengers and other predators, or where prey is scarce, are obliged to store their kills in the forks of trees, where they can consume the kill at leisure. As mentioned in section 2.1.2 on the highveld dolomitic region such trees are more likely to be found at the mouths of caves and fissures, or growing out of shafts and sinkholes. He has suggested (op. cit.) that leopards were obliged to use a tree such as the one shown in the reconstruction (Fig.21a) growing near the shaft leading to the Swartkrans cavern. Discarded portions of the kill would rot or be disturbed by vultures, and the bones would fall from the tree into the catchment area below, and so be funnelled into the cave.

A similar system may have operated at the Limeworks cavern at some stage of its history. It would therefore be wise, once the detailed characteristics of such leopard accumulations are published (Brain, in prep.) to evaluate the grey breccia bone accumulation in terms of these findings. A fossil form of leopard is present in the grey breccia.

9. Porcupines

Porcupines are widely acknowledged as being bone collectors, but apart from noting that various percentages of the bones collected by them appear to have been gnawed (Hendey and Singer 1965, Brain 1958) the other

characteristics of such bone accumulations appear to have been little studied. Thus all-important features such as the nature of the damage done by porcupines to the different skeletal elements appears never to have been described in detail; in addition, judging by the published and verbal comments of palaeontologists and palaeoanthropologists, there appears to be uncertainty concerning the behaviour of porcupines - for example, do they collect bones specifically for gnawing purposes, or do they accumulate bones and gnaw only a few of them?

The suggestion that porcupines may have been responsible for the Makapansgat Limeworks grey breccia bone accumulation has frequently been made, and perhaps as frequently, the suggestion that these animals may even have fashioned the osteodontokeratic artefacts described by Dart (1957a, b).

It has been the task of the present author to attempt to resolve these issues.

10. Early Man

Early man is known to have been an active accumulator of bones in caves and on open sites, where these bones may form a large part of the occupational debris. Apart from noting that the bone accumulations made by early man are characterised by a high degree of fragmentation and a high proportion of bone flakes (Brain 1969a,b,c), the characteristics of such accumulations, particularly in terms of Dart's claims concerning Australopithecus africanus , remain largely undocumented and require further detailed study.

It has not yet been conclusively demonstrated that Australopithecus did accumulate bones. One way of doing this would be to show that known human bone accumulations possess diagnostic characteristics possessed by none of the accumulations made by other agents, and then to demonstrate that an australopithecine bone accumulation resembled this type of accumulation closely. Alternatively, all other possible bone accumulating mechanisms could be eliminated at least as major agencies.

If, on the other hand, it could be demonstrated that A. africanus made and used tools and that some of the fossil bones are osteodontokeratic artefacts, the question as to the agency involved in their introduction would diminish somewhat in importance, particularly in so

far as the archaeologist and palaeoanthropologist are concerned.

It is probable that at various times (and the grey breccia probably represents an accumulation period of several thousand years) some or all of these agents may have operated, either simply or in various combinations. With regard to the grey breccia the present investigation has not been aimed at establishing which of the above mechanisms has predominated, but merely at investigating the possible role of porcupines, both in its accumulation and in the modification of the individual bones.

18. METHOD

An attempt was made at solving the first problem (that of assessing the extent to which fossil porcupines may have been responsible for the accumulation of the Makapansgat Limeworks grey breccia bone assemblage) by collecting the introduced contents, particularly bone, from the interiors of as many porcupine lairs as possible, and comparing these collections with that described by Dart (1957) from the above mentioned breccia, which he attributed to the activities of Australopithecus africanus. An attempt was made to collect from lairs situated in as many different environmental settings as possible, to see how the characteristics of the porcupine bone accumulations varied from area to area. Unfortunately, although several dozen lairs were observed, it was possible to make collections from only a few of them without having to resort to extensive digging or blasting which at the time was considered as being beyond the scope of this thesis. The author thus considers this section of the study as incomplete in that the collections available from reasonably 'intact' environments (environments where a full complement of naturally-occurring animals is present amidst an undisturbed vegetation) were few and small and thus do not permit conclusive formulation of the characteristics of porcupine bone accumulations. The problems connected with finding suitable lairs for study have been discussed in Chapter 21.

The second problem (that of establishing whether or not the contentious 'osteodontokeratic' tools described by Dart (op. cit.) from the grey breccia and attributed to australopithecine manufacture could have been wholly or partially manufactured by porcupines) was investigated by establishing how porcupines are able to damage the various skeletal elements and what this damage looks like and then comparing this damage with that apparent on corresponding skeletal elements from the grey breccia. For this purpose, the bone accumulation from the Hartebeesthoek porcupine lair, which is situated in a very disturbed environment in that the naturally-occurring fauna, particularly the carnivora, has long since been almost totally exterminated, was ideal for study. Once this lair had been completely cleared of introduced bones for the first time, it could safely be said that bones collected from the lair on the second and subsequent occasions were free from damage by carnivores prior to accumulation by porcupines. The first collection may

have contained a few very old bones collected during the period (at least 60 years ago) while carnivores were still present in the area. With the exception of porcupines, other bone damaging and scattering agents (such as humans and vultures) are now absent from the immediate vicinity of the Hartebeesthoek lair ($\pm$ 2 mile radius) and it is probable that the bones collected by the porcupines were available undamaged. This situation is ideal for the investigation of how porcupines are capable of damaging bone, especially as this information can be contrasted with bone damage from lairs where carnivores or humans have had access to bone (e.g. the Derdepoort and Winkelhoek lairs respectively) before it became available for collection by porcupines.

For comparative purposes it was necessary to attempt to isolate Dart's original 'osteodontokeratic' collection of 7,159 bones from the several tens of thousand specimens which have been prepared from the grey breccia since 1957. This could not be done, as the original collection was not marked in any way; only the few hundred specimens figured in the monograph could be relocated. These were sufficient for the second part of the study but for the first part the author was obliged to use Dart's original analytical table (1957 Table I p.36) as a basis for comparison as well as a personal knowledge of the total bone assemblage now available.

Partly in order to facilitate direct comparison with published analyses of other bone accumulations, and partly because it was suspected that they would serve to distinguish features characteristic of porcupine, carnivore, human or 'hillwashed' bone accumulations, the following features were analysed:

1. The species and broader taxonomic groups (e.g. Antelope size class II etc.) present
2. the minimum numbers and age distribution of individuals of each species present
3. the percentage survival of skeletal parts (skeletal part representation)
4. the incidence of bone flakes and slivers and unidentifiable fragments
5. The degree of fragmentation, particularly of bone flakes
6. the percentage of porcupine-gnawed bone

7. The incidence of carnivore damaged bone, insect borings, cut marks etc. and pathological specimens
8. The incidence of fired bone
9. The incidence and severity of weathering on bone
10. The nature and distribution of damage on each of the skeletal elements

18.1 The species list and broader taxonomic grouping present

The first step in the analysis of a bone assemblage should be the removal of those pieces of bone and teeth which can be specifically identified with certainty. These form the basis of a 'species list'. The remaining material should then be sorted to remove any pieces referable to various taxonomic groupings broader than species, for example 'suid', 'equid', small, medium or large 'carnivore' or to one of the four antelope size and weight classes proposed by Brain (1974) or Dart (1957).

Porcupines are able to collect only those dry bones available to them after predators and scavengers have finished with a carcass, and may spend up to three years collecting bone from one large undisturbed skeleton (see p.605). On the other hand, carnivores such as lion, leopard, cheetah, hyena and wild dog live by predation and/or scavenging from each other's kills. Each of these predators has distinct prey preferences and hunts animals of specific size, weight and age categories, so that the full spectrum of animals available is exploited. Humans (and presumably hominids) are capable of hunting a wide range of animals, the variety of species and the size of the animals hunted depending on the social organization and sophistication of their technology. Humans have a wider hunting range than porcupines (and some carnivores) and can utilize animals which occupy habitats differing widely from their home site environment.

The species list, coupled with the broader taxonomic groups present, can furnish information as to which of the above-mentioned animals are likely to have predominated as the bone-accumulating agents of a bone assemblage. A porcupine bone accumulation is likely to provide a fairly restricted species list, the various carnivore accumulations may show a slightly more varied species list (but with much higher estimated minimum numbers of individuals of each species present, while human and hominid bone accumulations will contain a wide range of species which come from a variety of environmental situations.

The antelope weight/size categories used by Dart (1957) in his analysis of the Limeworks grey breccia bone assemblage do not coincide with those suggested by Brain, and, as Klein (1975) has suggested, Dart's categories overlap to some extent. The original specimens could not be relocated in order to segregate the bovid post-cranial remains according to Brain's scheme, so in keeping with the aim of the project, Dart's scheme has been followed where necessary. It is intended to re-analyse the Limeworks assemblage at a later date.

The collections from porcupine lairs located in environmentally undisturbed areas are small and limited in number, while the only extensive collection (Hartebeesthoek Lair) contains the bones of mainly domestic animals. None of the porcupine bone accumulations available at time of writing thus provided a valid basis for comparison as far as number of species or broader taxonomic groupings present were concerned. Thus these aspects have been investigated on the broadest terms only.

18.2 The estimated numbers of individuals of each species present and their age classes

As outlined in 18.1, the numbers of individuals of each species present and their ages (newborn, juvenile, adult) will provide evidence as to the identity of the bone-accumulating agent predominantly responsible for a bone assemblage. The minimum number of individuals is estimated using the most frequently-represented skeletal part for a particular taxon as a basis : for example, if 115 left mandibular rami are found to occur, and if no other skeletal part category exceeds this number, one may conclude that the bones of at least 115 individual animals of this taxon contributed to the assemblage. The age of the specimens at death is estimated using tooth eruption, tooth wear and suture-fusion.

Dart's analysis (Table I p. 37) does not segregate left skeletal elements from right, merely giving the total number of pieces present. Dividing these totals by two will give a conservative approximation of the minimum number of individual species present, as the original collection could not be reassembled.

As for 18.1, and for the reasons cited under it, the minimum numbers of the various species present and their age classes have been investigated on the broadest terms only.

18.3 The skeletal part distribution and the percentage survival of the various skeletal elements

When Dart (1957) made his pioneering analysis of 7,159 bone fragments from the Limeworks, he noted some interesting disproportions in the skeletal parts represented; for instance, cranial fragments were exceptionally common (34,5% of all recognizable fragments), while vertebrae, except for the atlas and axis (which were strikingly abundant within the vertebra sample) were very rare, tail vertebrae not being represented at all. Similar disproportions were observed amongst the bones of the rest of the post-cranial skeleton; for example, the bones of the fore limbs were found to be far more abundant than those of the hind limbs. In the case of individual limb-bones, one end frequently appeared in superior number to the other, for example, Dart found that the distal end of the humerus outnumbered the proximal end by 10 to 1.

Dart attempted to explain these disproportions (op. cit.) in terms of australopithecine behaviour, suggesting that they were head hunters, used the vertebrae as missiles and tails as "whips or signals in hunting". Fore-limbs were favoured, but hind-limbs were not always brought back to the cave, while skeletal elements likely to make useful tools such as mandibles, maxillae and distal humeri were especially sought after.

Brain (1967c and 1969b) has disputed this interpretation and has suggested that the disproportions are due to the differing survival potential of the various skeletal elements and thus require no special explanation. Predictable survival patterns will result depending on the destructive treatment which has been brought to bear on a skeleton. He has suggested that the percentage survival of the skeletal elements of goat skeletons from a Hottentot settlement (goat bones subjected to destructive treatment by Hottentots and small dogs only) is closely similar to that shown by the bovid skeletons from Makapansgat Limeworks (Fig. 172A and B). The present author agrees with Brain that certain skeletal part disproportions may be explicable in terms of the survival potential of the bones concerned, but suggests that the survival pattern will differ according to the destructive treatment involved. With regard to this point, note how Klein's bovid skeletal survival pattern (1975, Fig. 2, Fig. 173 of this thesis) for the Swartklip I hyena accumulation differs from that of Brain (1969b, Fig. 4A, Fig. 172A this thesis) for the Namib Desert Hottentot goat bones. The great similarity of the

Hottentot and Makapansgat skeletal part survival histograms (Fig. 172A and B) suggests that the bone-destructive agent was similar in both cases viz. predominantly man, with slight contribution by carnivores.

Klein (1975) on the other hand, has argued (not very convincingly) that the Makapansgat assemblage resembles the non-hominid (probably hyena) bone accumulation from Swartklip I, South-West Cape (Fig. 173), underlining the need for documentation of the skeletal part survival patterns of all bone-accumulating and bone-destructive agents, including the mechanical process of "hillwash". The skeletal survival patterns of the bony food remains of leopards, cheetahs and humans is at present being studied (Brain, in preparation).

The survival pattern of a porcupine bone accumulation has not yet been documented. The Hartebeesthoek porcupine lair bone accumulation proved most useful as a 'control' in this respect because carnivores and humans are absent as bone-destructive agents, the only damage the bones show is that accomplished by porcupines. As Brain has done for the Limeworks skeletal histogram, only bovid remains were considered from the Hartebeesthoek collection. The skeletal parts represented are shown in Table XXI and their percentage survival in Fig. 174. The Hartebeesthoek lair contents are atypical in view of the absence of carnivores and the domestic nature of the local fauna, but the analysis of the bone-damaging potential of porcupines on their own is useful in that their activity can then be allowed for in the analysis of 'mixed' accumulations to which they are suspected of contributing.

18.4 The degree of fragmentation

Porcupines do not appear to be capable of crushing, splitting, flaking or otherwise fragmenting bones, and presented with a readily-available assortment, they appear to show a preference for collecting large, dry bones (see 22.2). Carnivores and man, and particularly the latter, are known to cause extensive damage to bone in the process of removing meat and extracting marrow, or in the production and utilization of bone tools and artefacts.

For these reasons we would expect a greater average fragment size to characterize the bone accumulations of the former whereas a high degree of fragmentation and therefore a smaller fragment size would characterize the bone accumulations of carnivores and man. Beaumont (pers. comm.) has accumulated evidence suggesting that in bone accumulations made by man,

the more advanced a technology, the smaller the fragmentation of bone becomes.

In the analysis of any bone accumulation, therefore, the assessment of the degree of fragmentation is important. Unfortunately, fragment size is affected by a number of factors:

- 1) The source of bone. For porcupines the source of bone could be any of the following, providing the bone was dry:
 - (a) the skeletal remains of an animal which has been killed or has died and been left to decay unmolested by carnivores. The skeletal elements will be largely complete allowing a choice of large (if the animal was large) bones and from all parts of the skeleton. There will be no initial skeletal part disproportions;
 - (b) skeletal remains of a carcass after the usual range of predators and scavengers have finished with it. These are likely to be smaller bone fragments which show carnivore damage of some sort. The skeletal parts surviving carnivore activity will show disproportions;
 - (c) scattered incidental bones discarded or ignored by carnivores showing sun-cracking and deterioration due to other forms of weathering;
 - (d) bone accumulations for which other animals (e.g. hyenas or leopards) may have been responsible. Bones collected from such accumulations usually show carnivore damage of some sort;
 - (e) bone accumulations for which man (and hominids) have been responsible. Bones from such accumulations may be fragmentary, flaked, fired or otherwise artificially damaged.
- 2) The size of the animal hunted (for carnivores and man) or the size of the skeleton collected from (porcupines).
- 3) The availability of bone. The extent to which the original length of bone may be reduced by porcupine gnawing may depend on the availability of bone in the vicinity of the lair; if large quantities of bone are readily available, individual bones may show less gnawing than bones from a lair where bone is scarce.
- 4) Trampling. Disturbance by trampling of the upper layers of a deposit will fracture bone. The effects of trampling are difficult to assess.

- 5) Breakage during archaeological retrieval of bone and its subsequent preparation. Freshly-broken specimens should be excluded from an analysis of fragmentation.
- 6) Fragmentation by other factors such as firing which comminates (shatters) bone, sun-cracking, acid soil, weathering, root penetration, fragmentation in water-logged conditions.

The degree of fragmentation of bones in an assemblage can be measured in a number of ways:

- i. by assessing the number of identifiable bones compared with unidentifiable flakes and slivers;
- ii. by calculating what percentage of the total assemblage is made up of bone flakes;
- iii. by measuring the longest axes of the bone flakes;
- iv. by examining the proportions of intact shafts of long limb bones;
- v. estimating the number of bones per kilogram;
- vi. by measuring the total average fragment size.

i, ii and iv are easy to assess and have few variables influencing them. Flake size (iii) depends partially on the size of the animal from whose limb bones they have been made while the number of bones per kilogram is influenced by the degree of mineralization, the freshness and the efficiency of cleaning of the bone. Average fragment size is influenced by all six factors discussed above.

18.5 The percentage of porcupine-gnawed bone present

Porcupines apparently collect bones within their lairs for the express purpose of gnawing them, although a few bones may be collected but ignored if bone is in plentiful supply. Usually however, it is the extent of gnawing and not its incidence that varies according to the availability of bone. Neither carnivores, humans nor hominids gnaw bone in the same way as porcupines. The percentage of porcupine-gnawed bones is thus the most reliable feature by which porcupine bone accumulations can be differentiated from the accumulations of other agents.

Only unmistakably porcupine-gnawed bones (see Fig. 154 for modern and Fig. 155 for fossil porcupine gnawing) have been considered in analyses. Porcupine gnaw marks are readily distinguishable from the gnaw marks caused by other rodents or carnivores, and from the marks which result from the butchering and feeding habits, and bone tool manufacture and

utilization by hominids and man.

Porcupines are the largest rodents in Africa and have proportionately wider incisors, so that their gnaw marks are not easily confused with those of smaller rodents. The irregular grooves and striations produced on bones by young 'practising' carnivores (see Sutcliffe 1970 Fig. 4) and the punctate depressions caused by the bone-crushing premolars of older animals cannot be confused with the straight-edged, even sized, regular grooves caused by porcupine incisors. Porcupines are capable of scraping out cancellous bone with their incisors, such scrapes often having the appearance of carnivore chewing, but the edges are usually surrounded with 'conventional' gnaw marks, unlike carnivore-damaged bones.

The variety of marks produced on bone by hominids and man are all easily distinguishable from the even regular marks caused by porcupine gnawing.

18.6 The incidence of carnivore-gnawed bone, insect borings and pathological specimens

The means by which such bones may be recognized has been discussed above, and figured in Sutcliffe (1970). A high incidence of such damage would suggest that the accumulation had been made, or at least heavily contaminated by carnivores. It should be borne in mind that porcupines could destroy such carnivore damage in the course of gnawing.

A high proportion of insect borings on the surfaces of the bones would indicate the presence of carrion, as it is bones which are 'wet' and covered or at least partially covered with decomposing flesh that are most prone to insect attack. Carrion is unlikely to litter the lairs of either porcupines or hyenas.

The incidence of pathological specimens would indicate the proportion of handicapped animals that is being preyed upon.

18.7 The incidence of fired bone

Important in indicating human bone accumulations only.

18.8 The incidence, nature and severity of weathering on bone

Porcupines have a preference for 'dry', defatted bones that have often been lying exposed to the elements for long periods. The bones acquired by carnivores and human or hominid hunters usually arrive in the lair or cave entirely or partially flesh-covered. Once protected from the sun within a cave or lair, these bones are slow to defat or dry out and thus

maintain their 'fresh' condition for a long time, perhaps until fossilization occurs, as in the grey breccia where most of the bones appear 'fresh'. Porcupine bone accumulations are thus likely to show a higher incidence of sun-cracked bones than those of either carnivores or humans.

Bearing in mind the possibility of accumulation by means of 'hill-wash', bones should be examined for water and rolling abrasion and weathering.

18.9 The nature and distribution of damage on each of the skeletal parts

This was investigated mainly in an effort to determine whether or not fossil porcupines could have been responsible for the damage to the bones in the Limeworks grey breccia attributed by Dart (1957) to the tool-manufacturing and utilizing activities of australopithecines.

Series of each bone type ranging in completeness from almost undamaged to almost totally destroyed by gnawing were assembled from the sample of porcupine lair bones available. The nature and position of the damage on each bone type was noted and compared with that described and figured by Dart (op. cit.).

19. MATERIAL

While many porcupine lairs in widely differing ecological settings were observed, from the dry southwestern Kalahari of Botswana (Figs. 134 and 137) to the high Natal Drakensberg at Cathedral Peak (cf. Fig. 135), it was possible to obtain collections from only five of them for reasons discussed in Chapter 21. The five lairs from which collections were made are as follows:

19.1 The Hartebeesthoek porcupine lair

For a locality map of this lair, see Appendix XI pp.347-351, Vol. II. It is figured in Figures 139, 141 and 142 and requires no further description. A very low deep recess under large exfoliating boulders of Ventersdorp Lava $\pm$ 4km north of Hartebeesthoek Satellite Tracking Station on the Broederstroom road. Local environment very undisturbed, naturally occurring carnivores exterminated, humans and their dogs occasionally present.

Total number of specimens = 479

Catalogue number series PPM 221-367a (1st collection, 15/2/71)

PPM 592-679 (2nd collection, 13/2/72)

PPM 680-697 (3rd collection, 5/3/72)

PPM 704-768 (4th collection, 24/6/73)

PPM 790-820 (5th collection, 16/2/74)

PPM 872-896 (6th collection, 6/2/75)

Number of bone fragments = 368

Number of isolated teeth = 70

Number of horns = 2

Number of gnawed stones = 14

Number of gnawed vegetation = 25

Number of miscellaneous
objects = -

Total 479

19.2 Kimberley porcupine lair

Very small collection from recess in sandy river bank near Kimberley, enlarged by porcupines (collected by A. Anderson and I. McLachlan of Bernard Price Institute for Palaeontological Research). Apparently moderately undisturbed local environment, most carnivores exterminated.

Total number of specimens = 22

Catalogue number series : PPM 769 - PPM 788 (two numbers with bones
A and B)

Number of bone fragments	= 18
Number of isolated teeth	= 4
Number of horns	= -
Number of gnawed stones	= -
Number of gnawed vegetation	= -
Number of miscellaneous objects	= -
Total	= 22

19.3 Hanglip porcupine lair

Very small collection from low recess (25cm) at base of rocky cliff on farm Louwskraal (also called Stepping Stones) near Koelemansrus, N. Transvaal, 32km northwest of Naboomspruit. Local environment moderately undisturbed. Leopards and jackals still present.

Total number of specimens = 51
Catalogue number series: PPM 821 - 871

Number of bone fragments	= 23
Number of isolated teeth	= 13
Number of horns	= -
Number of gnawed stones	= -
Number of gnawed vegetation	= 12
Number of miscellaneous objects	= 3
Total	= 51

19.4 Rand van Tweedepoort porcupine lair

For a locality map of this lair, see Appendix XI pp. 347-351 Vol. II. It is figured in Figures 138, 140, 143, 156, 160 and 162 and thus requires no further description. A very low deep recess at the base of a tufa deposit on a quartzite cliff near Zuni-Zuni southwest of Derdepoort, W. Transvaal, on road to Zeerust. Moderately undisturbed local environment. Leopard, jackal and brown hyena probably still present. Bovid fauna depleted.

Total number of specimens = 106
Catalogue number series: PPM 1 - 106

Number of bone fragments	=	47
Number of isolated teeth	=	3
Number of horns	=	-
Number of gnawed stones	=	2
Number of gnawed vegetation	=	16
Number of miscellaneous objects	=	38
Total	=	106

19.5 The Winkelhoek Cave porcupine lair

Sketch plans of the cave are shown in Appendix XI pp.347-351 Vol. II
A low recess leading from a larger sandstone cave used periodically in the past by Bushmen. On farm 'Winkelhoek' or Winkelhaak' near Wakkerstroom on the Natal-Transvaal border, northern Natal. Local environment very disturbed, very few wild animals present.

Total number of specimens = 463 excluding 93 rodent bones
Catalogue number series: PPM 127 - 220
PPM 367b - 591

Number of bone fragments	=	379 excluding 93 rodent bones
Number of isolated teeth	=	81
Number of horns	=	-
Number of gnawed stones	=	1
Number of gnawed vegetation	=	-
Number of miscellaneous objects	=	2
Total	=	463 excluding 93 rodent bones

The collections have mainly been made from areas which have been ecologically disrupted for some time. The bones available for collection by porcupines have probably been biased in some way, and the collections cannot be regarded as 'typical' - see Chapter 21.

20. THE HABITAT AND LAIR PREFERENCES OF HYSTRIX AFRICAEAUSTRALIS
AND THE MEANS BY WHICH PORCUPINE LAIRS CAN BE IDENTIFIED

20.1 The habitat and lair preferences of H. africaeaustralis

As can be seen from the distribution map (Fig. 24) Hystrix africaeaustralis is widely distributed over Southern Africa. The species is found in almost every type of countryside, whether wet or dry, open or bushy, flat, hilly or mountainous and thus appears to have wide ecological tolerance and no particular habitat preference. The occurrence of the species has been noted in the sparsely vegetated hot drier parts of the Kalahari in western Botswana where the rainfall averages less than 254mm (10 inches) per annum (Fig.134) as well as in the mountainous and cool Drakensberg (Fig.135) with a rainfall of about 1780mm (60-70 inches) per annum, and an altitude of up to 3387 m (11,000ft) although to date, quills have only been recovered from altitudes of 2440m (8,000 ft) and below. The presence of the species in large tracts of the Kalahari which are devoid of permanent sources of surface water seems to indicate that porcupines have no real requirement for the regular drinking of water, the moisture obtained from the underground roots, bulbs, tubers and other succulent food storage plants, which form a large part of their diet, being seemingly sufficient.

Porcupines are usually strictly nocturnal and remain deep in the shelter of their lairs or burrows during the day, generally emerging only after nightfall, and then not on every night. The author observed one emerging from its burrow for the first time on one particular evening at 11.40pm. Their emergence seems to depend on the adequacy and recency of the last feed for, if satisfied, they will remain within their lair or burrow and not appear at all for a few nights. An African resident in the Mosdene Private Nature Reserve (Springbok Flats, near Naboomspruit, northern Transvaal) well-acquainted with porcupine habits (he had on many occasions attempted to trap them on account of their extensive damage to his cultivated crops) reports that they are shy of emerging in heavily overcast weather, whether hungry or not, but can often be seen abroad on bright moonlight nights. Unfortunately, there has as yet been no opportunity to verify his statement, nor has it been possible

Fig 134

Maitlo-a- phuhuduhudu Pan, approximately 50km south of Takatshwane, Western Botswana.

A kalahari environment with a rainfall of less than 330mm (13 inches) per annum. Porcupine activity has been observed by the present author on pans such as this one, but appears to be more common around the sandy margins where aardvark burrows (as well as subterranean food plants) more frequently occur. After good seasons, water may be available for a few weeks in the form of small pools in the calcrete of the lower lying parts of the floor of such pans.

Fig 135

Drakensberg foothills near Little Switzerland, Oliviershoek, northwestern Natal.

A mountainous environment, with a rainfall exceeding 1780mm (70 inches) per annum. Porcupine activity has been noted up to an altitude of approximately 2440m (8500 ft) i.e. to about the level of the Cave Sandstone which forms the impressive cliffs in the picture.



Fig 134

or in other areas where the natural environment does not provide suitable rocky hide-outs, e.g. the Springbok Flats, most parts of the Highveld and the flatter parts of the eastern Transvaal Lowveld, porcupines frequently occur in small groups.



Fig 135

to check on the conflicting reports on whether the animal is solitary or gregarious in its social habits, the latter factor being of considerable importance when considering the rate of accumulation of bone within caves or lairs.

This nocturnal habit, coupled with their elusive disposition and the fact that their lairs are generally inaccessible for interior observation makes studies of porcupine behaviour and bone accumulation extremely difficult, and as a result virtually nothing is known of their biology.

The type of lair utilized depends largely on the local natural surroundings, but lairs are never in too close a proximity to permanent human habitations, as the animals seem very sensitive to disturbance. Lairs, whether subterranean rocky lairs or sandy burrows, are generally found in completely dry situations and frequently have more than one entrance.

In flat, exposed and entirely rockless areas such as the Kalahari or in other areas where the natural environment does not provide suitable rocky hide-outs, e.g. much of the Springbok Flats, most parts of the Highveld and the flatter parts of the eastern Transvaal Lowveld, porcupines frequently occupy disused aardvark (Orycteropus afer) burrows (Fig. 136 and Fig. 137), although they are recorded as being quite capable of digging their own (Roberts 1951 p.346; Dorst and Dandelot 1970 p.34) for which purpose they are equipped with stout digging claws. With regard to this, it is interesting to note that Orycteropus afer, although showing a distinct preference for open, dry, sandy savanna country and light forest, has (in suitable habitats) as wide a distribution as Hystrix africaeaustralis, and in areas where aardvarks occur the author has not observed a single example of a porcupine-excavated burrow. These porcupine-occupied aardvark burrows may be simple holes with a single entrance, as in Fig. 136, but more frequently the burrows form a maze of interconnecting underground tunnels with up to 20 or 30 surface openings and covering many hundreds of square metres.

In more broken country porcupines favour boulder-strewn bush-covered koppies or hillocks (Figs. 138 and 139) where they occupy small, low rock crevices which may be enlarged by digging and scraping out loose earth,

Fig 136

An abandoned aardvark (Orycteropus afer) earth burrow which had been appropriated by a porcupine (or porcupines) on the farm Zyferbult, near Naboomspruit, Springbok Flats, central Transvaal.

Note the small size of the entrance and its steeply downward-sloping approach. Note also the horseshoe shape of the tunnel, which corresponds to the end-on profile of an aardvark. Scrape marks made by the strong digging claws of the latter animal may be visible on the tunnel sides; alternatively striations caused by porcupine quills may be present. Spoor of various sorts are readily seen in the soft excavated earth at the burrow entrance; the 'freshness' of this earth often makes it possible to determine whether or not an aardvark is in residence. The growth of weeds on the excavated earth, the compaction of the excavated soil and the presence of spider webs across the entrance tunnel usually indicate that a burrow is unoccupied. Porcupines, which are smaller than aardvark, have no need to enlarge this type of burrow, and fresh excavated earth is therefore more likely to indicate the presence of the latter animal.

Fig 137

Porcupine occupied aardvark burrow near Nojane, western Botswana, which has been dug open by Bushmen in order to catch the porcupine.

Remnants of a collapsed tunnel, probably leading to a second entrance can be seen on the extreme right of the picture, at right angles to the main burrow, which has been enlarged by the Bushmen. Note the volume and extent of the excavated sand and its fresh appearance.



Fig 136



Fig 137

Fig 138

Part of the Rand van Tweedepoort, on the farm Zuni-Zuni, on the road between Derdepoort and Zeerust, western Transvaal.

A substantial labyrinthine limestone 'tufa' has developed in a series of carapaces over the quartzite escarpment, and small caves and recesses in this provide excellent lairs for porcupines and sheltering places for baboons. A dense fringe of vegetation at the base of the cliff provides additional protection as well as a variety of edible wild fruits and berries. The 'Rand van Tweedepoort' porcupine lair is at the base of the cliff a little to the right of the large cave near the left-hand extremity of the cliffs. Looking north-north-east.

Fig 139

A conical hill of Ventersdorp Lava, crowned with a series of large balancing granitic boulders and housing the 'Hartebeesthoek' porcupine lairs.

Approximately 3km (2 miles) north of the Hartebeesthoek Satellite Tracking Station on the road to Broederstroom, on the right hand side. On the high, grassy, undulating plains of the highveld (see background), porcupines tend to favour rocky outcrops such as the one shown. The Hartebeesthoek 'Main' and 'Side' lairs occur near the summit of the east-facing (right-hand) slope of the conical hill, under a series of large balancing boulders.



Fig 138

and in the lairs of some carnivores, collections of bone from the latter type of cave can be expected to show mixed characteristics of the bone accumulations of two or more of the above mentioned bone accumulating agents. (see Fig. 143)



Fig 139

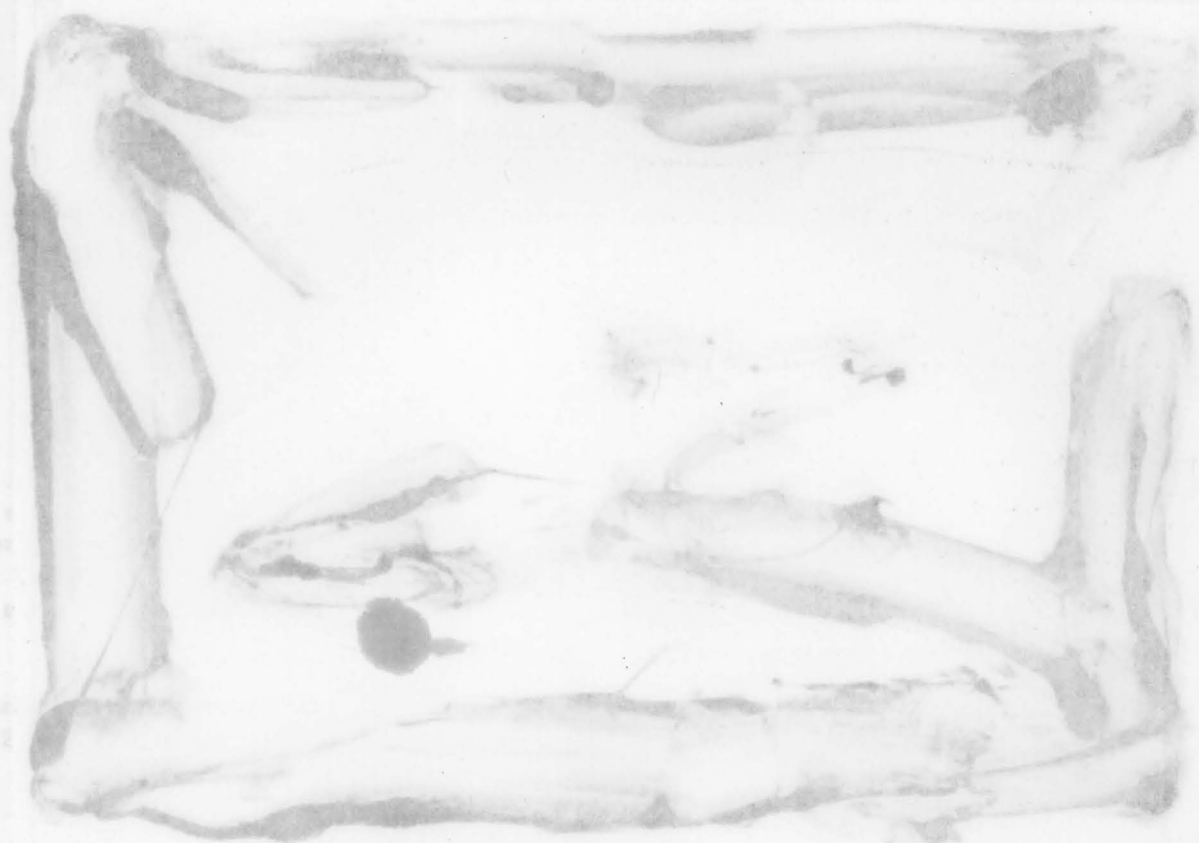
for example the 'Rand van Tweedepoort lair' (Fig. 140) and the 'side lair' at Hartebeesthoek (Fig. 141) or they may occupy larger but low recesses under and between boulder piles which require little or no enlarging, e.g. the 'main lair' at Hartebeesthoek (Fig. 142).

Still larger recesses and caves, suitable for use by larger animals such as hyenas, leopards, baboons or even for human occupation are as a rule not used by porcupines as lairs, since such places are not sufficiently dark by day nor do they offer adequate protection. However, low, dark recesses or narrow tunnels leading off such caverns may be used. It is highly improbable, however, that simultaneous human and porcupine (or porcupine-carnivore) occupation of any one such cave complex would have ever occurred; in all probability porcupines would occupy suitable recesses at the back of such caves between periods of human or carnivore occupation only. Since bone accumulations occur in the living sites of humans, porcupines, and in the lairs of some carnivores, collections of bone from the latter type of cave can be expected to show mixed characteristics of the bone accumulations of two or more of the above mentioned bone accumulating agents. (see Fig. 143)

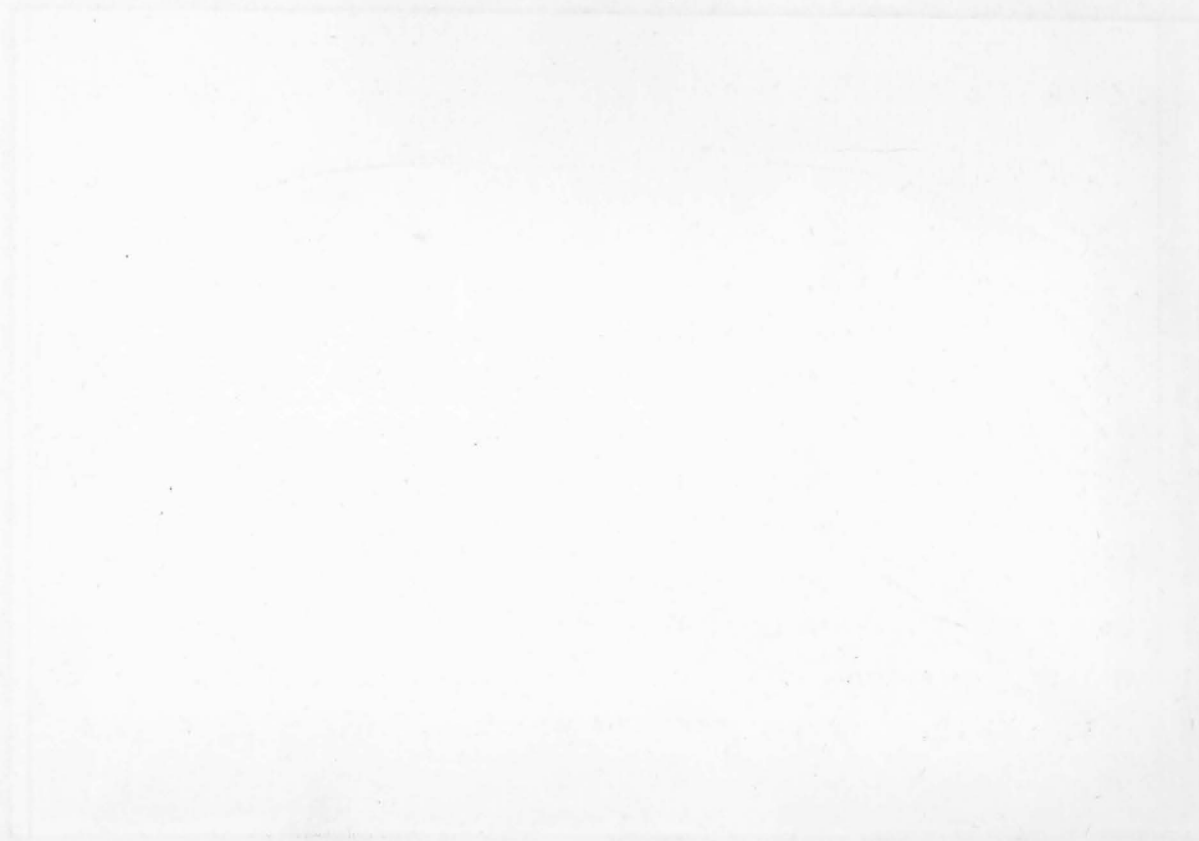
20.2 Means of establishing that a recess or burrow is a porcupine lair

In a study of this nature it is a matter of some importance to establish the identity of the occupant of a recess or burrow before a collection of the introduced bones is made. If possible, crevices, recesses and burrows should be watched both by day and night in order to establish unequivocally the identity of the occupant or occupants. If this is not possible, as often happens, the observations listed below should be made. These observations represent means by which it can be established whether or not a porcupine is occupying a burrow or recess, or has done so a short while previously. The presence of even a few of these features is often enough to confirm actual or very recent presence. Previous and concurrent occupation by other animals and therefore 'contamination' of bone accumulations should always be borne in mind.

lit 130



lit 138



- 105 -

205

Fig 140

The 'Rand van Tweedepoort' porcupine lair, an enlarged recess in the limestone 'tufa' (see Fig. 138).

Note the size of the mound of excavated earth at the entrance (compared with that shown in Fig. 137 which is aardvark excavated) and the small size of the entrance.

Fig 141

The 'Side Lair' at Hartebeesthoek.

Note the small size of the entrance, made still smaller by the piling of rocks to facilitate trap-setting. Note also the well-gnawed oblique-standing rock in the centre of the entrance and the much-gnawed tree roots above the matchbox. The excavated earth in the right foreground has been built up by the enlarging of a second entrance (not shown).



Fig 140

The entrance to the 'Main Lair' at Hartbeesthoek, the half loaf of bread at left centre providing a scale.



Fig 141



Fig 142

The entrance to the 'Main Lair' at Hartebeesthoek, the half loaf of bread at left centre providing a scale.

As in Fig. 141 the low entrance has been made still smaller by the piling up of large rocks. The porcupine occupied part of this low rock cave lay some 6m (20ft.) from the entrance and was made inaccessible by the approach of the roof to the floor, the gap between not exceeding 20cm (8 inches). More than 300 bones have been retrieved from this lair over a four year period.

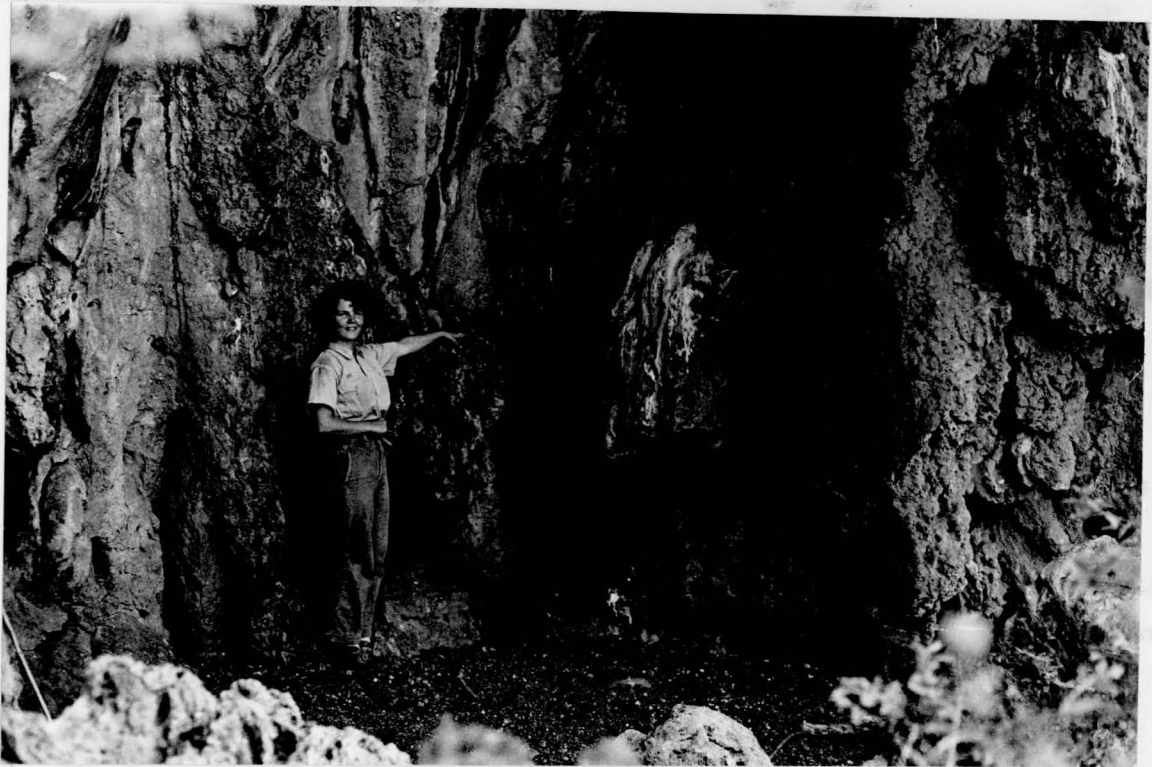


Fig 143

A ledge in the Rand van Tweedepoort limestone 'tufa' used as a sleeping place by a troop of baboons.

Note the mass of baboon droppings and fruit stones (mainly marula) littering the floor. There are signs that porcupines had used the narrow tunnel behind the standing figure as well as the narrow fissure indicated as lairs, probably prior to occupation of the ledge by baboons. The rock ledge which was partially roofed by an overhanging carapace of lime, had apparently also been used by humans, as evidenced by quantities of potsherds, wooden bowl fragments and other artefacts. Bones retrieved from a porcupine lair in this type of setting are likely to show mixed characteristics, as the porcupines would tend to accumulate bones left by the human occupants of the ledge.

value. Droppings had to be collected from the wild: animals in the wild were observed and their droppings retrieved. Natural variations had to be considered, these seemed to depend primarily on the health of the animal and local differences in diet.

Porcupine dung has a very distinctive appearance, giving the impression of being plaited (Fig. 145). It is almost impossible to confuse the droppings of porcupines with those produced by any other species; perhaps the closest in appearance are those of baboons (Fig. 146). Each of the segments constituting the 'plait' of porcupine dung (adult) is on average about the size and shape of an outside date and woody-

20.2.1 The presence of porcupine spoor

Porcupine tracks (Fig.144) are frequently found in the mound of soft excavated earth at the entrance to a lair or burrow. The earth at the entrance can be swept at intervals and examined for fresh spoor, and the identity of the occupant established in this way.

A knowledge of porcupine spoor, and that of other likely occupants of rocky lairs or burrows, for example aardvark, spotted and brown hyena, leopard, aardwolf, wild dogs, jackals, ratels, warthogs, dassies, hares and snakes is essential.

If a lair has been vacated for some time, spoor of any description may be absent, and the identity of the erstwhile occupant(s) will have to be established by other means.

20.2.2 The nature of the dung found in the vicinity of the lair

The nature of the droppings found in the vicinity of or within a lair or burrow can give some clue as to the identity of the occupant. The ability to recognise the droppings of the animals (including porcupines) that are likely to inhabit the rocky shelters or earth burrows favoured by porcupines, such as those species mentioned in 20.2.1 above, was considered a useful asset. For this reason, a brief study of the droppings of the animals involved was undertaken.

The droppings of any species of animal reflect the nature of its diet. Since most zoo animals (and civilized man, for that matter) subsist mainly on artificial diets, their droppings cannot be considered as typical, and therefore a collection from a zoo is of little value. Droppings had to be collected from the veld: animals in the wild were observed and their droppings retrieved. Natural variations had to be considered, these seemed to depend primarily on the health of the animal and local differences in diet.

Porcupine dung has a very distinctive appearance, giving the impression of being plaited (Fig.145). It is almost impossible to confuse the droppings of porcupines with those produced by any other species; perhaps the closest in appearance are those of baboons (Fig.146). Each of the segments constituting the 'plait' of porcupine dung (adult) is on average about the size and shape of an outsize date and woody-

Fig 144

Porcupine spoor (centre) and faint quill drag marks (below) in the soft excavated earth at the entrance to a porcupine-enlarged rock burrow.

Fig 145

Porcupine droppings. Note the fibrous texture and plaited appearance.



Burrows are frequently occupied by porcupines, are variable in shape, consistency and texture, but in instances can be fairly easily recognized by the presence of many ant and termite integuments, the rest of the soil being composed of wood and debris which is usually

Fig 144

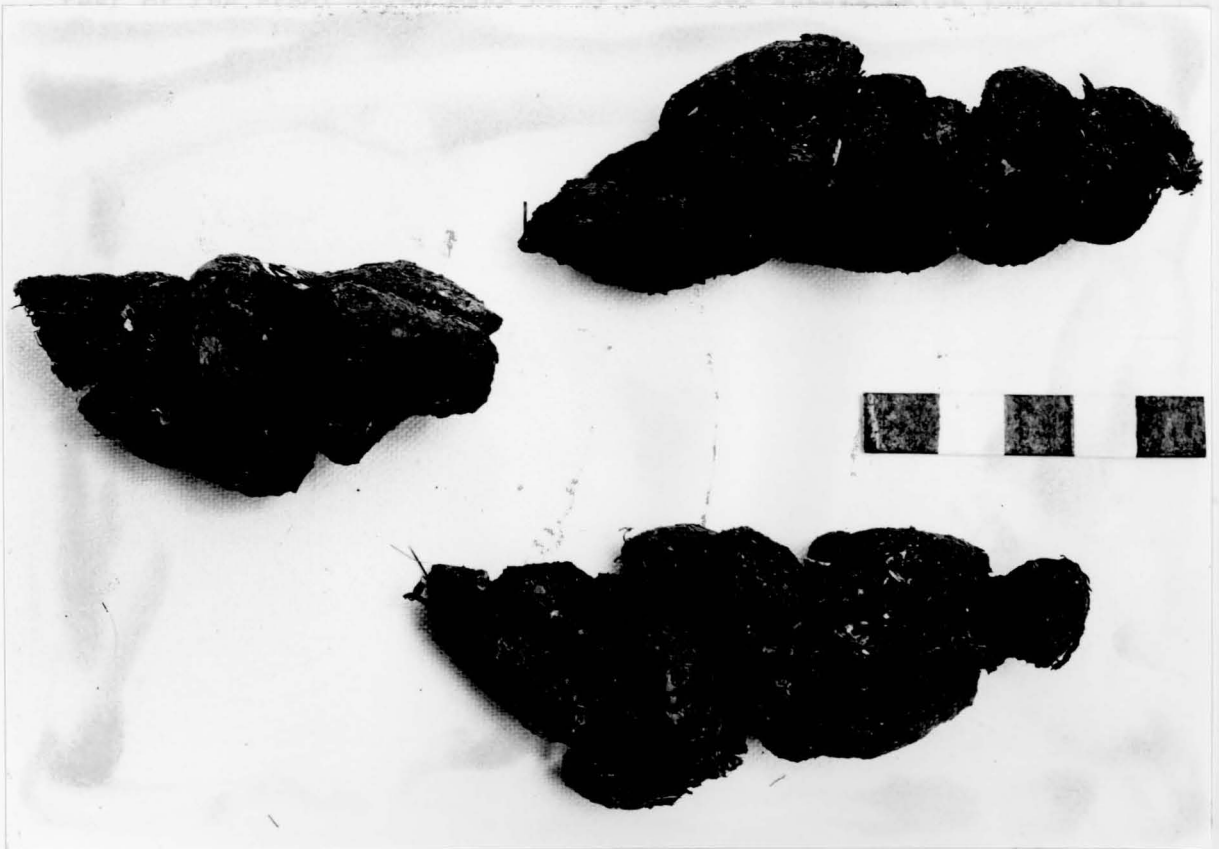


Fig 145

fibrous in texture. The colour ranges from almost black to pale beige-brown. On teasing out, each segment can be seen to consist mainly of fibrous, undigestible plant material, a certain amount of grit and sand and, occasionally, pips and seeds. One or two 'plaits' of adhering segments or a series of loose segments may be found lying together, but porcupines do not seem to return constantly to the same spot to defaecate. Their dung is found lying at intervals on the veld, where it is presumably deposited on the way to or from their feeding grounds. A lair or porcupine-occupied burrow which has been fouled by the porcupines themselves has not yet been encountered by the present author, neither has porcupine dung been found littering a lair entrance, or even the approach to a lair. The closest that dung has been found to an entrance was 5m distant. The absence of porcupine dung from the vicinity of a lair therefore does not preclude the possibility that a porcupine may be resident.

The droppings of the aardvark (Orycteropus afer) whose disused burrows are frequently occupied by porcupines, are variable in shape, consistency and texture, but in all instances can be fairly easily recognized by the presence of many ant and termite integuments, the rest of the stool being made up of sand and debris which invariably gets swallowed along with the ants on which these creatures live. The colour of the dung seems to depend on the soil colour of the area in which the aardvark is operating, whilst the shape, texture and consistency seems to depend on the proportion of ants to soil ingested. The two specimens in my possession apparently represent extremes in variation; the one is an aggregation of firm, smooth nodules composed mainly of fine grit (Fig.147), and the other being an amorphous mass of dark crumbs, each crumb being an ant exo-skeleton with a few adhering soil particles or a small aggregation of soil particles, the proportions of each being about equal and the whole weighing about 60g (4oz.). Aardvark normally deposit their dung in the loose excavated soil at the entrance to their burrows, after which they cover it with earth, making it difficult to retrieve.

Owing to the bony nature of the hyena diet (both spotted and brown hyena) their droppings are unmistakable, being almost pure white, dry and chalky in texture (Fig.148) and conspicuous on the veld. Small

Fig 146

Baboon (Papio ursinus) droppings.

Note the blunt (right hand) and tapering (left hand) extremities of the upper dropping and its segmented appearance. Note also their fibrous and pippy texture, particularly the lower dropping. The fruit stone visible in the segment second from the right of the upper dropping belongs to Mimusops.

Fig 147

Aardvark (Orycteropus afer) droppings, which are apparently composed of grit and ant integuments.

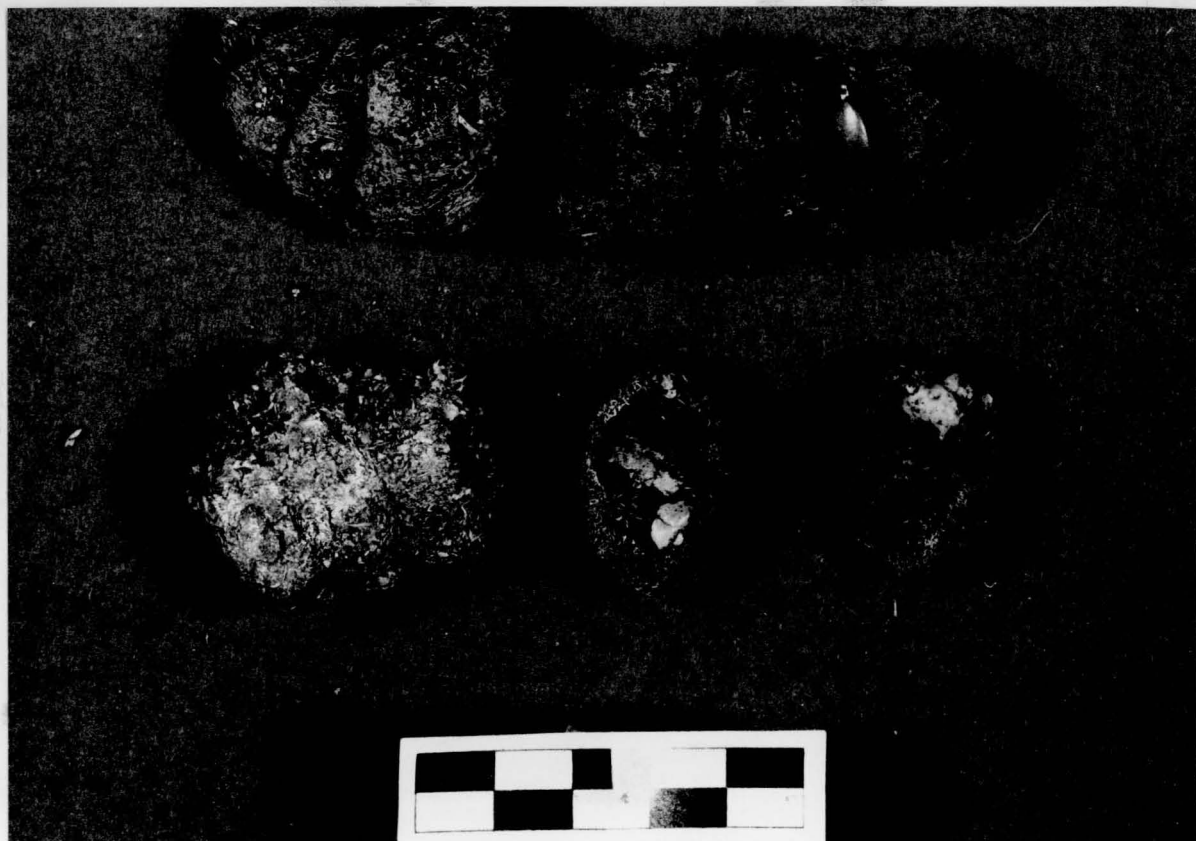


Fig 146

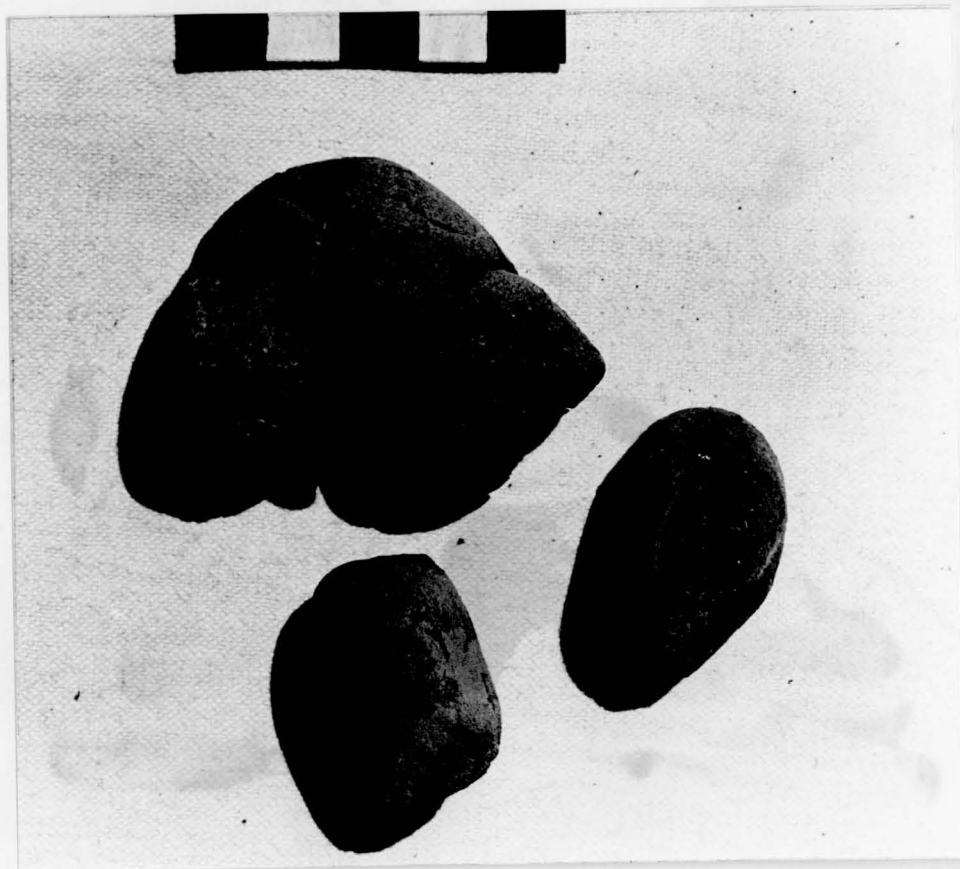


Fig 147

Fig 148

The almost pure white, chalky dung of the spotted hyena Crocota crocuta, consisting mainly of undigested bone and hair.

Fig 149

Fossilized hyena (Hyaena hyaena makapani) coprolites from the Makapansgat Limeworks grey breccia. Bone slivers may sometimes be seen on fracturing a segment.



Fig 148

therefore indicate the presence of these animals within.

Leopard droppings may on occasion resemble those of hyenas



Fig 149

reported to use Grycteropus snail earth burrows, but their defecating behaviour appears to be undocumented.

slivers of undigested bone and the hair of their prey can sometimes be discerned upon breaking a dropping open. Some fossilized hyena coprolites are shown in Fig. 149. According to Kruuk (1972 p.66) hyenas frequently deposit their droppings in special 'latrines' which are often situated on the boundary between two clan ranges, and hence at some distance from the lair. These have also been observed by the present author. Sutcliffe (1969) on the other hand has found that:

Droppings of spotted hyaenas were common on the surface not far from the lair described above, but only one dropping was found inside. This was associated with the juvenile hyaena skeleton in the lair In a cave..... a concentration of hyaena droppings was found beyond the limit of penetration of daylight but no bones were associated with it..... Hyaena droppings are often common on the surface around the entrances of lairs but rare within them. (p.3)

Brain (1958 Fig. 11) also describes and illustrates a hyena lair containing dung. Hyena dung in the vicinity of a lair or burrow may therefore indicate the presence of these animals within.

Leopard droppings may on occasion resemble those of hyenas except that they are of smaller diameter, less 'nodular', 'stringier' and contain less fur. Turnbull-Kemp (1967 p.95) describes leopard droppings as being viscous or tar-like. Leopards are not known to foul the interiors of their lairs but whitened dung may be encountered in the vicinity, especially on patches of bare rock, if the environment is rocky. In non-rocky areas, droppings may be encountered on open ground free of vegetation, but in such instances the leopard usually 'scratches over' and covers his scats with a layer of soil (Turnbull-Kemp op. cit. p.95). Such scratch marks or piles of droppings should therefore be looked for.

The dung of the predominantly insectivorous aardwolf or maanhaarjakkals (Proteles cristatus) contains masses of fragmented insect carapaces (mainly Isoptera), sand and sometimes short sections of undigested grass. That of the bat-eared fox (Otocyon megalotis) also a predominantly insectivorous animal, is similar, except in that it contains a greater proportion of Coleoptera exoskeletons as well as scorpion, solifugid and occasionally murid remains. Both species are reported to use Orycteropus and other earth burrows, but their defecating behaviour appears to be undocumented.

Silver jackal (Vulpes charma), sidestriped jackal (Canis adustus) and blackbacked jackal (C. mesomelas) are also reported to use disused aardvark and other burrows (Smithers 1971). The droppings of all three species (rather dog-like in appearance) would appear to be indistinguishable on account of the similar diets, and since all contain fragments of insect integuments, may easily be confused with those of O. megalotis (a little smaller) or P. cristatus (mainly ant exoskeletons present). The droppings of the ratel (Mellivora capensis) would appear to resemble those of jackals closely. Any dog-like droppings containing insect carapaces have thus been interpreted as indicating the possible presence of one of these six species.

The droppings of more exclusively carnivorous animals such as wild dog (Lycaon pictus) never have a woody fibrous or pippy texture, nor a pellet form, but are uniform-textured, smoothish, usually dark coloured, slender and often taper sharply at both ends. Undigested vegetable matter or grit is usually not present.

The droppings of the dassie (Procavia capensis) and the red rock hare (Pronolagus crassicaudatus) both have pellet form but are not easily confused, differing in size, shape, colour and composition (Figs. 150 and 151). The pellets of P. crassicaudatus are distinctly flattened, regular spheroids (oblate) approximately 10mm to 15mm in diameter, and composed entirely of minute fragments of undigested grass. They are very pale yellowish green, when fresh, fading to beige or ginger brown, and have a characteristic dry grass odour. The dung of dassies is much smaller and tends to have an elongated oval outline, the long axis of which seldom exceeds 12mm. Both the broad and the narrow end often terminate in a small pointed protuberance. On fragmentation the texture can be seen to be finer than the pellets of Pronolagus crassicaudatus, and the composition not so homogeneous - it is apparent that materials other than grass are also eaten. Their colour is much darker than the droppings of the rock hare, ranging from dark brown to almost black. Their odour is grassy but distinctly pungent.

Both species are commonly encountered in the rocky environment favoured by porcupines, and as both tend to defecate in specific spots (away from their lairs), accumulations of their droppings are frequently

Fig 150

The droppings of the red rock hare, Pronolagus crassicaudatus.

Fig 151

The droppings of the dassie, Procavia capensis.



Fig 150

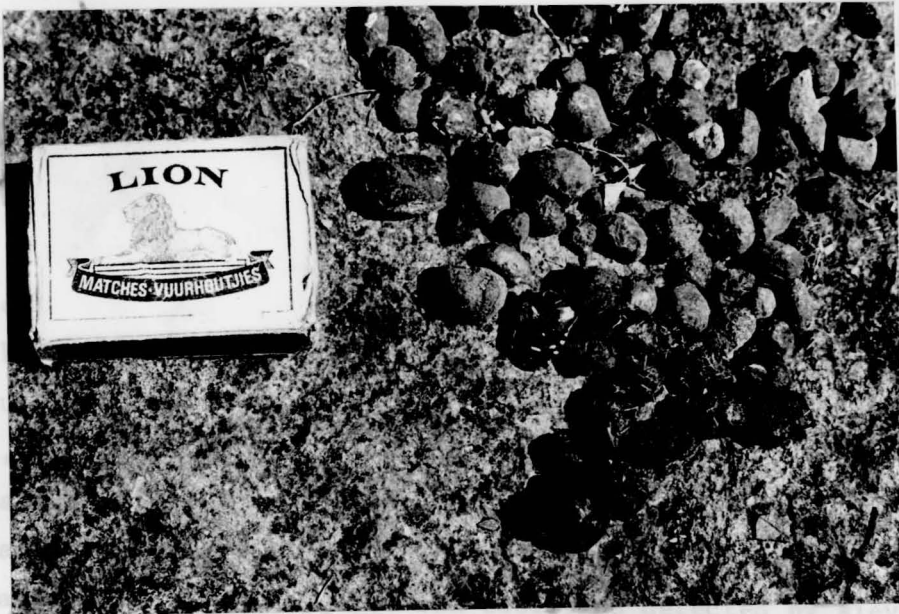


Fig 151

to be seen. On occasion these may occur at or near the entrance to an occupied porcupine lair, but this seems to be a matter of chance and not because either species was sharing a lair with Hystrix. The presence of Procavia capensis or Pronolagus crassicaudatus dung piles at a lair entrance therefore does not preclude the presence of porcupines.

The droppings of baboons reflect their omnivorous but predominantly vegetarian diet, being coarse-textured and fibrous, and containing pips, seeds and husks and, to a lesser extent, insect and scorpion integuments. One end is often blunt, the other tapering, faint constrictions at intervals demarcating each dropping into a series of stout disc-like segments. Baboon droppings are seldom encountered in those shelters preferred by porcupines, unless porcupines happen to be occupying low tunnels or recesses leading off a rock shelter, ledge or cave which is used by baboons as a sleeping place. As baboons have no scruples about fouling their living quarters, their dung may be found in the vicinity of this type of porcupine lair. However, in such situations, it is unlikely that a porcupine will be resident if baboons are occupying the large rock shelter regularly.

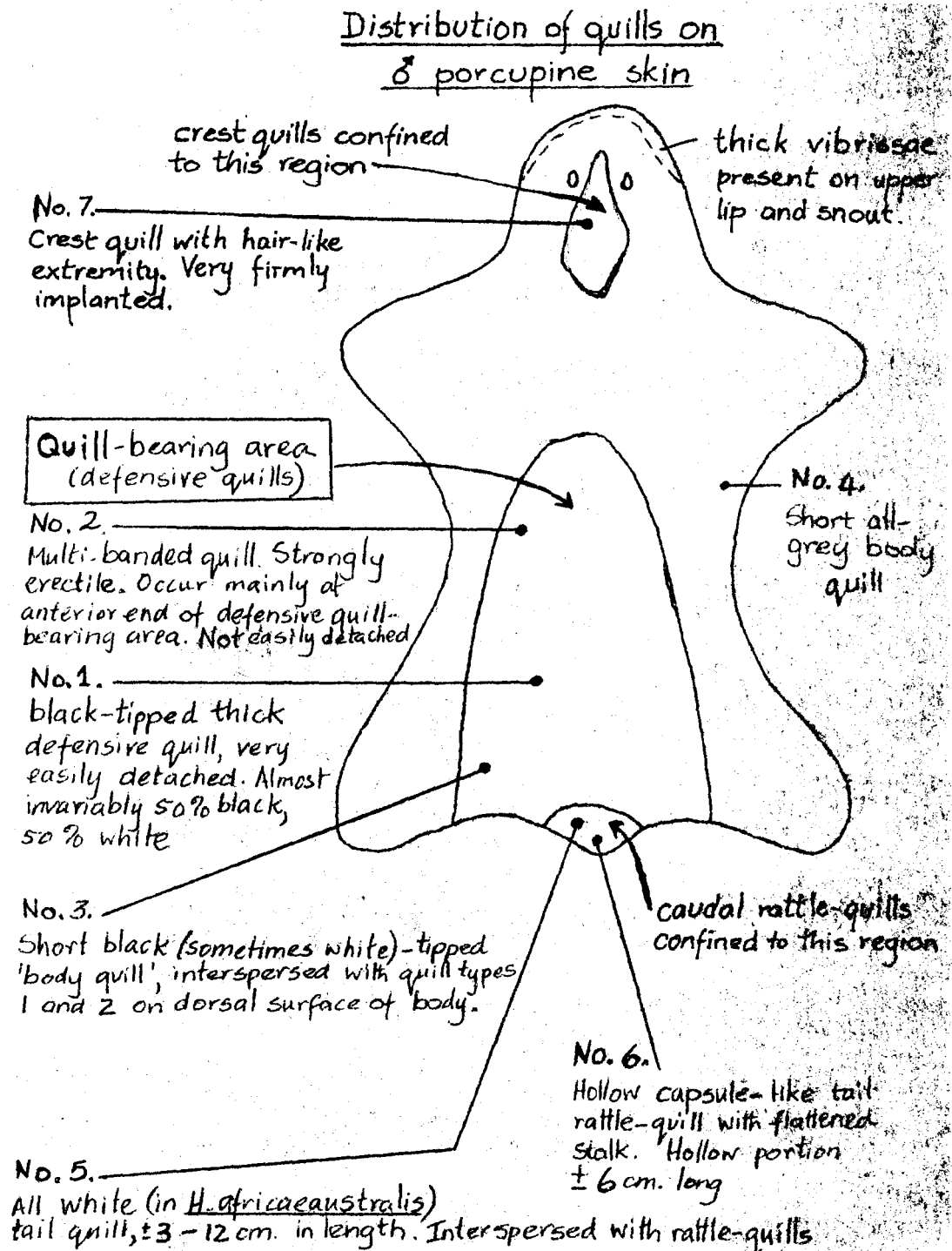
Animal dung is therefore a useful, though by no means infallible, means of establishing the identity of the occupant of a lair or burrow.

20.2.3 The presence of loose quills

Porcupine quills, of which there are several shapes, sizes and colour-banded varieties (Fig.152) are easily recognizable, and since they are very loosely embedded in the skin, (Roberts 1957, p.346) come out easily when the animal shakes itself or brushes firmly against objects. Quills, particularly the small, short type which cover the sides and belly of the animal, are frequently found within a lair (Fig.153) or scattered over and near the disturbed soil at the entrance. Because of the activity and trampling of the animal, quills may soon become buried in the soft earth at the lair entrance, but can easily be detected by sieving some of this soil through the fingers. The large thick defensive quills can

Fig. 152

Porcupine quill types: a: crest quills; b: body quills;
c: belly quills; d: defensive quills; e: tail quills;
f: rattle quills





1



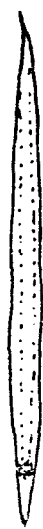
2



3



4



5



6



7

x1



Fig 153

Gnaw-damaged vegetation has been encountered in the vicinity of most Well-gnawed atlas, axis and cervical vertebrae littering the interior of a porcupine lair. Note also the numerous short belly quills lying in the vicinity of the section of spinal column. In others it seems as if the vegetation has merely been treated as a substance to gnaw (Fig.157). The presence of well-gnawed 'ring-barked' tree trunks or even completely felled saplings and numerous wood chips (Figs.159 and 160) in the vicinity of a likely-looking rock crevice or burrow thus indicates the presence of porcupines.

Porcupines appear to have favourite trees, some trunks being left untouched while others are extensively damaged, showing gnaw-marks of different ages, or intervals, the more recent being the palest and the older scars at varying stages of discolouration (Fig.158). The gnawing frequently extends up the stem to a level of about 45cm (18") above the surface, presumably as high as a porcupine can comfortably reach (Fig.156). Extensively gnaw-damaged stumps and branches of wood (Fig.159) and, in agricultural areas, fair numbers of maize cobs, portions of pumpkins and prickly pears are often dragged right into the lair, or are strewn about the entrance. The excavation and gnawing of underground roots, bulbs and tubers in the vicinity can also be indicative of porcupine activity.

frequently be found on the routes leading to and from the lair. Freshly dropped quills are easy to detect as they lie on top of the disturbed soil and their white bands are not earth-stained and reddish-brown, the freshness of the quills being a useful way of determining whether the lair is occupied or abandoned.

20.2.4 Gnawing of various objects

Porcupine gnawing (Figs. 154 and 155) is easily distinguishable from the gnawing of other rodents and from the gnawing damage done to bone by adult and juvenile carnivores (see Sutcliffe 1970, Figs. 1, 4 and 5). Being by far the largest rodent in Africa, the incisor teeth are proportionately larger and hence the grooves in bone and other materials caused by the gnawing action of these teeth are very much broader than those caused by the teeth of other rodents such as rats and mice.

20.2.4.1 Vegetation

Gnaw-damaged vegetation has been encountered in the vicinity of most porcupine lairs observed so far. In some instances it appears as if the vegetation has been systematically felled in order to make access to the lair easier (Fig. 156), while in others it seems as if the vegetation has merely been treated as a substance to gnaw (Fig. 157). The presence of well-gnawed 'ring-barked' tree trunks or even completely felled saplings and numerous wood chips (Figs. 159 and 160) in the vicinity of a likely-looking rock crevice or burrow thus indicates the presence of porcupines.

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Fig 154

Extensively porcupine-gnawed modern ungulate tibia, removed from the Hartebeesthoek Porcupine Lair.

Fig 155

Fossilised bovid tibial fragment from the Makapansgat Limeworks grey breccia, probably gnawed by the giant extinct porcupine Xenohystrix crassidens.

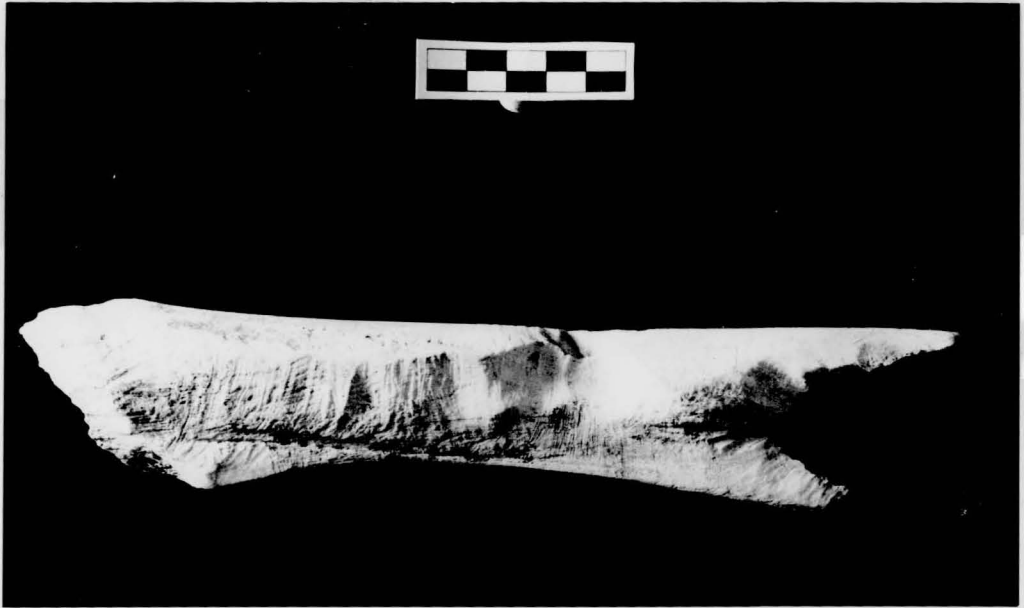


Fig 154



Fig 155

Fig 156

Gnawed-off shrubs and low mound of excavated earth outside the entrance of the Rand van Tweedepoort porcupine lair.

Fig 157

Extensively porcupine-gnawed stick, showing gnaw marks of differing ages, recovered from the Hartebeesthoek porcupine lair.



Fig 156



Fig 157

Fig 158

Base of the trunk of Pappea capensis growing about 3m from the entrance of the Hartebeesthoek Side Lair showing porcupine gnaw marks of differing ages. Note that the gnaw marks terminate about 45cm (18 inches) above ground level, presumably indicating the height beyond which a porcupine cannot conveniently gnaw.

Fig 159

Close up of scars caused by porcupine gnawing on the base of the trunk of the tree figured above.



Fig 158

nine smaller obviously gnawed stones were found in the vicinity (Fig. 160). Stone gnawing of this magnitude appears to be confined to the immediate vicinity of the lair. With regard to these porcupine-gnawed stones it



Fig 159

20.2.4.2 Bone

Perhaps the most characteristic feature of a porcupine lair is the presence of large numbers of extensively gnawed bones and teeth (Figs. 153 and 160) scattered near the entrance but particularly within the lair. Once again the bones may exhibit gnaw damage of differing ages or intervals. Porcupines are apparently compulsive collectors of bones, and dozens of bones are frequently found littering the floors of lairs. The majority of these gnawed bones are entirely devoid of meat and some of them are extensively sun-cracked, showing that they have been exposed to the natural elements for a considerable period before being collected, but at times a few may have adherent strips of dry shrivelled flesh, cartilage and skin attached.

20.2.4.3 Stone

Across the entrance to the Side Lair at Hartebeesthoek was a large rock that had been extensively gnawed by porcupines (Fig. 141) and a further nine smaller obviously gnawed stones were found in the vicinity (Fig. 161). Stone gnawing of this magnitude appears to be confined to the immediate vicinity of the lair. With regard to these porcupine-gnawed stones it is interesting to note that Alexander (1956), commenting on the activities of a captive porcupine, reported that

on no occasion could he be induced to carry a stone, but if the stone was well larded with human sweat he would lick and bite at it, taking it into his mouth and then dropping it again. (p.258)

20.2.4.4 Other

A variety of other materials such as gnawed bovid horns, hooves, ivory and even pottery and metal may also at times be encountered in porcupine lairs.

20.2.5 Excavation of the soil in vicinity of the lair

The volume and extent of excavated soil gives some indication of the size of the animal involved. Aardvark excavations or holes are so extensive as to be unmistakable, and the scrape marks of their powerful digging claws are often evident on the side of the tunnel. Where enlargement of actual aardvark tunnels has been undertaken, this is most likely

Fig 160

Gnawed-off sapling, stump and gnawed bone (centre) near the entrance to the Rand van Tweedepoort porcupine lair (extreme left).

Fig 161

Extensively gnawed small Ventersdorp Lava rock fragment removed from the entrance to the Hartebeesthoek Side Lair.



Fig 160

grunting sounds emanating from the depths of the burrow or lair can sometimes be heard." The distinctive sound of rattling quills, probably the hollow tail rattle-quills (Fig. 152), has been heard on several



Fig 161

the work of hyenas, wild dogs or warthogs and not of porcupines which are considerably smaller than aardvarks and have no need to enlarge the tunnels. However, where mounds of excavated earth occur in quantity along the bases of cliffs and kranzes or near boulder piles (a locality type not favoured by aardvark) this is in all probability due to porcupine activity (Figs.140 and 162). The disturbed earth may be scraped and kicked out to a distance of up to 8m (25ft) or more. In any case spoor of one description or another is usually evident on the excavated earth; porcupines frequently leave fine striations where their quills have dragged (Fig.144).

Localized smaller excavations to expose edible roots, bulbs and tubers etc. (which are often gnawed) also disclose the presence of porcupines.

20.2.6 Auditory and olfactory detection

It has been reported (Astley Maberly 1967 p.275) that "muffled grunting sounds emanating from the depths of the burrow or lair can sometimes be heard." The distinctive sound of rattling quills, probably the hollow tail rattle-quills (Fig.152), has been heard on several occasions by the author in the course of investigating lairs.

Although more subjective, the olfactory detection method is sometimes useful as different animals have characteristic smells. In India native sportsmen declare that the aroma from burrows is sufficient to distinguish the different species of porcupine (Sclater 1865 p.356).

20.2.7 The presence of body (external) parasites

The presence of outsize fleas in the fine loose dust inside some lairs was noted, but it is not known whether this extremely large variety is confined to porcupine lairs only. If fleas do occur on porcupines their manner of scratching themselves is a matter of some interest.

If regular observation is impossible, some of the above-mentioned points may make it possible to decide whether or not a porcupine is occupying a lair or has occupied it some time previously. However, as many animals besides porcupines, some of them potential bone accumulators, have been observed to use rock crevices and earth burrows as

Fig 162

The narrow (approximately 50-60cm wide and 20cm high) entrance to the Rand van Tweedepoort Lair.

Note the enlargement of the recess by the excavation of loose earth and the well preserved porcupine hind footprint (left centre).

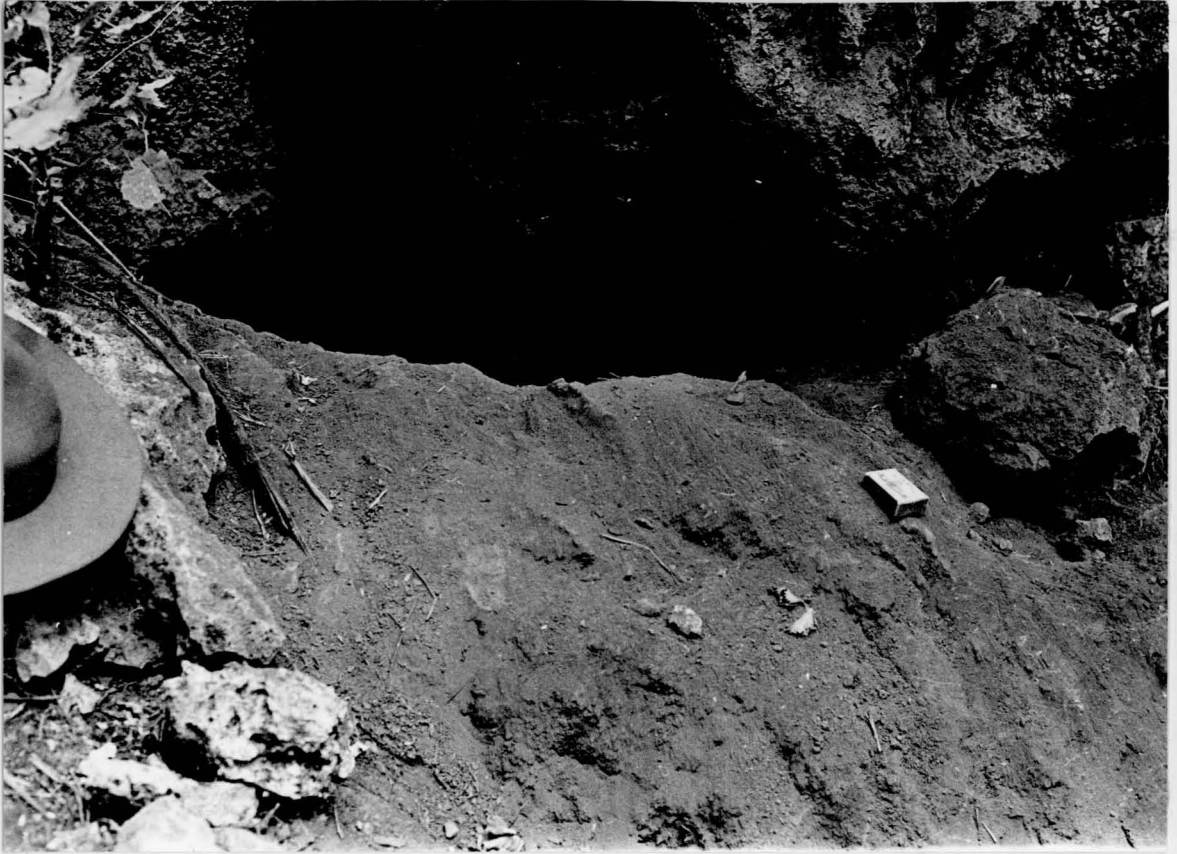


Fig 162

lair, any lair could have had a succession of different occupants, of which a porcupine may have been one. The question of 'contaminated' or 'mixed' bone accumulations should therefore constantly be borne in mind.

21. PROBLEMS CONNECTED WITH THE STUDY OF PORCUPINE LAIRS

The finding of lairs which are suitable for study and for the retrieval of bone is made very difficult by several factors.

21.1 Difficulty of access

Most of the rock crevice type of lair used by porcupines have low entrances which are too small to allow access to humans, whether adult or child, and are often so small that only head and possibly the shoulders can be inserted (Figs. 140 and 141). For example, the entrance to the Rand van Tweedepoort lair (Fig. 162) although 50-60cm (20-24 inches) wide, has an average height of only 20cm (8 inches), reaching 30cm (12 inches) only at its highest point. Inside, such lairs are usually extremely low-ceilinged, seldom being more than about 30cm (12 inches) from floor to roof. In many instances, the space available does not permit turning of the head from side to side, and movement can only be made by squirming or by the use of friction against ceiling and floor. Ceilings and floors are often sloping, curved and irregular. Rock projections from both roof and floor are common and if the lair takes the form of a passage, this is likely to have a number of bends or curves. Apart from hampered movement within the lair, these features make illumination of the innermost recesses of the lair difficult on account of the shadows. As a result of the restricted movement, generally confined to the entrance or its vicinity, gnawed bones and other objects deep within the lair are usually inaccessible, even when the collector is equipped with a long hooked collecting pole. Most rock lairs, therefore, require extensive blasting, removal of large boulders or excavation if the introduced contents are to be recovered in their entirety.

Abandoned aardvark holes which have been appropriated by porcupines sometimes have entrances which are large enough to squeeze through, (about 40 x 50 to 45 x 60cm and occasionally even larger), but the tunnel leading into the ground usually slopes steeply downwards and is often curved, with a floor of loose soft sand or soil which offers no traction, and cascades inwards when movements are made. As there is no turning space the soft material makes it extremely difficult to reverse out, as testified to by the following statement:

Three men entered and were lost in a very extensive and deep burrow in Zambia. After ten days' digging only one body was recovered, indicating the extraordinary extent of these burrows. (Foran, 1961)

21.2 The risk factor

Rock lairs and porcupine-occupied aardvark holes which are large enough to permit access, even though this may be for only a short distance of their total extent, present several hazards which are worthy of mention:

Collectors entering low rock lairs run the risk of dislodging precariously balanced boulders and rocks which may block the tunnel entrance and thus confine the collector within the lair. Another hazard is that of being confronted by dangerous occupants in the lair; for example, part of the cast-off skin of a large Black Mamba (Dendroaspis angusticeps) was found draped over the mound of excavated earth at the entrance of the Rand van Tweedepoort lair, and the author has on a number of occasions been startled by the rattle of porcupine quills at the first tentative investigation of a hole.

Apart from the danger of becoming stuck (see 21.1), the earth burrows of aardvark are known to harbour a wide range of potentially dangerous animals. In the hotter areas there is a strong possibility of encountering snakes such as various types of cobra, ringhals and mambas (Stevenson-Hamilton 1954 p. 242; Dorst and Dandelot 1970 p.106). Both brown and spotted hyenas, wild dogs, ratels and warthogs are recorded as making use of abandoned aardvark burrows at times. The (harmless?) aardwolf (Proteles cristatus) which feeds on termites and probably follows the aardvark about to benefit from its wasteful feeding habits, also uses aardvark holes.

Bats, bees and wasps are also a problem.

21.3 The difficulty of finding uncontaminated porcupine bone accumulations

The possibility that more than one bone-accumulating agent has contributed to a bone accumulation has to be constantly considered. This is especially true of bone accumulations retrieved from earth burrows,

where some bones may originally have been collected by hyenas and then gnawed by porcupines subsequently occupying the lair. In such cases, the porcupine gnawing may obliterate any evidence of carnivore damage and the contamination may be difficult to detect. On the other hand, if hyenas are contributing to a pre-existing porcupine bone accumulation, this may be evident in a lowered percentage of porcupine-gnawed bone, a higher incidence of hyena-damaged bone, and possibly a greater degree of fragmentation than is usual for 'pure' porcupine bone accumulations. The collections made by Hughes from two large 'porcupine' lairs in the Kalahari Gemsbok National Park probably represent mixed hyena-porcupine accumulations of this kind (Dart 1957 p.4; Hughes 1951).

In rock lair situations, either hyenas, leopards or humans may represent contaminative agents. Brain (pers. comm.) has said that while doing field studies on the food remains in the lairs of living leopards in South West Africa, he found it difficult to find leopard lairs that had not also been used by porcupines, or leopard food remains which had been left untouched by porcupines. The bones collected by Toerien and Brand in 1954 from the farm Goedgevonden near Krugersdorp, and described by Dart (1957 p.5) apparently represent a collection that has been complicated by the contributions of three bone accumulative agents, humans, hyenas and porcupines.

The larger the porcupine lair, the greater the likelihood that the bone accumulation will contain 'contaminants' left by occupants other than porcupines (see Chapter 19).

Both the Winklehoek Cave material (see Chapter 19) and possibly even the bone collection from the Cave of Hearths, may be mixed human-porcupine accumulations. In this instance, it is more correct to regard the bones collected by the porcupines as 'contaminants' of a predominantly human bone accumulation. As Dart (op. cit.) has pointed out, "these are complications such as are not easily evaded even in the Kalahari Desert today and presumably during the entire Pleistocene period" (p.6). From this statement it appears obvious to the present author that Dart did not consider either the Taung or Makapansgat australopithecine cavern deposit bone accumulations to be entirely the work of Australopithecus or any other one bone accumulating agent - the few porcupine and carnivore-gnawed bones may merely represent minor 'contaminants.'

The recognition of the characteristic features of the bone accumulations of all the major bone-accumulating agents is essential in order that contamination can readily be detected in collections made from lairs or caves. However, the definition of such characteristics depends on the locating of 'pure' bone accumulations made by each agent, and such assemblages are difficult to find.

In order to eliminate or at least substantially minimize the possibility of contamination by other bone-accumulating agents, the bone assemblage that was selected for analysis with a view to defining the characteristics of porcupine-accumulated bone deposits, was extracted from a porcupine lair in an area where lions, leopards and hyenas are not now known to occur. After initially clearing the lair of bones, it could be said with reasonable certainty that all bones that subsequently accumulated within it had been introduced by porcupines (see Chapter 18, Method). The inner recesses of this lair were in any case too low and confined to make it habitable by man or any other likely bone-accumulating agent.

21.4 The difficulty of finding 'analogous' lairs and defining 'typical' porcupine bone accumulations

The aim of part II of this thesis has been to determine the possible extent of fossil porcupine involvement in the accumulation and fracture of the bones in the Limeworks grey breccia. It was hoped that this could be achieved by collecting the bones from uncontaminated 'real' porcupine lairs and defining the characteristics of porcupine-accumulated bone assemblages, and then, by comparison, determining whether the grey breccia bone assemblage resembled this type of accumulation in any way.

Wolberg (1970) has pointed out that it is desirable to study modern analogues in an attempt to illumine past processes. Thus, with the above aim in mind, the ideal porcupine bone accumulation to examine would be one that had built up in as closely analogous a situation as possible to that which prevailed at the time when the grey breccia was being laid down. Unfortunately, the ape-man period environment is still largely a matter of speculation; for this and other reasons, a modern analogous situation is impossible to find.

For example, during ape-man times, porcupines would have had only the bones left from carcasses after predatory and scavenging carnivores such as sabre-toothed cats, lions, leopards, a variety of hyaenids, jackals and probably even australopithecines had finished with them. Alternatively, they could have collected any dry bones left littering the lairs of these same creatures. A fairly closely analogous modern situation would supposedly be one in which a porcupine was operating in an area where a full spectrum of normally behaving predators and scavengers was present. To allow for the 'australopithecine component', the normal activities of a primitive hunter-gatherer society would also have to be present. Such an undisturbed natural environment is difficult to find today, even in the remoter parts of the Kalahari. In the course of the ten weeks spent in the Kalahari, several lairs were observed (invariably disused aardvark burrows), but none proved suitable for study.

Even in game reserves, strictly natural faunas do not occur, on account of predator control and culling (both of which affect animal behaviour), and the hominid element as a bone dispersing, damaging and destroying agent is absent because of strict poaching control. In addition the carcasses of culled animals are often sold and others limed and burnt in an effort to control disease.

The most accessible lair and the one from which controlled collections were regularly made was situated on the Highveld about 4,8km (3 miles) north-east of the Hartebeesthoek Satellite Tracking Station on the righthand side of the road to Broederstroom which passes the Station. Unfortunately, from the time of the earliest settlers and the advent of stockfarming onwards, indiscriminate hunting has exterminated the larger predators and scavengers as well as the large ungulate populations they once preyed upon over large tracts of the Highveld, and indeed over southern and eastern Africa generally. Vultures (important bone-scattering agents) disappeared along with the disappearance of carcasses. The bones which find their way into porcupine lairs under conditions where the natural faunal balance has been disrupted in this way represent 'unnatural' accumulations from the point of view of the aim and method, as the bones available for collection will differ in a number of ways from those which would have been available to porcupines in a 'Pleistocene' environment. On the Highveld bones are derived mainly from the carcasses of a limited variety of mainly domestic animals such as horses,

donkeys and mules, cattle, sheep, goats, pigs and dogs. More important, however, is the fact that the carcasses of these animals are often left to dry out intact on the veld, unmolested by predators and scavengers, and bones can be picked up in complete or almost complete condition by porcupines. Brain (1967c, 1969b, 1970a) has repeatedly shown that certain parts of the mammalian skeleton survive the feeding activities of carnivores and hominids better than others, giving rise to predictable disproportions in the ensuing skeletal remains. A porcupine bone accumulation from an area in which the carnivorous element of the natural fauna has been eliminated will be very different from one in which the fauna is complete. Firstly, the initial skeletal part disproportions will not occur; secondly bones will be largely undamaged, and thirdly a wide selection will be available. For this reason, the results of the analysis of the Hartebeesthoek lair which is situated in a long-settled area, cannot be considered as strictly typical (see Method, Chapter 18).

The contents of porcupine lairs are likely to differ from locality to locality, depending on the nature of the environment, the local fauna and the source of bone. Therefore even if the accumulation may safely be regarded as 'pure', it appears to be impossible to define 'typical' porcupine bone accumulations. Brain (1970b) has pointed out a similar problem in the case of leopard behaviour and food remains, as has Kruuk (1972) in the case of spotted hyenas.

21.5 Disturbance

Porcupines are exclusively vegetarians, subsisting on both wild and cultivated bulbs (e.g. Gladiolus and Ornithogalum), roots, tubers, stems and fruits, pods and berries which have fallen to the ground. They are destructive and wasteful feeders (Roberts, 1951 p.346; Astley-Maberly 1967, p.275) and where they occur in numbers in cultivated regions cause extensive damage to both surface and subterranean agricultural crops. Grain of all kinds (particularly maize) and pumpkins, melons, turnips, potatoes and carrots are eaten. Generally only part of the melon or maize (which is gnawed down if the animal cannot reach the cob) is consumed, the rest being left to decay, while the animal moves on to gnaw at another.

Porcupines are reputed to make very tasty eating (Stevenson-Hamilton 1954, p.248; Roberts 1951, p.346; Astley Maberly 1967, p.276) to which natives in particular are partial. In the Kalahari, Bushmen pursue and dig porcupines out of their burrows, dispatching them with a blow over the snout, as the flesh under the back skin is considered to be 'one of the delicacies of the desert'' (Dr. H.J. Heinz, pers. comm., see Fig 137).

For the above reasons, porcupines are seldom left unmolested by farmer and native alike. Being of an exceptionally shy disposition they often respond to disturbance by departing. In the experiment conducted by the author to establish the rate of accumulation of bone within the Hartebeesthoek lair over a year (see 22.1) disturbance constituted an annoying factor, as traps were frequently found outside the lair and rocks were piled up to block the entrance. This in all probability interfered with the normal activities of the animal or animals within.

From the above five points it can be seen that accessible, safe, uncontaminated and undisturbed lairs in ideal Pleistocene-analogous situations are difficult to find. Although many lairs have been observed, it has been possible to make significant collections from only a few of them.

22. THE RATE OF ACCUMULATION OF BONE WITHIN PORCUPINE LAIRS AND THE TYPE OF BONE PREFERRED

22.1 The rate of accumulation of bone and factors affecting this

No published information is available concerning this important aspect. Brain (pers. comm. 1971, in a lecture to the Archaeological Society of South Africa) reported that over a twelve-year period, 500 bones accumulated within a previously cleared porcupine lair, or about 42 bones per annum. In an experiment conducted by the author, 44 bones, every one of them gnawed, in addition to 5 much-gnawed branches and sticks, 6 gnawed mealie-cobs and two extensively gnawed stones were retrieved from within a carefully cleared lair after the lapse of exactly one year, although 31 further bones were found near the entrance. This figure closely coincides with that obtained by Brain. Although the hillside in the immediate vicinity of the lair entrance was also cleared of bone, only the 44 bones from right inside the lair were taken into consideration since the bone retrieved from in front of the lair entrance could have been exposed by the removal of boulders and large slabs of rock by Africans in order to construct a trap; some of these bones probably had been lying under the rocks for many years. Three weeks later the same lair (i.e. the Main Hartebeesthoek Lair) was visited again to see if any more bones had accumulated in the interim and a further 3 freshly-gnawed bones were found, with saliva still dampening the ground below the gnawed portions. This gives a short-term average of one bone per week. A freshly-gnawed but obviously old branch which had probably been brought forward from some inaccessible corner of the recess was also found inside. The only additional information on the rate of bone accumulation within lairs is that it took 5 years for porcupines to remove an entire horse skeleton with the exception of a few phalanges and smaller bones (J.W. Kitching, 1971 pers. comm.).

A number of factors will affect the rate of accumulation of bone within porcupine lairs; these are discussed below.

22.1.1 The availability of bone in the vicinity

The availability of bone in turn depends on a number of factors, the chief of these being the local environment of the lair and the variety

and efficiency of predators and prey animals present; the number of animals killed; the variety, numbers and effectiveness of scavengers; the numbers of animals dying due to disease, starvation, snake bite, age or accident, and the extent of human hunting, farming and other activities.

As already mentioned (section 21.4), in environments where a full range of carnivores has had access to a carcass, very few bones will remain for collection by porcupines. For example, only 4 pieces of rib, 7 bone flakes, a scapula, the skull (complete) and fragments of the left mandible - i.e. 14 fragments in all - remained from the carcass of an old gemsbok male after lions and hyenas had finished with it, though the bush and grass over a 188 yards radius around the kill was thoroughly searched (Hughes 1958, p.113). Kruuk (1972), working on spotted hyenas in East Africa reports that:

a yearling wildebeest was chased for 5 min. by a hyena and died 2 min. after being caught by two hyenas; 7 min. after its death, one of the twenty-one hyenas eating off it ran off with a leg; another 3 min. later only the head and spine were left, and 3 min. more from the time of death there was only a dark spot on the grass..... (p.126)

It is becoming apparent (Brain 1970b) that the pressure exerted by aggressive scavengers and other predators will have a marked effect on the feeding habits and hence the food remains of predators such as leopards. Brain (op. cit. and in preparation) has shown that in areas where leopards are constantly harried by hyenas and other scavengers, extensive damage is done to their prey skeletons which are dragged up into the branches of trees to render them less accessible. In areas where no hyenas or other significant scavengers occur, comparatively little damage is done to prey skeletons. The leopard does not trouble to conceal its kill and eats only a small quantity of meat before moving on to make another (Brain op. cit. p.5). More bones would therefore be available to porcupines in the latter type of environment.

An extreme situation would be one in which all the predators (lion, leopard, cheetah, wild dog and hyenas) and all but the wildest of scavengers have been exterminated. Unfortunately such conditions prevail over large tracts of southern and eastern Africa, where the only 'common' surviving scavenger is the black-backed jackal (Canis mesomelas). Under such

conditions carcasses (mainly from domestic animals) are left to decompose unmolested and the bones left to desiccate undamaged on the veld, unless for health reasons such as the control of stock diseases like anthrax or rinderpest, the carcasses are incinerated or buried. Porcupines operating in such areas, like those occupying the Main and Side Hartebeesthoek Lairs, could obtain bones from such undisturbed carcasses, and also, it would appear, from the midden heaps of nearby human habitations, since some of the bones retrieved from these lairs appear to have been sawn through or otherwise damaged by a human agency. It is probable that more bone is available to porcupines operating in such artificial conditions than is available to porcupines in areas where the fauna is undisturbed. This in turn probably results in a more rapid rate of bone accumulation.

Primitive man is known to operate both as a predator and as a scavenger. Using circling vultures as guides, natives in the Magabeng area of the northwestern Transvaal chase predators or scavengers away from fresh (and even not so fresh) kills and dismember and carry the carcass away for consumption, (A. Boshier, pers. comm, 1972). Similar behaviour has been observed by J.W. Kitching in the Luangwa Valley, Zambia and by the author amongst the !ko Bushmen of western Botswana. Natives, particularly Bushmen, seem relatively oblivious of meat maggots and relish flesh even at an advanced stage of decomposition (Heinz, pers. comm. 1969, personal observations). In the case of either human hunting or scavenging it is unlikely that many skeletal parts will be left lying on the veld. Man would therefore constitute an important factor in bone removal from the veld, rendering it unavailable for collection by porcupines.

During Plio-Pleistocene times, a full range of predators and scavengers as well as australopithecines were present. Between them it is likely that the veld was kept relatively clean of bones. Australopithecine midden heaps, whether outdoor or cavern site, probably formed an important source of bones for porcupines, which prefer dried-out, meat-free bones to fresh ones (see 22.2). These would be collected after the hominid occupants had moved off or gone to sleep.

From the above it can be seen that the availability of bone will vary considerably from area to area and thus the locality of the lair is likely to have some influence on the rate of accumulation of bones within it.

22.1.2 The bone-collecting behaviour of porcupines

The rate at which porcupines accumulate bone apparently does not depend on the quantity of bone already present within the lair. They will accumulate still more if it is available. At the Hartebeesthoek Main Lair, for instance, it was noted that bones continued to be carried into the lair in spite of the presence of a profusion (nearly 200) of previously accumulated bones, many of them only slightly gnawed. Porcupines would thus seem to be compulsive bone collectors, and it would be interesting to observe the outcome of a situation where they were provided with an unlimited bone supply not too distant from their lair.

Fossil porcupines apparently collected bone for the same reason - gnawing - there would be no point in collecting bone if it were not for this purpose. The suggestion that porcupines gnaw bones as a source of calcium 'in order to make quills' (Singer 1959) appears to have no foundation, since quills are modified hairs and thus keratinous (i.e. a protein substance).

22.1.3 The number of porcupines occupying the lair

As already mentioned, regrettably little is known of the biology of these animals, and conflicting reports concerning their social habits and group size exist. Stevenson-Hamilton (1954 p.247) reports that porcupines are solitary in habit, while Astley-Maberly (1967, p.267) says that one to three offspring live with their mother, and Dorst and Dandelot (1970, p.34) report that they live "in pairs or in groups."

In the author's opinion, the number of porcupines which occupy a lair at any given time probably depends upon the size of the lair, the availability of food and the incidence of trapping and killing, and probably varies from time to time. Some lairs certainly seem to house only a single porcupine, others would seem to accommodate several, judging by the amount of porcupine activity evident in the vicinity. Disturbance, snaring, and predation would also account for fluctuations in the lair population.

22.1.4 Difficulty of terrain

Alexander (1956, p.257) discussing the activities of a captive porcupine in laboratory surroundings, reports that the creature took three nights to drag a large (2 kg.) tortoise-shell, by stages, into its den. Since the

animal is only active at night and since it is extremely flat-footed and lacks any ability to climb, difficulty of terrain can be considered a factor, though a minor one, which would influence the rate of accumulation of bone.

22.2 The type of bones preferred by porcupines

A small experiment, designed to test the preference of porcupines for particular bones was undertaken: thirteen ungnawed bones differing in shape, size and degree of freshness, were placed practically in a heap 5 metres from the entrance of a porcupine-occupied disused aardvark burrow. This lair is situated on an eastern Transvaal Lowveld ranch (Morea Estate, P O Klaserie) where bone is normally scarce on account of strict foot-and-mouth control measures. A note was made of which bones disappeared first, and the intention was to excavate the aardvark burrow after a certain time interval to recover the bones (which were marked A to M with an odourless indelible marking pen) to determine whether they had actually been taken into the lair and the degree of gnawing which had taken place. In due course, the bones were all dragged into the lair, although a few were left lying (gnawed) just within the entrance. However, the burrow, which was originally chosen on account of the soft nature of the sand in which it was dug, baked so hard during the three month period that the experiment was running, that spades and picks made little impression on its cement-like surface. Only a few bones, all showing signs of gnawing, were recovered by means of a rake and a walking-stick

The bones and their order of disappearance were as follows:

- A: Complete bovid tibia, defatted. Length 406mm; shape category: large, long, slender
- B: Complete bovid rib, defatted. Length 352mm; shape category: large, long, slender
- C: Complete bovid tibia, defatted. Length 330mm; shape category: large triangular
- D: Complete vulture limb bone, partially defatted at start of experiment. Length 270mm; shape category: medium-sized, long, slender
- E: Complete bovid thoracic vertebra, defatted. Length 276mm; shape category: medium-sized, irregular

- F: Complete bovid calcaneus, defatted. Length 158mm. Shape category: small to medium-sized, short, thick
- G: Complete cervical vertebra, defatted. Length 113mm. Shape category: small to medium-sized, irregular
- H: Rear portion (occiput) of fractured bovid cranium, defatted. Length 85mm; shape category: small, irregular
- I: Complete bovid phalange, defatted. Length 72mm. Shape category: small, short, thick
- J: complete bovid astragalus, defatted. Length 64mm. Shape category: small, compactly globular
- K: Complete bovid patella, defatted. Length 63mm. Shape category: small, compactly globular
- L: Complete bovid carpal, defatted. Length 35mm. Shape category small, compactly globular
- M: Complete bovid metatarsal with phalanges (a hoof attached). Undefined but cracked, initially with strips of partially dried flesh adherent. Length 420mm. Shape category: large, long, slender

- 24/6/72 - bones placed 5m from lair entrance on porcupine 'path'
- 28/6/72 - Day 4. All bones still present. Africans informed us that porcupine had been trapped and eaten
- 22/7/72 - Bones moved to new lair. Placed 3,5m from entrance
- 30/7/72 - Day 8. B(rib) and G (cervical vertebra) missing, E (thoracic vertebra) moved into lair entrance and spine gnawed, C(scapula) gnawed in situ outside
- 19/8/72 - Day 28. A (tibia), C (scapula), F (calcaneus), K (patella) and L (carpal) missing. E (thoracic vertebra) still visible in lair entrance, gnawed
- 31/8/72 - Day 40. H (occiput) and I (bovid phalange) missing, E (thoracic vertebra) now moved right into lair
- 17/9/72 - Day 57. No bones left where originally placed. M (undefatted metatarsal) missing, J (astragalus) and D (vulture limb bone) just visible, deep in lair.

Conclusions:

Porcupines seem to favour large, slender bones and vertebrae. Smaller more compact bones are less favoured. The undefatted greasy bones (D, bird limb bone and M, bovid metatarsal) were ignored till last, by which time

they were practically defatted, on account of lying exposed to sun and all weather for almost three months. The vulture bone, because it was only partially fatty at the start of the experiment, defatted earlier, and may have been ignored because of its light weight, different smell or texture. Clearly this type of experiment could be extended to confirm these preliminary results.

Fig 163

Eight bone flakes from the Makapansgat Limeworks grey breccia.

All, with the exception of the top right-hand specimen which is humeral and the bottom right-hand specimen which is tibial, are derived from metacarpal or metatarsal bones. Flakes resembling these are very rare or absent from the porcupine-accumulated bone assemblages studied, but many thousands occur in the grey breccia. There is no detectable evidence of porcupine-gnawing on any of these well-preserved flakes, but some of them show evidence of localized wear. Typical porcupine damage to metapodals is shown in Figs. 170 and 171; porcupines appear to be incapable of splitting metapodals or any other long limb bones to produce flakes of the type illustrated here.

Fig 164

A further four small pointed bone flakes from the Makapansgat Limeworks grey breccia, the central two broken at the butt end by blasting.

None show any detectable signs of porcupine gnawing but all show signs of localized wear, especially the awl-like metatarsal flake on the extreme right. Pointed and locally-worn flakes such as these are absent from porcupine-accumulated bone assemblages.

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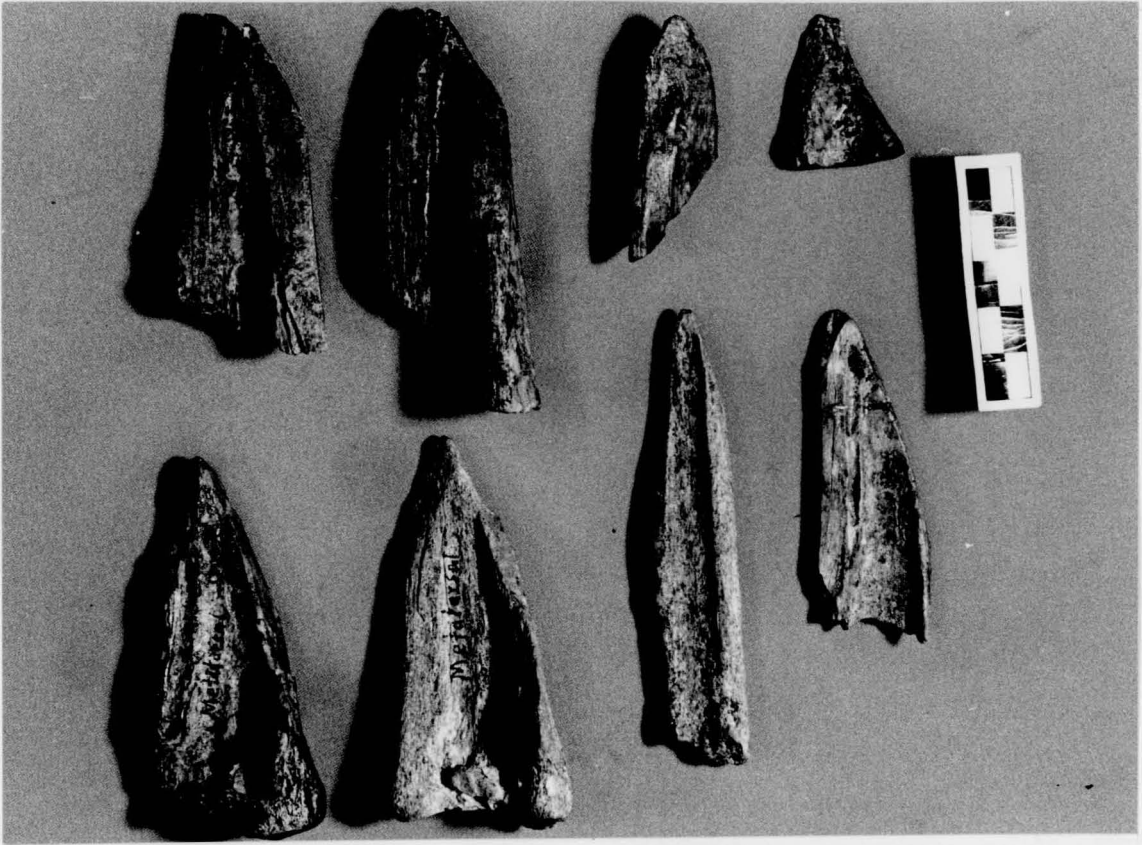


Fig 163



Fig 164

Fig 165

The distal ends of two humeri from the Makapansgat Limeworks grey breccia, both shafts showing spiral fracture.

Such spiral fracturing of the shafts of humeri is extremely frequent in the grey breccia but has not been observed on the humeri recovered from any of the porcupine bone accumulations. The humeri illustrated show no evidence of porcupine gnawing and contrast strongly with the typically porcupine damaged humeri shown in Fig 167.

Fig 166

The distal end of a humerus from the Makapansgat Limeworks grey breccia, its shaft showing spiral fracture.

Note the overall fine wear on the spiral fracture, particularly at the apex which appears to have been 'retouched' on both the visible and the reverse sides by the removal of several very small flakes. Note in this specimen that the sinus of the original spiral fracture appears to have been deepened considerably by strongly localized wear. None of the above-mentioned damage can be attributed to porcupine gnawing.

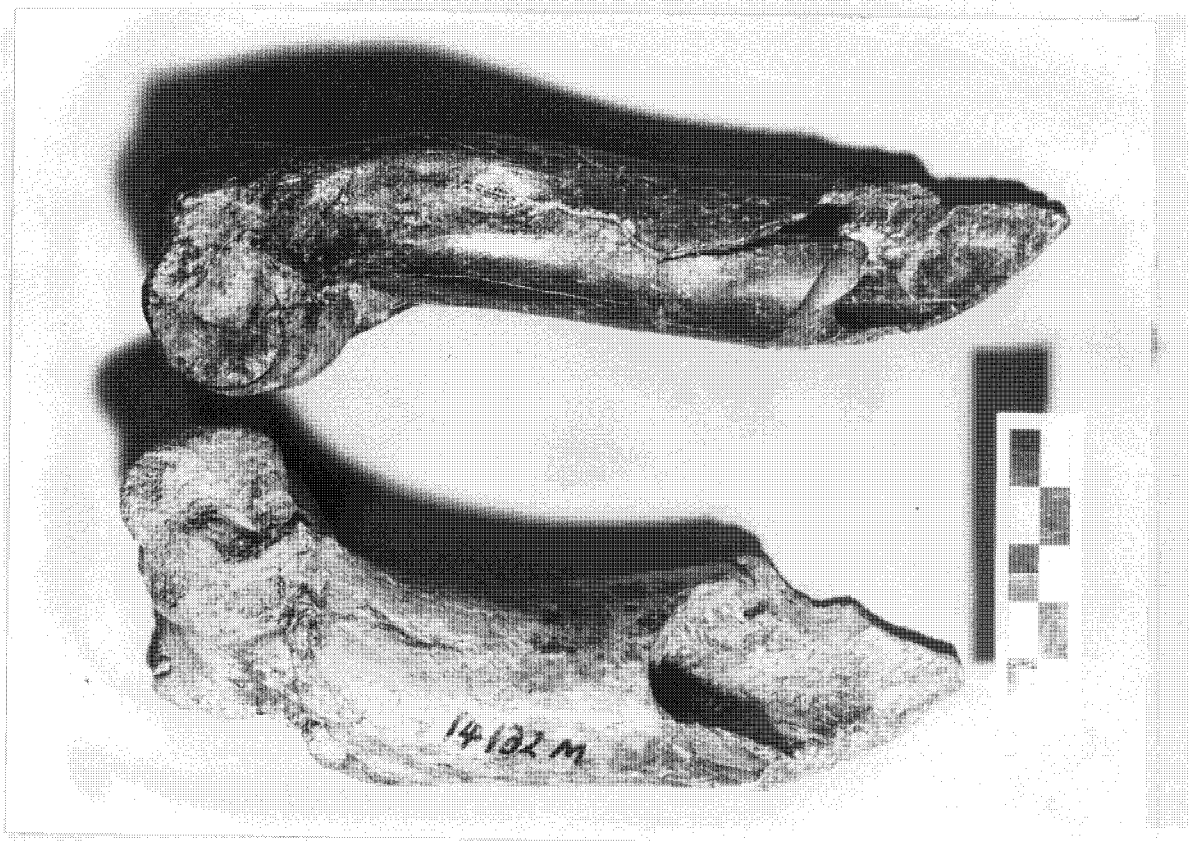


Fig 165

Fig 167



Fig 166



Fig 167

A series of porcupine gnawed humeri from the Hartebeesthoek porcupine lair.

Note that the distal articular ends of the humeri are as prone to destruction by porcupine gnawing as the proximal and that there is no evidence of any fracturing, spiral or otherwise. Note also the irregular 'ragged' shapes resulting from such gnawing damage and the groove-like scars produced by the incisor teeth. These should be compared with the spirally fractured humeri from Makapansgat illustrated in Figs 165 and 166.

Fig 168

The distal ends of three metapodal bones from the Makapansgat Limeworks grey breccia, showing severe damage to the posterior sides of their shafts.

The damage responsible for producing the scoop-like shape of the two specimens on the right has been repetitive, in contrast to the regular spiral fracturing of the humeral shafts shown in Fig 165. The mechanism responsible for this damage would appear to be the same as that which produced the conspicuous depressed fracture on the shaft of the specimen on the left. The distal parts of metapodals damaged in this way occur frequently in the grey breccia, but such damage has not been observed on the metapodal bones recovered from porcupine lairs (compare with Fig 171).

Fig 169

Two longitudinally split metapodal bones from the Makapansgat Limeworks grey breccia.

Note the sharp edges of the fractures in both cases and the absence of any evidence of porcupine gnawing. Longitudinal splitting of metapodal bones was not observed amongst those recovered from porcupine lairs - compare with Figs 170 and 171.

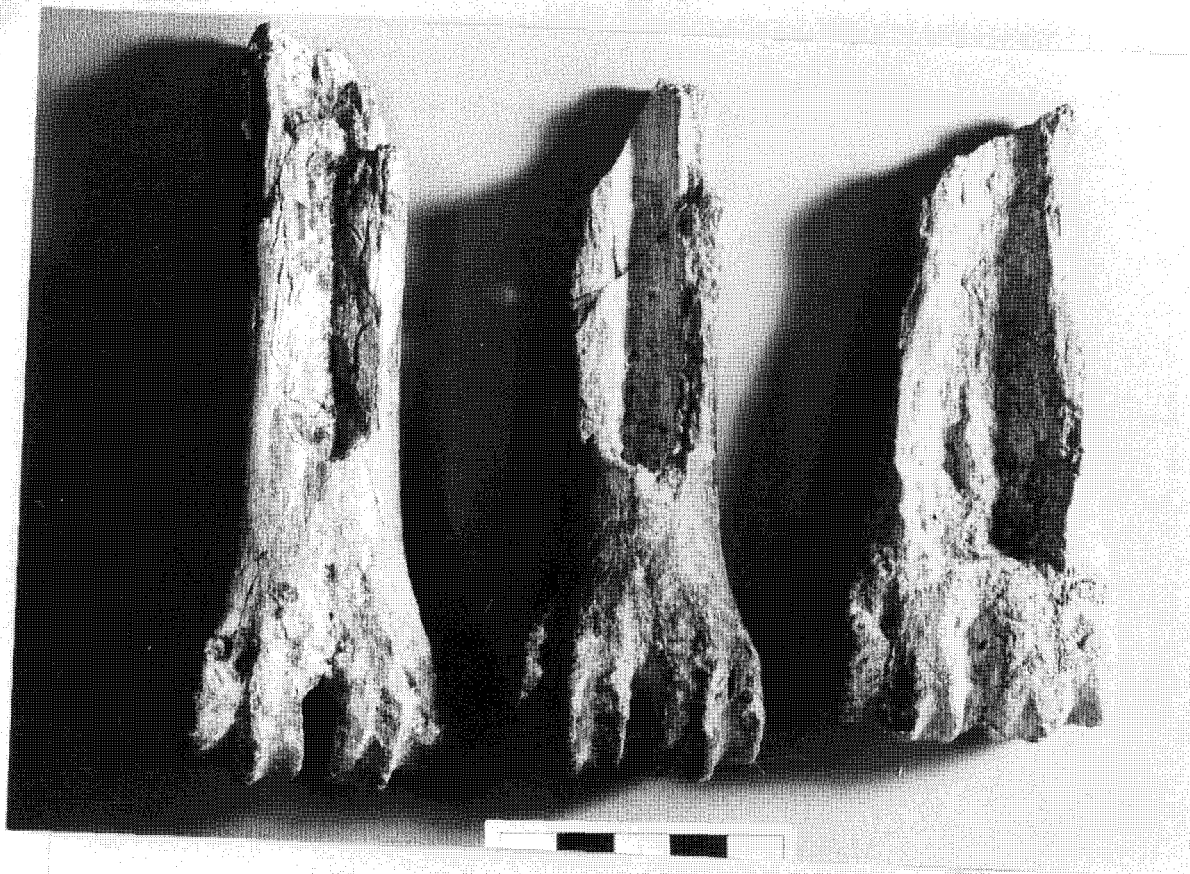


Fig 168

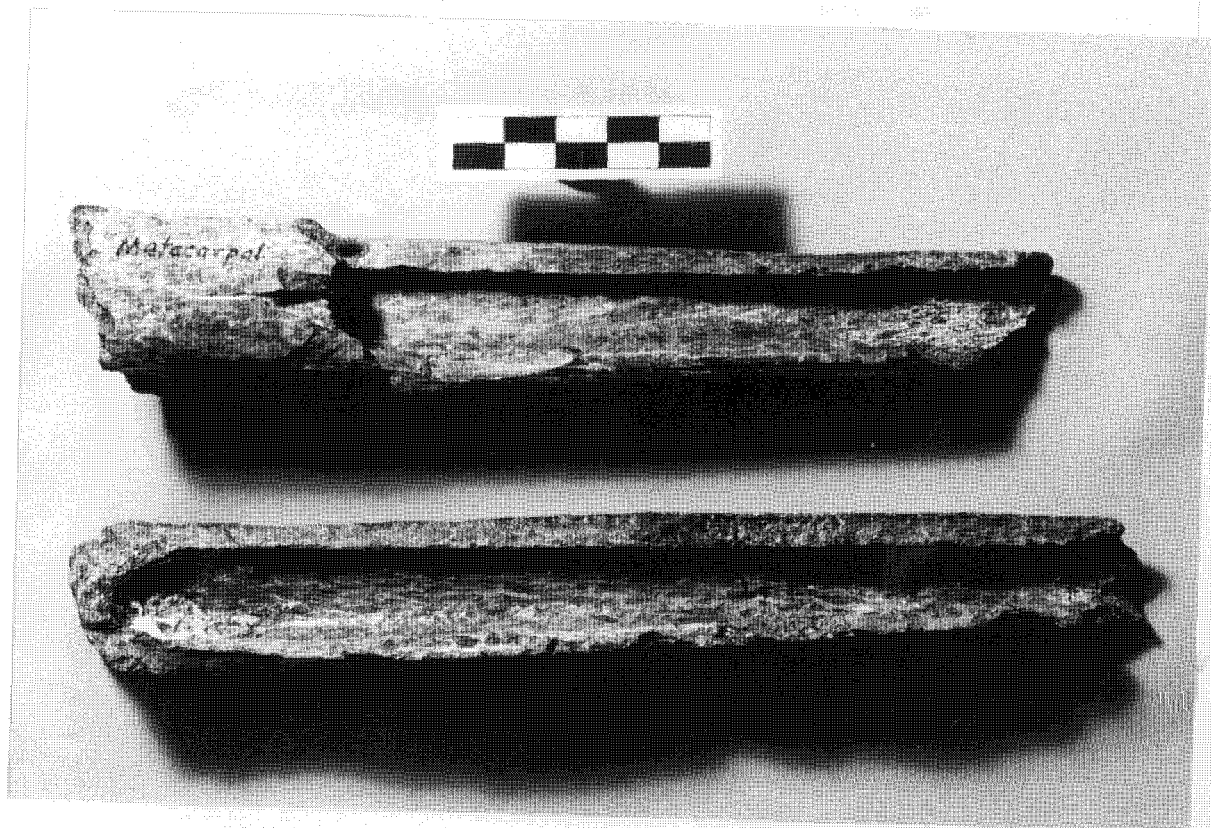


Fig 169

Fig 170

A metapodal bone showing damage caused by porcupine gnawing. Note the continuous and clearly diagnostic nature of the damage, the absence of fracturing and the irregular shape resulting from this damage. These features contrast strongly with those evidenced by the metapodals from the Makapansgat grey breccia, illustrated in Figs 168 and 169.

Fig 171

A series of metapodal bones showing varying degrees of damage by porcupines.

Note again the complete absence of evident fracture, the highly irregular resultant shapes and the diagnostic scars resulting from damage by the incisors. These features are not evidenced in the specimens from the Makapansgat Limeworks grey breccia shown in Figs 168 and 169.



Fig 170

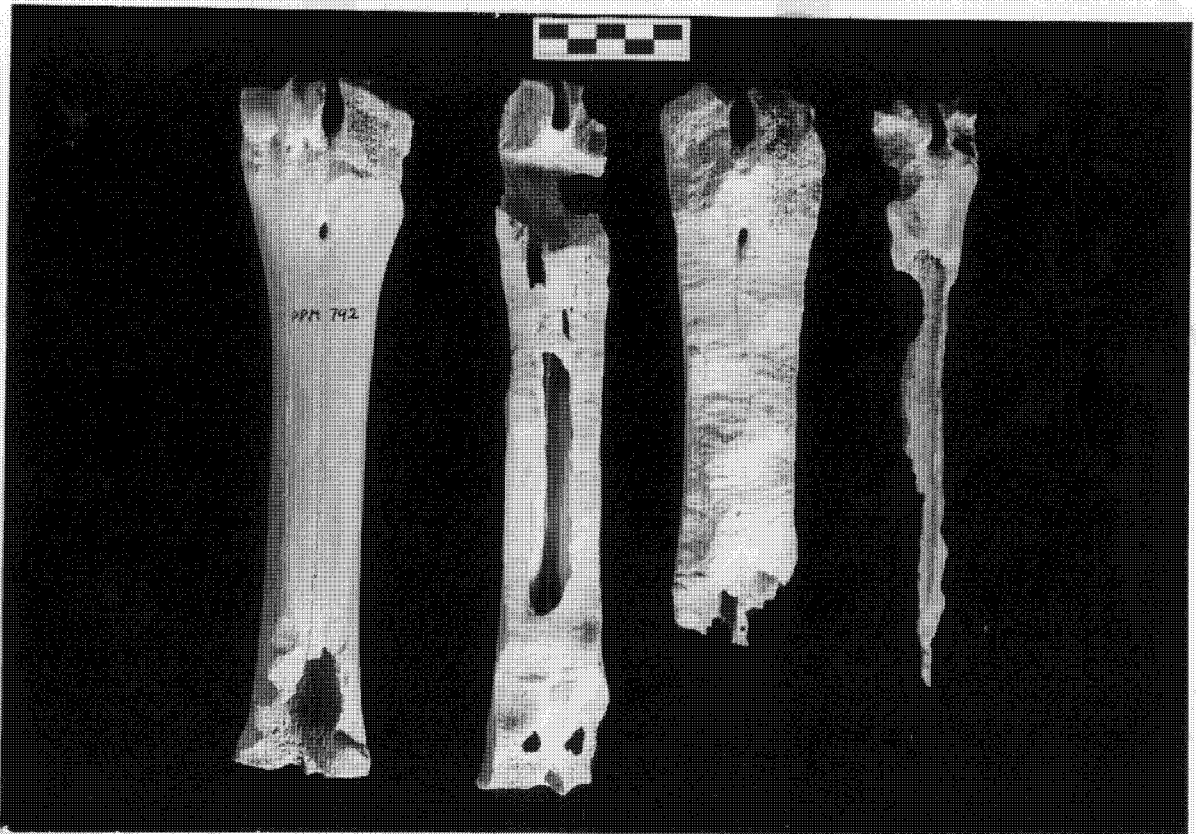


Fig 171

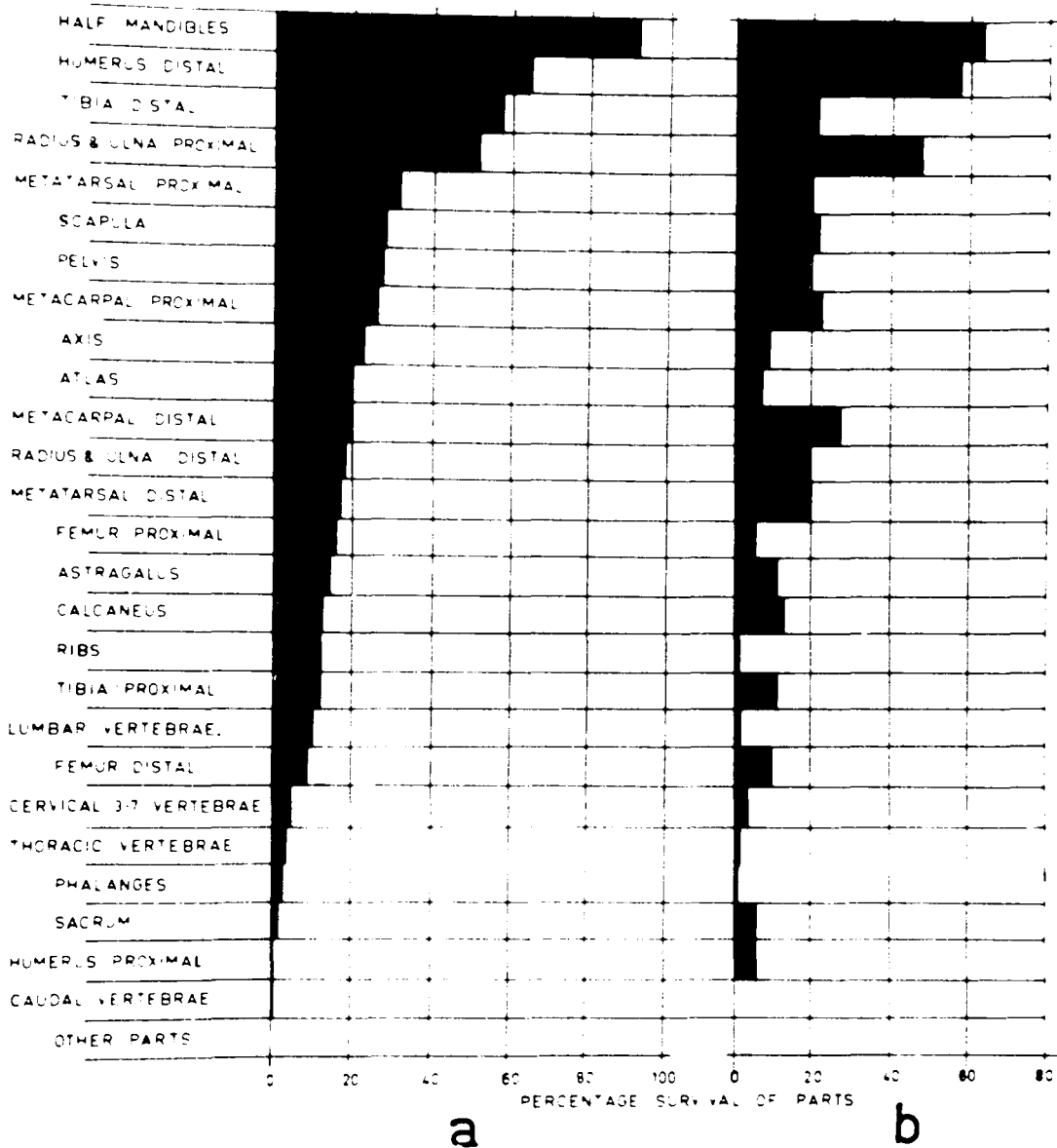


Fig. 172

A comparison of the percentage survival histogram of goat skeletal elements from a Hottentot settlement (a) with the percentage survival of bovid skeletal elements from Makapansgat Limeworks (b) (after Brain 1969 Fig. 4)

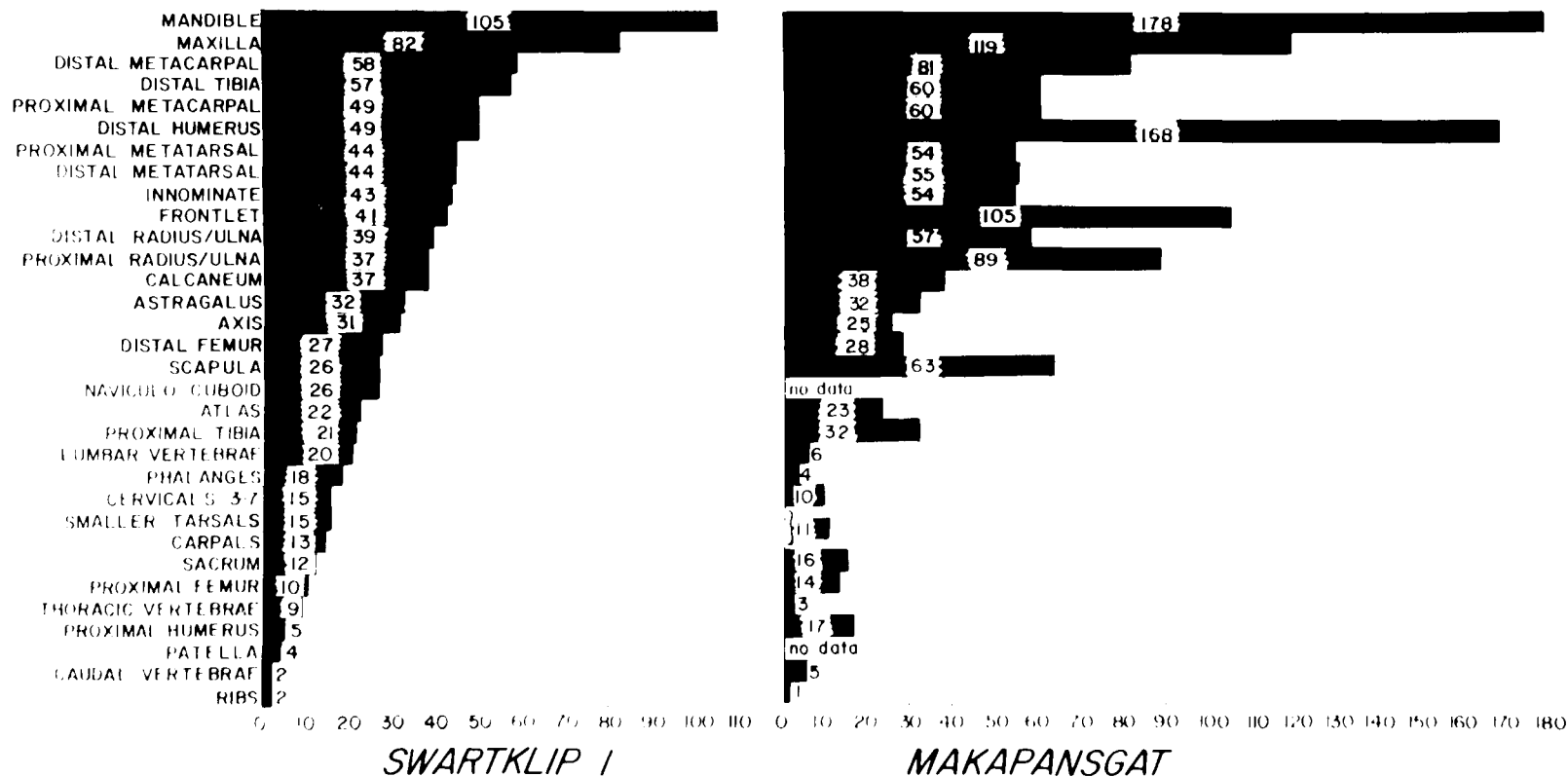


Fig. 173

Histograms used by Klein (1975 Fig. 2) to demonstrate the 'similarity' between the Swartklip I hyena bone accumulation and the Makapansgat australopithecine locality bone assemblage.

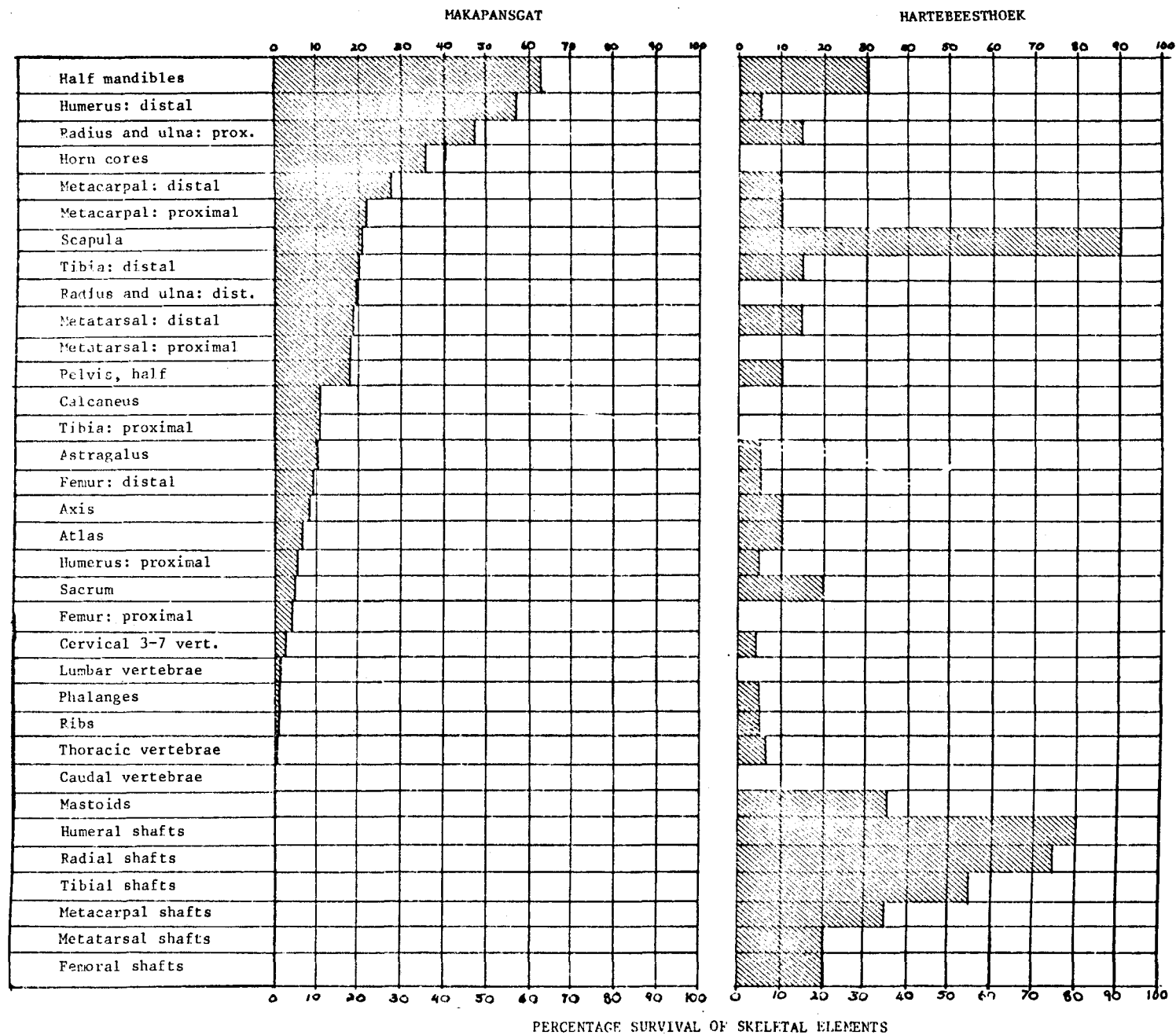


FIG 174

THE PERCENTAGE SURVIVAL OF BOVID SKELETAL ELEMENTS FROM MAKAPANGSAT COMPARED WITH THAT FROM HARTEBEESTHOEK PORCUPINE LAIR.

TABLE XXI

SKELETAL PART DISTRIBUTION OF BOVID REMAINS FROM HAPTEBEESTHOEK LAIR

	SKFLETAL PART CATEGORY	NUMBER	TOTAL
SKULL	horns and horn cores	-	
	cranial fragments	-	
	isolated mastoid regions	7	
	maxillary	-	
	mandibular	6	13
ISOLATED TEETH		24	24
VERTEBRAE	1st cervical (atlas)	1	
	2nd cervical (axis)	1	
	other cervical	4	
	thoracic	9	
	lumbar	-	
	sacral	8	
	caudal	-	
	fragments	13	36
RIBS	complete	8	
	fragmentary	5	13
SCAPULA	complete	3	
	head portion	5	
	fragmentary	10	18
PELVIS	complete	-	
	acetabular portion	2	
	fragmentary	-	2
HUMERUS	complete	1	
	proximal end	1	
	shaft pieces	16	
	distal end	-	18
RADIUS AND ULNA	complete	-	
	proximal ends	3	
	shaft pieces	15	
	distal ends	-	18
FEMUR	complete	-	
	proximal ends	-	
	shaft pieces	4	
	distal ends	1	5
TIBIA	complete	-	
	proximal ends	-	
	shaft pieces	11	
	distal ends	3	14
METACARPAL	complete	1	
	proximal ends	1	
	shaft pieces	7	
	distal ends	1	10
METATARSAL	complete	2	
	proximal ends	-	
	shaft pieces	4	
	distal ends	1	8
ASTRAGALUS	complete	1	
	fragmentary	-	1
CALCANEUM	complete	-	
	fragmentary	-	0
PHALANGES	complete	2	
	fragmentary	4	6
BONE FLAKES AND SLIVERS		55	55
MISCELLANEOUS UNIDENTIFIABLE		27	27
TOTAL			268

23. ANALYTICAL PROCEDURE AND RESULTS

23.1 Analytical procedure

The porcupine bone accumulations were analysed in the following way:

- 1) Specimens which could be referred with certainty to a definite taxon were removed from the sample, and a list of species represented drawn up.
- 2) The minimum number of individuals of each of these identifiable species present was then estimated. Usually, teeth were used, the most frequently occurring tooth class (e.g. left upper third molars) being taken as representing the minimum number of individuals. If degree of wear is considered, the minimum number arrived at in the above way can usually be increased.
- 3) The approximate age at death, judged only as broadly as 'new-born', 'juvenile', 'adult' or 'very old' and using tooth wear, suture-fusion and size as guides, was then assessed for all but the bovid taxa. The latter, on the basis of tooth eruption and occasionally horn-core development can usually be referred to more refined age-classes, for example, one of the seven proposed by Klein (1975 p. 3).
- 4) The remaining specimens which could not be specifically identified were resorted, and those which could be referred to broader taxonomic groupings such as small, medium or large 'suid' 'equid' 'primate' or 'carnivore', or referred to one of the four antelope size categories proposed by Dart (1957 p. 36) were removed. These are as follows:
 - a) LARGE - diameters of long bones exceed 2 inches ($\pm$ 5 cm) in length at both proximal and distal ends; diameters of maxillary tooth crowns in excess of 15 mm; diameters of mandibular tooth crowns 12 - 15 mm.

Dart lists kudu, eland, wildebeest, hartebeest, oryx, roan, sable and buffalo as examples. The domestic cow is considered as belonging to this size category.

- b) MEDIUM - diameters of long bones between 1 and 2 inches (2,54 - 5 cm) at both ends; maxillary tooth crown diameters 12 - 15 mm; mandibular tooth crown diameters from 9 - 12 mm.

Dart lists nyala, impala, bushbuck, springbuck, tsessebe, bontebok, blesbok, lechwe and waterbuck as examples.

- c) SMALL - diameters of long bones less than 1 inch (2,54 mm) at both ends; maxillary tooth crown diameters 9 - 12 mm; mandibular tooth crowns 6 - 9 mm.

Dart lists steenbok, grysbok, klipspringer, reedbuck and mountain reedbuck as examples.

To this list can be added the domestic sheep and goat.

- d) VERY SMALL - maxillary tooth crown diameters less than 9 mm; mandibular tooth crown diameters less than 6 mm.

Dart lists Cape, red and blue duikers as examples.

Brain (1974 p. 2) has proposed four slightly more refined antelope size classes but these, however convenient, could not be used without having to re-classify the 6570 bovid specimens analysed by Dart (1957), because Brain's categories do not coincide with those of Dart.

- 5) The minimum numbers of individuals contributing to each of these broader taxonomic groupings was then calculated, using the most frequently occurring skeletal element; for example, if there were 15 right humeri in antelope category a), or 'Large', and if this number was not exceeded by that of any

other skeletal element category, it was assumed that the remains of at least 15 large antelopes contributed to the bone assemblage. A useful check is to compare the minimum number obtained in this way with the total minimum numbers of bovid species which fall into this size category, based on the identifiable fragments. The size of fragment which can positively be referred to a specific skeletal category depends on the competence of the identifier; the more specimens being dismissed as unidentifiable 'residue' (bone flakes, fragmentary shaft pieces not referable to any skeletal category, and miscellaneous fragments) naturally reduces the potential calculable minimum number of individuals. The present author is of the opinion that even if a specimen falls into the category 'bone flake' as defined by Brain (1974 p. 3 - 'bone flakes (of long limb bones) in which less than half the circumference of the shaft is preserved') it should, if possible, be considered for inclusion in the data on which the minimum number of individuals is to be estimated.

The approximate age at death of the specimens referred to the broader taxonomic groupings is difficult if not impossible to judge.

- 6) The identifiable specimens were returned to the sample to enable its analysis into skeletal part distribution patterns. For each taxon or taxonomic group, the skeletal parts were listed under the headings shown in Table XXI, which has been modified after Dart (1957 Table I) and Brain (1967d Table I). The cranial category 'isolated mastoid regions' has been included because such fragments appear to be usually common in porcupine lairs, probably on account of the intractable gnaw-resistant nature of the mastoid. In the limb bone analyses, a category 'complete bones' has been included for each, because intact bones are frequently encountered amongst porcupine bone accumulations. A category 'miscellaneous unidentifiable fragments' has been included to accommodate unidentifiable bones not falling into the 'bone flake' cate-

gory. The percentage survival of skeletal parts was worked out using Table XXI as a basis.

7) The degree of fragmentation of bone was calculated in the following three ways, although other methods are also available:

- a) The percentage of bone flakes present, as opposed to shaft pieces (both as defined by Brain 1974 p. 8), miscellaneous unidentifiable fragments and larger identifiable bones present. Bone flakes are limited to fragments of the shafts of long limb bones in which less than half the circumference of the shaft is preserved.
- b) The size distribution of the bone flake category, i.e. the number and percentage of bone flakes referable to each of the size categories proposed by Dart (1957 pp. 62, 63). These are: small (less than 6 cm), medium (between 6 and 11 cm) and large (over 11 cm long). Most recent investigators of bone assemblages use much smaller size intervals (1 or 2 cm between each size class) but for the sake of comparison, Dart's subdivisions have been used. Only unbroken flakes should be used for this investigation, freshly broken flakes must be discarded. Dart (op. cit.) further discarded what he termed 'blunt' flakes, measuring only those that were pointed (p. 22, 23).
- c) Average fragment size, using the entire bone assemblage, including bone flakes.

The number of bones per kg was not calculated on account of the difference in weight between mineralized, fossilized bone and fresh but defatted bone.

8) The percentage of gnawed bone was calculated using the entire sample, regardless of specific taxa or taxonomic groups. If the origin of a mark on a bone was at all doubtful, it was not counted in either this category or in any of the following three.

- 9) The percentage of carnivore-gnawed bone was calculated in the same way as in 8).
- 10) The percentage of insect-bored bones was calculated as in 8).
- 11) The percentage of bones showing cut-marks, saw-marks, other butchering damage or decoration of human (or hominid) origin was calculated as in 8).
- 12) The percentage of fired bone was calculated as in 8). Fired bone is characteristic of human bone accumulations of a particular age.
- 13) The percentage incidence of two types of weathering were examined:
 - a) Percentage 'suncracked' bone (this was further subdivided into 'moderately' and 'severely' suncracked).
 - b) Percentage rolled or abraded bone present.The entire sample was considered in each case.
- 14) The nature and distribution of damage by porcupines on the various skeletal elements was examined by gathering all the bones of each skeletal category together and then arranging each category serially, from complete bones to those almost totally destroyed by porcupine gnawing. All bovid bones from all the lairs were included in the serial arrangements. In this way, the process and course of destruction of each bone type could be examined, and those areas vulnerable to damage by porcupine gnawing determined. This information was then compared with the damage described and figured for the corresponding skeletal elements in Dart's Osteodontokeratic monograph.

23.2 Results

23.2.1 The species list and broader taxonomic groupings present, and the minimum numbers and approximate age at death of each present

The results are inconclusive as a consequence of biased samples from almost all the porcupine lairs studied, the bias being due to the disrupted environments in which the lairs were situated. The local naturally-occurring fauna, particularly the carnivora, was absent or radically reduced in each case and mainly domestic animals were available for collection by porcupines (particularly in the case of the Hartebeesthoek lair). The collections thus offer no real grounds for comparison with the Makapansgat grey breccia bone assemblage. However, the species list and approximate minimum numbers of individuals of each from the Hartebeesthoek lair (from which the biggest collection is available)ⁱ⁾ is given as an example, based on the identifiable fragments only:

	<u>Min. no. individuals</u>	<u>Age at death</u>
<u>Primates</u>		
<u>Homo sapiens</u>	1	?
<u>Papio ursinus</u>	1	Adult
<u>Lagomorpha</u>		
<u>Pronolagus crassicaudatus</u>	2	Both adult
<u>Hyracoidea</u>		
<u>Procavia capensis</u>	6	All ages
<u>Carnivora</u>		
<u>Canis domesticus</u>	2	Both very old
<u>Perissodactyla, Equidae</u>		
<u>Equus</u> sp. domestic horse, donkey or mule	2	Adult

i) The Winkelhoek Cave collection has been excluded in this instance as it very definitely represents a 'mixed' human/porcupine bone assemblage.

Bovidae

<u>Bos</u> sp., domestic cow	5	Of mixed age
Bovidae sp. indet, (size class small)	1	Young adult?
Bovidae sp. indet, (size class medium)	1	Young adult?

The indications are thus that the range and size of species collected by porcupines is fairly broad and varied (not as limited as suggested in Method, Chap. 18) but with low minimum numbers of individuals of each species being represented, and with no emphasis on any particular size, weight or age category of animal.

From Makapansgat Limeworks grey breccia, on the other hand, an extensive and very varied list of 61 mammalian species had been described at the time Dart wrote his monograph (1957, see Ewer in Brain 1958 p. 130) and this number has since been substantially added to. Large but rather conservative minimum numbers of many of these species are present; for example 39 large antelope, 126 medium, 100 small and 28 very small (the size categories as defined in 23.1.4), giving a total of 293 bovids (Dart op. cit. Table I). In all, 433 individuals (all species included) were estimated to have contributed to the Makapansgat grey breccia assemblage analysed, a rather different situation to that existing in modern porcupine bone accumulations. Furthermore, Dart (1957 p. 23) mentions that 75 % of the bones and teeth are those of very young animals, the remaining 25 % being derived from very old, senile animals.

23.2.2 The skeletal part representation and percentage survival of skeletal elements

As in the case of 23.2.1, the results of the skeletal part representation analysis are inconclusive in that nearly all the lair contents that were available for study came from areas where the local carnivora had been exterminated, so that mainly complete bones from intact skeletons were available for collection by porcupines. There were thus no initial disproportions in skeletal parts represented, or fractured bones, a situation which would seldom occur in more natural conditions. The situation is not altogether disadvantageous in that the skeletal part analysis will show exactly what disproportions are likely to result when the sole bone-destructive agent is a porcupine.

The skeletal part distribution of the bovid remains from the Hartebeesthoek lair is shown in Table XXI and the percentage survival of skeletal parts calculated from this analysis in Table XXII, contrasted with the percentage survival of skeletal parts calculated for Makapansgat. The percentage survival calculation for the Hartebeesthoek sample was based on a minimum number of 10 individuals, as indicated by the occurrence of 10 left humeri, a number not exceeded by any other single skeletal element. The histograms based on the latter table, shown in Fig. 174a and b, contrast the percentage survival of skeletal parts at Makapansgat with that indicated by the Hartebeesthoek lair contents. A glance at these histograms will show how different the survival patterns from the hominid site and the porcupine lair are.

Bovid horn-cores, cranial fragments and maxillary fragments, are all very common in the Limeworks grey breccia, skull fragments making up 34,5 % of all recognizable fragments at the site. At the Hartebeesthoek porcupine lair assemblage, on the other hand, such fragments (at least amongst the bovid remains) are absent, and the author initially suspected that their absence may have been due to the fact that porcupines were incapable of retrieving bovid crania of the size that would be available in the vicinity of the lair, i.e. cow, although several smaller non-bovid crania (dog, baboon) were present. With the discovery of several bovid mastoids and parts of an adult human cranium amongst the lair contents, it became clear that this was not the case, and the conclusion was reached that

porcupines are capable of collecting large bovid crania, but gnaw them to the extent that they are totally destroyed, with the exception of the very resistant mastoid region. Six mandibles occur (30 % survival) but the total cranial remains (excluding isolated teeth) make up only 4,85 % of the total assemblage as opposed to 34,5 % in the grey breccia.

Amongst the post-cranial remains, the most significant feature of porcupine bone accumulations is the very low percentage survival of any of the articular ends of the long limb bones (proximal and distal ends of the humerus, radio-ulna, femur, tibia, metacarpal and metatarsal) but the relatively high percentage survival of their shafts, which usually remain as intact cylinders, see Fig. 167. At Makapansgat Limeworks, the proximal and distal ends of the long limb bones frequently occur in startling disproportions while shafts, without attached proximal or distal articular ends, tend not to survive at all (see Table XXII), probably on account of being smashed to extract marrow or in the course of tool manufacture. Porcupines appear to be incapable of splitting, spirally fracturing or crushing the shafts of bovid long limb bones (Figs. 167, 170 and 171) while the long limb bones from the Limeworks frequently show spiral fracturing (Fig. 165, 166), crushing (Fig. 168) and splitting (Fig. 169). The percentage survival of scapulae is very high in the Hartebeesthoek lair bone assemblage.

A second striking feature of the Hartebeesthoek porcupine bone accumulation is the low incidence of bone flakes (20,52 %) as opposed to 35,6 % in the Limeworks grey breccia bone accumulation. Even more interesting, only one of the 55 Hartebeesthoek specimens, which by Brain's 1974 definition fall into the bone flake category is a 'pointed flake' such as commonly occurs amongst the grey breccia bones (Figs. 163 and 164). 83,45 % of the bone flakes present at Makapansgat are of the pointed variety, and many show signs of localized wear or smoothing (Fig. 164). Bone flakes are also commented on in section 23.2.3.

Table showing percentage survival of skeletal elements as encountered in the Makapansgat Limeworks grey breccia bone accumulation compared with that encountered in the Hartebeesthoek porcupine lair collection.

SKELETAL PART CATEGORY ¹⁾	MAKAPANGGAT		HARTEBEESTHOEK			
	Number found	Original number	% survival	Number found	Original number	% survival
Half mandibles	369	586	62,9	6	20	30,0
Humerus: distal	336	586	57,3	1	20	5,0
Radius and ulna: proximal	279	586	47,6	3	20	15,0
Horn cores	210	586	35,8	0	20	0
Metacarpal: distal	161	586	27,4	2	20	10,0
Metacarpal: proximal	129	586	22,0	2	20	10,0
Scapula	126	586	21,5	18	20	90,0
Tibia: distal	129	586	20,3	3	20	15,0
Radius and ulna: distal	114	586	19,5	0	20	0
Metatarsal: distal	110	586	18,8	3	20	15,0
Metatarsal: proximal	107	586	18,3	0	20	0
Pelvis, half	107	586	18,3	2	20	10,0
Calcaneus	75	586	12,8	0	20	0
Tibia: proximal	64	586	10,9	0	20	0
Astragalus	61	586	10,4	1	20	5,0
Femur: distal	56	586	9,6	1	20	5,0
Axis	25	293	8,5	1	10	10,0
Atlas	20	293	6,8	1	10	10,0
Humerus: proximal	33	586	5,6	2	20	5,0
Sacrum	16	293	5,5	2	10	20,0
Femur: proximal	28	586	4,8	0	20	0
Cervical 3 - 7 vertebrae	47	1465	3,2	4	50	4,0
Lumbar vertebrae	30	1758	1,7	0	60	0
Phalanges	47	3516	1,3	6	120	5,0
Ribs	66	7618	0,9	13	260	5,0
Thoracic vertebrae	24	3809	0,6	9	130	6,92
Caudal vertebrae	1	4688	0	0	160	0
Mastoids	no data		0	7	20	35,0
Humeral shafts	-	586	0	16	20	80,0
Radial shafts	-	586	0	15	20	75,0
Femoral shafts	-	586	0	4	20	20,0
Tibial shafts	-	586	0	11	20	55,0
Metacarpal shafts	-	586	0	7	20	35,0
Metatarsal shafts	-	586	0	4	20	20,0

1) Arranged in descending order of percentage survival according to that found at Makapansgat

23.2.3 The degree of fragmentation

1. HARTEBEESTHOEK PORCUPINE LAIR

a) Number and percentage of bone flakes present	= 55; 20,52%
Number unbroken flakes	= 55; 100,00%
Number of freshly broken flakes	= 0; 0
b) Size of bone flakes: <u>small</u> (less than 6 cm)	= 17; 30,91%
<u>medium</u> (6 - 11 cm)	= 19; 34,55%
<u>large</u> (11 cm +)	= 19; 34,55%
c) Average fragment size	= 140mm

2. KIMBERLEY PORCUPINE LAIR

a) Number and percentage of bone flakes present	= 6; 27,27%
Number of unbroken flakes	= 6; 100,00%
Number of freshly broken flakes	= 0; 0
b) Size of bone flakes: <u>small</u> (less than 6 cm)	= 3; 50,00%
<u>medium</u> (6 - 11 cm)	= 3; 50,00%
<u>large</u> (11 cm +)	= 0; 0
c) Average fragment size	= 84,5 mm

3. HANGLIP PORCUPINE LAIR

a) Number and percentage of bone flakes present	= 20; 55,56%
Number of unbroken flakes	= 20; 100,00%
Number of freshly broken flakes	= 0; 0
b) Size of bone flakes: <u>small</u> (less than 6 cm)	= 8; 40,00%
<u>medium</u> (6 - 11 cm)	= 11; 55,00%
<u>large</u> (11 cm +)	= 1; 5,00%
c) Average fragment size	= 57,47 mm

4. RAND VAN TWEEDEPOORT PORCUPINE LAIR

a) Number and percentage of bone flakes present	= 19; 38,00%
Number of unbroken flakes	= 18; 94,74%
Number of freshly broken flakes	= 1; 5,26%
b) Size of bone flakes: <u>small</u> (less than 6 cm)	= 5; 27,78%
<u>medium</u> (6 - 11 cm)	= 10; 55,56%
<u>large</u> (11 cm +)	= 3; 16,67%

c) Average fragment size = 111,0mm

5. WINKELHOEK CAVE PORCUPINE LAIR

- a) Number and percentage of bone flakes present = 100; 26,39%
 Number of unbroken flakes = 92; 92%
 Number of freshly broken flakes = 8; 8%
- b) Size of bone flakes: small (less than 6 cm) = 50; 54,35%
 medium (6 - 11 cm) = 37; 40,22%
 large (11 cm +) = 5; 5,43%
- c) Average fragment size = 66,9mm

6. MAKAPANSGAT LIMEWORKS GREY BRECCIA

- a) Number and percentage of bone flakes present = 2552; 35,6%
 Number of unbroken flakes = 1432; 56,11%
 Number of freshly broken flakes = 1120; 43,89%
- b) Size of bone flakes: small (less than 6 cm) = 790; 55,17%
 medium (6 - 11 cm) = 357; 24,93%
 large (11 cm +) = 48; 16,55%
- c) Average fragment size: No information available, but probably
 intermediate between high degree of
 fragmentation at Winkelhoek (small
 average fragment size) and low degree
 apparent from porcupine lairs (large
 average fragment size).

The Hartebeesthoek porcupine lair bone accumulation is remarkable in its low bone flake content - in fact, porcupines appear to be incapable of producing the 'pointed' type of bone flake described and figured by Dart (1957 Fig. 32) and in Figs. 163 and 164 of this thesis, where, at least at one end, the margins of the flake meet at a point where two fractures of the 'spiral' type intersect. According to Behrensmeyer (1973 and 1975), such 'spiral' fractures can only be produced while the bone is still fresh, i.e. still containing a certain amount of fat. Once a bone has become defatted, it tends to develop fine hair fissures which run parallel to the long axis of the bone, with transverse cracks occasionally joining two or more; subsequent fractures are likely to run along these

cracks, resulting in a more rectangular bone flake. As porcupines are known not to favour the collection of fatty fresh bone (section 22.2), it is more likely that the flakes encountered amongst the bones from within their lairs were developed in the latter way. Flakes of the 'pointed' variety would occur if either humans or hyenas were present in the vicinity of the lair. The artificial environments in which the lairs occurred thus also affected the bone flake analysis in that the occurrence of pointed bone flakes is slightly lower than it should be.

23.2.4 The percentage of gnawed bones present

The most characteristic feature of porcupine-accumulated bone assemblages appears to be the high percentage (usually in excess of 75 %) of porcupine-gnawed bone, and the extensive nature of the gnawing damage to most of the bones (Figs 167 and 171). At Makapansgat, on the other hand,

only 11 of these 7,159 fragments appeared to me to carry curious scratchings, holes or porcupine gnawings. These markings, other than those caused by porcupines may be due to water drips, to the implements used by the australopithecines or to the teeth of other animals, but the trifling proportion in which such fragments occur does not indicate that either hyenas or porcupines played a part in accumulating this heap of bones
(Dart 1957 p. 22)

Even if all 11 bones showing marked surfaces were attributed to porcupine gnawing damage, the percentage of gnawed bone would only be 0,15 %. The percentages obtained from the five porcupine lairs is as follows:

1) The Hartebeesthoek porcupine lair:	96%
2) The Kimberley lair:	80%
3) The Hanglip lair:	100%
4) The Rand van Tweedepoort lair:	76%
5) The Winkelhoek Cave collection:	22%

The differences between the first four and the percentage gnawing present at Makapansgat (less than 0,15 %) are very striking.

The Winkelhoek Cave collection, which represents a mixed human/porcupine bone accumulation, occupies an intermediate position.

23.2.5 The percentage incidence of carnivore-damaged bones, insect borings, cut marked bones and pathological specimens

As with 23.2.2., the percentage of carnivore-damaged bones is probably artificially low on account of the disturbed environments in which the lairs occur. The incidence of the above features was as follows:

<u>Carnivore-damaged bones:</u>	1) Hartebeesthoek lair:	= 2;	0,54%
	2) Kimberley lair:	= 4;	22,0%
	3) Hanglip lair:	= 0;	0,0%
	4) Rand van Tweedepoort lair:	= 1;	2,13%
	5) Winkelhoek Cave collection:	= 3;	0,79%

At Makapansgat, carnivore-damaged bones make up less than 0,15 % of the assemblage (see quotation in 23.2.4).

<u>Insect-borings:</u>	1) Hartebeesthoek lair:	= 0;	0%
	2) Kimberley lair:	= 0;	0%
	3) Hanglip lair:	= 0;	0%
	4) Rand van Tweedepoort lair:	= 0;	0%
	5) Winkelhoek Cave collection:	= 0;	0%

Less than 0,15 % of the Makapansgat grey breccia bones analysed by Dart show insect borings - see 23.2.4.

<u>Cut marks, saw marks,</u>	1) Hartebeesthoek lair:	= 7;	1,90%
<u>butchering damage:</u>	2) Kimberley lair:	= 0;	0%
	3) Hanglip lair:	= 0;	0%
	4) Rand van Tweedepoort lair:	= 2;	4,26%
	5) Winkelhoek Cave collection:	= 16;	4,22%

Less than 0,15 % of bones damaged in this way occur in the sample of bones from the grey breccia at Makapansgat.

Pathological specimens:

- 1) Hartebeesthoek lair: 0%
- 2) Kimberley lair: 0%
- 3) Hanglip lair: 0%
- 4) Rand van Tweedepoort lair: 0%
- 5) Winkelhoek Cave collection: 0%

Dart (op. cit. p. 22) records less than 0,15 % of pathological specimens in the Makapansgat grey breccia bone accumulation. The present author has noticed the presence of several further pathological specimens but the percentage present would probably not exceed 1 %.

23.2.5. The incidence of fired bone.

Fired bone was absent from all porcupine lairs studied and was encountered only in the Winkelhoek Cave collection where the specimens involved obviously came from hearth areas in the open cave in front of the low porcupine recesses.

23.2.6 The incidence, nature and severity of weathering on bone.

The results of the analysis of the nature and severity of weathering on the bones from the porcupine lairs and on a randomly selected sample of 200 from the Makapansgat Lime-works grey breccia were as follows:

	SUNCRACKING	OTHER WEATHERING e.g. ROLLING ABRASION
1. Hartebeesthoek porcupine lair	28,0%	2,4%
2. Kimberley porcupine lair	23,0%	0,0%
3. Hanglip porcupine lair	62,0%	0,0%
4. Rand van Tweedepoort porcupine lair	30,0%	0,0%
5. Winkelhoek Cave porcupine lair	10,0%	3,0%
6. Makapansgat Grey Breccia	9,7%	12,6%

23.2.7 The nature and distribution of porcupine damage on each skeletal element type:

This analysis was conducted mainly on the Hartebeesthoek collection, where damage by other bone-damaging agents could be disregarded.

Crania:

Bovid crania, either complete or fragmentary, of a size which would match the post-cranial elements present were absent; 7 mastoid bones only being represented. However, numerous large isolated bovid maxillary teeth (many of them gnawed) and many large, almost complete bovid half-mandibles were present, indicating that large crania are collected but gnawed to total destruction with the exception of the resistant mastoid. The crania of a dog, a baboon, several dassies, a rock hare and a human, indicate that the siting of porcupine gnawing appears to be random and widespread. Cranial fragments of the type described by Dart (op. cit.) as picks or digging tools (mainly horn-cores with small adherent portion of crania, Dart op. cit. Figs. 34, 35, 36 and 37 and Text Figs. 17, 18, 19 and 20), daggers (Dart op. cit. Text Fig. 21), 'chalices' or bowls (Fig. 17) and maxillary scrapers (Figs. 38, 39, Text Fig. 22) were absent from any of the porcupine lairs studied. A gnawed cow's horn only was found (Rand van Tweedepoort lair).

Mandibles:

The symphyseal region and ascending ramus are the first to be destroyed by gnawing. The body of the ramus is the next to go, the mandibular teeth being shed as the sockets are penetrated by gnawing. The roots of these teeth frequently show gnawing damage. The angle of the jaw frequently remains till last.

At the stage where the symphysis and ascending ramus have been destroyed by gnawing the mandible looks somewhat like the mandibular fragments described by Dart as saws (1957 Fig. 41) except that instead of clean fractures demarcating the points of attachment of the ascending ramus and symphysis, gnawing damage is apparent, as well as on the periphery of the entire fragment.

Vertebrae:

Unlike in the Makapansgat Limeworks grey breccia bone assemblage, the atlas and axis vertebrae in the Hartebeesthoek lair assemblage do not show a higher percentage survival than the other cervical, thoracic, lumbar or sacral vertebrae, but as in the australopithecine deposits, caudal vertebrae are absent. The neural spine and transverse processes appear to be particularly prone to destruction by gnawing, after which the centra and articular zygapophyses tend to disappear. The end result is a highly irregular, almost unrecognizable fragment. These are far smaller and more irregular than those figured by Dart (1957, Fig. 14 - 16) from the Limeworks.

Ribs:

The articular and distal extremities of the ribs appear to be particularly prone to gnawing attack, but the body of the rib is also frequently gnawed. Once gnawing has penetrated the bony anterior and posterior edges of the ribs, the rib tends to split longitudinally, giving rise to very thin small fragments which appear to be too small to be 'handled' by porcupines for further gnawing, as such fragments commonly occur amongst the bony contents of porcupine lairs. Dart does not mention the use of ribs as Osteodontokeratic tools.

Scapulae:

Like crania, scapulae do not resist total destruction due to porcupine gnawing. Unlike in the grey breccia bone assemblage, the head portion of the scapulae does not survive better than

the rest of the blade in porcupine bone accumulations; in fact, paper-thin fragments of the flat part of the blade (which the porcupine probably finds unsatisfactory or impossible to gnaw), are the most commonly encountered type of scapular fragment. On the whole, the compact head portion of the scapula tends to be destroyed first. Fossil scapular fragments from Limeworks are figured in Dart op. cit. Fig. 19; these appear very unlike those retrieved from porcupine lairs in that the latter normally show gnawing scars around the entire periphery.

Pelves:

As in the Limeworks grey breccia bone assemblage, the head portion of the pelvis tends to survive in porcupine bone accumulations, but the remainder is largely destroyed by gnawing. Pelvic fragments very like those figured by Dart (1957 Fig. 18) are encountered in porcupine lairs, but these normally have a more irregular outline and show numerous gnawing scars.

The long limb bones: humerus, radius and ulna, femur, tibia, metacarpal and metatarsal.

Gnawing damage of the long limb bones appears to follow the same course regardless of limb-bone type. First, the proximal and distal articular ends are destroyed. In the case of the humerus, even the very resistant and dense bone of the distal articular end does not withstand gnawing attack (see Fig. 167 extreme left) although the spongier proximal articular end tends to disappear first. The distal ends of the metacarpal and metatarsal bones, however, do appear to be somewhat more resistant than the proximal ends (Fig. 171).

In all limb bones, gnawing proceeds down the shaft from both ends, usually leaving the shaft intact and unsplit (Fig. 169). The end result is often a bone which is shaped like a serviette ring, with gnawing scars round each circumference. Occasionally, the shaft may split along two or

more sun-crack fissures, resulting in 'bone flakes'; these are also gnawed until they become too small for a porcupine to handle, resulting in bone flakes which are gnawed around their entire margin.

Spirally fractured humeri (in which the shaft is broken by means of a 'spiral' fracture, Fig. 165, 166), split shafts (Fig. 169) and crushed and 'pulped out' metapodal shafts (Fig. 168) such as described by Dart as damage resulting from the manufacture of osteodontokeratic tools was not encountered in any of the porcupine lair contents studied.

Astragali, calcanei and phalanges:

Gnawing occurs randomly over the surfaces of all of these bones, which seldom occur split.

Bone flakes:

As mentioned in 23.2.2 and 23.2.3, very few bone flakes occur in porcupine lair bone accumulations and of those that do, still fewer are of the 'pointed' or 'spirally fractured' variety illustrated in Figs. 163 and 164. Such bone flakes from the Limeworks grey breccia frequently display localized wear or smoothing, e.g. Fig. 164, extreme right. Porcupine lair 'bone flakes' normally result from the spontaneous splitting along suncrack fissures of the shafts of long limb bones whose articular ends have been destroyed by gnawing, the length of the flake being determined by the extent to which the shaft had been gnawed before splitting occurred.

The gnawing damage to the various skeletal elements encountered in porcupine lairs appears to be very different from that demonstrated by Dart for the corresponding elements from the grey breccia.

24. SUMMARY, CONCLUSIONS AND DISCUSSION

24.1 Summary.

1. The background to the question of the bone accumulating agent responsible for the very extensive Makapansgat Limeworks grey breccia bone assemblage has been outlined. The question of the mode of origin of the 'Osteodontokeratic tools' described by Dart (1957 and elsewhere) from this assemblage has been reviewed.
2. The various means by which bones may become incorporated in cave deposits have been discussed.
3. A method for analysing bone accumulations (porcupine bone accumulations in particular) has been suggested.
4. The habitat preferences of porcupines and the appearance of their lairs has been investigated and described.
5. Means by which a lair may be identified as a porcupine lair or otherwise have been discussed.
6. The numerous problems associated with the study and retrieval of collections of bone from porcupine lairs have been outlined.
7. The rate of accumulation of bone within porcupine lairs and the type of bone preferred for collection have been investigated.
8. The introduced contents of five porcupine lairs have been analysed in order to ascertain whether:
 - (a) Fossil porcupines could have been the bone-accumulating agent responsible for the accumulation of the Makapansgat Limeworks grey breccia bone assemblage.
 - (b) Fossil porcupines could have produced any of the bone tools described by Dart (op. cit.) and attributed to australopithecine manufacture.

24.2 Conclusions

1. The habitat preferences of porcupines and the appearance of their lairs

The recent southern African porcupine, H. africae australis, appears to have a very widespread distribution, occurring in almost every type of country, whether wet (e.g. Drakensberg, up to altitudes of 2440m; rainfall 1780mm) or dry (e.g. Kalahari; rainfall less than 254mm), provided sufficient cover and suitable food is available. Diet, however, does not appear to be a very restricting factor, as porcupines eat a wide range of underground roots, tubers, corms and bulbs as well as curcubit fruits, seed pods and other fallen fruits and agricultural crops of all kinds. The occurrence of a fossil form of H. africae australis in the Makapansgat Limeworks breccias (Members 3, 4 and 5) therefore does not suggest much with regard to palaeoenvironment. The ecological preferences of H. makapanensis, a second species of Hystrix from the Limeworks deposit (Members 3 and 4 only) can be assessed only on the basis of its preserved morphology, and as the remains of this species are decidedly scant and fragmentary, this has been difficult. Its ecological preferences would appear to be similar to those of H. africae australis, except that its slightly more brachydont, better rooted teeth suggest a somewhat softer diet than that preferred by the latter species. This suggests no more than an environment providing niches for both species, which would not have to be very different from that of the present day. The third fossil hystricid present in the Limeworks breccias, the giant form Xenohystrix crassidens, (Members 3 and 4 only) is very probably adapted to forest conditions. This suggests that during the accumulation period of the grey breccias and at least part of the overlying pink breccia, the evergreen tropical forest which today is so restricted in the Makapan valley as to be termed 'relict', was more widespread, perhaps occupying the entire Cave of Hearths and Swartkrans 'arms' of the Makapan valley and spreading onto the floor of the main valley along the stream banks. The presence of a substantial forest during pink breccia and particularly grey breccia times is also indicated by the cercopithecoid fauna (Eisenhart 1974). The fewer numbers of both forest loving cercopithecoids and of Xenohystrix in the pink breccia (both are commoner than their savanna-loving counterparts in the

Eisenhart, W.L. (1974) The fossil cercopithecoids of Makapansgat and Sterkfontein. Harvard College, Faculty of Arts.

underlying grey breccia) probably indicates shrinkage of the forest environment, culminating in their extinction by the time the Phase II breccia (Member 5) was being deposited. The smallest of the three Limeworks porcupines, H. africae australis, is the only species encountered in the Phase II breccia and has survived to the present day.

The type of lair preferred by porcupines is apparently very low, dark and almost invariably inaccessible to humans. In most cases, the rock lairs encountered would have been inaccessible to larger carnivores such as hyenas, wild dogs and leopards as well. Earth burrows, such as disused aardvark burrows, are usually only accessible to humans after extensive digging. More open caves, such as those suitable for human occupation, were not seen to be used, but very low dark passages leading off the rearmost recesses of these are frequently used, if humans are not in occupation; for example the Historic Cave and Makapansgat Limeworks underground excavation at the present day. It is therefore probable that fossil porcupines occupied low recesses leading off the ancient Limeworks australopithecine cavern during periods when australopithecines or large carnivores were not in residence. It is also likely that they gnawed some of the bones left behind by other occupants of the cave and even contributed a few of their own accord. However, porcupine occupation could not possibly explain the large volume of ungnawed but otherwise damaged bone. Their contribution to the bone accumulation appears to have been minimal.

2. Problems associated with the study of bone accumulations from porcupine lairs

The main problems are:

- a) Finding lairs in ecologically undisturbed areas. Even in game reserves, predators are usually restricted and the human element is absent or very rigidly controlled (section 21.4)
- b) Access to lairs and retrieval of bones from within. Lair are often dangerous if not impossible to collect from (section 21.1)
- c) Contamination by other bone-accumulating agents (section 21.3)

3. The rate of accumulation of bone within porcupine lairs and the type of bone preferred by porcupines

Further experimentation is required for both of these aspects. However, five collections made at approximately yearly intervals from a lair in which probably no more than two porcupines were living indicated an accumulation rate of 42 bones per annum. This rate is affected by the availability of bone in the area and the number of porcupines occupying the lair (section 22.1).

The experiment on the type of bones preferred by porcupines indicated a preference for large limb bones and vertebrae. Fatty fresh bone held no appeal, although dried flesh and almost completely defatted bone is acceptable. Bird bones are not favoured.

4. The results of the analysis of the introduced bony contents of porcupine lairs

- a) The species list and broader taxonomic groupings present, the minimum numbers of individuals of each present, and their approximate age at death

The results of the analysis of the above points were inconclusive in that the samples of porcupine-accumulated bones studied come from lairs situated in regions where the local naturally-occurring fauna, particularly the carnivora, has been exterminated. The range of species available for collection is thus far more limited in number and variety and consists mainly of domestic animals. However, the results indicate that porcupines will collect whatever bone is available, from skeletons ranging in size from dassie and red rock hare to domestic cow and horse. The minimum number of individuals of each species present was low (six or less) and their age at death was random, both very young and very old specimens being present.

- b) The skeletal part representation and percentage survival of skeletal elements

The skeletal part survival pattern in porcupine-accumulated bone assemblages is very different from that demonstrated by Dart's analysis of the Makapansgat Limeworks grey breccia bone accumulation. The most striking differences were the almost total absence of either proximal or distal articular extremities from any of the long limb bones retrieved from

porcupine lairs, whereas certain of these articular extremities from the Limeworks showed a high percentage survival. Intact shafts of the long limb bones, which are extremely rare in the Limeworks assemblage, show a high percentage survival in porcupine bone accumulations. The most common type of limb bone fragment in porcupine lairs is thus an intact cylindrical shaft with both articular ends absent, their points of attachment marked by gnawing scars. This type of fragment was not encountered amongst the Limeworks assemblage.

A second striking feature is the lower incidence of bone flakes from porcupine lairs (20,52%) as opposed to 35,6% from Limeworks. Very few (less than 1%) of these flakes are of the pointed, spirally-fractured variety common in the Limeworks, and it is obvious that the bone flakes present in porcupine lairs have been produced in a different way from those in the Limeworks. Bone flakes are further commented on in the subsequent section.

The differences in the survival patterns are so strikingly different that it appears unlikely that fossil porcupines were the prime bone-accumulators involved at Makapansgat. The Hartebeesthoek lair contents were particularly useful in this respect in that the influence of carnivores on the survival pattern could be disregarded, because they are absent from the vicinity of the lair.

c) The degree of fragmentation

This investigation did not give a very clear result. The percentage of bone flakes (of the total number of bone fragments collected) ranged from 20,52% (Hartebeesthoek lair) to 55,56% (Hanglip lair). The percentage at Limeworks is 35,6%. The high percentage at Hanglip is most probably due to the scarcity of bone available for collection by porcupines; the local farmers inter or burn all domestic carcasses. The few bones available are very extensively gnawed and most of the shafts of the limb bones have split along natural drying cracks and fissures to become bone flakes. The absence of larger more intact specimens has led to the higher percentage of bone flakes present, while the extensive gnawing has resulted in a low average fragment size (57,47mm). The relatively high percentage obtained for the Rand van Tweedepoort lair is probably due to the fact that porcupines were collecting bone flakes from human occupation sites nearby. The surprisingly low percentage of bone flakes obtained for the Winkelhoek cave porcupine lair, which is a low rocky passage leading

off a large open cave once occupied by Bushmen, is probably due to the fact that larger more easily identifiable bones and teeth were selectively collected while smaller, more insignificant fragments and bone flakes were ignored (the collection was made on behalf of the author by a farmer friend). The most striking feature about the flakes from the porcupine lairs was that none of them (with the exception of one or two from the Winkelhoek lair, which were probably collected from the human occupational debris) are of the pointed variety, where at least at one end of the flake, the margins meet by means of two intersecting curved fractures of the 'spiral' type. Such spiral fractures are usually apparent even after a substantial amount of gnawing has occurred. Pointed flakes on the other hand, some of them locally smoothed or worn, are a feature of the Limeworks grey breccia assemblage, and also, it appears, of human occupation sites (Beaumont, pers. comm.). The blunt square-tipped flakes found amongst porcupine bone accumulations have obviously been produced in a different manner - this has been explained in section 23.2.3. Porcupines therefore did not produce the bone flakes present in the grey breccia.

Flake size is apparently also affected by the local availability of bone as well as by the size of the animal to whose skeleton it once belonged.

Average fragment size is apparently also affected by the local availability of bone - if this is scarce, the individual bones will be very extensively gnawed, resulting in small fragments. On the whole, the average fragment size tends to be large in porcupine bone accumulations; 140mm for the Hartebeesthoek lair, 111mm for the Rand van Tweedepoort lair and 84,5mm for the Kimberley porcupine lair. The average fragment size for the mixed human/porcupine Winkelhoek bone accumulation is only 66,9mm.

d) The percentage gnawed bone present

The high percentage of gnawed bone present is the feature most characteristic of porcupine bone accumulations - the percentages for the four 'pure' porcupine bone accumulations were all high, ranging from

76% (Rand van Tweedepoort lair) to 100% gnawed (Hanglip lair). The local availability of bone does appear to affect the percentage of bones that are gnawed to some extent, collections from lairs in regions where bone is plentiful showing somewhat lower percentages of gnawed bone (e.g. Rand van Tweedepoort, 76%) than collections from lairs where bone is scarce (e.g. Hanglip, 100%). However, the extent to which individual bones are gnawed is more noticeably affected by bone availability, bones from lairs where bone is in short supply frequently being gnawed to small fragments (e.g. Hanglip, average fragment size 57,47 mm) whereas bones from lairs where bone is freely available are often only slightly gnawed and left almost complete and new bones are collected (e.g. Rand van Tweedepoort lair, average fragment size 111,0 mm, see section 23.2.3). The author is of the opinion that if the percentage of gnawed bone drops below 70% and if gnawing is extensive on only a small proportion of the bones present, the presence of an additional bone accumulating mechanism should be suspected.

It is highly improbable, even provided with an inexhaustible supply of bones, that fossil porcupines living in the ancient Makapansgat Limeworks would have collected 7,159 bones (the total number of prepared fossil bone specimens from Limeworks now exceeds 250,000) and gnawed less than 0,15% of them. It is equally improbable, bearing in mind the superb state of preservation (except for fracture) of most of these bones, that some form of weathering could have destroyed all traces of gnawing off any sizeable porportion of them, as has been suggested. It is more likely that the less than 0,15% of not very extensively porcupine-gnawed fossil bones (fig. 155) from the grey breccia represent an insignificant contamination in the large bone accumulations of some other bone accumulating agent or agents.

e) The percentage of carnivore-damaged bones, insect-bored bones cut-marked bones and pathological specimens present

i) Carnivore-damaged bones

The incidence of carnivore-damaged bones is low at all the porcupine lairs studied (less than 2,13%) with the exception of the Kimberley lair (22,0%) where it was apparent that most of the bones collected had come from one animal, a large hare, which appeared to have been killed by a carnivore of some sort. It is possible, even probable, that many carnivore gnaw-marks are obliterated by porcupine-gnawing, but even amongst the bones practically undamaged by gnawing from porcupine lairs where bone was in abundant supply, carnivore-damaged bones did not figure prominently. Little can be said about the absence of carnivore-damaged bone from a porcupine bone accumulation; an abundance of such bones would perhaps suggest much carnivore activity in the vicinity of the lair, and possibly even contribution to its contents by carnivores.

ii) Insect borings

Insect borings on bones, such as those produced by carrion beetle larvae, were not encountered amongst the contents of any of the porcupine lairs studied. Their presence would suggest that decomposing flesh, attractive to carrion beetles, once covered the bones which bear such marks. The experiment on the bone preferences of porcupines (section 22.2) has demonstrated that fresh undefatted bone is not favoured for collection by porcupines; those covered with flesh or decomposing flesh would be even less attractive. The absence of bones damaged by carrion beetle larvae from their lairs is therefore not surprising. The presence of somewhat less than 0,15% of insect-bored bones from the Limeworks grey breccia probably indicates that

occasionally, bones covered with flesh were brought into the cavern, discarded, and the meat left to decompose. Such a situation is unlikely to occur in a lair occupied by hyenas, which would consume all available meat. Leopards are known to be fastidious about the fouling of their lairs with any odouriferous material (Turnbull-Kemp 1967 p. 35) but flesh-covered bones might frequently drop to the base of a tree into which a leopard has dragged a kill. If such a tree happens to be growing in the catchment area near the top of a shaft type entrance to a dolomitic cavern, a situation which Brain (19706) has reconstructed for Swartkrans, flesh-covered or partially flesh-covered bones could be funnelled into the cavern deposit. Such bones are prone to carrion beetle attack. The presence of insect-bored bones can thus be explained in a number of ways.

iii) Cut marks, saw marks, butchering damage

The incidence of such marks was low in all procupine bone accumulations studied (0% - 4,22%), the highest of these low percentages being associated with porcupine bone accumulations from lairs where human bone accumulations were accessible (e.g. Winkelhoek lair, 4,22% and Rand van Tweedepoort lair, 4,26%) and probably used by the procupines as a source of bone. A high incidence of such marks is characteristic of human bone accumulations.

iv) Pathological specimens

These were absent from all the lairs studied. The Makapansgat grey breccia contains approximately 1% (probably more) of pathological specimens, indicating that disabled animals were exploited when encountered. The presence of pathological specimens in an accumulation is not very informative with regard to its accumulating agent, since all predators, including humans and hominids, exploit handicapped animals.

f) The incidence of fired bones

Fired bone was absent from all but the Winkelhoek Cave porcupine lair, the presence of such bones in the accumulation being due to its close proximity to the human bone accumulation in the adjacent Winkelhoek Cave, from a hearth in which it was it was probably removed. High percentages of gnawed bone are indicative of human bone accumulations of approximately 250,000 years B.P. and younger.

g) The incidence nature and severity of weathering on bone

Fairly high percentages of mildly suncracked bone are characteristic of procupine accumulations. Bones weathered by other means are rare. In the Makapansgat Limeworks grey breccia bone accumulation, however, sun-cracked bone is less common but bones weathered by other means (rolling, other abrasion and possibly chemical weathering) are far more common. This probably has something to do with the means by which the bones in the grey breccia have been concentrated in the lowermost rear recesses of the Limeworks cavern, a means which has not yet been determined. The vast majority of the bones in the grey breccia do not show suncracking, and it is probable that they were introduced into the cavern in the un-defatted, fresh state, left to dry and defat slowly, at which time they developed a few widely-spaced longitudinal fissures, such as are normal when bones defat, dry out and contract. Some of the bones collected by procupines apparently have been lying on the veld for some time prior to collection.

h) The nature and distribution of procupine gnawing damage on the various skeletal elements

An examination of Figs. 163 to 171 will demonstrate how different porcupine damage on the various skeletal elements is from that apparent in the bones from the grey breccia. It is impossible that porcupines could have been responsible for any of the damage on the bones referred to as tools by Dart (1957 and elsewhere). Spiral fracturing of the shafts

of long limb bones and the production of pointed spirally-fractured flakes, both types of fracture common amongst the bones of the grey breccia, appears to be impossible for porcupines. Some other agent has therefore been responsible for the production of the specimens referred to as osteodontokeratic tools.

To sum up, fossil porcupines appear to have contributed only minimally to the very extensive accumulation of bones in the Makapansgat Lime-works grey breccia, the gnawed bones present representing an insignificant contamination in the accumulation of some other agent or agents. Fossil porcupines could not have been responsible in any way for the production of any of the osteodontokeratic tools described by Dart (op. cit.).

24.3 Discussion

The aim of part 2 of this thesis was to investigate the extent to which fossil porcupines could have been responsible for the accumulation of the grey breccia bone assemblage, and to establish whether they could have caused the damage to the bones which Dart (1957) referred to as 'Osteodontokeratic tools' and attributed to australopithecine manufacture. From the above results it is clear that porcupines have had very little to do with either the accumulation of, or the fracture and other damage to, the grey breccia bones; some other bone-accumulating agent (or agents) or mechanism must have been responsible.

The remarkable similarity of the percentage survival of skeletal parts histogram for the Makapansgat grey breccia assemblage (Fig. 72B) to that obtained for the Kuiseb River Hottentot settlements assemblage (Fig. 72A) - a far greater similarity than that apparent when the grey breccia histogram (Fig. 73B) is compared with the Swartklip 'hyena' bone accumulation (Fig. 73A) - suggests to the present author that a hominid (as suggested by Dart, op. cit.) was involved although probably not exclusively as a bone-accumulating and bone-destructive agent in the grey breccia. The large numbers of pointed, spirally fractured and often locally abraded bone flakes (not carnivore damaged), the large numbers of bone splinters present and the wide range of species present in the grey breccia, ranging in size from rhinoceros to cane rat, tends to support the latter contention.

To test this suggestion, the entire grey breccia assemblage requires re-analysis in terms of the characteristics of the bone accumulations of all the other bone accumulating agents, particularly human. By a process of elimination, it should be possible to establish which bone accumulating agent has predominated. If it could be demonstrated that a hominid was mainly responsible, the case for the Osteodontokeratic culture would be further strengthened.

The relatively high proportion of frequently severely 'weathered' bones - the nature of the weathering remains to be established - requires investigation, and may provide an explanation for the manner in which the grey breccia bones have become so densely concentrated in the low rearmost recesses of the ancient Limeworks cavern. Conversely, the very much larger percentage of completely unweathered, 'mint-fresh' bones needs to be explained.