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

J M MAGUIRE

VOLUME ONE, PART I

MAIN TEXT
(pp. 1 - 317)

Thesis submitted to the Faculty of Science at the University of the Witwatersrand, Johannesburg in fulfillment of the requirements for the Degree of Doctor of Philosophy.

Johannesburg, May 1976

I hereby certify that this thesis is my own work unless otherwise stated in the text, and has not been submitted for degree purposes at any other university.

J M Maguire

J M MAGUIRE



The Taung skull: Australopithecus africanus Dart 1925
Photo: P. Nagel

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VOLUME ONE

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ABSTRACT

The taxonomy of modern and fossil Hystricidae and the evolutionary history of the family has been reviewed, with particular reference to 203 undescribed South African specimens from the Transvaal australopithecine deposits and Cave of Hearths. After comparison with all contemporaneous fossil forms (only 10 of the 28 described fossil species seem valid) it was concluded that Xenohystrix crassidens Greenwood 1955, Hystrix makapanensis (Greenwood 1958) and H. africaeaustralis Peters 1852 are present at Makapansgat Limeworks, whereas only the latter species is present at the remaining australopithecine sites, with the possible exception of a few tentatively referred specimens of H. makapanensis. There are insufficient grounds for erecting a distinct species for the fossil form of H. africaeaustralis present in the australopithecine deposits and the Cave of Hearths material is likewise referred to the modern species. The distribution and minimum numbers of individuals of porcupine species present in the different breccias of the five sites is detailed and a reconstruction of the skull and mandible of X. crassidens attempted. The environment, stratigraphy and potential ages of the source deposits is discussed; it is concluded that with the exception of Taung, the dates suggested by Partridge and Vrba agree with the limited evidence provided by the fossil Hystricidae. Numerous skull characters used in the diagnoses of new Hystrix were examined for variability within a single modern species (only 3 of the 77 extant species proved to be valid) and then tested for diagnostic significance by comparison with the remaining valid species. Special attention was paid to mandibular and dental characters, particularly the crown enamel pattern, but the only reliable diagnostic characters were found to be associated with the anterior part of the cranium, which is seldom preserved in fossil form. The sequence of tooth replacement, a method for identifying isolated teeth, methods for segregating specimens into growth stages, and a standard terminology have been outlined.

A taphonomic study, attempting to determine the extent to which fossil porcupines may have been responsible for the accumulation of the Makapansgat Limeworks bone assemblage and for the manufacture of the bone tools described by Dart, was undertaken. Unlike the fossil assemblage, porcupine bone accumulations are characterized by a high percentage of much-gnawed bones, a large average fragment size, a high proportion of intact shafts with the concomitant near-absence of bone flakes and a low survival potential

for the articular ends of all limb bones. Comparison showed that the damage done by porcupines differs from that evident on the corresponding skeletal elements from Makapansgat. It is concluded that fossil porcupines had very little to do with either the accumulation or fracture of the Makapansgat Limeworks bones.

INTRODUCTION

This thesis encompasses two discrete topics: Part I deals with the taxonomy of modern and fossil Hystricidae (Table III) and attempts to identify and describe 112 fossil porcupine specimens from the four Transvaal australopithecine cavern deposits - Makapansgat Limeworks, Sterkfontein, Swartkrans and Kromdraai, and 91 from the Cave of Hearths, while Part II is a taphonomic study which attempts to determine to what extent fossil porcupines may have been responsible for the accumulation of the extensive bone assemblage found at the Makapansgat Limeworks australopithecine site and for the damage exhibited by the individual bones, both the accumulation and damage being attributed by Dart (1957a, b) to australopithecine activity. The background to both aspects of study has been discussed fully in the introductory chapters to Parts I and II; a brief summary only, outlining the scope of the thesis, is given here.

Greenwood's 1955 paper was the first and has so far been the only one describing South African fossil Hystricidae although Broom (Broom and Schepers 1946 p.82) erroneously mentions the occurrence of Hystrix cristatus in the Sterkfontein breccias. H. cristata Linn. 1758 is one of the two living representatives of this genus in Africa, the present range of this species being confined to North and north-eastern Africa. Broom's Sterkfontein material is thus probably referable to H. africaeaustralis Peters 1852, the living southern African porcupine.

From the meagre sample of only eleven specimens available at that time, Greenwood (1955) described three species of porcupine: Xenohystrix crassidens (gen. et sp. nov.), a gigantic porcupine some 3,5 times larger than the living African species and sufficiently different to warrant separate generic status, Hystrix major (sp. nov.), a porcupine larger than any extant or fossil Hystrix known, and a species tentatively described as H.cf.africaeaustralis,the teeth of which were thought to approximate in size and appearance to those of the living southern African porcupine. Greenwood later discovered that H. major Greenwood 1955 was a junior homonym of H. major Gervais 1859, and subsequently (1958) renamed her species H. makapanensis.

Since 1955, further collection and preparation of fossil material from the Makapansgat Limeworks site has increased the sample to seventy-one. In order to obtain as complete a picture as possible of the South African Hystricidae an attempt was made to assemble all available material

from the remaining four australopithecine localities. No fossil Hystricid material was available from Taung but the other sites yielded a combined total of 112 specimens. About 75% of this total is made up of isolated teeth, many of them fragmentary, while most of the remaining specimens are small, very fragmentary, maxillary or mandibular pieces. The sample is thus statistically inadequate for taxonomic purposes, especially in view of the fact that three distinct taxa are represented. This collection is the largest sample of fossil Hystricidae at present available from the australopithecine period. Ninety-one fossil and subfossil specimens from the more recent Cave of Hearths deposit (Later Early Stone Age to Iron Age) that have been included in the study give an overall total of 203 specimens of which only 10 have been described.

In view of the fragmentary nature of the fossil remains, it was considered that a prior study of both living and fossil porcupines in general and of the extant southern African form in particular would assist in an assessment of the scanty fossil sample, and many of the conclusions concerning the taxonomy of fossil forms have been based on the results obtained from a detailed study of the diagnostic characters, particularly those involving the dentition, of the three living species in the subgenus Hystrix.

The taxonomic study has taken the following course:

1. The stratigraphy and potential ages of the source deposits have been reviewed in order to provide a stratigraphic and temporal frame of reference for the fossil material. The time-setting of fossils is essential in discussions of the evolutionary history of any group, and no review of the dating of the four australopithecine sites has been undertaken during the twenty-year period since that of Ewer (1956) was published, with the exception of that of Sampson (1971) which deals only with the sequential dating of the sites. The last stratigraphic review of the australopithecine deposits was that of Brain (1958), and as much that is new has come to light since that time, it was felt that a review, collating the discoveries of the last 18 years, would not be out of place.

2. A list was made of the all the named forms, both living and fossil, in the genus Hystrix. It was found that in all, 95 forms have been named. 69 of these are extant, of which only three, Hystrix (Hystrix) cristata Linn. 1758, Hystrix (Hystrix) indica Kerr 1792 and Hystrix (Hystrix) africaeaustralis Peters 1852, proved to be valid species of the subgenus Hystrix.

Of the 28 fossil forms named, only 10 have been regarded as valid or potentially valid species. Closely related fossil genera (Sivacanthion, Atherurus and Xenohystrix) were also considered.

3. The skull characters (cranial, mandibular and dental) used to diagnose new species of Hystrix were listed, defined and tested for variability within a sample of 32 modern H.(H.) africaeaustralis specimens. Particular note was taken of differences that could have been due to the geographical source of particular specimens. The diagnostic validity of these characters, particularly mandibular and maxillary characters, was then tested by comparing the characters for dissimilarity or overlap within the three modern species. These three species were then redefined. Dental characters have long been considered as taxonomically unreliable for modern species (Hooijer 1946) but because fossil porcupine remains are so frequently confined to isolated teeth a special attempt was made to find whether any of the numerous dental characters that have been used to define new fossil species actually have any significance. In all some 146 characters were examined.

4. The South African fossil material was then identified and described, after comparing the specimens with all contemporaneous fossil forms. For comparative purposes, a catalogue of all fossil Hystricidae was compiled, with particular attention being paid to their validity, geological age and appearance. The minimum numbers of individuals of each species present in each breccia at the various South African sites has been estimated.

5. A reconstruction of the cranium and mandible of X. crassidens was attempted. The fossil material referred to H. makapanensis and H. africaeaustralis is too fragmentary to attempt reconstruction.

6. Finally, the evolutionary trends amongst modern representatives of the family and the possible evolutionary history of the group have been discussed, with particular reference to the South African fossil forms.

In passing, the tooth replacement, a method of positionally identifying isolated teeth and a method for segregating fossil specimens into age groups by means of either tooth eruption or crown enamel pattern have been devised. Because of the almost exclusive use of external morphological characters and cranial characters other than dental ones as definitive criteria, there is a great lack of information on the dentitions of both modern and fossil Hystricidae. The provision of tables of measurements

for the three modern species as well as for all fossil forms, and the investigation of the crown enamel pattern and root systems of modern forms attempts to rectify this omission.

When the first australopithecine, Australopithecus africanus Dart 1925a was described, Dart, using the evidence provided by the morphology of the fossil itself, its geographical and palaeoenvironmental setting, its depositional environment and the associated fossil fauna, concluded that Australopithecus was erect or semi-erect, cursorial, omnivorous, troglodytic and predatory, and that the bones found in association with the australopithecine remains were the result of the predatory, carnivorous and troglodytic behaviour of this creature. Later, failing to find any recognizable lithic artefacts in direct association with A. africanus remains, and seeking defensive and predatory weapons of some sort, particularly a weapon which could have been responsible for the double-depressional cranial fractures he found in an unusually high number of associated fossil baboon crania, Dart (1957a,b) undertook the analysis of the entire bone assemblage then available from the Makapansgat Limeworks australopithecine deposit to ascertain whether any of these bones had been fashioned and used as tools. After the examination of some 7,000 specimens, he concluded that many of the bones, teeth and horn-cores had been artificially damaged to form a variety of tool types (clubs, scoops, saws, knives, digging tools, scraping tools, ripping tools, piercing tools, pounding tools and compound tools), and that these constituted the varied elements of an 'Osteodontokeratic Culture.'

Many objections to both these views - that the australopithecines were responsible for bone accumulations and the view that they used and fashioned bone tools - immediately followed and many opponents still exist. As far as the accumulations of the bones was concerned, arguments have centred round predators, and it has been suggested by numerous authors (Leakey 1953; Washburn 1959, 1960; Sutcliffe 1969, 1970, and others, see Chapter 17) that Australopithecus, rather than being a predator, instead constituted the prey of carnivores such as hyenas, leopards, lions and sabre-toothed cats and that these animals, rather than the hominid, were responsible for the bone accumulations found in the australopithecine deposits. Porcupines, long recognized as active accumulators of bone, have also been implicated as the agent possibly responsible for the Limeworks assemblage (Hughes 1974, pers. comm.), while Partridge (1975)

has suggested that 'hillwash' (the characteristics of which are undocumented) may have been responsible for the accumulation of the bones in the grey breccia stratum at this site.

At the time, these claims were difficult to prove or disprove because little was known about the biology or bone accumulating propensities of the animals in question. Dart's claims thus stimulated research into the feeding behaviour, bony food remains and bone accumulating habits of hyenas (Hughes 1954a,b, 1958, 1961; Sutcliffe 1969,1970) leopards (Brain 1968, 1969a) cheetahs (Brain, pers. comm. as a possible modern analogue for the extinct sabre-tooths) and modern primitive humans (Brain 1967c, 1969b, 1969c). The results of these field studies are gradually making it possible to differentiate the bony food remains of the various carnivores from those produced by primitive man. It now remains for the bone accumulations from the various australopithecine sites, particularly that from Makapansgat Limeworks, which has thus far escaped attention since Dart's pioneering analysis, to be assessed in terms of this new information. Brain (1969a, 1970b) has already argued convincingly in favour of leopards as the agent largely responsible for the Swartkrans bone accumulation while Vrba (1974a) has suggested that a super predator, possibly a sabre-toothed cat, may have been responsible for the Sterkfontein Type Site bone accumulation, and a hominid for the Sterkfontein Extension Site accumulation.

The characteristics of porcupine bone accumulations are as yet undocumented, except for passing mention of the high percentage of porcupine-gnawed bones they contain. The bone accumulating habits of porcupines have frequently been commented upon (Alexander 1958; Hughes 1958, 1961; Brain 1958). One of the aims of Part II of this thesis has been to establish the characteristics which typify such accumulations and to assess in broad terms the extent to which porcupines (three species of which occur as fossils in the Makapansgat deposit) may have been responsible for the accumulation of the grey breccia bone accumulation at this site. This was done by making collections of the introduced contents of as many porcupine lairs as possible and comparing the characteristics of these with those described by Dart (op. cit.) as characterizing the Limeworks grey breccia australopithecine deposit. Experiments were undertaken to investigate the bone preferences (size, shape, freshness, fattiness, etc.) of porcupines, and the rate of accumulation of bones within lairs has also been investigated.

As with the postulation that australopithecines were bone accumulators, Dart's claims concerning their 'osteodontokeratic Culture' were also almost universally rejected, although the recent accumulation of data demonstrating the tool-using, tool-making and cooperative hunting abilities of chimpanzees by Goodall (1964*, 1968*, 1971), Khronstov (1964*), Kortland and Kooij (1963*) and Teleki (1973*) have led to a gradual decline in published objections to Dart's claims. Again, porcupines have been implicated in the problem, since it has been suggested that these animals may have been responsible for the 'manufacture' of at least some 'Osteodontekeratic' tools (Singer 1956*, 1959). This argument has been tested in this thesis by comparing the damage encountered on bones from a porcupine lair situated in a locality where damage to the bones by carnivores or any other bone-damaging agent could safely be excluded, i.e. the bones compared showed only porcupine damage, with the damage shown on corresponding skeletal elements from the Limeworks grey breccia.

It should be noted that the methods employed in solving both the taxonomic (Part I) and taphonomic (Part II) sections are discussed fully in the appropriate chapters (3 and 18 respectively) while the conclusions to each are summarized and discussed separately in Chapters 16 and 24.

Further, it should be noted that Part II does not attempt to be a definitive account of the characteristics typical of porcupine bone accumulations. At the time of writing the best collections available came from a lair situated in a somewhat 'artificial' environment for deciding this point in that :

1. the bones available for collection by porcupines were derived from the skeletons of a limited number of species of mainly domestic animals
2. other bone dispersing and bone damaging agents (carnivorous birds, carnivores and scavengers) were absent or present only in limited numbers; whole bones were therefore available for collection by porcupines

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* Goodall,J. (1964)Tool using and aimed throwing in a community of free-living chimpanzees Nature 201, 1264-1266)

* Goodall,J.(1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. In Animal Behaviour Monographs 1(3)161-311

* Khroustov,H.F.(1964) 8th Int.Congr.Anthrop.Ethnol.Sci., Moscow

* Kortland A. & Kooij M.(1963) Symp.Zool.Soc.Lond., 10, 61-87

* Teleki, G.(1973) Scientific American 228, 32-46

* Singer, R.(1956) American Anthropologist 58: 1127-1134

Both factors would radically affect the characteristics of any porcupine bone accumulations made in this area. On the other hand, this somewhat 'artificial' collection has enabled an assessment of exactly how and where porcupines are capable of damaging the various skeletal elements without having to allow for possible damage by carnivores. Collections from less disturbed environments were often inadequately small, mainly on account of the long-term and expensive nature of obtaining such collections. Part II should be regarded as a preliminary account only.

The two aspects of this study which are of a general nature, namely the geological and stratigraphical review of the source localities and the discussion of their age, have been dealt with first (Chapter 2) and should be regarded as introductory. Since considerable controversy still exists concerning the temporal placement of the Plio-Pleistocene boundary, the South African australopithecine sites have been loosely referred to as being of 'Plio-Pleistocene' age.

2 THE SOURCE OF THE FOSSIL MATERIAL

This chapter aims at providing a frame of reference for the fossil material dealt with by broadly discussing the past and present environment, the stratigraphy and the age of the five Transvaal cavern deposits from which the fossil materials were extracted.

Four of the five fossil-porcupine-bearing cavern deposits, Sterkfontein, Swartkrans, Kromdraai and Makapansgat Limeworks, are also well known australopithecine-bearing localities which, broadly speaking, cover the period of time from the Middle Pliocene (approximately 3,6 m.y.B.P.) to the terminal part of the Lower Pleistocene. The Plio-Pleistocene boundary has been taken at 1,8 m.y.B.P. as suggested by Van Couvering (1972) and the Lower Pleistocene-Middle Pleistocene boundary at 700,000 years B.P., at the interface between the Matuyama Epoch of reversed magnetic polarity and the Brunhes Epoch of normal polarity. The Miocene-Pliocene boundary is at 5,0 m.y.B.P. (Van Couvering, op. cit.).

No porcupine remains have been recovered from Taung, the only other known South African australopithecine site, and the type locality of Australopithecus. This site, near Buxton in the extreme north-eastern Cape, an area bordering the Kalahari (Fig. 1), yielded the skull of the first-discovered australopithecine. The significance of the skull was immediately recognized by R.A. Dart, who named the creature Australopithecus africanus (Dart 1925 a) (see frontispiece). As far as can be determined from the faunal lists of this locality (Broom 1934, 1948; Peabody 1954) only smaller rodents were recovered from the Taung breccias, and since the breccia deposits were subsequently almost completely destroyed by mining activities, it is unlikely that any further fossil faunal material will be recovered from the site. In view of the total lack of porcupine remains from Taung, possibly a Lower Pleistocene locality, it has been largely omitted from the present investigation.[i)]

Up to the time of writing, neither australopithecine nor porcupine remains have been recovered from the limited Plio-Pleistocene deposits elsewhere in South Africa, including the richly fossiliferous 4 million year old (Hendey 1970, 1972, 1973) Langebaanweg sites in

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i) It has been suggested (Partridge 1973) that the Taung locality may be only approximately 0,87 m.y. old, in which case it would be terminal Lower Pleistocene.

the western Cape (Fig. 1). Apart from the Hystrix material recovered from archaeological sites dating from the Middle and Upper Pleistocene (apparently all referable to the living H. africaeaustralis), all the South African Plio-Pleistocene fossil porcupine remains available up to the end of 1974 have been considered in this review.[i)]

The Cave of Hearths deposit, the fifth source of fossil porcupine material, is not ape-man-bearing but considerably younger than the australopithecine sites. This deposit (see Table II p. ?) covers the period from approximately 260,000 years B.P. to the end of the Iron Age. Several human fragments have been recovered from it, including a right half of a corpus mandibulae from the symphysis menti to the area posterior to the second molar, found in association with Earlier Stone Age (Later Acheulean) artefacts. This jaw fragment was initially described as exhibiting neanderthaloid affinities (Dart 1948a) and has recently (Tobias 1971) been assigned to the taxon Homo sapiens rhodesiensis Campbell 1963. However, Coon (1967 p.379), Klein (1974) and Beaumont (1975, in press) consider the latter taxon to represent a late form of Homo erectus.

The locations of the South African australopithecine deposits and the Cave of Hearths are shown in Fig. 2. The Makapansgat Limeworks and Cave of Hearths are situated in the rugged mountainous country near Potgietersrus in the northern Transvaal whilst Sterkfontein, Swartkrans and Kromdraai are all located in the Blaaubank valley, which winds across the open grasslands of the gently undulating southern Transvaal highveld near Krugersdorp, some 288km (180 miles) to the south.

A large number of publications relating to the geology and dating of the australopithecine deposits has accumulated since the Taung discovery of 1925. However, although the more obvious features of their geology and stratigraphy now appear to be understood, many controversial issues remain, and the question of the ages of the sites, both absolute and relative, remains unresolved.

The main environmental, geological and stratigraphical features

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i) A large fossil Hystrix has recently (June 1975) come to light from Langebaanweg, but since the material was acquired after the completion of the present study, it has not been considered here.

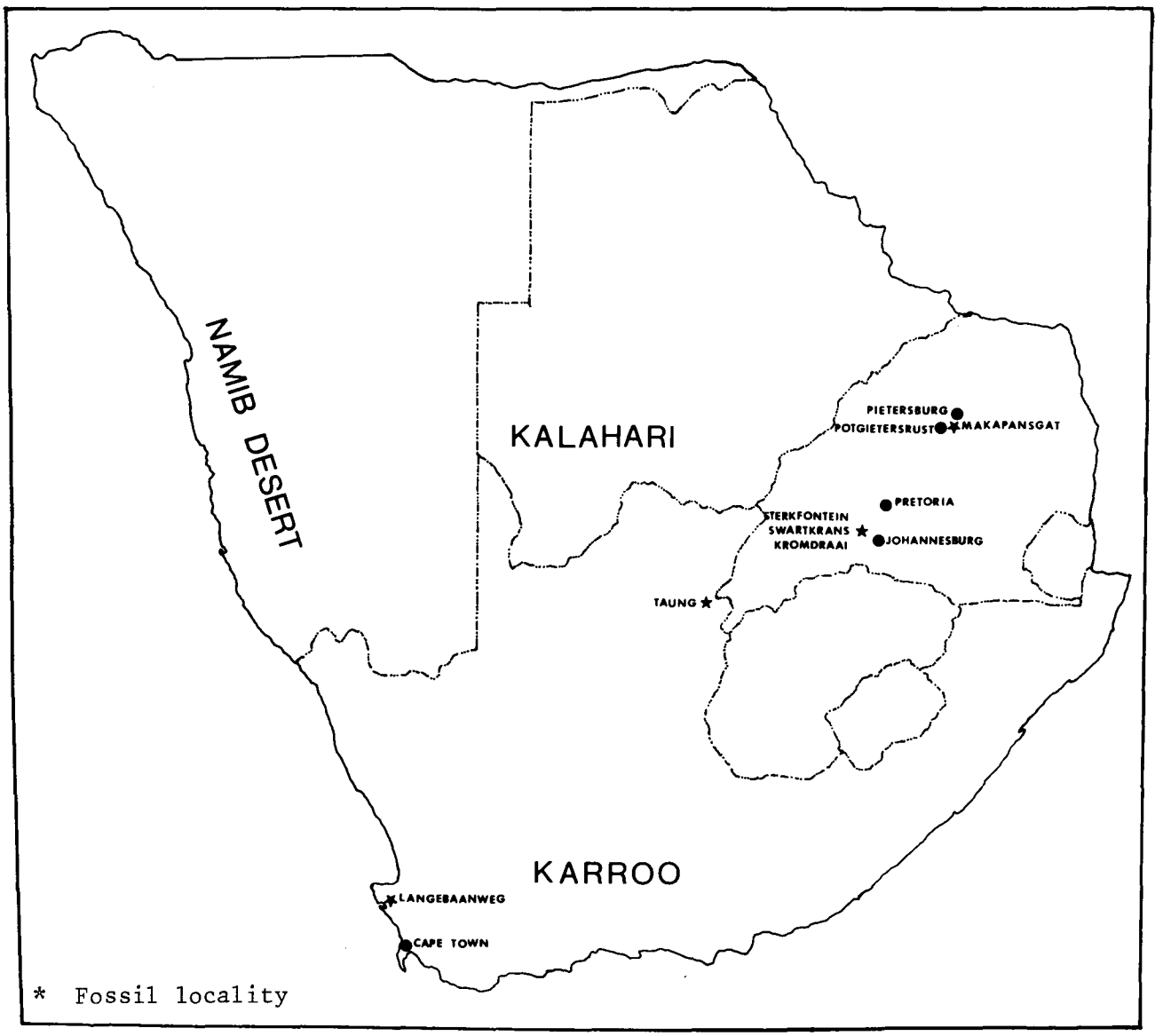


Fig I

Map of Southern Africa showing locations of major fossil sites

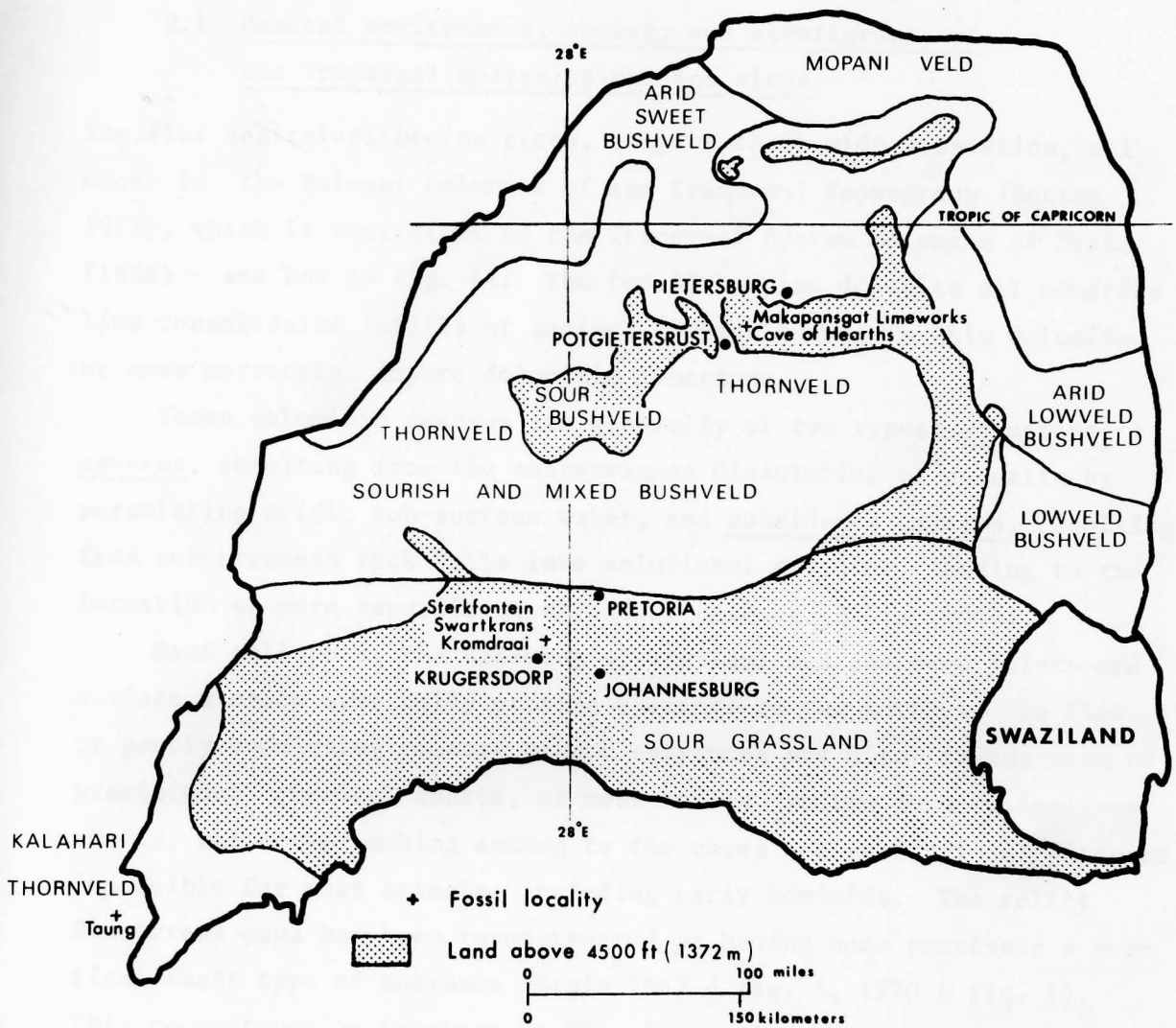


Fig. 2 **Map of the Transvaal showing the principal vegetation zones and the location of the five South African australopithecine sites and the Cave of Hearths.**

of each site are described in section 2.1 below, whilst a broad outline of the dating problem with a discussion of past and present opinions is given in section 2.2.

2.1 General environment, geology and stratigraphy of the Transvaal australopithecine sites

The five australopithecine sites, despite their wide separation, all occur in the Malmani Dolomite of the Transvaal Supergroup (Button 1973), which is equivalent to the Transvaal System Dolomite of Brain (1958) - see key to Fig. 16. The fossil-bearing deposits all comprise lime-consolidated infills of ancient caverns formed in this dolomite, or more correctly impure dolomitic limestone.

These dolomitic caverns are generally of two types: solutional caverns, resulting from the subterranean dissolution of dolomite by percolating acidic sub-surface water, and subsidence caverns, resulting from subterranean rock falls into solutional cavities, leading to the formation of more superficial secondary caverns (Brain 1958).

Roof collapses, the widening of vertical and inclined joints and surface erosion eventually provide openings to the surface. In flat or gently undulating country cavern entrances are often in the form of precipitous vertical shafts, or more rarely, in the form of inclined shafts, the former making access to the caves for habitational purposes impossible for most animals, including early hominids. The relict Swartkrans cave has been reconstructed as having once possessed a vertical shaft type of entrance (Brain 1967 d fig. 5, 1970 b fig. 1). This reconstruction is shown in Fig. 21 a. In country of more broken relief, caverns in the dolomite frequently open into the sides of valleys by means of a break-through in one of their side walls, thus giving rise to a lateral type of entrance. The modern caves in the Makapansgat valley, namely the Historic Cave (Fig. 12), Ficus Cave and Peppercorn's Cave, provide excellent examples of this type of entrance, and it is probable that the relict Makapansgat Limeworks cavern and Cave of Hearths once possessed entrances of this kind.

It is important to note that the history of dolomitic caverns is not static: successive roof collapses, rock falls, subsidences, erosion and deposition progressively modify the original cavern form and may render previously habitable caverns uninhabitable. For this reason periodic changes in the nature of the cavern frequenters and hence in

the method of bone accumulation within the caverns should be expected.

The development of an entrance allows surface-derived materials to enter a cavern which, together with the earthy and rocky infill of intracavernous origin, become cemented by percolating lime drip from the cavern roof. These lime-consolidated infills, irrespective of the nature of their bony or lithic inclusions, have been termed 'cavern breccias'. The breccias dealt with differ widely in their fossil content, degree of calcification, colour and general characteristics, but may be broadly differentiated (Brain 1958 pp. 18-22) into two types:

(1) Phase I breccias, which are composed of materials of intracavernous or predominantly intracavernous origin and which form prior to the development of a large cavern entrance, and

(2) Phase II breccias, which are composed largely of surface-derived materials and which are considered to have accumulated only after considerable enlargement of the cave entrance permitted the relatively rapid entry of surface-derived materials.

The sites investigated have all been subjected to long and intensive surface erosion, speculative estimates indicating that 15 to 30m (50-100ft) of dolomite has weathered from the surface of the local hillsides since the beginning of the Pleistocene (Cooke 1970 pers. comm., Brain 1970b p.1113, fig. 1). At all of these sites, therefore, the original cavern roof or most of the roof as well as the upper part of the consolidated infill has been eroded away, the weathered surface of the breccia outcropping at the surface (Figs. 7, 14, 20 and 21b) except where covered with a shallow overburden derived, at least in part, from the decalcifying breccial mass itself.

Although basically similar in mode of formation and geology, these geographically widely separated and environmentally very different sites are discussed as two separate groups:

2.1.1 The Makapansgat Valley sites: Makapansgat Limeworks and Cave of Hearths

These two sites, only 0,8km (0,5 miles) apart, are situated in the Makapansgat valley on the farm Makapansgat, some 19km (12 miles) east north-east of the town of Potgietersrus in the central Transvaal

(see Figs. 2 and 3).

The Makapansgat valley has formed on the western side of an isolated north-south running spur of the Strydpoort Mountains which is separated from the western extremity of the main range by a gap of 5 to 6km (3-4 miles). This short, northward-veering spur or Makapan-Strydpoort plateau (sometimes called the Makapansberg) therefore lies at right angles to the main range, which runs eastwards for 64km (40 miles) to join the Transvaal Drakensberg near Haenertsberg.

Approximately 19km long and 10km wide (12 x 6 sq. miles), the elevated Makapan-Strydpoort plateau is particularly well defined along its escarpment-like eastern margin, its broken relief characterised by ruggedly rolling dolomite and Black Reef quartzite mountains deeply incised by kloofs and valleys leading down to the flats below. The highest point, 2040m (6700 ft) above sea level, lies at the summit of the Black Reef quartzite mountains forming the eastern escarpment some 6,5km (4 miles) south east of the Limeworks, at the more easterly of the two beacons marking the common boundary of the farms Spanje and Portugal. The escarpment drops steeply and often precipitously to the plains below, where flatter country, averaging 1090m (3500 ft) above sea level, extends eastwards and through the gap between the plateau and the main range into the southward-lying vast expanse of the Springbok Flats.

The western slopes of the plateau, although less abrupt than those of the eastern escarpment, are nevertheless very irregular and broken. Fig. 4 shows the narrow upper part of the Makapan valley itself, which is terminated by the rugged 90m (300 ft) Black Reef quartzite cliffs forming the head. The Makapan stream leading down from the plateau above drops 55m (180 ft) over the lowest part of the cliff into the valley.

The Cave of Hearths and Limeworks lie respectively 1,6 and 2km (a mile and a mile and a half) to the west of these cliffs, on the south side of the stream running down the valley. The Cave of Hearths, with a north-eastern aspect, is situated 46m (150 ft) above the stream, within the narrow upper part of the valley, whilst the Limeworks, with a north-western aspect lies just outside, where the valley widens conspicuously and assumes a more south-westerly than north-westerly direction (Figs. 3 and 5).

The altitude of the valley drops gradually westwards from 1425m

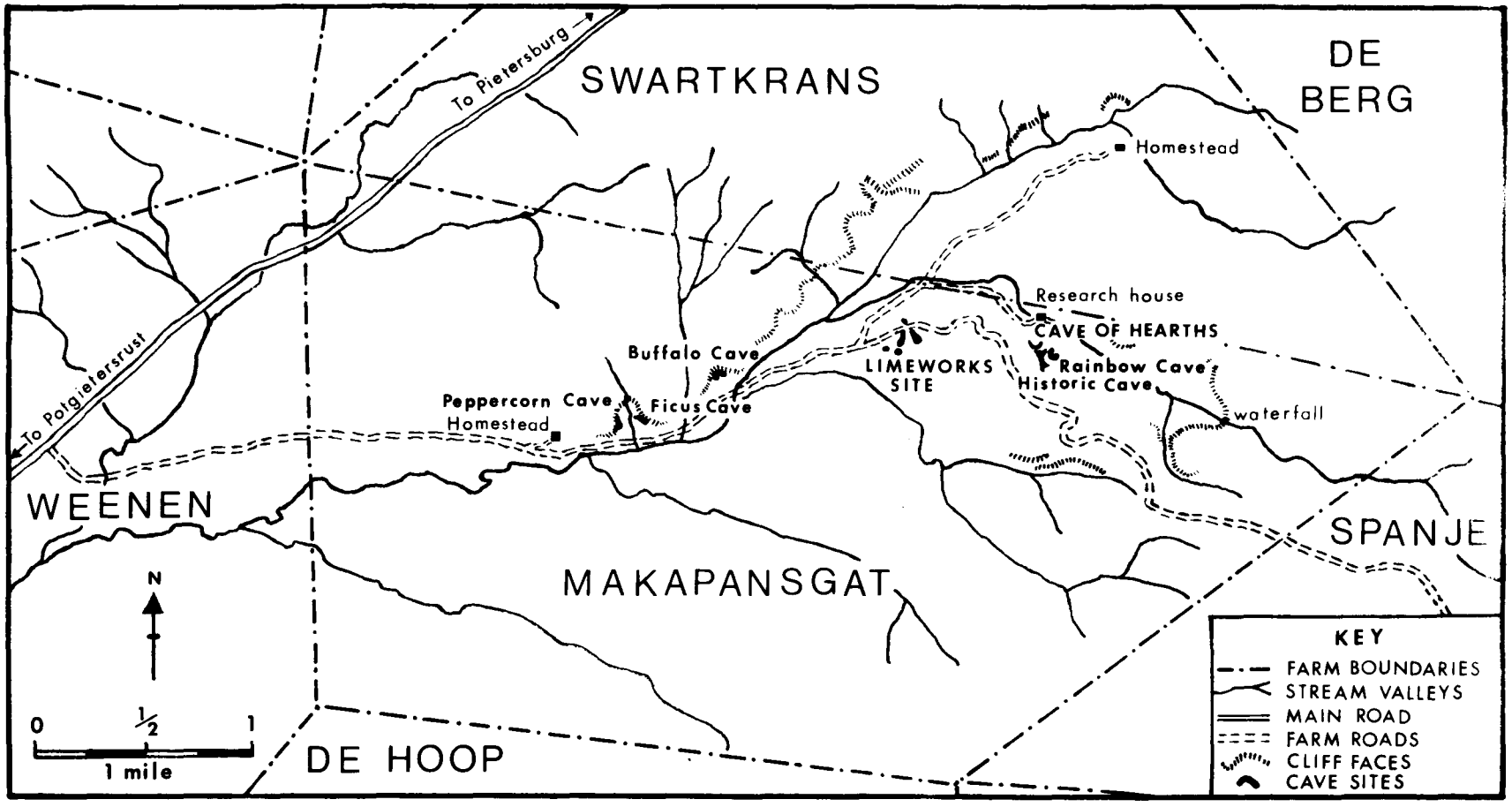


Fig. 3 Plan of the Makapansgat valley showing the location of the Limeworks and Cave of Hearths and other caves of palaeontological or archaeological interest. (after Wells and Cooke 1956)

Fig. 4

A wintertime view from the eastern mouth of the Historic Cave looking eastwards towards the Black Reef quartzite cliffs forming the head of the Makapansgat valley.

The Protea-covered mountain slopes lying above and beyond the cliffs rise to 2040m (6700 ft) 6,5km (4 miles) to the south-east. A 55m (180 ft) waterfall drops through a cleft in the middle of the cliffs into the dark patch of sub-tropical evergreen relict forest seen below them. This forest extends up two narrow gullies formed between the sharply-defined quartzite ridges seen on the left.

Fig. 5

A view from the hillside immediately above the Limeworks excavation looking westwards down the Makapansgat valley.

Potgietersrus, some 19km (12 miles) distant, lies in the valley of the Magalakwyn river, i.e. between the mountain range seen in the background and that traversing the picture from left to right. Prior to cultivation the valley was probably covered with a sourish mixed bushveld flora. The line of trees on the valley floor (right of centre) marks the course of the Makapan stream.



Fig. 4



Fig. 5

(4700 ft) opposite the Limeworks to some 1180m (3800 ft) near Potgietersrus. In this part of the valley, termed 'Mwaridzi' by the local Bantu inhabitants, the water carried by the Makapan stream disappears underground for some miles to reappear several miles downstream near Potgietersrus.

The annual rainfall is estimated at between 695mm and 710mm (27-28 inches) in the Makapansgat valley and probably approaches 900mm (35 inches) in the mountains above, while Potgietersrus receives an average of only 605mm (24 inches). Precipitation usually occurs in the form of brief but sharp summer thunderstorms, but on the higher parts of the Makapan-Strydpoort plateau, where dense mists occur during the summer months, periods of rain may be much prolonged. Although during much of the year the Makapansgat stream flows for only a short distance beyond the waterfall, water is available throughout the year in several permanently shaded deep rock pools both above and below the waterfall. This was probably the case even during the drier interludes of the fluctuating Pleistocene climate.

The annual range of temperatures is wide, summer day temperatures rising to 26,7°C or 32,2°C (80°F or 90°F) or more, while sharp frosts are frequent on winter nights. On the more exposed higher slopes of the plateau, winter night temperatures not infrequently drop to -3,9°C or even -6,7°C (25°F to 20°F) and occasionally even lower (climatic figures B. Maguire 1970 pers. comm.).

It is evident that the above-mentioned variations in local climate and geology combined with the highly broken relief provide a wide range of ecological niches which are ideal for the support of a rich and varied fauna and flora.

The area within an 8km (5 mile) radius of the Limeworks and Cave of Hearths supports more than 1000 plant species, and of this number, some 100-120 provide edible parts (B. Maguire, in preparation). The vegetation of the mountains rising above and generally eastwards of Makapansgat exhibits a fairly strong Cape element, with Protea dominating large tracts of the cool Black Reef quartzite uplands where soils are acid. The deeper, more protected, kloofs or ravines and notably the narrow gullies at the head of the Makapansgat valley shelter patches of tropical to semi-temperate relict evergreen forest, whilst the lower more open valleys and slopes are covered with a rather open Sourish Mixed Bushveld flora (Acocks 1953). The vegetation at the

head of the Makapansgat valley is shown in Fig. 3, although much of the relict forest sheltering within the northern gullies is concealed by intervening ridges of quartzite.

The local older inhabitants report that a wide variety of mountain, bush and plains-loving larger mammals (about 39 species) occurred in considerable numbers up to fifty years ago. This fauna has been severely depleted or rendered locally extinct by indiscriminate hunting and extermination, animals such as leopards, baboons and porcupines being regarded as vermin by local farmers. Analyses of the Makapansgat Limeworks grey-breccia fossil fauna indicate that the Pliocene or Pleistocene fauna of the area was quite as rich as if not richer than that recorded in historical times.

The Makapansgat valley, with its varied flora and fauna, abundant rocky shelters and limestone caverns of various sizes offers much in the way of protection for man and animal. The palaeontological and archaeological evidence indicates that the valley has been favoured by both from australopithecine times during the Pliocene some two to three million years ago up to the present day.

The Limeworks has yielded evidence of man's earliest attempts at tool manufacture, both in bone (Dart 1957a, 1957b) and stone (Brain, van Riet Lowe and Dart 1955; Dart 1962; Maguire 1965, 1968) whilst the Cave of Hearths has provided the earliest evidence in Africa of the controlled use of fire (Oakley 1957b; Mason 1962a).

The geology and stratigraphy of the Limeworks and Cave of Hearths are discussed below:

2.1.1.1 Makapansgat Limeworks

The Limeworks deposit represents the weathered remains of a vast ancient cavern of the subsidence type and its consolidated infill, the present extent of which covers some 1,5ha (over 3 acres). Surface erosion has destroyed almost the entire ancient cavern roof save for a limited stalactite-encrusted section on the western side of the deposit and a small fragment on the south-western side of the 'collapsed cave'. The weathered surface of the breccial infill occasionally outcrops through a 15-30cm (6-12 inch) layer of chert-rubbly overburden, largely, it is presumed, derived from decalcified breccia itself. Although erosion has destroyed an unknown depth of breccia, an average depth of 12 to 18m (40 to 60ft) of breccial deposit still

remains. The main surface features of the site and excavation are shown in Fig. 6, and when used in conjunction with the site photograph (Fig. 7), some idea of the general appearance of the Limeworks may be obtained.

An accurate reconstruction of the original cavern form does not appear possible, the combined effects of erosion and limestone mining activities having destroyed much of the evidence on which such a reconstruction might have been based. It is generally conceded, however, that at some stage the entrance was probably of the lateral type, and a 2,4m (8 ft) layer of fossilized rodent bones, once the contents of ancient owl pellets, on the north-eastern side of the deposit, in Bed A of Member 4 (Partridge 1975) may well indicate the approximate position of the original entrance, since it is known that owls roost at no great distance from cave mouths. The lateral entrance would probably have made access to the cavern possible for most animals as well as hominids, and it is probable, especially in view of its warm, sunny, north-facing aspect, that the ancient Limeworks cavern was habitable from a relatively early stage in its development. However, the presence of almost completely articulated fossilised skeletons in some of the lower levels or members of the deposit may be indicative of animals falling down shaft or fissure-like openings which may have preceded the opening of the lateral entrance.

Many stratigraphic details of the deposit have been revealed by extensive limestone mining and by the subsequent collapse of a conical mass of several thousand tons of undermined (mainly Phase II) breccia onto the floor of the miners' excavation. The stratigraphy has been investigated by a number of workers, the first detailed sequence being proposed by Dart in 1947 (published 1952). The importance of the site had by this time been realised and reports by King (1951), Howell (1955), Wells and Cooke (1956), Brain (1958) and most recently Partridge (1975 in preparation) followed. Of these, (apart from Partridge's unpublished work), Brain's is the most intensive study, and his composite stratigraphic profile for the Limeworks (op. cit.) is shown in Fig. 8.

The grey breccia, which may be regarded as a bone-contaminated travertine, forms part of Brain's Lower Phase I material (Member 3 of the Makapansgat Formation of Partridge 1975), and overlies a basal

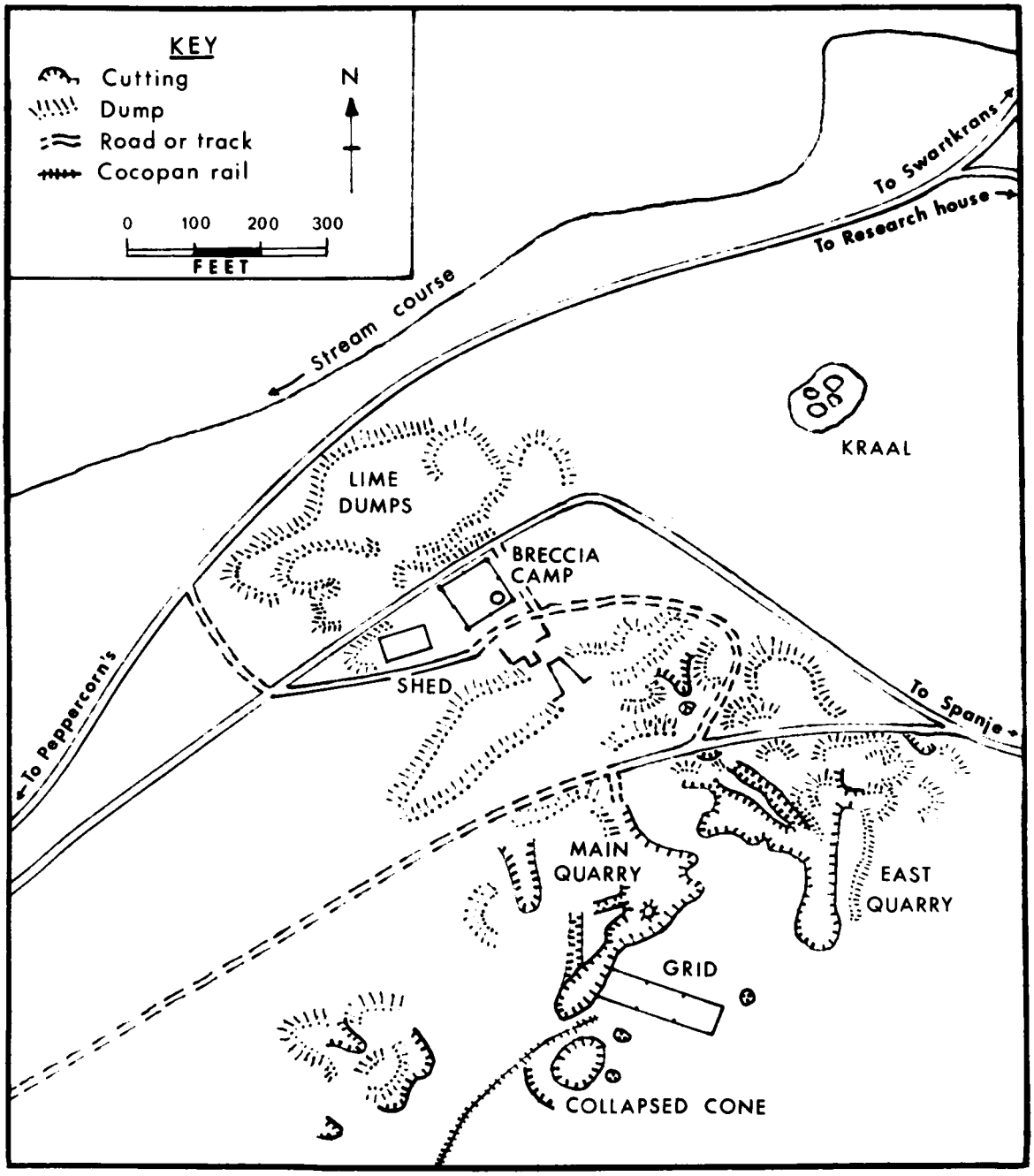


Fig. 6 Map showing the surface features of the area surrounding the Limeworks site. (after Brain 1958, modified by Maguire, pers. comm.)



Fig. 7

A wintertime view looking northwards across the Makapansgat Limeworks site from the hillside above.

Note the numerous specimens of Aloe dolomitica covering the dolomite hillside in the foreground. Part of the cone mouth is seen on the extreme left, and just beyond it, the main quarry. On the right, and leading down to the main quarry is the excavation grid which has been cleared of vegetation and decalcified overburden exposing the Pink Breccia and the abundant solution cavities pocking its surface. Beyond the shed and breccia camp, at the foot of the hillside, are the extensive lime dumps left by the limeworkers. The line of trees on the valley floor marks the course of the Makapan stream.

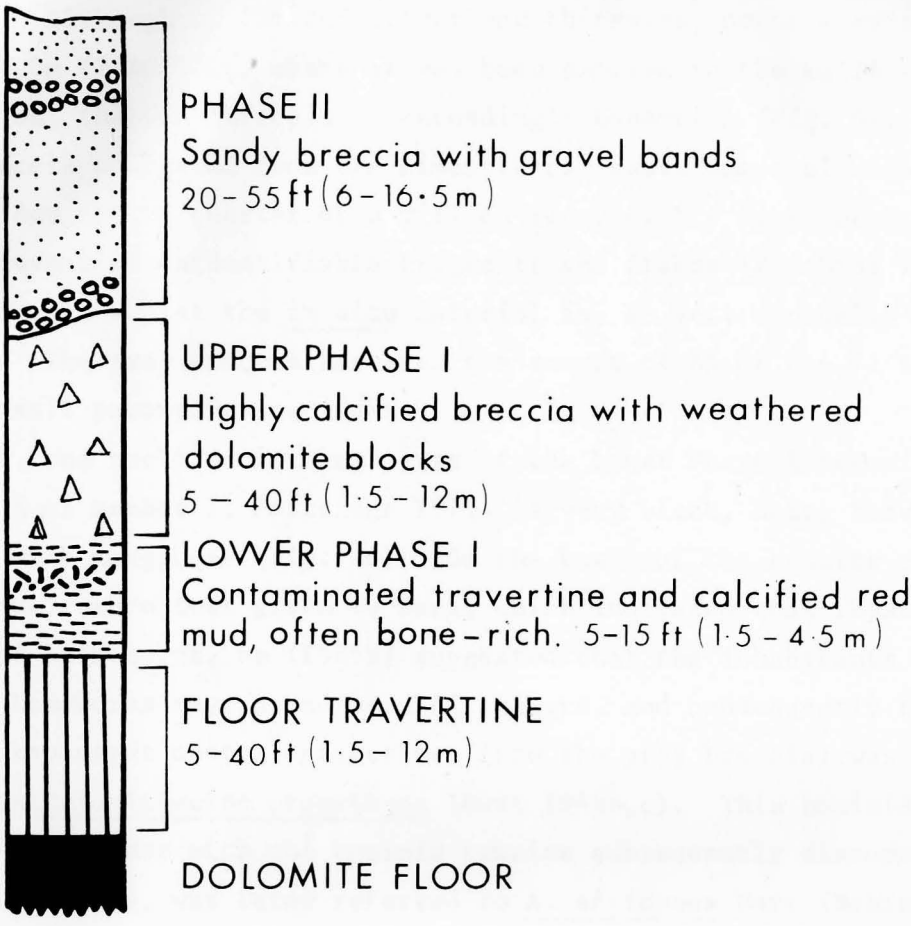


Fig. 8 Composite stratigraphic profile for the whole of the Limeworks deposit. (after Brain 1958)

layer of calcified red mud (Bed A of Member 2 of Partridge 1975), from which the rare articulated skeletons referred to above have been derived. Although of limited extent and thickness, nowhere exceeding 0,5 to 1,0m (2 to 3 ft) where it has been exposed in the walls of the excavation, the grey breccia is exceedingly bone-rich (Fig. 9). The grey breccia collected from the Limeworkers' waste dumps alone has so far yielded over a quarter of a million identifiable specimens and many thousand of unidentifiable fragments and flakes (Kitching 1972 pers. comm.), whilst the in situ material is, as yet, virtually untouched. The grey breccia has been the source of 65 of the 71 Limeworks fossil porcupine specimens.

The bone enclosed in some parts of the Lower Phase I breccia (in Bed B of Member 2, Partridge 1975) is very black, being heavily stained with manganese (Fig. 10). On the basis of the results of a fallacious carbon test given to Dart, which indicated that these bones had been burnt, he (1925b) suggested that the inhabitants of the ancient Limeworks cavern had been fire-users, and consequently the first Makapansgat australopithecine (from the grey breccia) was named Australopithecine prometheus (Dart 1948b,c). This hominid material, together with the hominid remains subsequently discovered at the Limeworks, was later referred to A. africanus Dart (Robinson 1954). However, an A. robustus (questionable?) from the grey breccia has recently been described from the existing Makapansgat hominid sample (Aguirre 1970, vide Tobias 1973).

The Lower Phase I breccias are succeeded by the exceedingly hard, heavily calcified pink or Upper Phase I breccia, Bed B of Member 4 (Partridge 1975), which has been eroded down to the present maximum thickness of 12 to 15m (40 to 50 ft). This breccia, which is markedly less fossiliferous than the grey breccia, is characterized by numerous dolomite and chert inclusions and constitutes the bulk of the Limeworks deposit. Whilst the fossil fauna of the grey breccia has a 92% bovid component (Dart 1957b p.84), the fauna of the Upper Phase I is characterized by a predominance of fossil primates, particularly of cercopithecids. As to date only four fossil porcupine specimens have been recovered from this breccia.

The pink Upper Phase I breccia is, in turn, overlain by the rather reddish Phase II breccia (Member 5, Beds A, B, C and D Partridge 1975), in the vicinity of the collapsed cone. The seeming contact

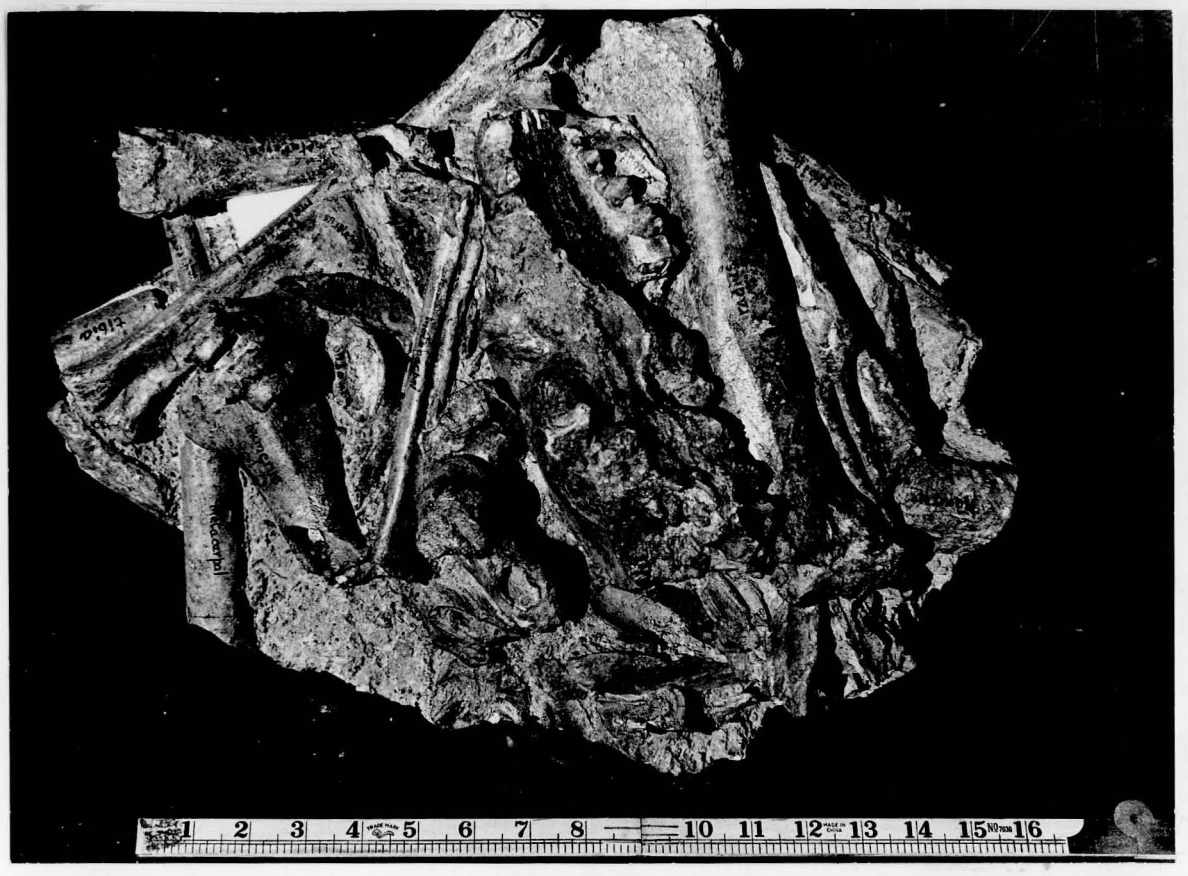


Fig. 9

A block of the exceedingly bone-rich grey breccia from the Makapansgat Limeworks.

Note the Hyaena makapani skull lying rather centrally in this block which contains relatively few flakes and an unusually high proportion of intact bovid metapodal bones.

Fig. 10

In situ bone stained black by manganese in an exposure of the Lower Phase I breccia in the Main Quarry at the Makapansgat Limeworks.

Fig. 11

A profile exposed by the collapse of the cone, on the east wall of the cone mouth.

The travertine fragment seen just above the standing figure formed part of the floor of the ancient Limeworks cavern. Note the faint concentric lines indicative of its mode of formation and the breccia-filled cracks running through it, resulting from instability in this part of the ancient cavern floor. Limeworkers have removed most of the 12m (40 ft) depth of pure limestone which formed the floor at this point. A well-defined contact between the Upper Phase I breccia and the overlying Phase II breccia (top left hand corner) is seen in this profile. Partridge (1975 pers. comm.) considers that this 'contact' is merely the interface between somewhat decalcified and less decalcified Member 5 breccia, and that the only 'Upper Phase I' breccia visible in this section is a thin lens immediately overlying the larger of the travertine fragments at the origin of the three cracks.



Fig. 10



Fig. 11

between the Upper Phase I and Phase II breccias seen in the profile exposed by the collapse is shown in Fig. 11. It is uncertain whether the less compact Phase II breccia was initially less heavily calcified than the Upper Phase I or whether it subsequently suffered decalcification by weathering. Partridge (1975) considers that the colour difference is due to decalcification and places both breccias in this region in Member 5. The Phase II breccia contains two bands of predominantly dolomite pebbles, many of which have been rounded to some extent, and from which Brain recovered 17 suspected 'Kafuan' artefacts (Brain et al. 1955). The validity of these stone tools has generally been questioned (Mason 1962a; Tobias 1965; Inskeep 1969). However, on the basis of a variety of evidence accumulated during extensive independent excavations conducted at the site between 1960 and 1965, Maguire (1965, 1968; pers. comm. 1972) has concluded that large numbers of crude artefacts of dolomite and chert are present in both the Phase II and Upper Phase I breccias; also that relatively small-numbered water-worn quartzite pebbles present in the Phase II breccia represent lithic materials foreign to the site, and were intentionally introduced into the ancient cavern, primarily for use as simple percussion tools . After an examination of the quartzite specimens recovered from the Phase II breccia M.D. Leakey (1970) concluded, in a footnote, that a number of flakes and utilized pieces were indeed present.

Only two porcupine specimens have thus far been recovered from the latter breccia, both having been retrieved from the surface of the collapsed cone. Australopithecus africanus occurs in all breccias above and including the grey breccia, Aguirre (1970) suggesting, on the basis of a single specimen, that A. robustus is also represented in the grey breccia. As yet (July 1975), no more advanced hominid has been found.

The Pliocene climate prevailing during the accumulation of the australopithecine deposits has received attention by C.K. Brain (1958) who concluded that between the rainfall range of 500-1000mm (20-40 inches), the angularity of sand grains in dolomite soils could be used to deduce the rainfall conditions under which the soils were formed; a high degree of sand-grain angularity being indicative of wetter climatic conditions than low sand-grain angularity. A quantitative assessment of sand-grain angularity could be obtained by measuring

the porosity of the sand in question under compaction, samples containing angular grains giving a higher porosity reading than those containing rounded grains. Since surface-derived sand grains become incorporated in cavern breccias, this method can be employed on decalcified breccial residues to determine the nature of the extra-cavernous climate which prevailed during their accumulation.

Using a table of porosities for dolomite soils from areas of known rainfall as a basis of comparison, Brain (op. cit.) concluded that if the present rainfall at Makapansgat is 710mm (28 inches) per annum, the Phase II breccia must have accumulated during a drier period when the annual rainfall dropped to approximately 500mm (20 inches). Although the assessment of climate from porosity measurements of Phase I breccias is difficult since only a low proportion of surface-derived material is incorporated in them, Brain nevertheless concluded that the Upper Phase I breccia must have accumulated under even drier climatic conditions than those prevailing during Phase II times, that is, with a rainfall of less than 500mm (20 inches). The Lower Phase I breccia contains far too little surface-derived material to employ this method.

Butzer (1971) has challenged Brain's climatic deductions stating that:

> I am of the opinion that Brain's (sedimentological) analyses have little bearing on the environments actually contemporary with active deposition at the different sites. (p.1119)

apparently because of the time-lag between pedogenesis and the incorporation of outside soils as part of the cave-fills. He further states that:

> ....consequently the cave breccias do not provide convincing evidence of a fluctuating climate through time, at least not contemporary with active sedimentation..... The great bulk of the sediments at each site implies accumulation under relatively dry conditions ..... Any palaeo-climatic deductions will have to be based primarily on biological data. (p.1200)

With regard to the latter statement, and considering the Makapansgat Limeworks, Wells and Cooke (1956) concluded that:

> The total impression conveyed by the bovid fauna (of the grey breccia) suggests a moderately well-watered bushy valley opening out onto nearby plains, which at no great distance, were decidedly dry. (p. 49)

Eisenhart (1974) states that the cercopithecoid fauna of the grey breccia (which includes Cercopithecoides, Cercocebus and a large colobine) suggests that a gallery forest, flanked by brush, savanna, woodland and bushveld was present in the Makapan valley during grey breccia times. The decrease in the frequency of the three cercopithecoid forms mentioned above during the succeeding Upper Phase I period probably indicates that the gallery forest along the Makapan river was receding at this time. The paleo-environment and ecology of the Makapan valley has been discussed at some length in a subsequent chapter.

2.1.1.2 The Cave of Hearths

The Cave of Hearths, Historic Cave and Rainbow Cave are situated close together on a warm, bush-covered northeast facing hillside just within the narrow upper confines of the Makapansgat valley. Immediately adjacent to the Cave of Hearths, on its southeast side, is the double-entranced Historic or Makapan's Cave (the scene of a clash between the Voortrekkers and local Bantu in 1854) from whence the name of the farm and valley is derived. The Cave of Hearths and Historic Cave lie some 46m (150 ft) above the valley floor and immediately below the eastern entrance of the latter is Rainbow Cave, so named due to the presence in its breccial infill of several bands of ochreous-coloured ash. A general view of the Cave of Hearths hillside and the above-mentioned caves is shown in Fig. 12.

The Cave of Hearths was named in 1937 by Van Riet Lowe after he had noted the presence of a number of substantial hearths in the cave infill. The lowermost of these, overlying a bed of calcined bat guano which covered the travertine cave floor, proved to be the earliest evidence of the controlled use of fire in Africa (Oakley 1957b). A few hearths, one of which is shown in Fig. 13, are still visible today, recognizable by the distinctive coloration of fired cave earth and by the localized presence of fire-shattered and calcined bones.

As at the Limeworks, erosion has removed the original roof of the cave, so that the infill, except where covered with overburden and sparse vegetation, outcrops at the surface (Fig. 14). Little remains from which a reconstruction of the original cave form can be made, except that, like the adjacent Historic Cave, the Cave of Hearths probably had a lateral entrance. The occurrence of hearths close to the travertine floor indicates that the cave was accessible to humans almost

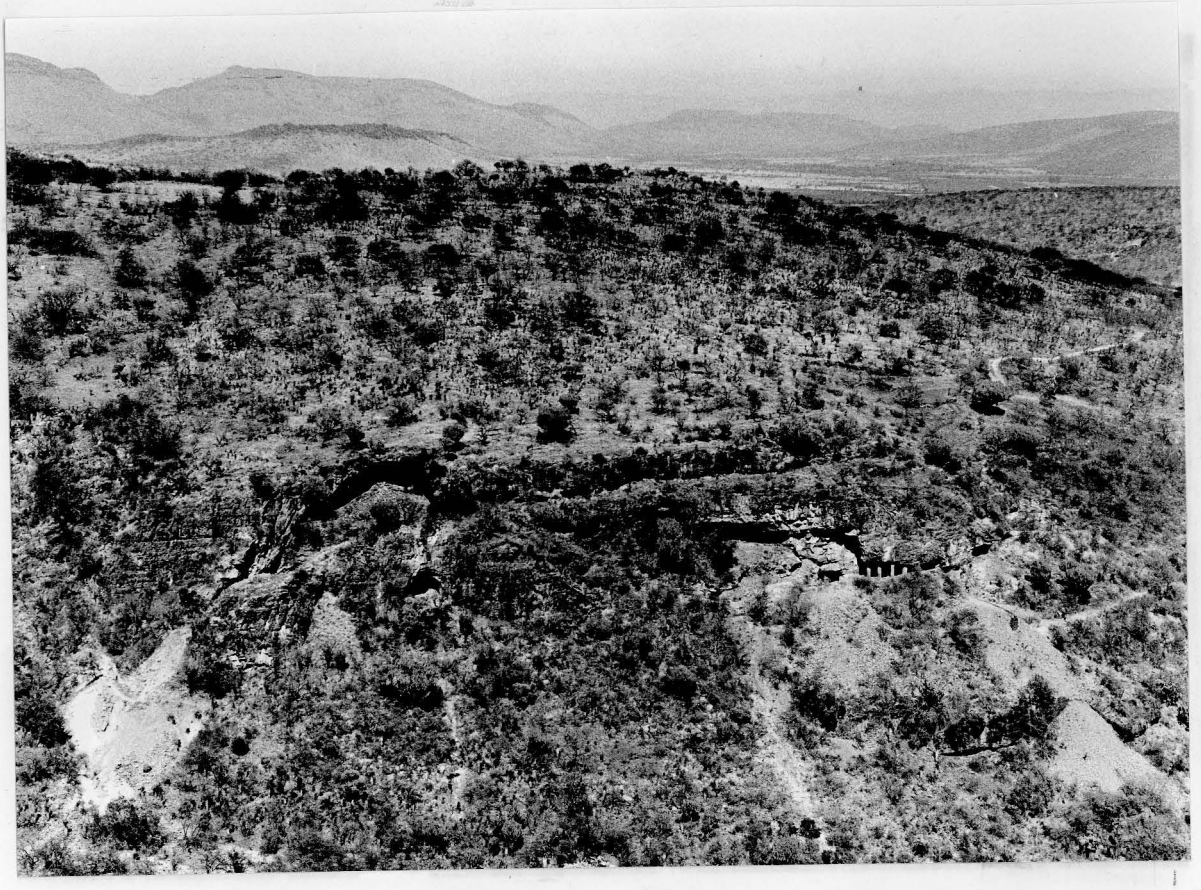


Fig. 12

The Cave of Hearths hillside as seen from the opposite slopes of the valley and looking south-westwards (June 1969).

The four pillars supporting the unexcavated breccial infill of the Cave of Hearths can be seen right of centre, and immediately to the left of the Cave of Hearths breccia is the wide, low, northern entrance of the Historic Cave. The large eastern mouth of the Historic Cave is seen towards the left of the picture, and directly below it the shadowed entrance to the Rainbow Cave. The pale-coloured scree littering the hillside has resulted from lime-mining and excavating activities.



Fig. 13

A hearth exposed on the lower surface of the pillar-supported unexcavated breccia in the Cave of Hearths.

The breccia at the site of the hearth is different in colour from the surrounding breccia. The splitting and fine fracturing (comminution) of bone is characteristic of the damage suffered by bones subjected to firing (De Graaff 1961).

Fig. 14

View of the pillar-supported remnant of the breccial infill of the Cave of Hearths (July 1970).

The breccia, except where covered with sparse vegetation, outcrops at the surface. The dolomite back wall of the cave is seen on the extreme left. The white streak crossing the entire depth of remaining breccia above the pillar, second from right, is the impression left by an ancient stalactite. In front of the standing figure lies the fractured remnant of the travertine floor, part of which subsided some 4,6m (15ft) giving rise to the sinkhole, partially visible in the left foreground. The stable floor travertine adjacent to the sinkhole supports Mason's 1,5m (5 ft) witness section of unexcavated breccia (partially shadowed), above which was the breccia from which the specimens marked CH were derived.

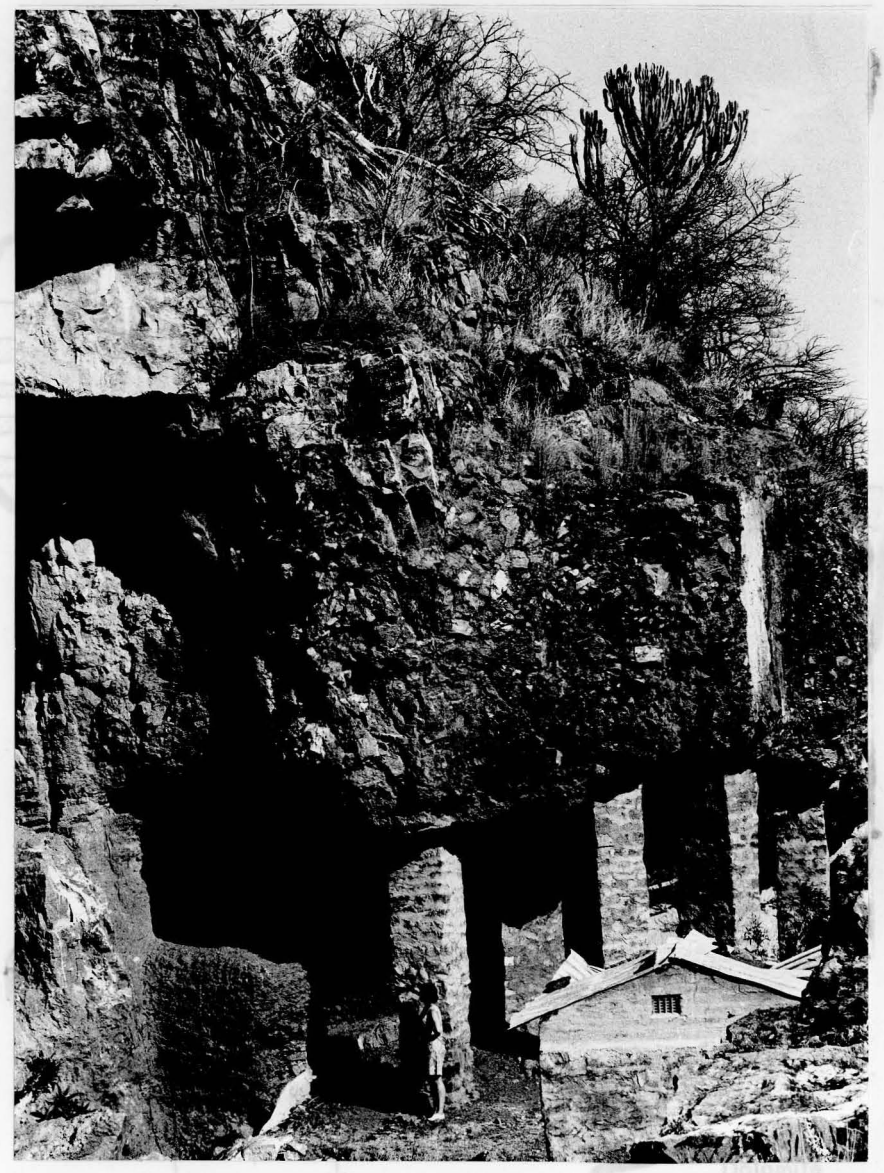


Fig. 14

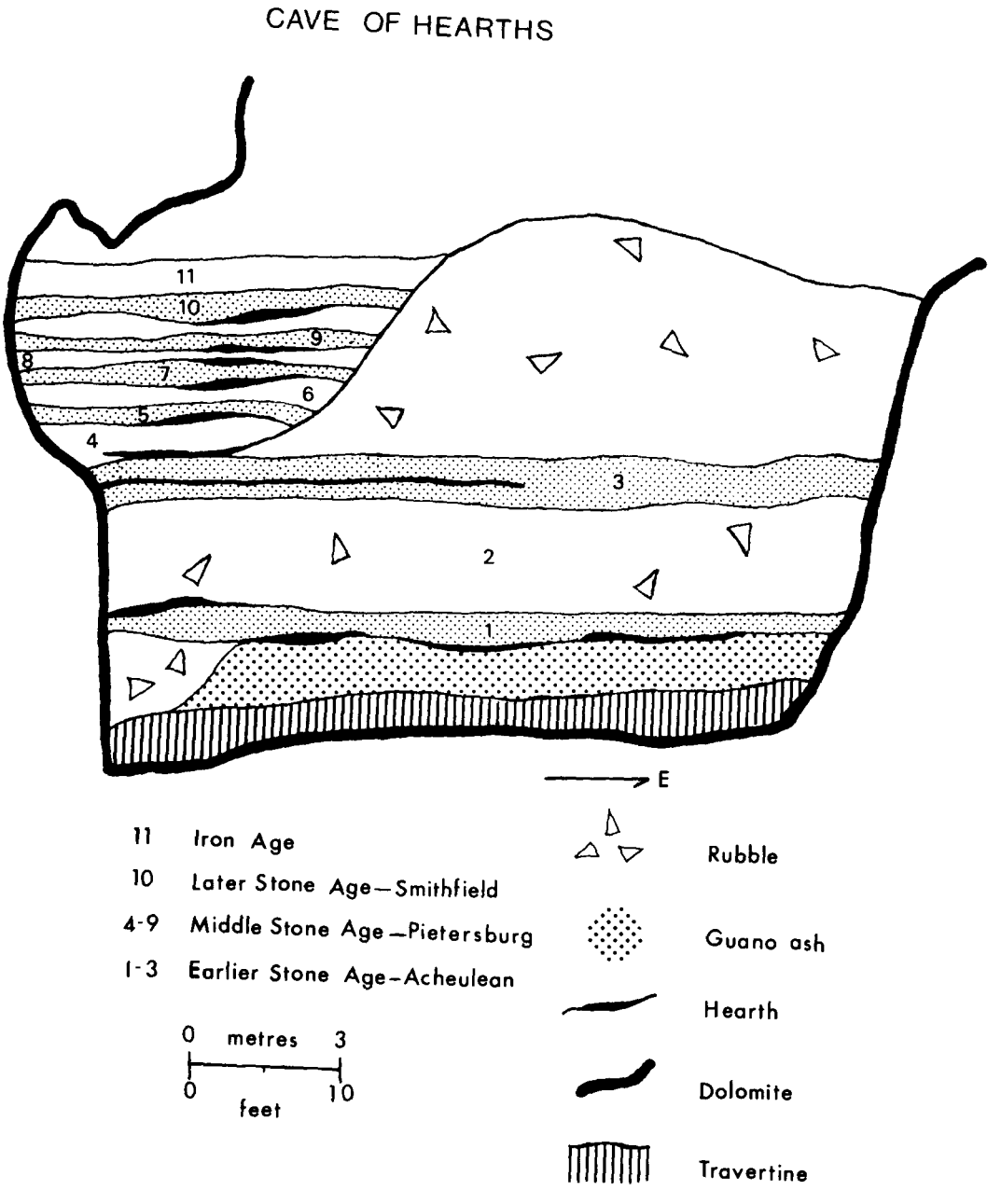


Fig. 15 Mason's 1962 stratigraphic profile of the Cave of Hearths. (Mason 1962 fig. 51)

from the time at which it first acquired an entrance, and the succession of hearths, bones and artefacts preserved in the deposit show that it was almost continually occupied throughout the period of time during which the infill was accumulating.

Systematic excavation of the Cave of Hearths breccia, which is all of the Phase II type, was begun in 1947 and was continued during 1953 and 1954 by Mason and Kitching; the former was finally able to suggest a stratigraphic sequence (Mason 1957; see also Appendix I, Table 1, p. 3).

Later (1962a), Mason published a diagrammatic reconstruction of the archaeological stratigraphy of the site. This reconstruction redrawn (from op. cit. fig. 51) and shown in Fig. 15, does not strictly agree with his 1957 stratigraphic interpretation. In the 1962 reconstruction it appears that the two LSA levels shown in the earlier sequence, Beds 10 and 11, have been combined to form one bed, Bed 10; consequently, the overlying Iron Age level is designated Bed 11 instead of Bed 12 as in the 1957 stratigraphic interpretation.

The stratigraphy and cultural terminology have since been rerevised (Mason 1971, pers. comm. 1972), based mainly on a multivariate analysis of the MSA artefact assemblage from Beds 4 to 9. The latest revision affects mainly the MSA levels, the original six beds having been divided into 15 stratigraphic units. The latest revision and the amended stratigraphic and cultural terminology ~~is~~ are shown in Appendix I, Tables I and II, pp.3, 4, Vol. II. Since the depth figures and bed numbers appearing on the porcupine material recovered from the site all refer to the 1957 stratigraphy, it is this sequence which is referred to throughout the present work.

The Cave of Hearths stratigraphy has been complicated by post-accumulation collapses of parts of the deposit due to the instability of the floor. One such collapse gave rise to a pocket at the back of the cave known as the 'swallow-hole' or 'sinkhole'. In this part of the deposit, a section of the travertine floor, together with the breccia supported by it, collapsed and slumped some 4,6 to 6,0m (15 to 20 ft), presumably into a subterranean chamber. Some degree of mixing of the deposit in this area was therefore inevitable, and the sinkhole was found to contain the fossilized remains of both Iron Age domestic animals and extinct species. Unfortunately, this 'mixed' breccia in and around the sinkhole has furnished most of the total

sample of identifiable bone fragments.

Ninety-one porcupine fragments have been recovered from the cave, representing almost every bed from the Earlier Stone Age in Bed I through to the Iron Age in Bed 12 (or 11). More than half of these (56) have come from the sinkhole, and a fair number of the remainder (27) have been derived from the 'CH breccia' immediately adjacent to the sinkhole (Fig. 14). J.W. Kitching, who has been associated with the excavation since its inception in 1947, has said that most of the sinkhole specimens probably belong to MSA levels (1970 pers. comm.).

The Cave of Hearths reflects almost all of the main stages of human activity known in southern Africa, from the final stages of the Earlier Stone Age towards the end of the Middle Pleistocene or early Upper Pleistocene to the arrival of the European in the area approximately a hundred years ago. However, the cultural evidence from the uppermost Phase II breccia at the Limeworks and the lowermost of the Earlier Stone Age levels (Bed 1) at the Cave of Hearths indicates that a considerable time lapse exists between the two deposits. This period covers part of the Early Pleistocene and much of the Middle Pleistocene, hence the valley provides no record of the long interval lying between later australopithecine times at the Limeworks and the advent of Homo sapiens rhodesiensis in the Later Acheulean levels at the base of the Cave of Hearths deposit.

2.1.2 The Blaaubank Valley Sites: Sterkfontein, Swartkrans and Kromdraai

These sites lie approximately 53km (33 miles) northwest of Johannesburg, and occupy small hillocks on either side of that part of the Blaaubank valley which winds with a very shallow gradient north-eastwards across the southern Transvaal highveld some 9,6km (6 miles) north of Krugersdorp (Fig. 2). Their relative positions are shown in Fig. 16.

The Highveld, which occupies the greater part of the southern Transvaal and adjacent parts of the Orange Free State, stretches from the Swaziland border in the east almost to the Botswana border in the west and is terminated in the north by the Magaliesberg. The terrain is one of low, rather uniform relief, forming a vast grass-covered upland of between 1390 to 1875m (4500-6000 ft). The Blaaubank valley itself has an elevation of approximately 1490m (4800 ft) in the vicinity of the three hillock sites. To the north, west and east of the valley, the country stretches away in a series of gently undulating

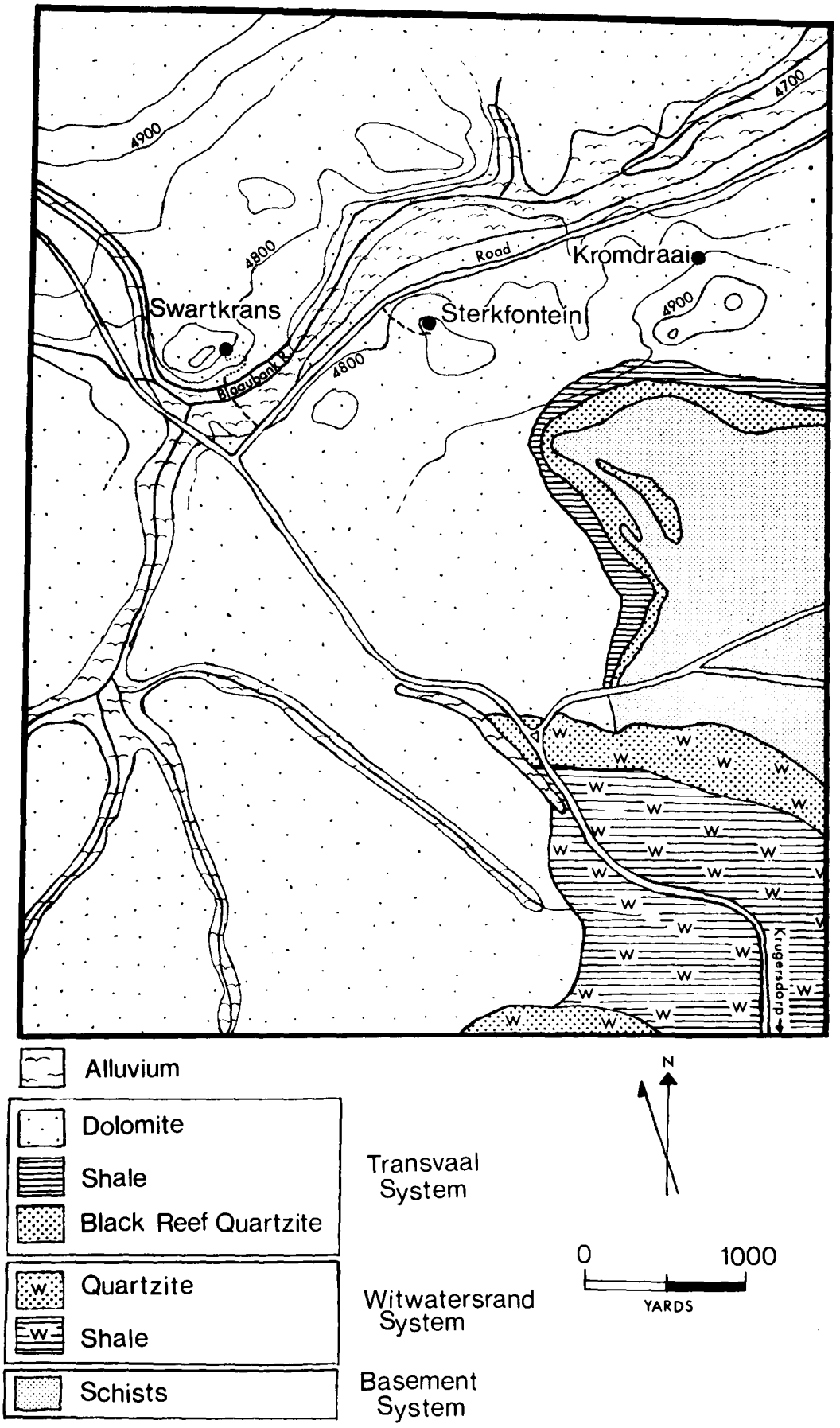


Fig.16 Map of the Sterkfontein area, showing geology and altitude and the positions of Swartkrans, Sterkfontein and Kromdraai relative to roads and to the Blaaubank stream. (after Brain 1958. figs. 37 and 38.)

low hills (Fig. 17). To the south is the Witwatersrand ridge which rises to almost 1875m (6000 ft) in places.

The rainfall in this part of the Highveld is moderate, averaging 760mm (30 inches) per annum (Brain 1958). However, the Blaaubank stream below the fossil sites is intermittent, as frequently happens in dolomite country, being perennial only from a point almost opposite and eastwards of Sterkfontein. Rainfall occurs mostly during sharp summer thunderstorms.

The summers are pleasantly warm with day temperatures of approximately 27°C (80°F) but the winters may be very cold with frequent heavy frosts and icy winds sometimes sweep the exposed hills.

The local relatively temperate climate favours a grassland, which covers the entire southern Highveld region (Figs. 2, 17). The tree cover is very distinctly sparser than at Makapansgat, and the trees that do occur are frequently found along stream courses or concentrated at the mouths of caves, fissures and sinkholes; the hills are often relatively bare. There are considerably fewer plant species than in the Makapansgat area, 401 species occurring in the immediate vicinity of the three cavern sites (Mogg 1972, pers. comm. and in press).

The area supports a less varied fauna than does the Makapansgat area, but according to the reports of early explorers and hunters, plains-loving antelope herds and those animals favouring open grassy country once occurred in countless numbers (Harris 1852). Their numbers rapidly dwindled with the arrival of European settlers in the area towards the turn of the last century.

Two types of australopithecine have been recovered from the Blaaubank valley sites, Sterkfontein having yielded remains of the lightly built or 'gracile' australopithecine, Australopithecus africanus, whilst A. robustus, the more heavily-built australopithecine, has been recovered from both Swartkrans and Kromdraai. In addition, a possibility exists that Homo habilis may be present at Sterkfontein (Tobias 1972). Cranial fragments of a more advanced hominid, generally thought to belong to either H. habilis or, more likely, to the pithecanthropine H. erectus have been recovered from Swartkrans. Recently, Robinson (in Brain et al. 1974) has assigned a hominid innominate from the Paranthropus breccia at Swartkrans to H. erectus. The importance of the Blaaubank valley sites can be gauged by the fact that, by 1972, Swartkrans and Sterkfontein between



Fig. 17

A view of the Swartkrans hillock from the Sterkfontein site (foreground) looking slightly south of west across the shallow valley formed by the Blaaubank stream.

The position of the Swartkrans excavation is marked by the trees and shrubs near the building on the low hillock (left). Note the low, gently-undulating grass-covered hills, which contrast strongly with the Makapansgat landscape (Fig. 4).

them had contributed nearly two-thirds of the total number of australopithecine specimens recovered from the whole of Africa, providing the largest and second largest site samples respectively (Tobias 1972).

The stratigraphy of these three sites is discussed briefly below:

2.1.2.1 Sterkfontein

The palaeontological significance of Sterkfontein was first recognised in 1935 with the discovery at the site of several specimens of a small extinct baboon. Dr. Broom's subsequent discovery (1936) of the first adult australopithecine skull made Sterkfontein world famous. The skull, first described as Australopithecus transvaalensis (Broom 1936, 1937a) and later as Plesianthropus transvaalensis (Broom 1937b) is currently considered to be conspecific with the original infant A. africanus skull from Taung (Robinson 1954). All the australopithecine fragments since recovered from the Sterkfontein breccias have likewise been referred to this taxon, although Tobias (1972) suggests the possibility that Homo habilis may be represented in the existing hominid sample from the West Pit. The possibility of discovering further hominids of course still exists.

The Sterkfontein site, like the Limeworks, represents the weathering remains of an ancient cavern and its breccial infill. Situated on the south-facing slope of a low hill on the south side of the Blaaubank valley, the Sterkfontein fossil site comprises the Type Site (STS), East Pit, Extension Location including the West Pit, (SE), the New Excavation, which is an extension of the Extension Locality, and several fossiliferous breccial dumps which were all once part of the Sterkfontein breccial mass (Fig. 18). The present known extent of breccia covers an area of roughly 75 x 33m (84 x 36 yds). Whilst the north, south and east walls of the ancient cave have been located, the western extremity of the breccia and its contact with the dolomite west wall has not yet been established (compass directions as indicated by I.B. Watt in Tobias and Hughes 1969 p.159). It is hoped that current work in the New Excavation will reveal this contact.

Reconstructions of the original form of the ancient cavern have been attempted by Brain (1958) and Robinson (1962). Robinson has suggested that the long fissure-like ancient cavern would have been inaccessible to all but the most agile of animals for a long time after

it had first acquired an entrance, because of a high vertical front (south) wall, or the steeply-inclined shaft which may have connected the cavern with the surface. Only after accumulation of infill had continued long enough to provide a sloping scree of material from the entrance to the floor of the cavern would occupation have become possible. This would account for the relative sterility of the lower levels of the breccia.

Mining activities and subsequent clearing-up operations have made observation of much of the stratigraphy possible. The first geological account was published by Cooke (1938). Reports by Haughton (1948), King (1951), Robinson (1952, 1962) and Brain (1958) followed, whilst the most recent stratigraphical comments are those of Tobias and Hughes (1969) and Partridge (1975, in preparation). The descriptions by Brain (1958), Robinson (1962) and Partridge's unpublished paper are the most detailed geological and stratigraphical records available.

Robinson in his paper describes three distinct breccias, and although his three-fold subdivision of the Sterkfontein deposit may require revision and supplementation in view of Partridge's recent work, it has been referred to throughout this text on account of its well-established position in the literature, and because of the lack of a published contradiction or improvement.

1. The Lower Breccia, Type Site Breccia or Pink Breccia
   (STS of Vrba 1974a and b; Member 4 Beds C and D of Partridge's unpublished work)
   The lower levels of this breccia are extremely stony and almost sterile, and have yielded no foreign lithic material or stone artefacts. Until recently, the upper levels have been regarded as the source of almost the entire australopithecine sample and associated fossil fauna.
2. The Middle Breccia, Artefact-bearing Breccia or Red-Brown Breccia
   (SE of Vrba 1974a and b, sensu lato, Member 5 of Partridge's unpublished work)
   This breccia, which Robinson thought rested unconformably upon the lower breccia mainly occupies the Extension Locality. It is the source of many diabase and quartzite artefacts (materials foreign to the Sterkfontein site) as well as a number of australopithecine remains and possibly the remains of a hominid more

advanced than Australopithecus, i.e. Homo sp. (See Tobias 1965 and Wallace 1972). Brain recently raised the question whether all the hominid remains formerly thought to have been derived from the lower breccia did not in fact come from the middle breccia (see Tobias and Hughes 1969).

3. The Upper Breccia or Chocolate Brown Breccia
(Member 6 of Partridge's unpublished work)
This is the most limited of the three breccias. It attains a maximum thickness of only three feet, and has yielded a number of lithic artefacts and a certain amount of bone amongst which Equus remains are more common than in the middle breccia.

Hughes (pers. comm. 1972) considers that the upper breccia simply represents decalcifying middle breccia whilst Tobias and Hughes (1969) state that:

> the whole question of the lower (Type Site) and middle breccias must be considered to be once more in the melting pot (Tobias and Hughes 1969 p.164).

Current opinion thus tends to support Robinson's interpretation of at least three discrete breccias, whilst Partridge's work indicates the presence of additional breccias at the site. Furthermore, an analysis of the fossil bovidae from the Type Site, Extension Site and breccial dumps has shown evidence that these have been accumulated at three different periods and under varying ecological conditions (see Vrba 1974a and b; 1975).

Seventeen of the 22 fossil porcupine specimens from Sterkfontein have been recovered from discarded miners' waste dumps, namely Dumps 1, 2, 8, 10 and 13 (Fig. 18) whilst the remainder have supposedly been retrieved from the Type Site (STS) to which Broom's fossil collecting was confined. (The Sterkfontein specimens borrowed from the Transvaal Museum were collected by Broom). According to Vrba (1974a) it is possible, on the basis of the fossil bovid content, to relate stratigraphically certain of the breccia dumps to their probable site of origin within the cavern deposit; thus Dump 13 has affinities with the Type Site (STS), whilst Dump 1 shows affinities with the Extension Locality (SE). Dump 8 has more in common with Dumps 16 and 6 than with either the Type Site or the Extension Locality; these three dumps appear not to be related to any specifically named Sterkfontein breccia. It was also not possible to correlate Dumps 2 and 10 on account of their low fossil

bovid content.

With regard to the climate that prevailed during the accumulation period at Sterkfontein, Brain (1958), on the basis of sand-grain angularity and chert-quartz ratio determinations, concluded that a general increase in rainfall, with minor fluctuations, had occurred at Sterkfontein from Type Site breccia times onwards.

The evidence of the fossil bovids (Vrba 1974a and b; 1975) seems to contradict this to a certain extent. Basing her argument on the premise that high percentages of Alcelaphines and Antilopines in the bovid fauna are indicative of grassland conditions, she has concluded that the relatively wet STS breccia period (only 51-55% Alcelaphines and Antilopines, and therefore a substantial bush cover) was followed by a drier or perhaps colder period, during which grassland conditions prevailed, as indicated by the substantial increase in the percentage of Antilopines and Alcelaphines (81-85%) present in the Extension Site and West Pit breccias, which stratigraphically overlie the Type Site breccia. This grassland period was in turn succeeded by a period of increased rainfall or temperature (or both), during which the D16 material was accumulated.

A ground plan, a stratigraphic section and a site photograph have been provided in explanation of the general appearance of the Sterkfontein site (Figs. 18, 19, 20).

2.1.2.2 Swartkrans

Swartkrans, the world's richest fossil hominid site, lies on the south-facing slope of a low hillock on the northern bank of the Blaaubank valley, less than 1,6km (1 mile) to the west of the Sterkfontein site. Excavations were started there in 1948,and almost immediately the remains of a robust australopithecine were blasted out of a pink breccia. These were assigned to Paranthropus, a genus which had been described by Broom from the nearby Kromdraai locality ten years previously, but a new species, P. crassidens Broom 1949, was created to accommodate the new material. The P. crassidens material from Swartkrans is at present usually classified as Australopithecus robustus crassidens (Campbell 1963) and is considered to be conspecific with Paranthropus robustus Broom 1938 (now Australopithecus robustus robustus) from Kromdraai. Many authors, however, consider that the gracile (Australopithecus) and robust (Paranthropus) australopithecines are

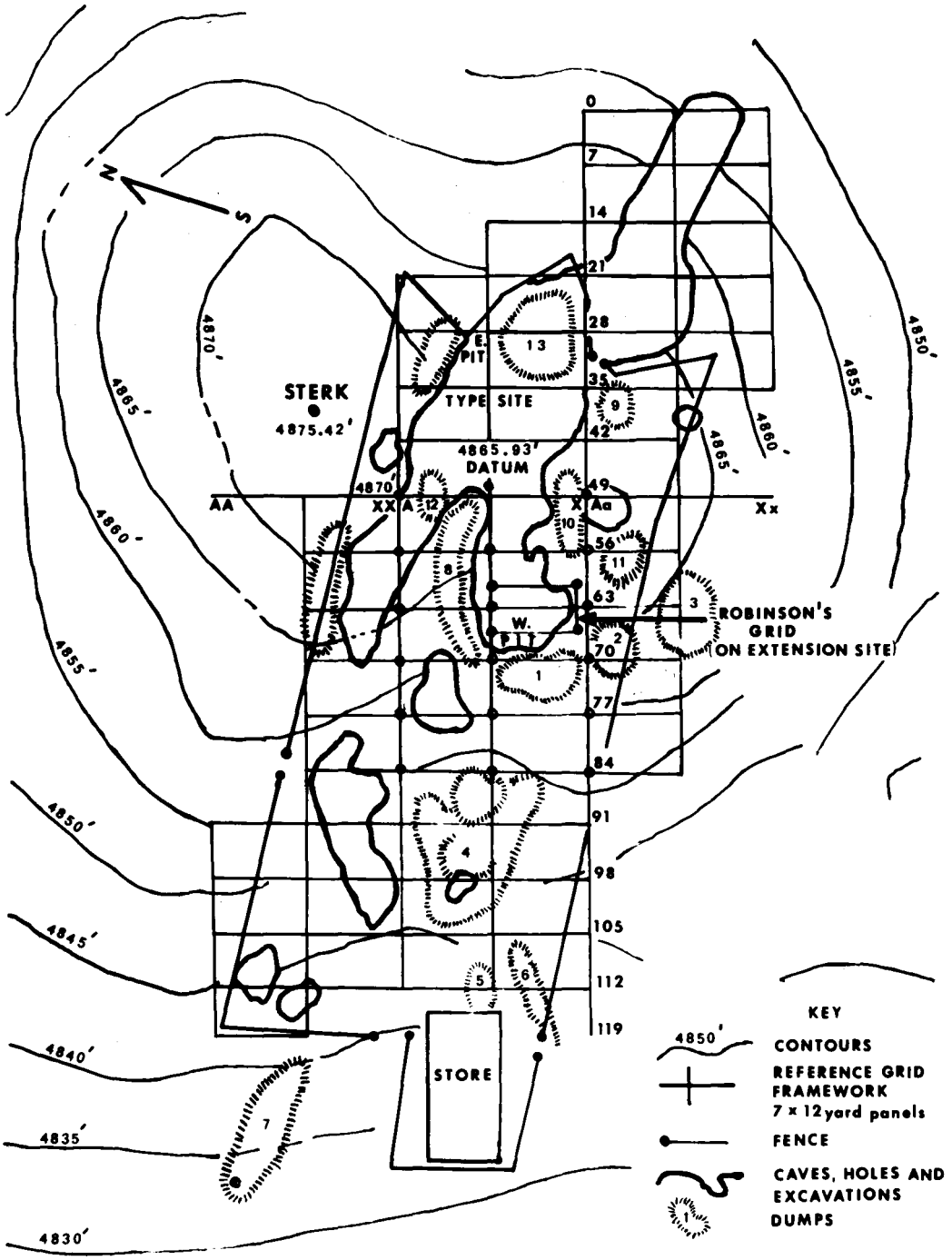


Fig. 18 Contour plan of the Sterkfontein koppie showing excavations and the present grid framework. (after Watt, I.B. in Tobias and Hughes 1969)

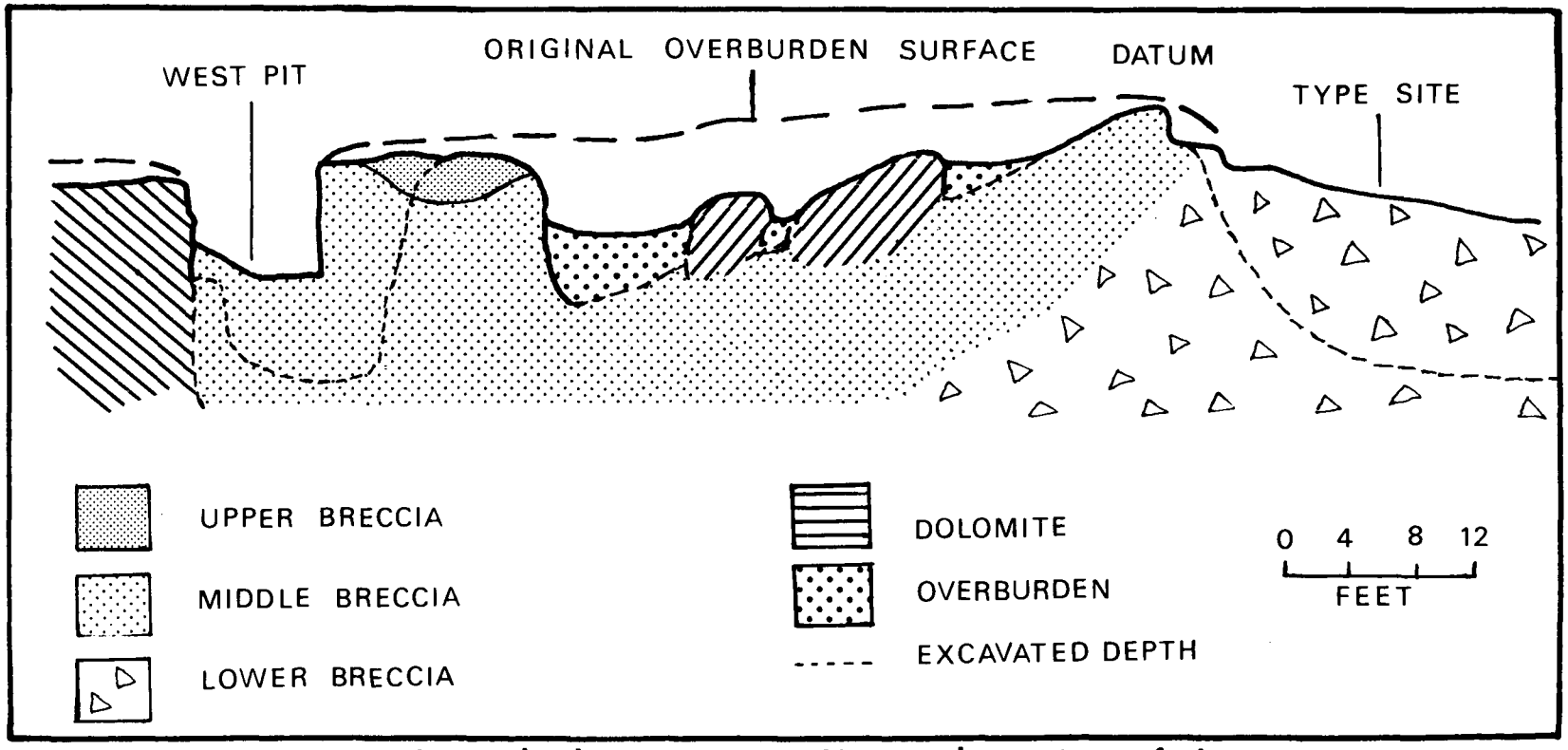


Fig. 19 E-W section through the Extension Site and portion of the Type Site showing breccias. (after Robinson 1962)

Fig. 20

A view across the Sterkfontein Type Site looking slightly north of west.

The Type Site breccia, containing many dolomite blocks and fragments cemented together with lime, occupies the foreground. Part of the original roof of the ancient cavern is still intact and can be seen sloping down to the right from the centre of the picture. Large blocks of dolomite which have collapsed from it lie erratically on the left. A narrow band of white travertine (right of centre) separates the so-called Type Site breccia from the overlying Middle breccia. The Upper breccia cannot be seen clearly in this photograph, and much of the overburden has been removed. The posts mark the grid of the New Excavation, which incorporates Robinson's Extension Site. A small part of the Swartkrans hillock can be seen in the background (extreme left).



Fig. 20

generically distinct and the term 'Paranthropus' is frequently upheld in reference to the robust form. Recent discoveries of both male and female specimens of the robust type of australopithecine in the East Rudolf region of East Africa seem to preclude the possibility that Australopithecus africanus may represent the female of A. robustus (or Paranthropus robustus): it therefore appears that sexual dimorphism does not account for the differences between A. africanus and A. robustus (A. Walker 1972 pers. comm.) as was thought by some workers.

In 1949 the mandible of a hominid seemingly more advanced than either A. robustus or A. africanus was recovered and named Telanthropus capensis (Broom and Robinson 1949). Later examination revealed that the form exhibited too many advanced features for it not to be included in the genus Homo and it was renamed Homo erectus (Robinson 1961, Tobias and von Koenigswald 1964), since it resembled the East African 'Pithecanthropine' hominids of the same name from Bed II at Olduvai Gorge. However, there is as yet little finality as to the true taxonomic status of this fossil, speculation revolving around the question of whether it is actually pithecanthropine or whether it has closer affinities with the ultra-gracile Olduvai hominid, Homo habilis. Until this matter is resolved, it is perhaps best to refer to it as Homo sp. indet. (A hominid innominate recently retrieved from the 'Paranthropus' breccia has been referred to as H. erectus (Robinson, in Brain et al. 1974)).

The presence of an indisputable lithic industry in the breccias at Swartkrans has been attributed to the activities of the last-mentioned hominid, since it is the most advanced hominid present. Dr. M. Leakey, in comparing these stone tools with artefact assemblages from Olduvai Gorge, has found striking similarities with assemblages from Bed II of the latter site, which also yielded H. erectus (Leakey, M.D. 1970).

By 1967, Swartkrans had provided almost half the total African australopithecine sample available, the remains of at least 70 A. robustus individuals having been distinguished from the more than 530 hominid fragments recovered (Brain 1967d; 1972 pers. comm.). A rich varied fossil fauna represented by more than 14,000 specimens has been found in association with the hominid remains. Fifteen fossilized porcupine fragments have been recovered from various breccias at the site.

Despite the high concentration of hominid and faunal remains in the Swartkrans breccias, it seems improbable that hominids ever actually

occupied the cavern itself, because if Brain's reconstruction (1967d; 1970b) of the original cavern is correct, access to the cavern would have been impossible for almost all creatures except bats and owls (See Fig. 21a). It is probable, however, that the rock shelter shown in Fig 21a was occupied from time to time, and that bones and artefacts dropped in its vicinity were funnelled downwards into the cavern below where they became fossilized and incorporated in the breccia. The deposit is therefore largely a reflection of events occurring in the catchment area above the cavern during the accumulation period.

The Swartkrans cavern was originally thought to have contained two breccias: an outer cavern unstratified pink bone-rich breccia and an inner cavern stratified brown relatively bone-sterile breccia (Brain 1958). A plan and stratigraphic section of the site as originally interpreted is shown in Fig 22A and B. Later investigations at a lower level in the cavern revealed the presence of a third breccia, the exact nature of which has not yet been fully determined (Brain 1970b) and even more recent discoveries at the site have made it essential that the entire stratigraphic interpretation be revised (Brain 1975, in press).

Initially, it was thought (Brain and Voight pers. comm. 1973) that 14 of the 15 Swartkrans fossil porcupine specimens had been derived from what Brain (1958) had termed the 'outer cavern unstratified pink breccia', the single exception being a specimen derived from a dump of decalcified breccia. The Outer Cave now appears (Brain 1975, in press) to contain deposits of at least three distinct ages instead of a homogeneous unstratified pink breccia as proposed in 1958. The oldest of these is a pinkish breccia ('Primary Breccia', Brain et al. 1974; 'Swartkrans Member 1' Butzer 1974) equivalent to the 'outer cavern unstratified pink breccia', Brain (1958) and termed SKa by Vrba (1975): this is followed by a younger brownish breccia ('Secondary Breccia' Brain 1974; 'Swartkrans Member 2' Butzer 1974) which is the same as the 'inner cavern stratified brown breccia' (Brain 1958) and earlier termed SKb by Vrba (op. cit.). These two breccias are separated by an erosional unconformity of long standing. Cutting into both 'Primary' and 'Secondary' breccias are erosion channels, the fills of which constitute an even younger breccia, exhibiting varying degrees of calcification. It appears likely that the channel fills are of differing ages, the latter being termed 'Inter SKb' by Vrba (op. cit.).

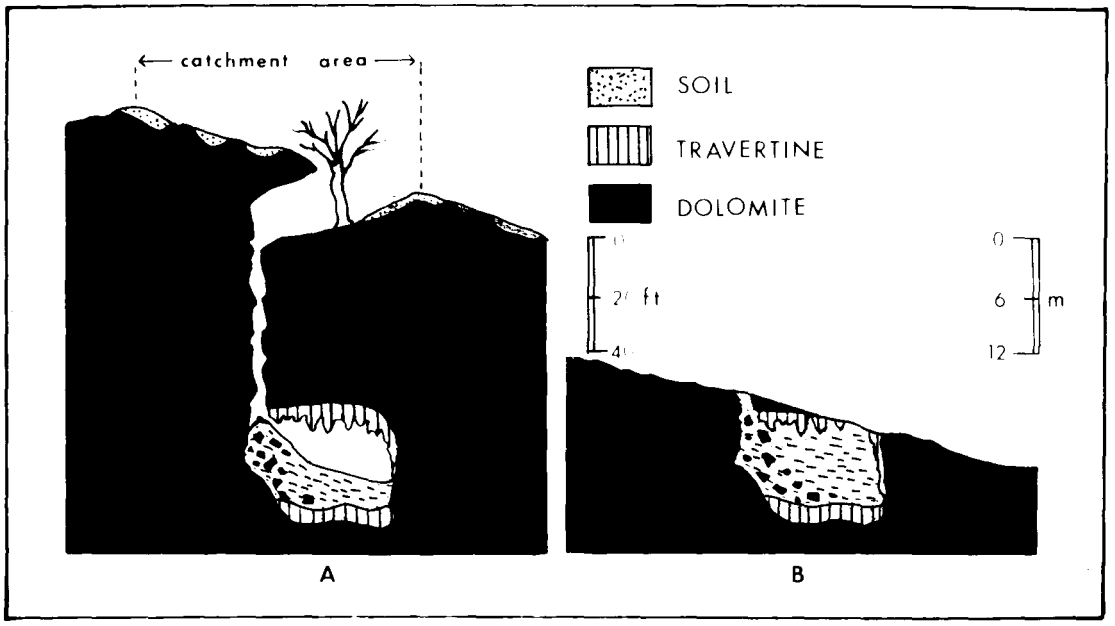
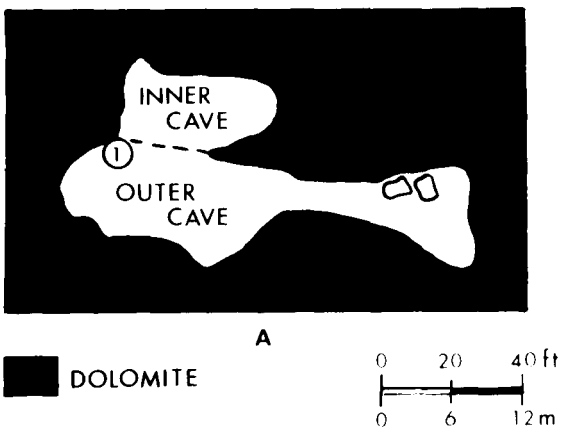


Fig. 21 Diagrammatic N–S vertical section through the Swartkrans hillside: A: reconstructed original rockshelter and shaft and B: with the shaft removed by erosion as it is today. after Brain 1967d and 1970b



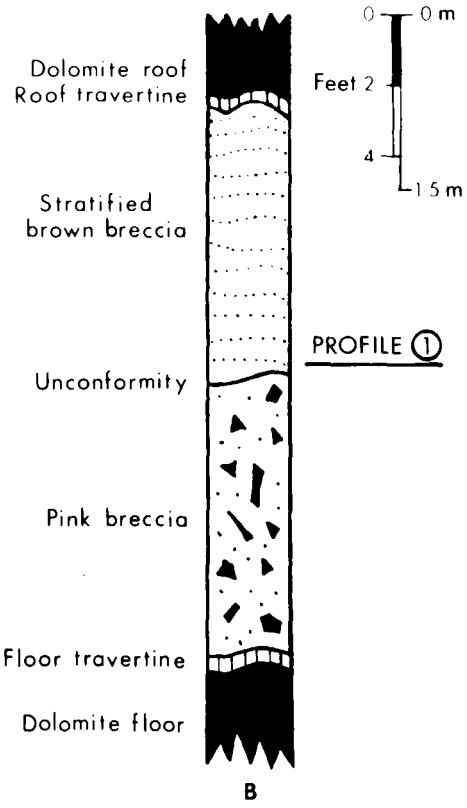


Fig. 22 A: Plan of the Swartkrans site showing extent of inner and outer caves and the location of profile 1. B: Stratigraphic profile through point 1, showing breccias. (after Brain 1958)

The 'Primary Breccia', apart from its pinkish colour, is apparently characterized by the presence of numerous rodent bones and manganese-free chert inclusions, as well as by the fact that the fossil bone is frequently manganese-stained. The 'Secondary Breccia', on the other hand, is characterized by a lack of micro-faunal remains and by the presence of manganese-stained chert inclusions. An examination of the breccia still adherent to some of the Swartkrans porcupine fossils has shown that the creature is represented in both the 'Primary' and 'Secondary' breccias, and probably in the channel fills as well. Other specimens have unfortunately been entirely cleared of matrix so that their exact breccial source will probably remain undeterminable.

It has recently been demonstrated (Brain, in preparation) that the type specimen of Telanthropus capensis mentioned above was actually embedded in what is at present termed the 'Secondary Breccia' of the outer cave, although additional material was also recovered from the underlying and much older 'Primary Breccia'. The Paranthropus material, however, appears to be confined to the older 'Primary Breccia'. Lithic artefacts are present in both breccias, those from the secondary breccia seemingly being more advanced.

With regard to the extra-cavernous climate which prevailed during the accumulation period, Brain (1958) concluded that:

> .....the accumulation of the Swartkrans deposit began and ended under conditions comparable with those of the present day. The middle breccia levels reflect a drier interlude which, however, was probably not very intense. It is probable that the climate became appreciably wetter than that of the present day in times immediately following the accumulation period. (p.85)

Vrba (1975 p.303) has concluded that the fossil antelopes making up the Swartkrans bovid fauna (from both SKa and SKb) are predominantly antilopines and alcelaphines (80%) of various sizes, many of which show drought adaptations, implying a drier and/or colder environment that that which prevailed during Sterkfontein Type Site times.

2.1.2.3 Kromdraai

The Kromdraai locality comprises two separate pockets of breccia: Kromdraai A, which has yielded many well-preserved faunal specimens but no hominid material, and Kromdraai B, which has yielded all the hominid material so far discovered, but comparatively few faunal remains.

It was from the Kromdraai B breccia that Broom obtained the type specimen of the robust form of australopithecine which he named Paranthropus robustus (Broom 1938), a taxon which was subsequently re-named Australopithecus robustus robustus (Campbell 1963). Since no faunal remains seem to have been associated with the Paranthropus material at the time, Broom undertook the excavation of the nearby Kromdraai A exposure, thinking that as the two breccias were so close together he could safely associate the faunal remains from this bone-rich deposit with the Paranthropus breccia of the Kromdraai B deposit. The Kromdraai A fauna, which includes 4 specimens of a fossil porcupine, were subsequently considered to be contemporaneous with Paranthropus but Vrba (1972 pers. comm.) is of the opinion that the faunal material since analysed from the Paranthropus-bearing Kromdraai breccia differs considerably in several respects from the Kromdraai A fauna, and that there appears to be no valid justification for this association, or for assuming that the two deposits are contemporaneous.

Erosion has been so intense that no vestige of a roof (if ever such existed) is evident at either the Kromdraai A or the Kromdraai B sites, and a reconstruction of the original form of the sites, whether cavern or fissure, is not possible.

The only stratigraphic investigation of these exposures is that of Brain (1958). The faunal-bearing Kromdraai A breccia is an almost rectangular exposure of some 24 x 6m (80 x 20 ft). According to Brain (op. cit.) the breccia which is all of the Phase II type, is divisible into a coarse-grained bone-sterile stony breccia which occupies the eastern end of the site, and a finer-grained well-stratified breccia filling the remaining volume of the cave (Fig. 23). The breccia is deep chocolate brown in colour, tinged in places with red and becoming appreciably pinker towards the surface.

After an analysis of the porosity of sand-grains incorporated in the Kromdraai A breccia, Brain (op. cit.) concluded that the deposit was formed under conditions rather drier than the present; this conclusion appears to be supported by Vrba's (1975) deductions based on a study of the bovid fauna from the site.

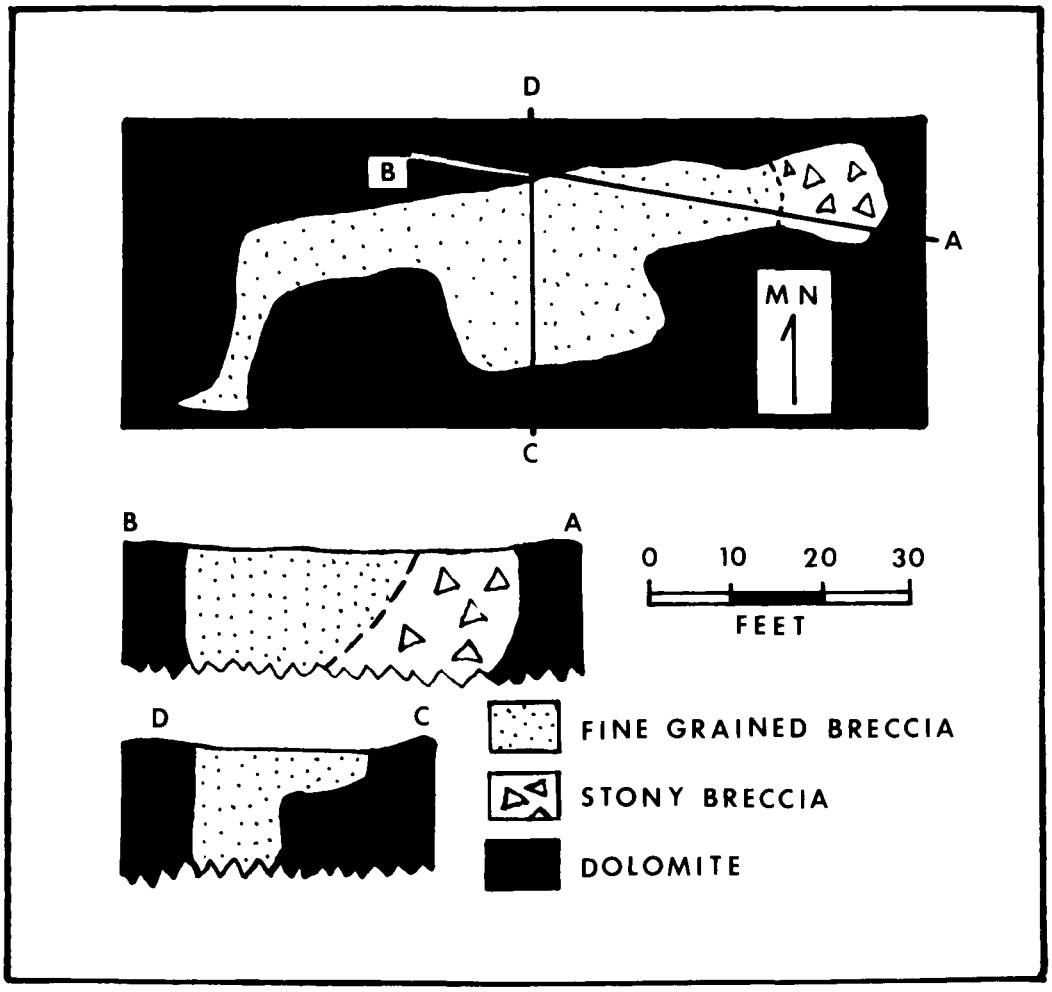


Fig. 23 A plan and vertical sections through the Kromdraai A cave. (after Brain 1958)

2.2 The age of the fossil deposits

2.2.1 The age of the australopithecine deposits

Together, the five South African australopithecine deposits provide an important body of evidence for the study of human and cultural origins and evolution. As such, it is unfortunate that not one of the sites has as yet provided an 'absolute' date, despite the variety of modern dating techniques available. Consequently, the manner in which these deposits and their contents relate to the calibrated faunal, hominid and cultural evolutionary sequences rapidly being established for East African Miocene, Pliocene and Pleistocene deposits remains tantalizingly uncertain. Until dates are available for the South African deposits, it will remain difficult to formulate a unified picture of African faunal and cultural evolution.

The failure of 'absolute' dating techniques to provide even tentative ages for the South African cave deposits has meant that their ages relative to one another are equally conjectural, sequential arrangements arrived at being based largely on the indirect and less secure method of correlating local uncalibrated faunal assemblages. The results of some of the more important attempts at both relative and absolute dating of the above sites have been tabulated in historical order in Table I; this Table shows that despite fifty years of investigation the answer to both absolute and relative aspects of the age question is still uncertain.

However, in order to provide some sort of temporal background for the fossil material described, a summary of the conclusions reached on both absolute and relative dating aspects has been given below, attention being drawn to several factors which might substantially affect the reliability of the dates given.

2.2.1.1 The absolute ages of the australopithecine deposits

The main techniques available for obtaining 'absolute' dates from geological deposits are listed below:

1) Radiocarbon ($^{14}C/^{12}C$) assays
2) Potassium-Argon ($^{40}K/^{40}Ar$) assays
3) $^{40}Ar/^{39}Ar$ dating, using the step-heating technique
4) Heavy isotope dating, including the Rubidium-Strontium, Uranium-Lead, $^{234}U/^{231}Pa/^{230}Th$ and $^{16}O/^{18}O$ decay series in the dating of carbonates

SUMMARY OF THE ABSOLUTE AND RELATIVE DATING OF THE SOUTH AFRICAN AUSTRALOPITHECINE LOCALITIES

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT*	BASIS
Dart 1926	pre-Pliocene	-	-	-	-	-	Geological and geomorphological considerations
Cooke 1938	-	Upper Pleistocene	-	-	-	-	Sedimentological analyses, palaeoclimatological comparisons
Cooke 1941	Late Lower Pleistocene (Taung) → Early Upper Pleistocene (Kromdraai)					-	
Broom 1946	Middle→ Upper Pliocene	Upper Pliocene	-	-	Lower Pleistocene	Taung, Sterkfontein, Kromdraai	Faunal comparisons with European occurrences
Haughton 1948	All sites contemporaneous, no absolute age suggested. Makapan not mentioned.					-	Geology, sedimentology
Broom 1950	Upper Pliocene	Upper Pliocene	Upper Pliocene	Not specifically mentioned	Lower Pleistocene	Makapansgat, Taung Sterkfontein, Swartkrans, Kromdraai	Faunal comparisons
Cooke 1951, 1952	All sites contemporaneous,'(faunal comparison) favours a broad correlation of the ape-man fauna with the lower Quaternary stage known as the Villafranchian'					-	Faunal comparisons
King 1951	All sites contemporaneous, = 'Older Red Sand' or late Pliocene					-	Geology, sedimentology
Robinson 1952	'the youngest of these deposits is not later than Lower Pleistocene ...Upper Pliocene seems the most reasonable date as an approximation for the deposits as a whole.'					Sites of varying ages, no definite sequence provided	Geology, faunal comparisons

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT*	BASIS
Oakley 1954	Late Kageran, First Pluvial (Lower Pleistocene)	Late Kageran First Pluvial (Lower Pleistocene)	Late Kageran First Pluvial (Lower Pleistocene)	Early Kamasian Second Pluvial (Early Mid. Pleist.)	Early Kamasian Second Pluvial (Early Mid. Pleist.)	Makapansgat Taung Sterkfontein Swartkrans Kromdraai	Sedimentology, palaeoclimatology faunal comparisons
Howell 1954	Final Kageran Pluvial	Final Kageran Pluvial	Final Kageran Pluvial	Early Kamasian Pluvial	Early Kamasian Pluvial	Makapansgat Sterkfontein Taung	
Howell 1955	Early→ Middle Kageran Lower Pleistocene (Villafranchian)	Early→Middle Kageran Lower Pleistocene, (Villafranchian)	Upper Kageran Lower Pleistocene (Villafranchian) (pink breccia)	Upper Kageran Lower Pleistocene (Villafranchian)	Upper Kageran Lower Pleistocene (Villafranchian)	Sterkfontein,Taung (either older or younger than STS) Makapansgat Swartkrans Kromdraai	Stratigraphic and palaeoclimatological analyses, faunal comparisons
Ewer 1956 1957	Kageran Villafranchian	Kageran Villafranchian	Kageran Villafranchian	Kageran Villafranchian	Kageran Villafranchian	Sterkfontein,Taung (either older than contemporaneous with or younger than STS), Makapansgat Swartkrans Kromdraai	Age is 'mean age' based on comparisons of % extinct genera and species with dated deposits elsewhere
Oakley 1957a	Late Kageran	Late Kageran	Late Kageran	Early Kamasian	Early Kamasian	Taung,Sterkfontein Makapansgat Swartkrans Kromdraai	Palaeoclimatology, faunal comparisons, geology

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT*	BASIS
Wells and Cooke 1956	Middle Kageran First Pluvial	Middle Kageran First Pluvial	Late Kageran First Pluvial → Kageran-Kamasian Interpluvial → Lower Kamasian Second Pluvial	Kamasian Second Pluvial	Kamasian Second Pluvial	Taung, Sterkfontein Makapansgat Swartkrans Kromdraai	Faunal and palaeoenvironmental evidence
Oakley 1958	Late Villafranchian = Günz 500,000	Late Villafranchian = Günz 500,000	Late Villafranchian = Günz 500,000	Probably Cromerian	Probably Cromerian	-	Faunal, geological and palaeoenvironmental evidence
Brain 1958	-	Lower Kageran-Kamasian Interpluvial	Middle Kageran-Kamasian Interpluvial	Upper Kageran-Kamasian Interpluvial	Middle Kamasian Pluvial	Taung not considered Sterkfontein Makapansgat Swartkrans Kromdraai	Sedimentological analyses and palaeoclimatological evidence
Kurten 1957 1960	Cromerian (Mid-Middle Pleistocene)	Cromerian (Mid-Middle Pleistocene)	Cromerian (Mid-Middle Pleistocene)	Mindel (Upper Middle Pleistocene)	Mindel (Upper Middle Pleistocene)	-	Faunal comparisons with Europe
Robinson 1961 1962	-	STS: Lower Kageran-Kamasian Interpluvial SE: Upper Kageran Kamasian Interpluvial (= Upper Bed I Olduvai Gorge 1,23 m.y.B.P.)	Middle Kageran-Kamasian Interpluvial	Lower Kamasian Pluvial	Middle Kamasian Pluvial	Sterkfontein Type Site Makapansgat Sterkfontein Extension Site Swartkrans Kromdraai	Palaeoclimatological comparisons with East Africa

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT *	BASIS
Wells 1962	Sterkfontein Faunal Stage Lower Pleistocene	Sterkfontein Faunal Stage Lower Pleistocene (Type site) Swartkrans Faunal Stage (Extension Site)	Sterkfontein Faunal Stage	Swartkrans Faunal Stage	Swartkrans Faunal Stage	Sterkfontein Type Site, Taung? Makapansgat Sterkfontein Extension Site Swartkrans Kromdraai	Composition of faunal assemblages, % extinct forms. No absolute ages suggested
Cooke 1963	Villafranchian (Günz)	Villafranchian (Type site) Cromerian or Uppermost Villafranchian (Extension Site)	Villafranchian (Günz)	Cromerian or Uppermost Villafranchian	Cromerian or Uppermost Villafranchian	Sterkfontein Type Site, Taung Makapansgat Sterkfontein Extension Site Swartkrans Kromdraai	Faunal comparisons with Europe
Ewer and Cooke 1964 Cooke 1967	Sterkfontein Faunal Stage or Span	Sterkfontein Faunal Stage or Span	Sterkfontein Faunal Stage or Span	Swartkrans Faunal Stage or Span	Swartkrans Faunal Stage or Span	-	Composition of faunal assemblages, proportions of extinct and extant forms. No absolute ages suggested
Wells 1969	Swartkrans Kromdraai Faunal Span?	Sterkfontein Faunal Span (Type Site)	Sterkfontein Faunal Span	Swartkrans-Kromdraai Faunal Span or Swartkrans-Kromdraai → Cornelia Faunal Span or Swartkrans Faunal Span	Swartkrans-Kromdraai Faunal Span or Swartkrans-Kromdraai → Cornelia Faunal Span or New Faunal span intermediate between Swartkrans and Kromdraai	Makapansgat Sterkfontein Swartkrans Kromdraai Taung not the oldest. Position of Taung not indicated	Composition of faunal assemblages, proportions of extinct and extant forms. No absolute ages suggested

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT*	BASIS
Leakey M.D. 1970	-	Artefact-bearing breccias = Bed II Olduvai Gorge	Quartzite flakes and utilized pieces not assignable to any recognised East African Culture	Artefact-bearing breccias = Bed II Olduvai Gorge	-	-	Correlation of artefact assemblages with those at Olduvai Gorge
Cooke 1970	-	2,5-3,0m.y. B.P. = Middle Shungura Formation (Omo) = Lowest Koobi Fora (East Rudolf)	2,5-3,0m.y. B.P. = Middle Shungura Formation (Omo) = Lowest Koobi Fora (East Rudolf)	Upper Member of Olduvai Gorge Bed I < 1,8 m.y. B.P.	-	-	Comparison of Sterkfontein and Makapansgat suids and the Makapansgat proboscids with East African occurrences
Partridge 1973	< 0,87 m.y.B.P.	3,26 m.y.B.P.	3,67 m.y.B.P.	2,57m.y.B.P.	-	Makapansgat Sterkfontein Swartkrans Taung	Geomorphological dating (see text)
Tobias 1973 1974	0,8-0,7 m.y.B.P.	2,5-3,0 m.y.B.P.	2,5-3,0 m.y.B.P.	2,0-< 2,2 m.y.B.P. (From Fig.1, 1973)	> 1,5-2,0 m.y.B.P. (From Fig. 1, 1973)	Makapansgat Sterkfontein Swartkrans Kromdraai Taung	Based on synthesis of Partridge's geomorphological dates and faunal dates of Cooke (1970)

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT*	BASIS
Butzer 1974	Swartkrans Kromdraai Faunal Span	-	-	-	-	-	Geomorphological, sedimentological and faunal evidence
Vrba 1974a	-	Sterkfontein Faunal Span (Type Site and Dumps 13,14, 15) Swartkrans Faunal Span or Cornelia Faunal Span (Extension locality and Dumps 1,5 and H2) Florisbad or Florisbad-Vlakkraal Faunal Span (Dumps 16,8, 6), = MSA	Sterkfontein Faunal Span	Culturally similar to the developed Oldowan in Bed II Olduvai Gorge Swartkrans Faunal Span	-	Makapansgat Sterkfontein TS i) or Sterkfontein TS Makapansgat Sterkfontein Extension Site, Swartkrans, or Swartkrans Sterkfontein ES ii) Kromdraai Sterkfontein Faunal Stage C (Dumps 16,8,6)	Analysis of Bovid faunal content

i) Type Site

ii) Extension Locality

AUTHOR	TAUNG	STERKFONTEIN	MAKAPANSGAT	SWARTKRANS	KROMDRAAI A	CHRONOLOGICAL ARRANGEMENT*	BASIS
Vrba i) 1974b	-	1,7-2,0 + m.y. B.P. Sterkfontein Faunal Span (Type Site) < 0,7 m.y.B.P. Cornelia Faunal Span (Extension Site) < 50,000-100,000 yrs. B.P.,Florisbad Faunal Span Dump 16)	Sterkfontein Faunal Span	SKa: 1-1,8 m.y.B.P. Swartkrans Faunal Span SKb (earlier): Late Cornelia Faunal Span SKb (later): Florisbad Faunal Span < 50,000-100,000 yrs. B.P.	+- 0,7-1,0 m.y.B.P. Early Cornelia Faunal Span (Kromdraai A) Cornelia Faunal Span (Kromdraai B)	Makapansgat Sterkfontein TS Swartkrans Member 1 or a, Kromdraai Faunal locality Sterkfontein Extension Locality Kromdraai australopithecine locality Early Swartkrans Member 2 or b, Later Swartkrans Member 2 or b Sterkfontein Dump 16. Taung not placed	Analysis of Bovid faunal content
Hendey 1974b	-	Early Makapanian (Plio-Pleistocene)	Early Makapanian (Plio-Pleistocene	Late Makapanian (Lower Pleistocene)	Late Makapanian (Lower Pleistocene)	No absolute ages suggested. Makapanian span covers 700,000-3,0 m.y. B.P.	Composition of faunal assemblages

* From oldest to youngest

i) Vrba's age estimates for Makapansgat Limeworks and Sterkfontein Type Site represent upper limits only

5) Fission-track dating
6) Dating using the racemization or epimerization rate of the residual amino acids in bone collagen
7) Thermoluminescence
8) Geomorphological dating
9) Transregional faunal and cultural correlations
10) Sedimentological analyses and palaeoclimatological dating
11) Palaeomagnetic reversals

Of these, the first seven are direct means of obtaining 'absolute' dates. The geomorphological method is an indirect means of obtaining an estimate for the maximum date of the original opening of the caves to the surface. The remaining three are also indirect methods in that the primary information is used in a comparative way with dated sequences or events elsewhere.

Only 8) and 9) have provided any results worth mentioning, this being due to the failure of the sites to provide materials suitable for direct dating.

The geomorphological method, developed by Partridge (1973) dates the earliest possible time at which the australopithecine caves could have first acquired entrances and thus become accessible for the accumulation of surface-derived deposit and hominid, faunal and cultural remains. The method relies on the established date of the last uplift of the African continent and the rate of recession inland of nickpoints associated with the ensuing erosion cycle, which was also responsible for exposing the caverns to the surface. The following dates for the first opening of the australopithecine caverns and hence for the base of the introduced deposit have been suggested (op. cit. p. 77) :

Taung	0,8 m.y. B.P.
Swartkrans	2,6 m.y. B.P.
Sterkfontein	3,3 m.y. B.P.
Makapansgat	3,7 m.y. B.P.

The suggested figures predate by an unknown period of time the fossil-bearing sections of the deposits; at Sterkfontein and Makapansgat at least, the main fossiliferous layers are underlain by considerable depths of sterile breccia. This may account for the discrepancies observable between the

geomorphological dates and those obtained by means of faunal comparisons.

The geomorphological method appears to embody a variety of variables and the reliability of the methodology employed has yet to be established. Until such time, the dates proposed should be regarded as approximations.

The negative results of all attempts at dating the cave deposits using direct methods has meant that the comparison of South African faunal and cultural assemblages with those from dated sequences in East Africa and elsewhere is still the most successful means of obtaining age estimates. However, there are several factors which affect the reliability of 'absolute' dates derived by this method. These are discussed below. These factors equally affect the reliability of the numerous sequential arrangements of the five cave sites arrived at using faunal and cultural comparisons.

1) The derived dates are only as reliable as the 'absolute' dates for the comparative faunas and,as Cooke and Maglio (1972) have pointed out, such 'absolute' age determinations are still subject to error. With regard to this, it has recently been discovered (Clark Howell 1975 pers. comm.) that percolating carbonaceous solutions in the East Rudolf sediments appear to have caused the material selected for dating to register ages considerably in excess of what they should be; for example 2,6 m.y. B.P. for the KBS tuff of the Koobi Fora deposit as opposed to a revised date of 1,8 m.y. B.P. The dates reported for the richly fossiliferous sediments of this region should therefore be treated with caution, as should dates for South African fossils derived by comparison with the faunal and cultural assemblages from this area.

2) There is a need to compare total faunal assemblages and for the compilation of comprehensive faunal lists to facilitate this, because, as Ewer (1957) has pointed out

> ".....it would be possible, by picking out individual genera as our examples, to support almost any conceivable view on the question of dating." (p. 135)

This stems from the fact that some genera are extremely conservative, persisting virtually unchanged for long periods of time. For example, some of the Makapansgat and Sterkfontein bovidae and

the black and white rhinoceroses from the former site are indistinguishable from their modern counterparts. Used in isolation such conservative forms are unsuitable for correlative purposes. On the other hand, other forms and notably members of the Suidae, Elephantidae and Equidae were evolving rapidly. Furthermore, members of these groups (as are their modern representatives) were widely distributed in Africa and their fossil remains are well represented at both open (East Africa) and in cave (South Africa) sites. Obviously then, different genera have differing comparative value, emphasizing the need for comparing the total fauna present. However, correlations between East and southern Africa using rapidly- evolving widely distributed groups is feasible whereas the use of conservative genera or those with low ecological tolerance and restricted occurrence is not.

Even the use of forms having the latter requirements can be unsatisfactory. The pigs, for example, seem to indicate an age between 1,7 and 2,6 m.y.B.P. for the Sterkfontein site, whereas the elephant Elephas ekorensis, reported to occur at Sterkfontein (Cooke and Maglio 1972) has an East African time range of +- 3,8 - 4,2 m.y.B.P. (op.cit.), much in excess of the age for the site as indicated by the Suidae. Again, the need for comparison of total faunas is indicated, but comprehensive faunal lists are lacking in both areas due to the following factors:

i) The rate of recovery of fossils far outstrips their description, and few people are available to perform identifications.

ii) The frequently very fragmentary condition of the fossil material makes identification difficult, tentative or impossible. As a result, frequent renaming of fossils as additional or more complete material comes to light is common, so that faunal lists have to be constantly updated.

iii) The opinions of taxonomists frequently differ as to the identity of fragmentary or juvenile specimens. This is particularly significant when there are several workers on a particular group of animals working in widely separated areas. For example, in a recent unpublished experiment conducted by R.G. Welbourne of the Witwatersrand University Archaeological Department three prominent specialists in the field of mammal palaeontology were asked to identify 25 recent bovid tooth specimens. In only one case, that of the Kudu specimen, did

the opinions of all three agree; in many cases three different identifications were given for one specimen. The 'lumper-splitter' problem is also a perennial one.

iv) Certain groups of animals such as hominids, baboons and other primates, the carnivores and bovines are 'popular' and have been intensively studied whereas others remain neglected.

v) The South African australopithecine sites are incompletely excavated, most of the fossils having come from rubble and breccia dumps left by limestone-mining activities. The fossils available for description therefore represent a sample only of the sample of the total fauna that has been preserved. One site, Taung, has been completely destroyed, so that no further additions to the faunal list from this site can be expected.

vi) The extraction of specimens from their rock-hard breccial matrix is a slow and exacting process.

3) Variation in the fossil faunal composition of two localities may be due either to a time separation, or to ecological differences between the two areas or to a difference in the agent or agents responsible for the accumulation of the bones. Obviously, in the case of sites which are in close proximity to one another faunal differences are more likely to be attributable to the latter two factors. The wide separation and ecological differences between the East and southern African fossil localities and even between Taung, the Blaaubank Valley sites and Makapansgat constitute a problem in faunal correlations - a whole range of species might be absent from one deposit because the environment did not support them. The actual present day extent of these claimed ecological differences has never been examined and would make a worthwhile modern comparative study; there seems no reason to suppose that these differences would have been exaggerated in past times and the information would assist fossil faunal correlations.

As mentioned in 2 above, animals that have a wide ecological tolerance are usually also widely distributed and of particular use in faunal dating, provided that they are not evolutionary 'conservatives'. Ecologically sensitive species with restricted habitat preferences such as hippo, bushbuck, gemsbuck and many other bovids are usually neglected in faunal comparisons but are

useful indicators of past climatic conditions. Complete faunal lists would be useful in establishing the degree and nature of the environmental differences between two areas so that this could be allowed for.

4) Differences in the modes of accumulation and preservation of the fossils in the East African open lacustrine and fluviatile deposits and in the South African cave fills are bound to cause fundamental differences in their faunal compositions.

At both, and at cavern sites particularly, the range of species preserved depends largely on the nature of the bone accumulating agent or agents in operation. These agents probably varied from site to site depending on the local environment and on the original form of the cave and the suitability of its immediate vicinity for hominid or carnivore habitation.

Since the cave deposits are now known to cover substantial periods of time it is probable that bone accumulating agents changed with time, so that different agents were responsible for various parts of the fossil bone accumulation within them, as Vrba (1974a) has suggested for Sterkfontein. Although bones do accumulate within caves by means of wash-in and 'accidents', the main agents are humans and hominids, porcupines and carnivores such as leopards, hyaenas and perhaps sabre-tooths. Apart from porcupines, which are largely indiscriminate bone collectors, each of the other agents would tend to accumulate the bones of only a certain range of species, because as predators and scavengers each has definite prey preferences and hunting capabilities. Each of these agents is therefore likely to provide a different sample of the total existing fauna, so that potential bone-accumulating agents should be considered when comparing fossil faunas. The whole matter of bone accumulating agents and the characteristics of the bone assemblages resulting from each has been discussed at length in Part II.

5) Another point to bear in mind concerning the derived ages for the South African sites is that until recently the faunal remains from different sections or 'site units' at each locality were 'lumped' and considered as a whole when faunal comparisons were made. Although little is known about the rate of accumulation of cave deposits, it is now generally recognized that the cave fills

represent many hundreds of thousands of years (Butzer 1971; Tobias 1974; Vrba 1974a) and Brain (1975, in preparation) reports that at Swartkrans a time-unconformity of long standing separates SKa and SKb (see section 2.1.2.2). With this lapse of time, it would be unreasonable not to expect changes in faunal composition from site unit to site unit within one deposit. The faunas of different site units should therefore be considered as separate entities for purposes of correlation. However, in many cases this is no longer possible: as mentioned previously, most specimens have been derived from breccial dumps and many of these have had all traces of their encasing breccial matrix removed, so that it is no longer possible to relate them with certainty to in situ portions of the deposit. This is true also of many lithic artefacts. Furthermore, every one of the cave sites has been extensively damaged by limestone-mining activities, whole site units may have been removed or displaced, leaving no trace in the remaining exposed sections of in situ deposit. Faunal uncertainty is greatest at Taung, where almost the entire breccial deposit at the site has been destroyed, or covered by rubble from mining activities.

For all these reasons, dates derived from faunal correlations should be treated cautiously.

Some of the ages proposed for the South African sites using faunal correlations are shown in Table I. Corroborative faunal evidence not included in the age derivations shown in Table I stems from the following:

At Makapansgat, the spotted hyaena Crocuta cf. crocuta makes its first appearance in Phase II Breccia times (Member 5, Partridge 1975 in preparation), apparently having displaced hyaenids typical of the earlier grey breccia period, namely Hyaena hyaena makapani (small striped hyaena) and Hyaena cf. brevirostris (large hyaenid) (Randall 1973; Collings et al. 1975, in preparation). In East Africa, the White Sands locality in the Omo Basin has yielded the earliest record of Crocuta crocuta, dated at 2,75 m.y.B.P. (Howell et al. 1969). Since there is no record of this genus below the Phase II breccia, the latter may be at least as old as 2,75 m.y.B.P.

According to Hooijer (1975 pers. comm.) the presence of both Diceros bicornis and Ceratotherium simum (black and white rhinos,

indistinguishable from recent) in the grey breccia indicates that the Limeworks is no older than 4,0 m.y.B.P. as these species do not occur before this date.

To date, the Hystricidae have not provided much information on the dating problem because the Hystrix remains occurring in dated East African deposits have not yet been determined. Porcupines have been recorded in the fossil faunas of the following East African localities:

Koobi Fora II, III (East Rudolf)	1,3-2,6 m.y.B.P.	Large Hystrix (Maglio 1971)
Olduvai Gorge Bed I (Lower, Middle and Upper i)	1,75 m.y.B.P.	Large Hystrix (Leakey, L.S.B. 1965) (Leakey, M.D. 1971)
Olduvai Gorge Bed V	+- 250,000 B.P.	H. galeata (Leakey L.S.B. 1965)
Laetolil	2,00 m.y.B.P.	H. galeata (Leakey 1967)
White Sands (Usno Formation)	2,75-3,1 m.y.B.P.	H. sp. (Howell et al. 1969)
Brown Sands (Usno Formation)	2,75-3,1 m.y.B.P.	H. sp. (Howell et al. 1969)
Chemeron	<2,0->5,4 m.y.B.P.	cf. Xenohystrix crassidens (Bishop 1972)
Kanapoi	4,0-4,5 m.y.B.P.	H. sp. (Patterson et al. 1970)
Kaperyon	<5,0 m.y.B.P.	Hystricidae (Bishop 1972)

The distinctive giant porcupine Xenohystrix crassidens, common in the Makapansgat grey breccia, is represented in the overlying Upper Phase I breccia by only two fragmentary juvenile specimens; it does not occur in the Phase II breccia or at any other South African australopithecine site. If Makapansgat is indeed the oldest of the five South African australopithecine deposits, it seems as if Xenohystrix became extinct during the period immediately following grey breccia

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i) At Olduvai Gorge, Hystrix sp. has been recorded from Lower Bed I (DK, L/2) Middle Bed I (FLK 'Zinj' Level'; FLK NN, L (1) and Upper Bed I (FLK, N, L/1, 6), and also at site MK I of Bed I.

times. In East Africa, this easily-recognizable form has tentatively been recorded from the Chemeron formation, which has a date of 2,0-5,4 m.y.B.P. In conversation with Bishop at the 1975 SASQUA conference (Cape Town) he mentioned that the cf. Xenohystrix crassidens specimens come from the lowermost fossiliferous horizons at Chemeron. The basal basalt at the site, dated at 5,4 m.y.B.P. has a weathered surface, which indicates that the overlying fossiliferous horizons are somewhat younger than this date, and Bishop suggests an age of ± 3,0 m.y.B.P. for the specimens in question. The date of ± 2,75 m.y.B.P. for the Phase II breccia suggested above therefore seems not unreasonable. Until such time as the East African forms are identified, little more can be said concerning the Hystricidae and age determinations.

Artefact-bearing localities present the possibility of trans-regional cultural comparisons in the same way as fossil faunas are used. Thus M.D. Leakey (1971) on the basis of the artefact assemblages from Sterkfontein and Swartkrans (in both instances derived from more than one site unit) has concluded that they compare very closely with the Developed Oldowan from the middle of Bed II at Olduvai Gorge, suggesting a date of 1,0-1,7 m.y.B.P. (Hay, in Leakey, M.D. 1971) for the breccias from which the artefacts were derived.

The presence of indisputably flaked stone tools of considerable refinement in the 2,6 million-year old Koobi Fora deposit suggests that stone tool-making probably had its origin prior to this date, perhaps as early as 3,0 million years (Leakey, M.D. 1970; Fitch et al. 1970) or a little later (± 2,75 m.y.B.P.), if the date for the Koobi Fora deposit proves to be younger. At Makapansgat Limeworks, some crude stone artefacts extracted from the Phase II breccia by Brain et al. (1955) and initially assigned to the now discredited 'Kafuan Culture' were subsequently and probably incorrectly (B. Maguire, pers. comm.) attributed to natural causes. However, it now seems evident that very crude stone artefacts of lithic material both endogenous and foreign to the site are clearly present in the Upper Phase I, the Phase II and in the decalcified overburden at the site (Maguire 1965, 1968; Partridge 1965; Leakey M.D. 1970; Tobias 1973). Their primitive nature suggests that they predate the 2,6 million-year old tools from Koobi Fora, but as to date it has not been possible to equate them with any part of the cultural sequence established in East Africa. Since, with the exception of the very occasional

* But see section 16.2.1 p.518 for further discussion on the age and identity of the Chemeron porcupine

utilized fragments of stalactite, only bone, tooth and horn tools (the Osteodontokeratic Culture of Dart 1957a and b) are present in the grey breccia, the stone tools in the overlying Upper Phase I and Phase II breccias probably represent the earliest known experiments in stone tool manufacture.

In sum, the geomorphological, faunal and cultural evidence indicates the following ages for the South African deposits:

Taung:	Estimates range from > 0,7 m.y.B.P. to about the age of STS
Kromdraai B:	Cornelia Faunal Span
Kromdraai A:	$\pm$ 0,7-1,0 m.y.B.P., early Cornelia Faunal Span
Swartkrans:	
SKb (later):	< 50,000-> 100,000 years, Florisbad Faunal Span
SKb (early):	Late Cornelia Faunal Span
SKa:	1,8-2,57 m.y.B.P.
Sterkfontein:	
D16, D8, D6:	< 50,000-100,000 years, Florisbad Faunal Span
SE:	< 0,7 m.y.B.P., Cornelia Faunal Span - 1,23 m.y.B.P.
STS:	1,7-3,26 m.y.B.P.
Makapansgat:	
Phase II:	$\pm$ 2,6-2,75 m.y.B.P.[i]
(Member 5, Partridge 1975 in preparation)	
Upper Phase I:	$\pm$ 2,75-3,0 m.y.B.P.
(Member 4, Partridge 1975 in preparation)	
Lower Phase I:	$\pm$ 3,0-3,67 m.y.B.P. but not much older than 4,00 m.y.B.P.
(Members 2 and 3, Partridge 1975 in preparation)	

If a date of 1,8 m.y.B.P. is accepted for the Plio-Pleistocene boundary (Van Couvering 1972) then the bulk of the South African australopithecine deposits should be regarded as Pliocene.

2.2.1.2 The relative ages of the australopithecine deposits

In the absence of absolute dates, the commonest means of obtaining a chronological arrangement for a series of localities is by means of analysing and comparing their respective fossil faunas. Various

i) Partridge (1975 in prep.) describes an unconformity between the Upper Phase I and Phase II breccias which may represent a considerable lapse of time. If this is so, the base of the Phase II breccia could be younger than 2,75 m.y.B.P.

analyses are made, the most usual being an assessment of the number of species common to two or more sites (sites with a high ratio of shared species are likely to be close to one another in time) and assessments of the number of extinct, or conversely, extant species present (sites with a high proportion of extinct species are likely to be older than localities which have few extinct species).

Many factors influence the reliability of arrangements arrived at in this way and items 2), 3), 4) and 5) of the preceding section apply equally well to relative dating by faunal comparisons. With reference to the methods outlined above, Vrba (1974b) has pointed out a few additional problems:

1) Site units with few identified species have less chance of contributing 'shared species';

2) Few and fragmentary specimens may provide insufficient information for distinguishing a species that is really extinct from a modern form,

> In other words, a site unit with a high proportion of such peripheral species may assume an undeservedly modern aspect, in comparison with one of similar antiquity, but containing ample material per species.
> (Vrba 1974b p.127)

3) Extinct species at different sites (or in different site units) may be diagnostic of different time periods.

The sequential arrangements of a large number of authors have been shown in Table I. These may be summarized as follows, from youngest to oldest:

Dumps 16, 8 and 6 at Sterkfontein
Swartkrans Member 2 or b 'Secondary Breccia' (SKb)
Kromdraai australopithecine locality (KB)
Sterkfontein Extension Locality (SE)
Kromdraai faunal locality (KA)
Swartkrans Member 1 or a 'Primary Breccia' (SKa)
Sterkfontein Type Site locality (STS)
Makapansgat Limeworks

It is obvious from the dates proposed at the end of the preceding section that part of the Makapansgat Limeworks deposit may overlap with part of Sterkfontein.

The position of the Taung locality in relation to the above sequence is uncertain. Partridge, using geomorphological methods, has

proposed a date of < 0,87 m.y.B.P. for the site and would therefore place it as contemporaneous with or immediately following KA, as the absolute dates provided in the preceding section indicate. Using faunal correlations, however, Taung has usually been placed as the oldest site (preceding Makapansgat or Sterkfontein), overlapping with the latter two localities or immediately following Sterkfontein. Since the faunal list from Taung is an abbreviated one, and since the site no longer exists, the uncertainty concerning its age is likely to persist, at least until very comprehensive faunal lists are available for the other four australopithecine localities.

Furthermore, because there were at least three distinct breccial bodies in the vicinity of the Taung australopithecine locality (Dart's Cave, Hrdlicka's Cave and Spier's Cave; Peabody, 1954), probably of differing ages, and because it is usually not possible to relate the fossils from Taung with any certainty to any definite breccial body, faunal comparisons are made more difficult.

Examination of Table I will show that there is further uncertainty concerning the relative ages of Makapansgat and Sterkfontein, most modern arrangements placing the former locality as earlier than Sterkfontein and therefore the oldest South African australopithecine site. To date, the Makapansgat locality has been treated as a unit, though there is evidence that the fossil fauna from this site should be treated as coming from at least five different units: the basal red breccia; the grey breccia; the 'rodent breccia'; the Phase I breccia and the Phase II breccia (Maier 1970; Kitching 1974 pers. comm.). Once this is done, it is probable that the breccias overlying the grey breccia will be found to overlap in time with those from one or more of the other localities.

2.2.2 The age of the Cave of Hearths

The Cave of Hearths stratigraphic sequence was published by Mason in 1962 and with it appeared the first absolute dates for various ash levels incorporated in the deposit. The samples for dating were processed by Libby (see Mason 1962) but the results, achieved in the pioneering days of radio-carbon dating, exhibit several anomalies and can no longer be accepted (Mason 1971, p.1). Unfortunately, further direct radiocarbon dating appears out of the question as no further charcoal samples from the site are available.

Dates for various levels in the Cave of Hearths sequence have been obtained indirectly by comparing their artefact assemblages with dated artefact assemblages from other archaeological sites in South Africa and elsewhere. Recently published ^{14}C dates (GrN-5116, 51,000 B.C. Vogel 1969) for Middle Stone Age (MSA) artefacts at Bushman Rock Shelter near Olrigstad in the eastern Transvaal, which are very similar to the Middle Pietersburg MSA artefacts present in Bed 5 of the Cave of Hearths (see Table II), seem to suggest that the latter were in production before 52,000 yrs. B.P. This estimate is far older than the 11,000-15,000 yrs. B.P. as suggested by Libby.

Recent discoveries would seem to indicate that much of or even the entire MSA lies beyond the normal dating range of radiocarbon, i.e. $\pm$ 40,000 yrs. B.P. Beaumont (1973) has found that levels which yielded Final MSA-type artefacts at Border Cave, Ingwavuma, northern Natal, give dates in excess of 48,000 yrs. B.P. whilst the Later Stone Age artefacts in overlying levels are dated at ca. 37,000 yrs. B.P. This suggests that the MSA terminated at ca. 40-45,000 yrs. B.P., that is, near the limit of radiocarbon dating.

Wymer and Singer (1972) have reported the occurrence of MSA artefacts from the 6-8m beach at Klasies River Mouth on the Tzitzikama coast, which Butzer and Helgren (1972) consider to have accumulated during the last or Eemian Interglacial. The most recent date for this Interglacial is ca. 120-130,000 yrs. B.P. (Kukla, Matthews and Mitchell 1972) which suggests that at least part of the MSA extends to 130,000 yrs. B.P. or beyond. This gives at least an approximate age for the Early Stone Age-Middle Stone Age interface at the Cave of Hearths (see Table II).

The Later Acheulian Culture present in Beds 1-3 at the Cave of Hearths must therefore predate 130,000 yrs. B.P. In connection with this Clark Howell et al.(1972) have published ^{230}Pa and ^{231}Pa dates of 260,000 $\pm$ 70,000 - 40,000 B.P. and > 170,000 B.P. respectively for bone from an Acheulian site at Isimila in Tanzania, which gives some indication of the possible age of Beds 1-3.

Since the onset of the Eemian Interglacial is supposed to mark the beginning of the Upper Pleistocene, the entire ESA, and possibly the early part of the MSA falls within the Middle Pleistocene.

A summary of the dating of the Cave of Hearths is given in Table II.

TABLE II

SUMMARY OF THE DATING OF THE CAVE OF HEARTHS

Stratigraphic Unit	Cultural Status	Radiometric date (Libby in Mason, 1962a)	Extrapolated date B.P. (Mason 1971, pers. comm.)	Maximum possible date B.P.
Bed 11	Iron Age		1,000	1,600 i)
Bed 10	LSA 'Smithfield'		20,000	37,000 ii)
	Epi-Pietersburg			> 50,000 ii)
Bed 9	MSA Later Pietersburg		30,000	
Bed 8	MSA Later Pietersburg			
Bed 7	MSA Later Pietersburg		40,000	
Bed 6	MSA Later Pietersburg	15,100 ± 730 B.P.		
Bed 5	MSA Middle Pietersburg	11,600 ± 700 B.P.	53,000	
Bed 4	MSA Early Pietersburg	11,700 ± 610 B.P. 11,811 ± 960 B.P.	60 - 70,000	> 120,000 iii)
Bed 3	ESA Later Acheulian		100,000	
Bed 2	ESA Later Acheulian		> 100,000	
Bed 1	ESA Later Acheulian			< 260,000 iv)

i) Beaumont and Vogel (1972a)
ii) Beaumont and Vogel (1972b)
iii) Klein (1973)
iv) Howell, F.C., et al. (1972)

PART I

THE TAXONOMY, CRANIAL AND DENTAL MORPHOLOGY OF LIVING AND FOSSIL PORCUPINES

3 BACKGROUND AND METHODS

The primary aim of Part I of this thesis is to identify and describe the fossil porcupine material (Order Rodentia, Subfamily Hystricinae, see Table III) from the breccias of the four Transvaal australopithecine deposits and Cave of Hearths, a collection numbering 203 specimens. Of these, only 11 have previously been mentioned in publications. Greenwood (1955, 1958) distinguishes two genera and three species from the 11 original Makapansgat Limeworks specimens, Xenohystrix crassidens, a truly giant form, sufficiently different from other Hystricids to warrant separate generic status, Hystrix makapanensis Greenwood 1958 (= H. major Greenwood 1955), a very large porcupine, larger than any living or fossil Hystrix known, and H. cf. africaeaustralis, which seemed to compare very favourably in all respects with the living southern African porcupine.

Although a considerable number of 'new' fossil porcupine remains have been recovered from the various australopithecine breccias since Greenwood's publication (a total of 112 from the australopithecine breccias and 91 from the Cave of Hearths), the available remains are very scant and extremely fragmentary, comprised mainly of isolated teeth and a few dentigerous maxillary and mandibular fragments (see Chapter 4, MATERIALS). Furthermore, this sample incorporates the remains of at least three different taxa. In view of these limitations it was decided that a detailed morphological study of modern and fossil Hystricidae, and particularly of the dentition of Hystrix, should be attempted as an essential prerequisite to any competent taxonomic consideration of the fossil remains. An extensive investigation of the taxonomy of the living and fossil Hystricidae with particular attention to cranial, mandibular and dental morphology, was therefore undertaken.

As a first step, the taxonomic literature on the living and fossil porcupines was reviewed in order to establish which morphological characters have been considered of significance in the differentiation of species, particularly within the genus Hystrix. Most of the early species, especially those named prior to 1920, were not differentiated on any feature differences from existing species, but simply described in great detail, the description constituting the diagnosis, with the result that a host of features appeared to have taxonomic

TABLE III

Classification of the Suborder Hystricomorpha
(modified from Simpson 1945 pp. 93 - 94)

SUBORDER	SUPERFAMILY	FAMILY	SUBFAMILY	GENUS
HYSTRICOMORPHA	HYSTRICOIDEA	HYSTRICIDAE	HYSTRICINAE	Hystrix * Acanthion Thecurus ** Sivacanthion ** Miohystrix ** Xenohystrix
			*** ATHERURINAE	Atherurus Trichys
	ERETHIZONTOIDEA	ERETHIZONTIDAE	** ACAREMYINAE	
			ERETHIZONTINAE	Coendou Erethizon Echinoprocta
			CHAETOMYINAE	Chaetomys
	CAVIOIDEA	Not applicable		
	CHINCHILLOIDEA	Not applicable		
	OCTODONTOIDEA	Not applicable		

* Most modern authors class Acanthion as a subgenus of Hystrix.
** Entirely fossil genera and subfamily.
*** Ellerman (1940) does not uphold the division of the family into two subfamilies, arguing that there is a gradation from the less-specialized Trichys to the highly developed Hystrix.

significance. The numerous characters that have been used can be grouped under six broad headings: (1) external morphological characters, (2) cranial morphological characters, (3) mandibular morphological characters, (4) dental characters, (5) post-cranial morphological characters and (6) internal anatomical features. (See Chapter 6, LIST OF CRITERIA USED IN THE DIAGNOSIS OF NEW SPECIES OF HYSTRIX).

The intention was first to evaluate the validity of these characters as diagnostic criteria, before employing any of them in the determination of the fossil material. However, the list of characters used proved so extensive (approximately 250) that it was decided to limit validity investigations to those which have been adequately defined or to those which seemed of potential use in the differentation of the fossil remains. In view of the fragmentary condition of the fossils, features investigated were mainly taken from the cranial, mandibular and dental morphological lists. At this stage it was noted that some potentially useful characters such as curvature of incisors and of the maxillary teeth, and the position of muscle attachments, etc. had not previously been used in descriptions or diagnoses of species.

As many possible characters as were suggested by the fossil remains were added to the list for evaluation. The 203 characters assessed for diagnostic significance are discussed in Chapter 6. It was hoped that the investigation would reveal, for each character assessed, the normal range of variability that can be expected within a species and within any one growth stage of that species, and also which of the characters have diagnostic significance and are therefore suitable for differentiation between species.

The evaluation ~~for~~ of diagnostic significance was done as follows: First the variability of each character was examined within a sample of one of the three valid living species of Hystrix. Thirty-two H. africaeaustralis crania and mandibles ranging from new-born to very mature individuals (a 'growth series') were assembled for this purpose. The specimens were retrieved from as wide a range of environments as possible (Chapter 4, MATERIALS) so that the full morphological range of the species could be established. By means of such a collection, the effects of growth, age, environment and sex on the various criteria could be assessed. This sample of modern porcupines is probably the largest and best growth series that has been available for study to date. It soon became evident that most characters varied

tremendously with age, in fact very few characters (apart from a very few indices and ratios) seemed age-independent. It was therefore decided to divide the sample into a series of growth stages, so that more refined and significant comparisons could be made. The growth stages used were based on the eruption of teeth, as partly suggested by Corbet and Jones (1964), and have been fully discussed and figured in section 7.1.4. For each character, the sample maximum, minimum and mean has been calculated, as well as the maximum, minimum and mean for each growth stage.

The method of dividing a sample into growth stages is only effective for specimens with in situ teeth; it was found necessary to devise a means of referring isolated teeth (a frequent phenomenon in fossil remains) to the appropriate growth stage. This was done by studying the crown enamel pattern of each cheek tooth characteristic of each growth stage; the method has been discussed in detail in section 7.1.4. The growth stage method of comparison was found invaluable in the taxonomic assessment of the fossil remains, where the small sample available would make the conclusions based on less refined comparisons more uncertain.

Once the variability of the characters had been established within H. africaeaustralis, the diagnostic significance of each was evaluated by comparison of each feature with its counterpart in the other valid Hystrix species; substantial diagnostic characters should change sharply between species while poor characters will grade or overlap or be identical in two or more species. It was also necessary to establish which of the many extant species mentioned in the literature are currently considered valid, and to note the features that have been used to differentiate them. For this purpose an alphabetical list of all the published species of Hystrix was compiled (see Appendix III, ALPHABETICAL LIST OF THE PUBLISHED SPECIES OF HYSTRIX) and, from the literature, all synonyms were noted. Of the list of 108 published species, only three proved valid: H. cristata Linnaeus 1758, H. indica Kerr 1792 and H. africaeaustralis Peters 1852. The distribution of the three species is shown in Figs. 42, 43 and 44. Appendix IV lists the valid species in the extant genera and families of Erethizontidae and Hystricidae and all the former species of Hystrix that are now considered synonymous with them, together with the synonymizing authors.

As mentioned, the various characters were assessed for diagnostic significance by examining the variability between the three valid species, growth stages being taken into consideration. Unfortunately only one skull of H. cristata and none of H. indica was available, with the result that, unsatisfactorily, comparisons had to be conducted from available published data and figures. With regard to this, it was discovered that much of the published metrical data was of limited use because the parameters measured and their method of measurement are very ill-defined. It was thus deemed advisable to define all parameters measured very accurately, for future comparative purposes. (See section 7.2).

The only previous investigation to assess the reliability of 'diagnostic criteria' was that undertaken by Corbet and Jones (1964), who examined the specific characters of the subgenus Hystrix. This involved evaluating 14 characters, only one of which - length of maxillary tooth row - might have been of use in the taxonomic determination of the South African fossil material. The 14 characters evaluated by Corbet and Jones have been marked with an obelus (†) in the list of characters used to define the species of Hystrix (Chapter 6); these have not been re-examined for significance in this thesis, only their variability within the larger sample of H. africaeaustralis at the disposal of the present author has been investigated.

Most dental criteria have generally been dismissed as highly variable or not mutually exclusive and are widely considered as unreliable (Greenwood, 1955). Because of this, description and discussion of dentitions in any detail are lacking in the literature, and the data on fossil dentitions has been confined to rather general statements of size, shape and degree of wear of individual teeth. However, fossil porcupine remains the world over seem to consist primarily of small tooth-bearing upper and lower jaw fragments and isolated teeth, probably on account of the extreme fragility of the much-inflated and weak cranial structure. This situation has enforced the use of dental features almost exclusively as diagnostic criteria in the taxonomic determination of fossil porcupines, and the lack of data on the reliability of such features and particularly on porcupine dentitions as a whole, whether modern or fossil, became obvious. Most careful attention was therefore paid to this aspect.

Only after the reliability of the various characters had been established were the determinations of the fossil material undertaken. Once again, it was necessary to establish what fossil species have been described and which of these are considered valid. It was also necessary to be familiar with the appearance, measurements and geological age of the latter species, in order that the South African fossil material could be compared with them. For this purpose a catalogue of fossil species was compiled in which every fossil Hystricid described as to date, approximately 30 forms, have been figured and discussed in terms of the above requirements (Appendix X). The actual methods employed in the identification of the fossil material are more fully described in Chapter 11 (SYSTEMATIC PALAEONTOLOGY).

A summary of the general method of approach is given below:

1 Adaptive and evolutionary trends within the living genera of the family Hystricidae were studied.

2 Literature was reviewed to extract morphological characters of supposedly or actual diagnostic significance. To this list were added further characters, not previously utilized in diagnoses, which were considered of potential diagnostic significance for the fossil sample.

3 The parameters measured were accurately defined.

4 Variability of these characters was then assessed within a sample of H. africaeaustralis. For this purpose a 'growth series', including individuals from a wide range of environmental settings was assembled.

5 Taxonomic literature was reviewed in order to determine valid extant species.

6 Characters were assessed for diagnostic significance by comparing each between the 3 valid extant species. Information concerning the characters involved for H. cristata and H. indica had first to be extracted from the literature. Growth stage significance was considered.

7 Taxonomic literature was reviewed to determine what fossil species have been described, and their ages, appearance, measurements and validity.

8 In light of above information, the South African fossil material was compared with other fossil porcupine material.

9 Diagnosis and description of South African taxa were reviewed.
10 Finally, any inference that may be drawn from the South African fossil material with regard to climate, environment and behaviour was discussed.

Evolutionary trends within the family Hystricidae had to be taken into consideration, the knowledge of those characters considered primitive and those considered advanced being necessary in order to 'place' the fossil species into an evolutionary line.

After the specimens in the fossil sample had been identified, an attempt was made to relate morphology to function and function to behaviour, in an effort to explain the synchronous occurrence of three closely related forms in the same area or deposit: a possible environment and mode of life for each species has been suggested, and climatic deductions have been advanced where possible.

4 MATERIALS

The material studied comprised three categories: a comparative collection of the living southern African porcupine Hystrix africaeaustralis; fossil porcupine remains recovered from the breccias of the four Transvaal australopithecine caves; and those excavated from the Cave of Hearths deposit.

4.1 Recent Hystrix comparative material

The crania and mandibles of 32 individuals of Hystrix africaeaustralis were available. Sixteen of these were kindly lent by the Transvaal Museum, Pretoria (catalogue code TM), and one by the University of the Witwatersrand Medical School (code Za), whilst the remaining 15 were either donated to or collected by the author (code PPM or BPI/C). The sample includes animals of both sexes, but the sex of most of the specimens is unfortunately not known. The crania, mandibles and teeth show no obvious differences which can be attributed to sexual dimorphism and, from the sample available, there appears to be no reliable means of establishing the sex of a specimen by means of cranial, mandibular and dental morphology alone. An attempt was made to obtain specimens from widely separated localities with differing environments so that the full morphological range of the species could be assessed. The collection therefore includes specimens from arid regions (South West Africa and the Kalahari) as well as from the lush coastal forest regions of Natal. The material is listed in order of increasing maturity and by locality in Table IV. For locality distribution see Fig. 24.

The sample, although rather small for taxonomic purposes, provides an excellent growth series, ranging from an exceedingly young individual (PPM 113) in which only the incisors and newly-erupted deciduous premolars are functional, to two extremely large, old and partially edentulous individuals (TM 6066 and PPM 123). The sample has been divided into a series of growth stages to facilitate the comparison of measurements of specimens at equivalent stages of growth. The growth stage to which each specimen belongs is indicated in the Table, and the method of subdivision discussed in section 7.1.4

Nineteen of the skulls are those of juveniles, i.e. lacking permanent premolars, the remaining 13 being those of adult individuals, i.e. with permanent premolars. This growth series has facilitated the study of a number of features not observable in samples comprising

Fig 24

Map of Southern Africa showing source localities of the comparative Hystrix (H.) africaeaustralis material. (Refer to Table III)

The position of one locality (Legg's Island) could not be traced and localities which are broadly defined, such as 'Albany District' are indicated only as accurately as descriptions will allow. Specimens described as having come from 'Kaokoveld', 'Karroo' and 'Nyasaland' are not shown as these are large regions rather than localities.

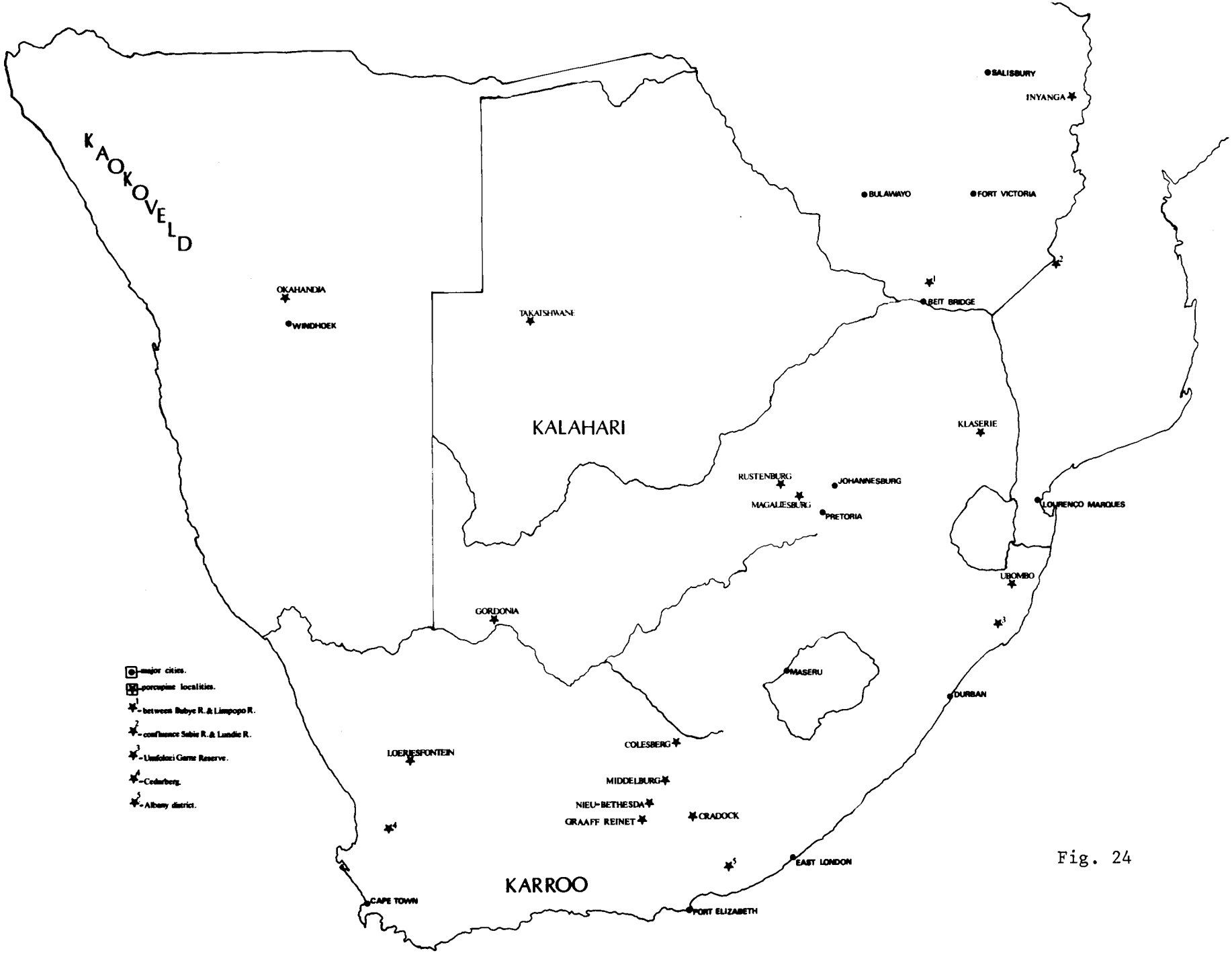

KAOKOVELD
OKAHANDJA
WINDHOEK
TAKATSHWANE
KALAHARI
SALISBURY
INYANGA
BULAWAYO
FORT VICTORIA
BEIT BRIDGE
KLASERIE
RUSTENBURG
JOHANNESBURG
MAGALIESBURG
PRETORIA
LOURENÇO MARQUES
UBOMBO
GORDONIA
MASERU
DURBAN
COLESBERG
LOERIESFONTEIN
MIDDELBURG
NIEU-BETHESDA
GRAAFF REINET
CRADOCK
EAST LONDON
KARROO
CAPE TOWN
PORT ELIZABETH
-major cities.
-porcupine localities.
1 - between Bubye R. & Limpopo R.
2 - confluence Sabie R. & Lundie R.
3 - Umfolozi Game Reserve.
4 - Cedarberg.
5 - Albany district.

Fig. 24

TABLE IV

Recent Hystrix africaeaustralis material used in Taxonomic studies*

Catalogue No.	Specimen Description	Locality	Sex	Growth Stage
PPM 113	Mandible only	Nieu-Bethesda, Karroo Cape	-	2
TM Nyasaland	Cranium & mandible	Nyasaland	-	2
TM 5662	Cranium & mandible	Mkuze river, Ubombo Natal	-	2
TM 5661	Cranium & mandible	Mkuze river, Ubombo Natal	-	2
TM 12698	Cranium & mandible	Kaokoveld, South West Africa	-	3
PPM 114	Partial cranium & mandible	Klaserie, E. Transvaal	♀	3
PPM 126	Mandible only	Takatshwane, Botswana	-	3
PPM 115	Partial cranium & mandible	Klaserie, E. Transvaal	♂	3
TM 12697	Cranium & mandible	Kaokoveld, South West Africa	-	3
PPM 116	Cranium & mandible	Graaff-Reinet, Karroo, Cape	-	4
PPM 124	Cranium & mandible	Loeriesfontein, W. Cape	-	4
PPM 125	Mandible only	Takatshwane, Botswana	-	4
TM Mt Zebra Park	Cranium & mandible	Mt. Zebra Natnl. Park, Cradock, Cape	-	4
TM 94F	Cranium & mandible	Rustenburg, Transvaal	♀	4
TM 2A	Cranium & mandible	Inyanga, S.E. Rhodesia	-	4
PPM 789	Mandible only	Takatshwane, Botswana	-	4
TM 753	Cranium & mandible	Quickborn, Ohahandja, S.W.A.	-	4
TM 594	Cranium & mandible	Between Bubye R. & Limpopo R., Rhodesia	-	4
BPI/C 682	Cranium & mandible	Magaliesburg, Transvaal	-	4
TM 12165	Cranium & mandible	Confluence of Sabie R. & Lundie R. Mocambique	-	5
PPM 117	Cranium & mandible	Karroo, Cape (?)	-	5

TABLE IV
continued

Recent Hystrix africaeaustralis material used in Taxonomic studies

Catalogue No.	Specimen Description	Locality	Sex	Growth Stage
PPM 118	Cranium & mandible	Middelburg, Karroo Cape	-	5
TM 866	Cranium & mandible	Albany, E. Cape	-	5
TM 8289	Cranium & mandible	Albany, E. Cape	-	6
Za 911	Cranium & mandible	Albany, E. Cape	-	6
PPM 119	Mandible only	Middelburg, Karroo Cape	-	6
TM 657	Cranium & mandible	Umfolozi Game Reserve, Natal	-	6
PPM 122	Cranium & mandible	Cedarberg, W. Cape	-	6
TM 623	Cranium & mandible	Rustenburg, Transvaal	-	6
BPI/C 641	Cranium only	Gordonia, W. Cape	-	6
TM 6066	Cranium & mandible	Legg's Island Botswana ?	-	6
PPM 123	Cranium only	Colesberg, Cape	-	6

* Specimens PPM113 to BPI/C682 juvenile, TM12165 to PPM123 adult

individuals of more homogeneous age. These features include(i) a study of the sequence of tooth replacement; (ii) a study of the changes in crown enamel pattern with progressive wear, and (iii) a study of the changes in cranial, mandibular and dental proportions with increasing maturity. The series has enabled the assessment of natural morphological variation and has hence facilitated the selection of those features most suitable for diagnostic purposes. The range of maturity represented has allowed each fossil specimen to be compared with a modern specimen at an equivalent 'growth stage', no matter what phase of tooth wear may be shown.

As far as it could be established from the literature, this is the largest sample of Hystrix africaeaustralis that has hitherto been studied.

One skull and mandible of Hystrix cristata was borrowed from the University of the Witwatersrand Zoology Department and was used in the assessment of the validity of diagnostic characters.

4.2 Fossil porcupine material from the australopithecine breccias

This is a collection totalling 112 specimens from the breccias of the Makapansgat Limeworks (catalogue code M: 71 specimens), Sterkfontein (codes STS and SFN: 22 specimens), Swartkrans (code SK: 15 specimens) and Kromdraai (code KA: 4 specimens). The sample provides a total number of 166 measureable teeth; although this may seem a fairly large number, it is quite inadequate taxonomically on account of the extremely fragmentary condition of the material, and in view of the fact that the collection incorporates the remains of at least three taxa. In addition, a number of specimens are those of juvenile individuals, which are taxonomically less useful than adults.

No intact or even reasonably complete cranium or mandible has been recovered from the above-mentioned sites; however, it has been possible to reconstruct partially the cranium and mandible of one of the three species represented: Xenohystrix crassidens, from Makapansgat Limeworks, using several specimens. The difficulty of identifying porcupine post-cranial fragments and the frailty of post-cranial bones perhaps accounts for the seeming absence of the latter from the cavern deposits. For this reason, there has been no other choice but to base the taxonomy of fossil porcupines almost entirely on dental and mandibular characters.

Almost all of the other fossil rodent material that has been recovered from the Transvaal australopithecine breccias can be assigned to the micro-mammalian category and has been derived from so-called 'rodent breccias', which contain the fossilized microfaunal regurgitations (owl pellets) of ancient owls. Even infant porcupines, and especially those of the giant form Xenohystrix crassidens, were probably too large and spiny to form part of the usual owl diet; it is thus unlikely that the porcupine fossils have found their way into the breccias via this means. The two instances where porcupine remains have been found in a rodent breccia, one at Swartkrans (SK 3082) and one at Kromdraai (KA 1432), are probably due to the remains being deposited immediately below an ancient owl perch by some other means. At Makapansgat, all the porcupine remains have been found in close association with the remains of numerous large mammals, and are more likely to represent the food remains of Australopithecus or some other predator or scavenger. On the other hand, if Brain's hypothesis (1968, 1969, 1970b) that ancient leopards were largely responsible for the Swartkrans bone accumulation proves to be correct, it is not unlikely that the fossil porcupines from this particular site were introduced into the deposit by leopards, since the latter seem to be one of the very few natural enemies of porcupines (Schaller 1970).

The stratigraphy and age of the deposits from which the fossils have been recovered are discussed in Chapter 2 (SOURCE OF THE FOSSIL MATERIAL). Illustrations and discussions of the taxonomic status of the fossil material appears in Chapter 11 (SYSTEMATIC PALAEONTOLOGY), and each specimen has been dealt with in a descriptive and identificatory catalogue forming Appendix II. Finally, the minimum number of individuals present at each site has been discussed in Chapter II. 3.

4.2.1 The Makapansgat Limeworks material

The 71 specimens available from the Makapansgat Limeworks deposit represent the largest collection of fossil porcupine remains from any known australopithecine site. Sixty-five of these come from the Lower Phase I (grey) breccia, 4 from the Upper Phase I (pink) breccia and 2 from the Phase II breccia. The specimens are numbered as follows:

Lower Phase I (grey) Breccia

M 1000 - M 1013	14
M 1016	1

M 1802 - M 1825	24
M 2516 - M 2523	8
M 2525 - M 2527	3
M 8220	1
M 8233	1
M 8276	1
M 8286 - M 8294	9
M 8362 - M 8364	3
	65 specimens

Upper Phase I (pink) Breccia

M 8277 - M 8278	2
M 8281 - M 8282	2
	4 specimens

Phase II Breccia

M 8284 - M 8285 2 specimens

The material consists of the following:

Dentigerous mandibular fragments	14
Dentigerous maxillary fragments	5
Isolated teeth or tooth fragments	52
	71

The mandibular and maxillary fragments and the 52 isolated teeth provide a total number of 104 fully or partially measureable teeth. Of these specimens, only eleven - M 1000 to M 1010 - have previously been described (Greenwood, 1955, 1958).

The mandibular and maxillary specimens are all very fragmentary, frequently consisting of from two to four consecutive teeth surrounded by very little supporting bone, the most intact specimen (M 1007) being about two-thirds of a left half-mandible. Preservation, however, is magnificent, distortion being absent, and details such as pressure facets and fine striations on the occlusal surfaces of the incisors caused by gnawing and tooth-sharpening activities being clearly visible. On the other hand, the fragmentary nature and relatively small number of specimens makes the sample inadequate for taxonomic purposes. The above material is housed and catalogued in the collections of the Bernard Price Institute for Palaeontological Research.

4.2.2. The Sterkfontein material

None of the 22 specimens available from the Sterkfontein deposit has previously been mentioned in publication. Broom (in Broom and Scheepers, 1946) records the presence of *Hystrix cristatus* (= *cristata*) in the Sterkfontein breccias, stating that

> A number of teeth of a porcupine have been obtained in various deposits. They differ little from those of the living South African species and probably belong to *Hystrix cristatus* (p. 82)

However, the author considers that since the present range of the latter species is confined to suitable areas north of about 10°S (Figs. 43 and 44) and since none of the Sterkfontein fossil material can be differentiated from the living southern African species, (*H. africaeaustralis*) Broom's identification is incorrect. Neither catalogue numbers nor sketches were provided with Broom's diagnosis, so that the specimens from which the original diagnoses were made are untraceable, and the identification cannot be checked.

The 22 Sterkfontein specimens are numbered as follows:

STS 957a - e
STS 1662
STS 2061
STS 2078
STS 2095
SFN 1 - 17

Specimens STS 957a - e have had every vestige of the surrounding breccial matrix removed during acetic acid preparation so that it cannot be stated with certainty from which breccia they were extracted, although their probable source is the upper levels of the Type Site breccia, from which most of the specimens collected by Broom have reputedly been recovered. All the remaining STS specimens were embedded in a very compact highly calcified brownish-pink breccia, probably representing Broom's Type Site breccia, the upper levels of which are thought to have yielded almost all the australopithecine material as well as most of the associated fossil faunal material. The SFN specimens, all isolated teeth, have recently been recovered from the various breccial dumps in the vicinity of the Sterkfontein excavations

(Fig. 18): 5 from Dump 1, 1 from Dump 2, 9 from Dump 8, 1 from Dump 10 and 1 from Dump 13. According to Vrba (1974) the fossil material from Dump 1 has affinities with that derived from the Extension Locality, whilst that from Dump 13 shows affinities with the Type Site material. The specimens from Dump 8 were probably derived from a more recent breccia than either the Type Site or Extension Locality breccias. The material from Dumps 2 and 10 has not as yet been related to any definite part of the Sterkfontein excavations.

A total of 29 measureable teeth is available for study, but as with the Limeworks sample, the material is regrettably fragmentary.

Specimens with the catalogue code STS are housed in the Palaeontology Department of the Transvaal Museum, Pretoria, while the SFN specimens are housed in the Bernard Price Institute for Palaeontological Research.

4.2.3 The Swartkrans material

There are 15 fossil porcupine specimens from the Swartkrans breccias, providing a total number of 20 measureable teeth. None of this material has previously been described, although the presence of a porcupine in the Swartkrans deposit has been noted incidentally in several publications.

The above specimens are numbered as follows:

SK 2040
SK 2045
SK 2466a, b
SK 2835
SK 2875
SK 3063
SK 3082
SK 4315
SK 6945
SK 7155
SK 14235 - SK 14238

Six of these (SK 2466a,b, 2875, 3082, 4315, 14236 and 14237) come from the 'outer cavern unstratified pink breccia' of Brain (1958) (= the *Paranthropus* breccia' or 'Primary Breccia' (Brain et al.1974) or 'Swartkrans Member I' (Butzer 1974) or SKA (Vrba 1974a,b). The remaining eight

(SK 2040, 2045, 2835, 3063, 6945, 7155, 14235 and 14238) come from a more recent brownish breccia (= 'Secondary Breccia' (Brain 1974) or 'Swartkrans Member 2 (Butzer 1974) or SKB (Vrba 1974a, b, 1975)) which is equivalent to the 'inner cavern stratified brown breccia ' of Brain (1958).

SK 3082 was found in association with a very large number of fossil micro-mammalian bones in a 'rodent breccia'. This could be explained by the nature of the original cavern form of Swartkrans, where a vertical shaft provided access to the subterranean cavern as well as a large number of perches for owls, in the form of protruding uneroded chert ledges. The talus cone of surface-derived material which accumulated below this shaft (which included mammalian remains) became extensively 'contaminated' with the micro-mammalian content of owl pellets falling from above (Brain 1974, pers. comm.).

4.2.4 The Kromdraai material

The presence of porcupines at Kromdraai has hitherto not been recorded. There are only 4 specimens from this site, probably all derived from the somewhat reddish-brown finer-grained Kromdraai A Phase II breccia, from which the majority of the Kromdraai A fossil specimens have been recovered. KA 1432 is associated with a large number of rodent bones and teeth.

The four Kromdraai specimens provide a total of 11 measureable teeth and are numbered as follows:

KA 757
KA 1432
KA 1607
KA 1912

The specimens from Swartkrans and Kromdraai and some of those from Sterkfontein are housed in the Department of Palaeontology, Transvaal Museum and were kindly made available for study purposes by Dr. C.K. Brain, the Director.

4.3 The Cave of Hearths material

There are 91 porcupine specimens from the Cave of Hearths. The only published information regarding any of the faunal material from this site is contained in Cooke's appendix to 'Prehistory of the

Transvaal' (Mason 1962a, pp. 447 - 453), where the porcupine has been identified as Hystrix africaeaustralis. The 91 porcupine specimens represent only a small fraction of the thousands of bones and teeth that have been recovered from this cave, which include the remains of 47 mammalian, 3 reptilian, 2 avian and one molluscan species (Cooke, in Mason 1962). There can be little doubt that humans were responsible for the accumulation of this faunal material, and that the porcupine remains in all probability represent the remains of their meals. Indeed, several of the specimens show evidence of firing and have been recovered from the vicinity of ancient hearths, where the bones were thrown after the meat had been removed. Many others show an abnormal degree of fragmentation or distinct signs of intentional pre-fossilizational damage.

However, in view of the fact that some of the mammalian bones from the deposit (± 10%, Kitching 1973, pers. comm.) show extensive porcupine gnawing, it is possible that the cave was intermittently occupied by porcupines in the absence of human occupation, during which periods they may have accumulated a few bones. Because the cave-dwellers would have left large numbers of readily accessible bones littering the cave floor, it was probably unnecessary for the porcupines to retrieve many bones from outside. Occasional deaths in the innermost recesses of the caves during such periods could have contributed to the number of porcupine specimens in the deposit, but on the whole it appears as if the porcupine remains, together with the wide variety of animal bones recovered from the site, were the food remains left by the different human occupants of the cave.

The 91 specimens are numbered as follows:

COH 717 - COH 769	58	
COH 2356 - COH 2358	3	
COH 2381 - COH 2410	30	
	91	specimens

Although many specimens are exceptionally fragmentary, the preservation is good, fine rodent gnaw-marks and evidence of artificial pre-fossilizational damage being clearly visible. Specimens which have been excavated from the vicinity of or from within hearth areas are often shattered due to the high temperatures to which they have been exposed, and are held together by a hard matrix of baked cave earth.

The material consists of the following:

Mandibular fragments	34
Maxillary fragments	6
Isolated mandibular teeth	27
Isolated maxillary teeth	23
Cranial fragments	1
	91

The mandibular and maxillary fragments together with the 50 isolated teeth contribute to a total of 122 teeth, of which only 103 are measureable or partially measureable, the remainder being either not fully erupted or too fragmentary for measurement. Since mandibular and maxillary remains would normally be expected to occur in roughly equal numbers, the disproportionately high number of mandibular fragments (34 as opposed to only 6 maxillary) requires explanation, as does the fact that 26 of the 34 mandibular fragments have broken incisor alveoli and missing incisors, a form of damage which seldom occurs naturally.

Of the 91 specimens, more than half (56) have been recovered from an area known as the 'sinkhole' which contains a mixed assemblage of stone tools, mainly MSA, and other materials so that it is impossible to assign these specimens to any particular bed or beds. The remaining 35 have been derived from almost all of the beds within the cave deposit suggesting that porcupine flesh, in all probability, was relished from Acheulean times, approximately 260,000 years ago up to the Iron Age; these animals are at present still snared for food by the local inhabitants of the Makapan Valley.

One specimen came from an ESA hearth in Bed 1, 4 from Bed 5, 2 from Bed 6, 1 from Bed 7, 4 from Bed 8, 6 from Bed 9 and 8 from Bed 10 - Beds 4 to 9 representing the Middle Stone Age. Three specimens have been derived from the Iron Age levels (Bed 11 and/or Bed 12), and one from the surface. Thus porcupine remains have been recovered from every bed except Beds 2, 3 and 4. Five specimens have no grid co-ordinates or depth markings so that their location in the deposits is unknown.

All specimens which have been assigned to a definite bed are marked 'CH' and came from a column of breccia adjacent to the sinkhole at the back of the cave. Both the sinkhole and the 'CH breccia', part of which has been left as a witness section, are shown in Fig. 14 of Chapter 2.1.1.2. A stratigraphic profile of the cave is shown in Fig. 15

of the same chapter and the stratigraphy has been tabulated in Appendix I.

Each specimen is recorded in a descriptive catalogue (Appendix II) which also lists the grid co-ordinate and Bed number of each, according to the 1957 stratigraphy. The minimum number of individuals occurring in each stratum and in the deposit as a whole is dealt with in Chapter 11. The catalogue and material ~~is~~ housed in the Bernard Price Institute for Palaeontological Research.

5 TAXONOMIC HISTORY OF THE FAMILY HYSTRICIDAE AND EVOLUTIONARY/ ADAPTIVE TRENDS WITHIN THE GROUP

Hystrix, a Latin word meaning 'porcupine', had been in common use long before the time of Linnaeus, and a large number of animals described in the pre-Linnaean period have been prefixed with this name. In 1758 Linnaeus formally defined the genus Hystrix as:

Dentes primores II, oblique scissi	=	2 anterior incisors, obliquely cut
Molares octo	=	eight molars
Corpus spinis tectum	=	body covered with spines (p. 56)

This definition was too broad, since practically anything that was spiny could be included in it, and for more than a century after this definition, all North and South American spiny 'porcupines' were listed under Hystrix.

In 1844 Wagner suggested that the living 'porcupines', which at that time were all included in a group known as Family Hystricina, should be divided into two groups: a) The Philogeae or Old World Porcupines, and b) the Philodendrae or American Porcupines. This suggestion was based on the fact that the Old World Porcupines had molars which were complicated by enamel folds with roots that were not distinctly divided; they had an 'orbital process' situated above the third molar; nude palms and soles, their tails were never prehensile and they were adapted for digging. The American porcupines, on the other hand, had simple molars with distinctly divergent roots, an 'orbital process' situated above the first molar, long tails which were often prehensile, and were adapted for climbing. Wagner's Philogeae and Philodendrae were later more precisely defined and were given familial status, being known as the Hystricidae and Erethizontidae respectively (see Table III). This accounts for the large number of 'Hystrix' species that have been synonymized within the New World genera Coendou, Erethizon, Echinoprocta and Chaetomys (see Table III and Appendix IV).

By 1907, all five living genera included in the Family Hystricidae- Hystrix Linnaeus 1758, Acanthion Cuvier 1822, Atherurus Cuvier 1829, Trichys Günther 1876 and Thecurus Lyon 1907 - had been defined. Of these only the genus Acanthion (sub-crested and crested short-tailed porcupines)

seemed to be controversial, in that no clear distinction could be drawn between this genus and the genus Hystrix (crested short-tailed porcupines), to which it appeared very closely related. Many authors ignored Cuvier's genus Acanthion, referring species listed under it to Hystrix.

Lyon (1907), after an analysis of the characters that had been employed in the definition of the five genera and an examination of examples of living south-east Asiatic porcupines, decided to re-instate Acanthion. Furthermore, he suggested that there was sufficient difference between the two more unspecialized, primitive porcupine genera Trichys and Atherurus on the one hand and the more advanced genera Thecurus, Acanthion and Hystrix on the other, to warrant the division of the family into two sub-families, which he termed the Atherurinae and Hystricinae respectively (see Table III). The former group could be distinguished by the possession of a long tail, which had a well-marked scaly portion between the tail base and apex, and which was terminated by a long tuft of modified hairs or bristles (hence the 'brush-tailed porcupines' as they are sometimes called); the back was covered with stiff grooved spines instead of thick, long, well-developed quills and the molars were brachydont and rooted. The Hystricinae, on the other hand, had short tails with no well-marked hairless scaly portion between base and apex, the terminal tail hairs were modified into hollow, capsule-like structures (rattle-quills, see Fig. 37), and they were in possession of well-developed thick quills on the back. Their molars were hypsodont and semi-rooted or rootless.

Lyon (1907) recognized that Trichys was the most primitive or generalized genus, and the most unrelated to the other four. He noted that although Atherurus had affinities with Trichys, it nevertheless appeared in certain ways to be related to Thecurus. On the other hand, Thecurus, Acanthion and Hystrix all appeared to be closely related to one another. He then suggested the following serial arrangement for the five Old World genera:

Hystrix * Acanthion ** Thecurus — Atherurus **** Trichys

In 1922, Lönnberg analysed all previously published diagnoses of the genera Acanthion and Hystrix, and concluded that no satisfactory

diagnosis effectively separating the two genera had been devised. At the same time he observed that there was a wide difference between the more primitive members of 'Acanthion' and the most highly developed members of Hystrix, with a series of forms bridging the two extremes. He therefore proceeded to use Acanthion in a subgeneric context.

Ellerman (1940) in a complete review of the Order Rodentia, upheld the subgeneric status of Acanthion, but opposed the division of the Hystricidae into two subfamilies, stating that:

> although the Atherurus group is much less specialized than the Hystrix group both in spiny covering, reduction of tail, and in the more brachydont cheek teeth, there appear to be too many essential characters common to both groups for this division to be maintained; the pattern of the cheek teeth and the structure of the feet, for example, are essentially similar in both groups; and the cranial characters of Thecurus, the lowest member of the Hystrix group, are very similar to those of Atherurus, including the rather important character of length of nasals. (p. 198)

Despite suggesting abandoning the subfamilial division, Ellerman nevertheless groups Trichys and Atherurus in what he calls the 'Atherurus group' and Thecurus and Hystrix (including Acanthion) in the 'Hystrix group'.

The only more recent review of Hystricid taxonomy is that of Mohr (1965) who agrees that the subfamilial division is unnecessary. Mohr, however, accords Acanthion full generic status.

With regard to the status of Acanthion, the present author supports the view of Lönnberg and Ellerman. For ease of reference, the three valid species of the subgenus Hystrix (cristata, indica and africaeaustralis)are referred to simply as H. cristata, etc. while all members of the subgenus Acanthion have been identified by including the subgenus (bracketed) in their name, e.g. Hystrix (Acanthion) subcristata.

The main diagnostic characters of the four extant genera of the Old World porcupines, arranged in ascending order of specialization, are given below; views of the crania, lateral views of the mandibles and illustrations of the external appearance of representatives of each of the four genera and of the subgenus Acanthion, also serially arranged, are shown in Figs. 25 to 36.

1 TRICHYS (Günther 1876 (Figs. 25, 26a and 26b))

i) Skull long and narrow with slender rostrum

ii) Skull with well-marked post-orbital process and strong inter-orbital constriction

iii) Nasals short and narrow, shorter than frontals, extending back to level of anterior zygomatic root

iv) Cheek teeth brachydont, rooted, lower incisors laterally compressed, toothrow short

v) Palate straight, moderately wide; palatal foramen (= foramina incisiva) short, far in front of toothrow

vi) Prominent horizontal groove on external surface of jugal

vii) Coronoid process of mandible high, nearly as high as condyle

viii) Body covered with poorly-developed flexible spines, head and underparts hairy

ix) Tail long and scaly, tipped with cluster of parallel-sided bristles

x) Body size smaller than is usual in the family

2 ATHERURUS Cuvier 1829 (Figs 27 and 28)

i) Skull shorter and broader than in Trichys, with less compressed rostrum

ii) Post-orbital process scarcely marked or absent, little interorbital constriction

iii) Nasals short but broader than in Trichys, extending back to about level of anterior margin of infraorbital foramen; frontals long, becoming slightly arched and inflated in A. africanus

iv) Cheek teeth brachydont, rooted, lower incisors not compressed

v) Palate as in Trichys, palatal foramina (= foramina incisiva) much reduced

vi) No groove on jugal, which sometimes reaches lachrymal

vii) Mandible with low coronoid, rather low condyle; traces of a ridge beside the condyle may be present

viii) Body covered with stronger spines than in Trichys, sometimes mixed with true quills, some African species with thick round quills characteristic of all members of the Hystrix group; quill cover thus better developed than in Trichys

ix) Tail long, less naked than in Trichys, tip formed by quills that are alternately expanded and contracted

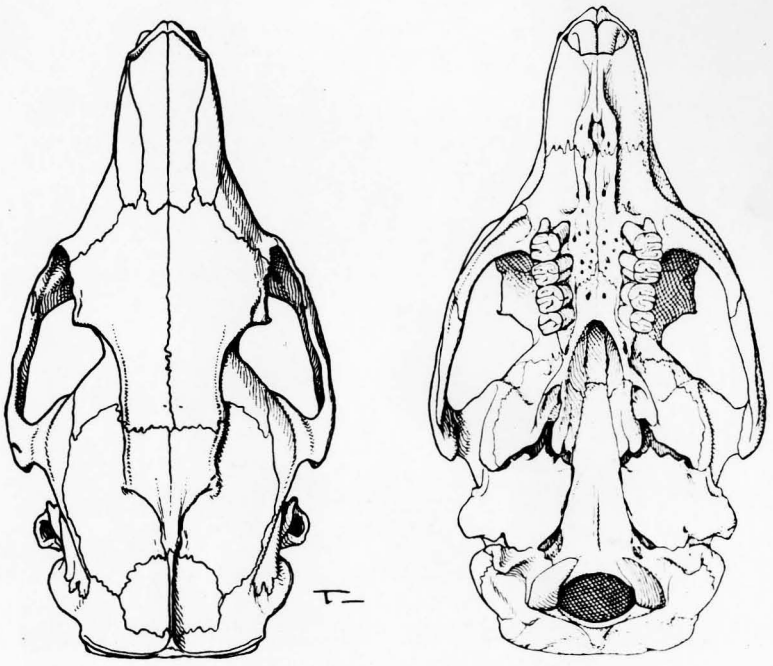


FIG. 56. TRICHYS MACROTIS, Miller.
B.M. No. 16.11.16.2; × 1.

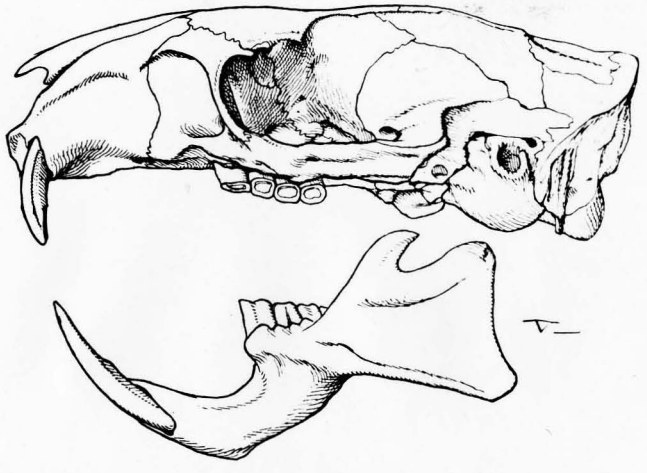


FIG. 57. TRICHYS MACROTIS, Miller.
B.M. No. 16.11.16.2; × 1.

Fig. 25

Views of the cranium and mandible of Trichys macrotis Miller, re-photographed from Ellerman 1940 p. 204 (×1)

Fig. 26a

Illustration of Trichys lipura Günther, re-photographed from Günther 1876 Pl. 71. The tail of this specimen was probably lost prior to illustration.

Fig. 26b

Illustration of Trichys fasciculata (Shaw), re-photographed from Shaw 1801 Pl. 124 opposite p. 9

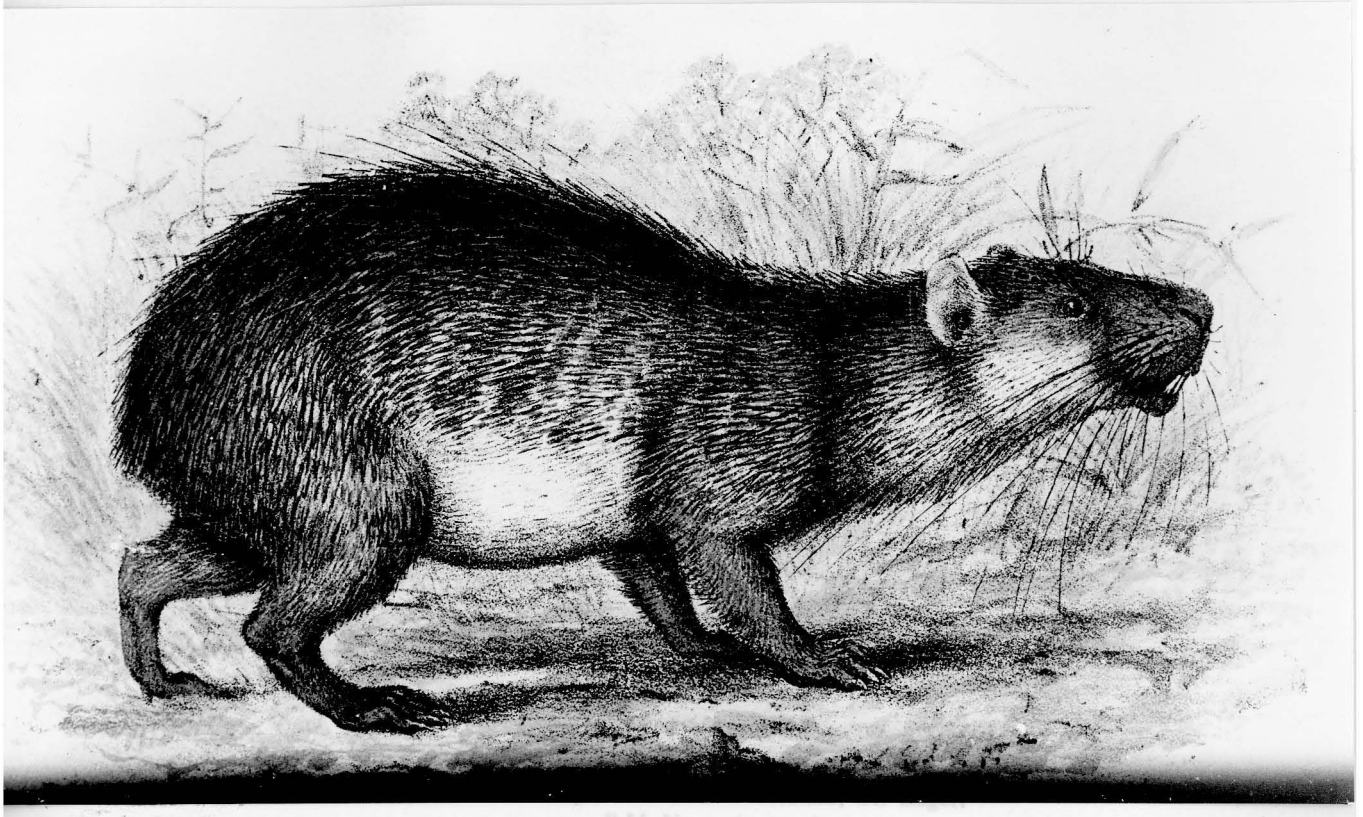


Fig. 26a

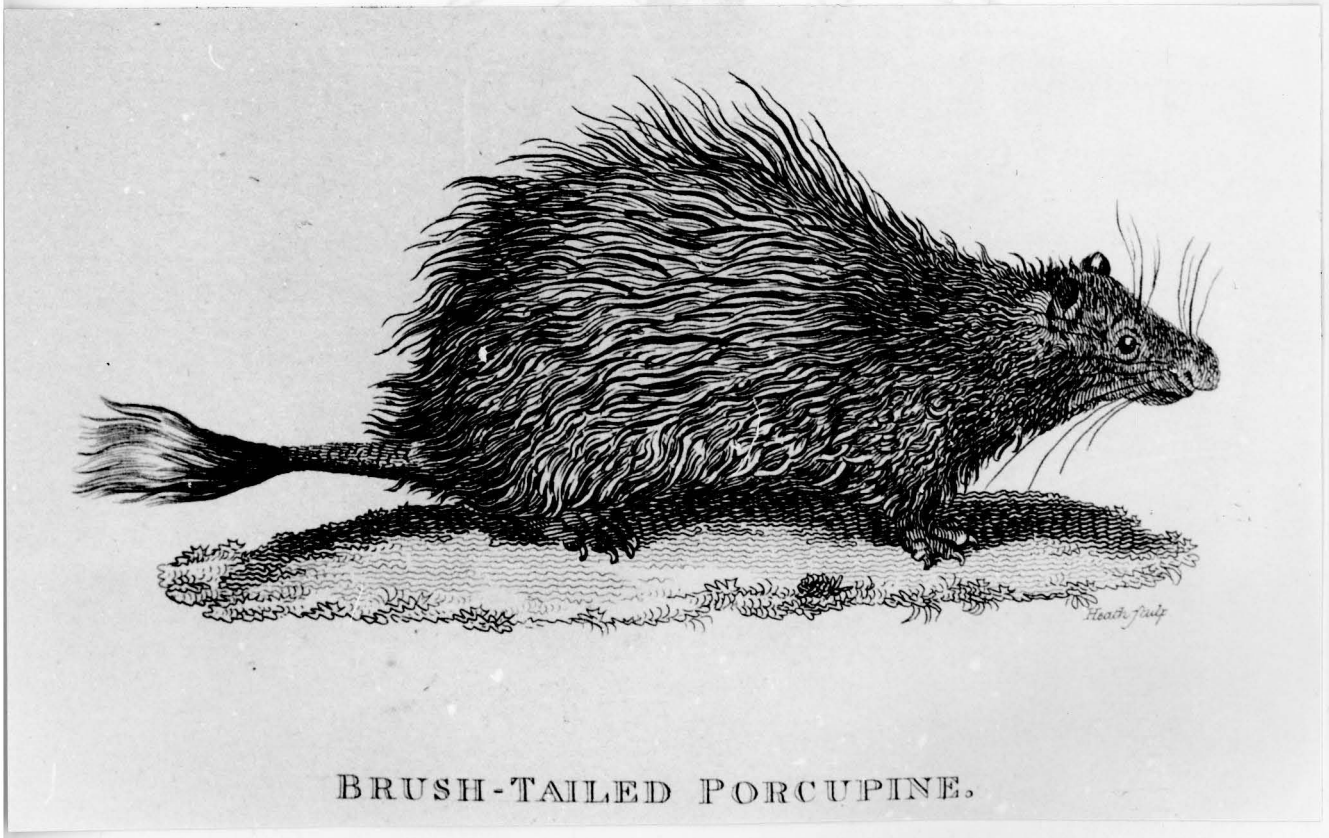


Fig. 26b

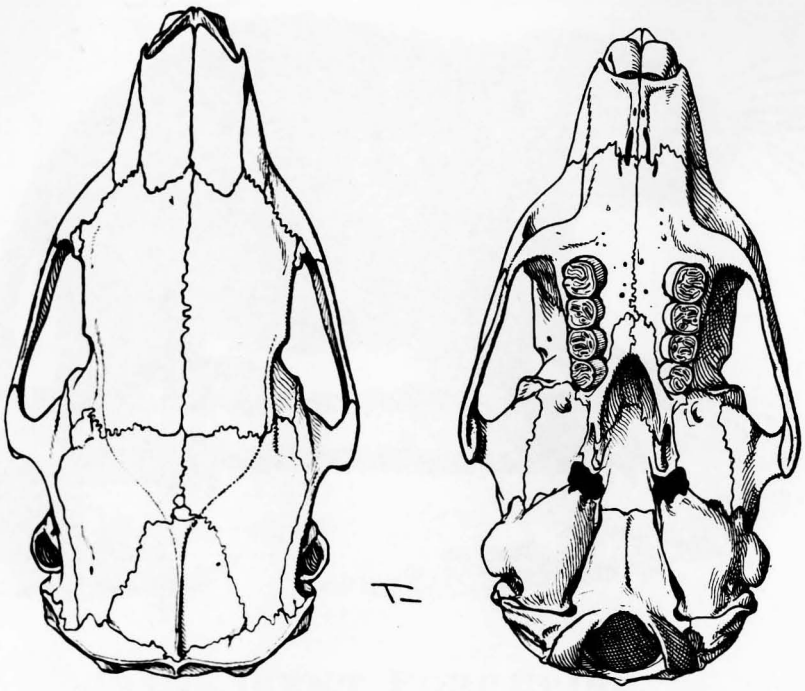


FIG. 58. ATHERURUS TURNERI, St. Leger.
B.M. No. 34.6.2.77, ♂; × 1.

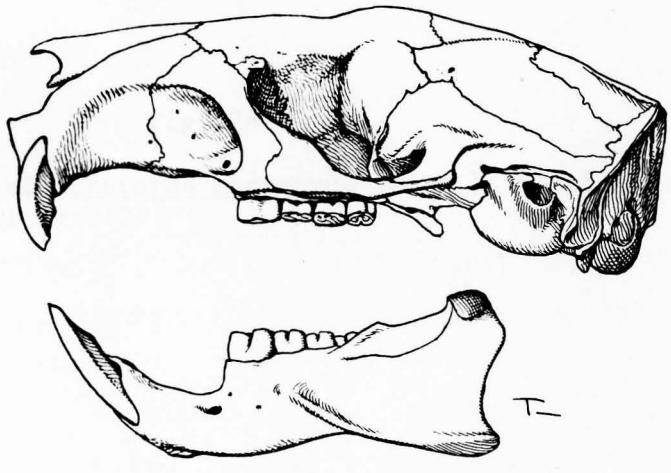


FIG. 59. ATHERURUS TURNERI, St. Leger.
B.M. No. 34.6.2.77, ♂; × 1.

Fig 27

Views of the cranium and mandible of Atherurus turneri St. Leger, re-photographed from Ellerman 1940 p. 207 (x1)



Fig. 28

Illustration of Atherurus macrourus (Linn.), re-photographed from Shaw 1801 Pl. 124

x) Body size larger than in Trichys

THECURUS Lyon/1907 (Figs. 29 and 30)

i) Skull intermediate in size and shape between Atherurus and Hystrix, but flatter and with narrower rostrum than any Hystrix

ii) Postorbital process rudimentary, interorbital constriction may be suggested

iii) Nasals narrow, extending back to about the level of the anterior margin of the infraorbital foramen, frontals longer than nasals

iv) Cheekteeth strongly hypsodont

v) Palatal foramina (= foramina incisiva) very small

vi) Coronoid process of mandible low, lower than condyle, thickened dorsally to form a ridge

vii) Body covered with true quills, which are sometimes highly developed e.g. Thecurus crassispinis

viii) Tail with rattle-quills, but these are smaller than those of Hystrix

ix) Body size as large as or larger than Atherurus

HYSTRIX Linnaeus/1758

HYSTRIX (Acanthion) Figs. 31a, 31b and 32

HYSTRIX (Hystrix) Figs. 33, 34, 35 and 36

i) Skull larger than in Thecurus, rostral portion not strongly offset from rest of skull, cranium faintly to strongly arched

ii) Postorbital process and interorbital constriction absent or very rudimentary

iii) Nasal, even in primitive forms of subgenus Acanthion, longer and broader than in Thecurus, extending to lachrymal level in H.(A) brachyurus group and progressively lengthened and broadened in more advanced species, ultimately approaching the level of the posterior zygomatic root; longer than frontals

iv) Cheek teeth strongly hypsodont, semi-rooted, upper molars curved, incisors broad

v) Palate broad, extending about to end of tooth row behind, and straight, palatal foramina (= foramina incisiva) short, far in front of tooth row

vi) Coronoid process of mandible low

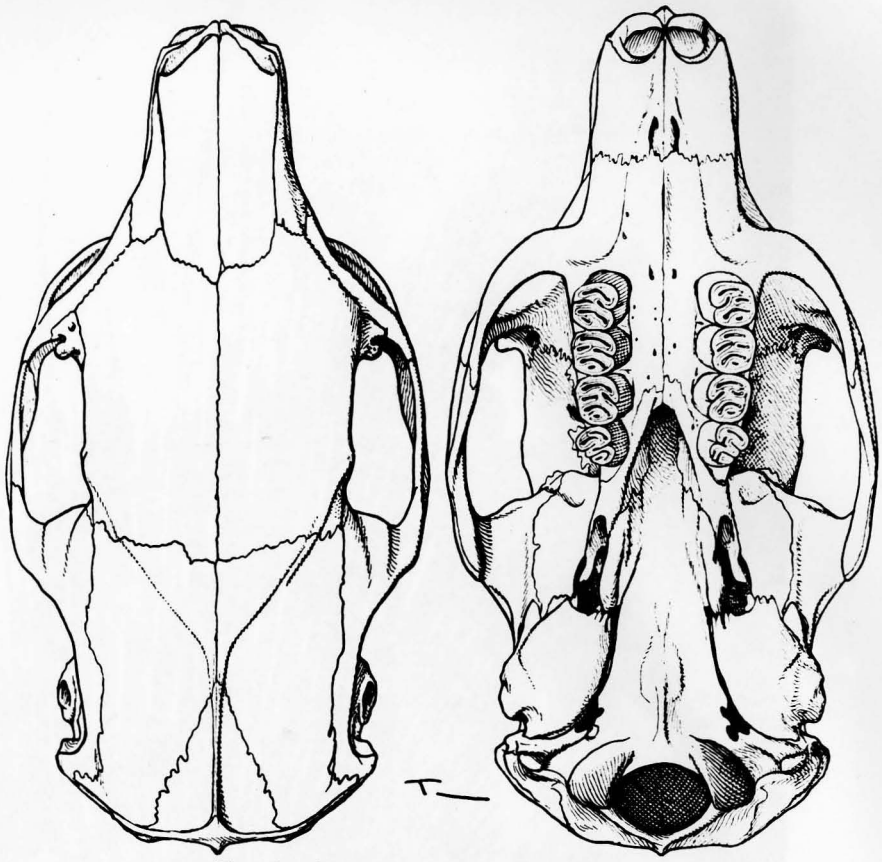


FIG. 60. THECURUS CRASSISPINIS, Günther.
B.M. No. 92.9.6.17; × 1.

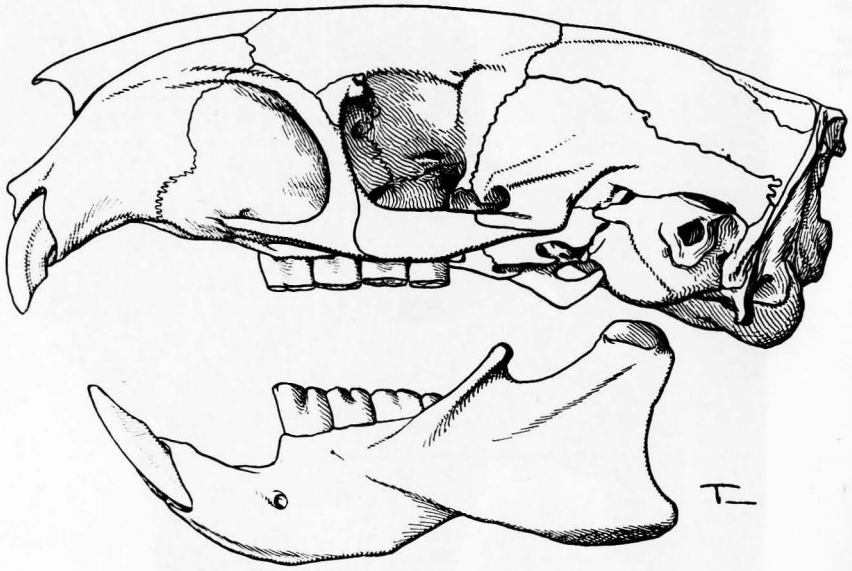


FIG. 61. THECURUS CRASSISPINIS, Günther.
B.M. No. 92.9.6.17; × 1.

Fig 29

Views of the cranium and mandible of Thecurus Crassispinis (Günther) re-photographed from Ellerman 1940 p. 210

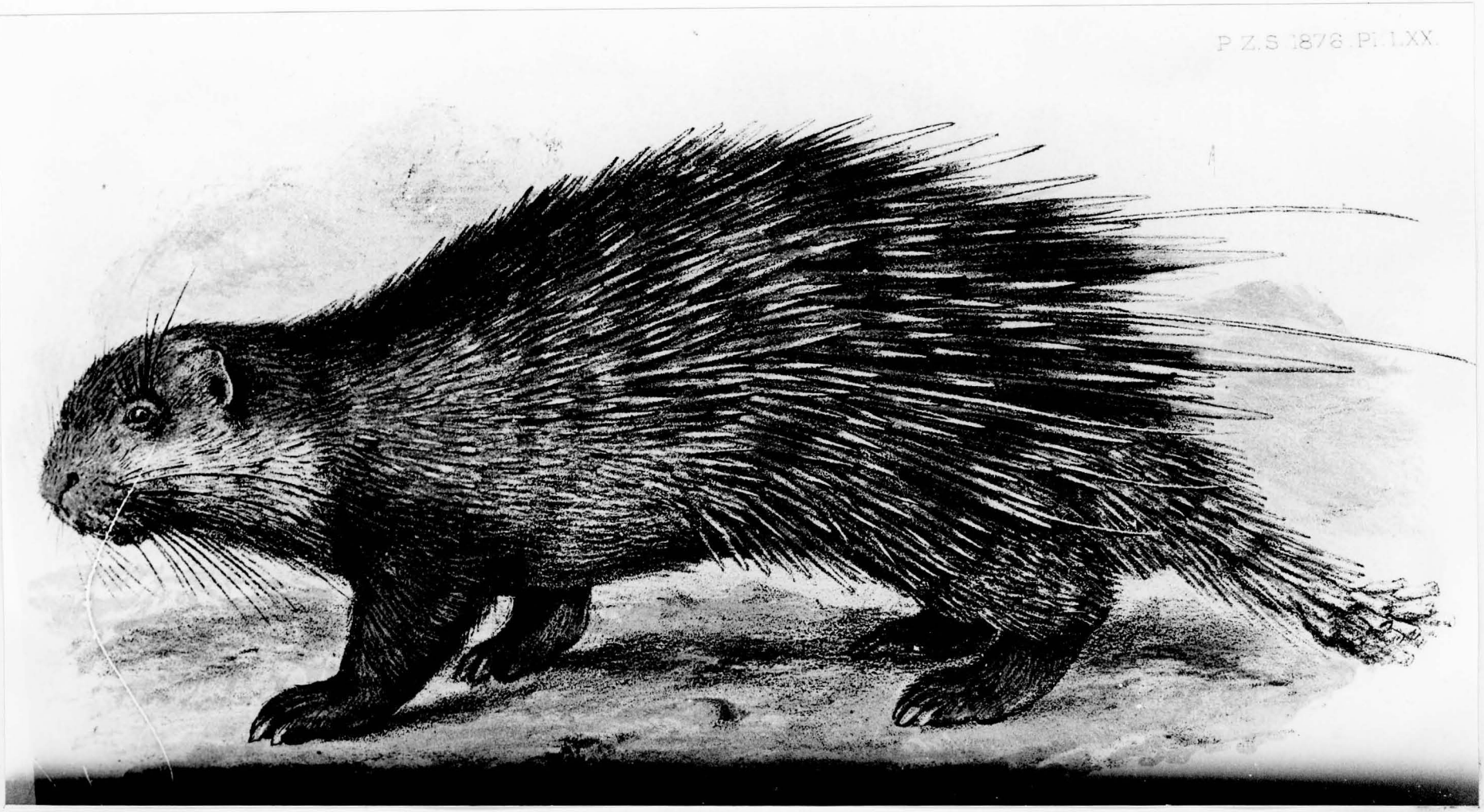


Fig 30

Illustration of Thecurus crassispinis (Günther), re-photographed from Günther 1876 Pl. 70

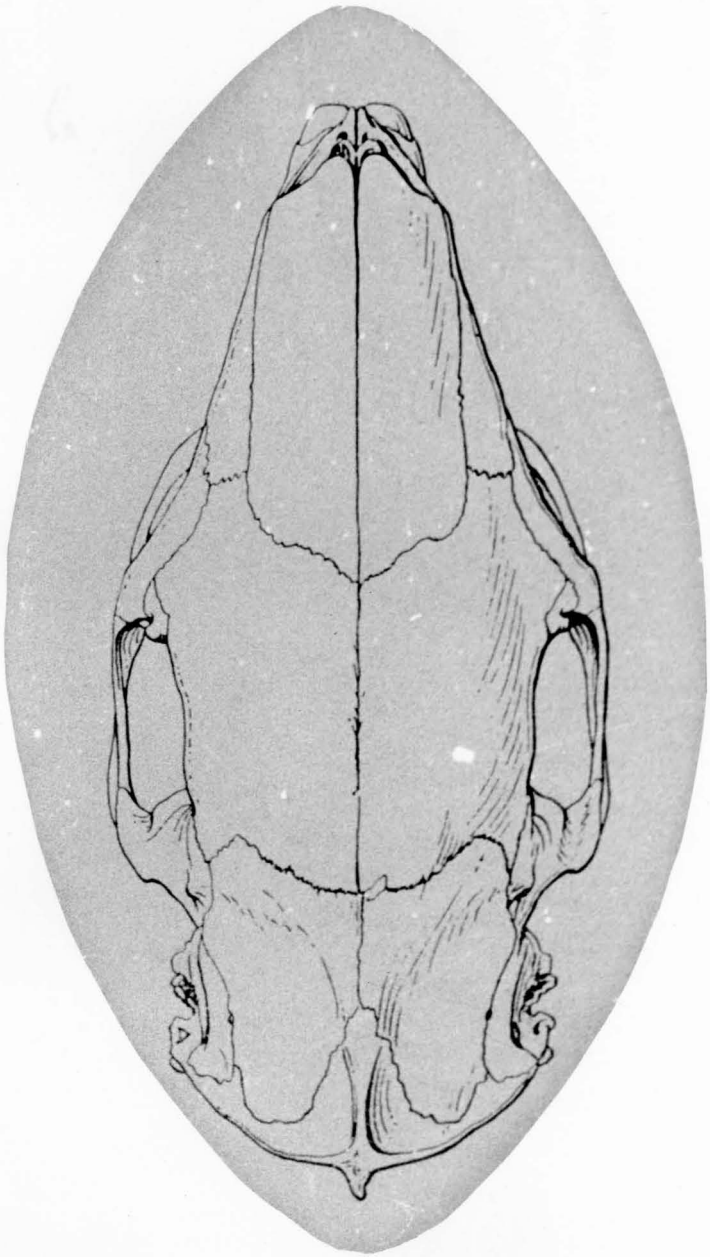


Fig. 31A

Dorsal view of the cranium of Acanthion sp., re-photographed from Lyon 1907 Pl. 54. Approximately x 1.



Fig 31B

Lateral view of the cranium and mandible of Hystrix (Acanthion) sp. re-photographed from Lyon 1907 Pl. 55. Approximately x 1.

Fig 32

Illustration of Hystrix (Acanthion) hodgsoni (Gray 1847) (= H. alophus (Hodgson)) re-drawn from Hodgson 1847 Pl.32 opposite p.771 (G. Smith).

Note the generally poor quill covering, the lack of crest or nape quills, and the few black bands on the quills when compared with subgenus Hystrix (Fig 36).

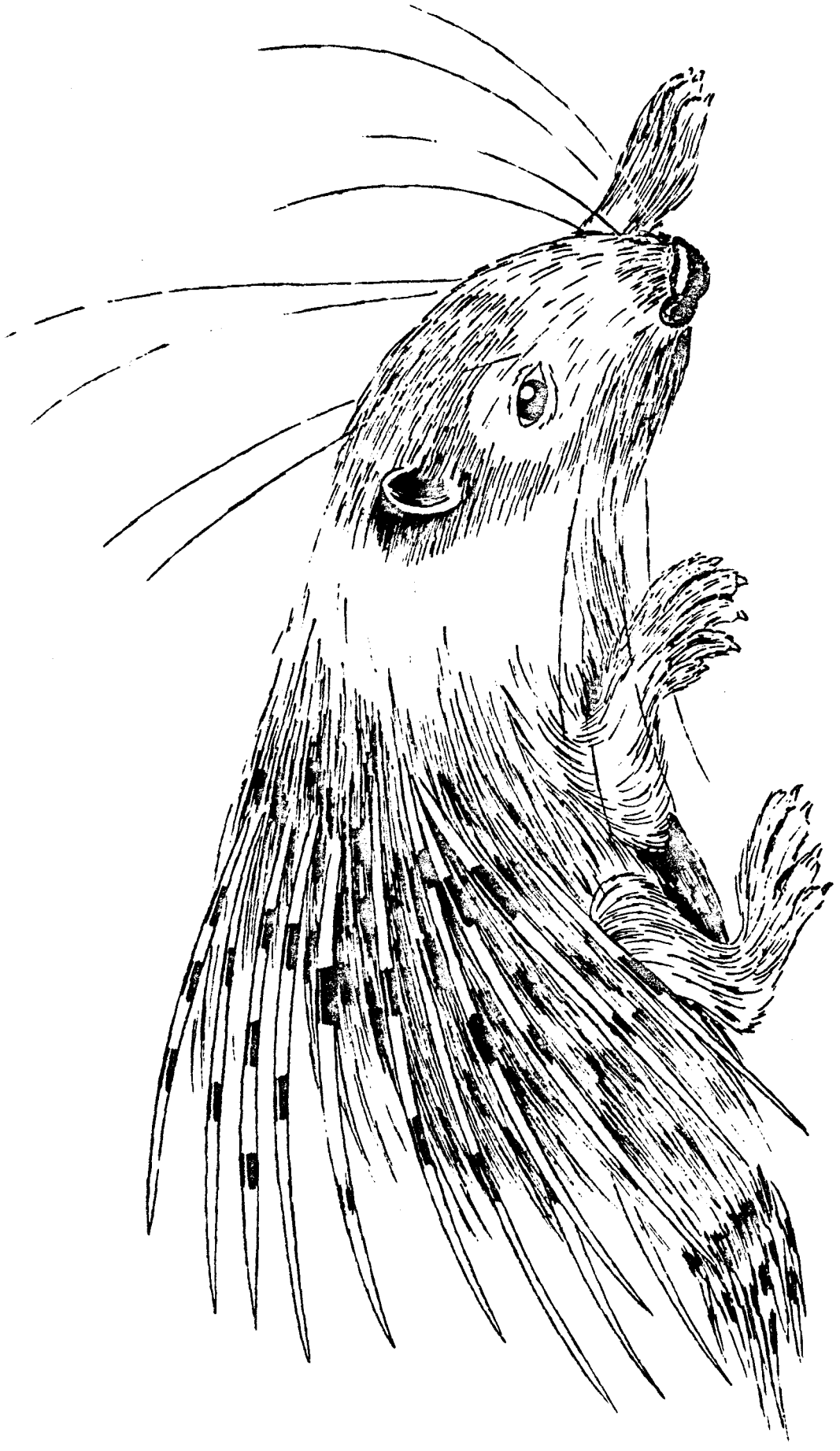


Fig 32

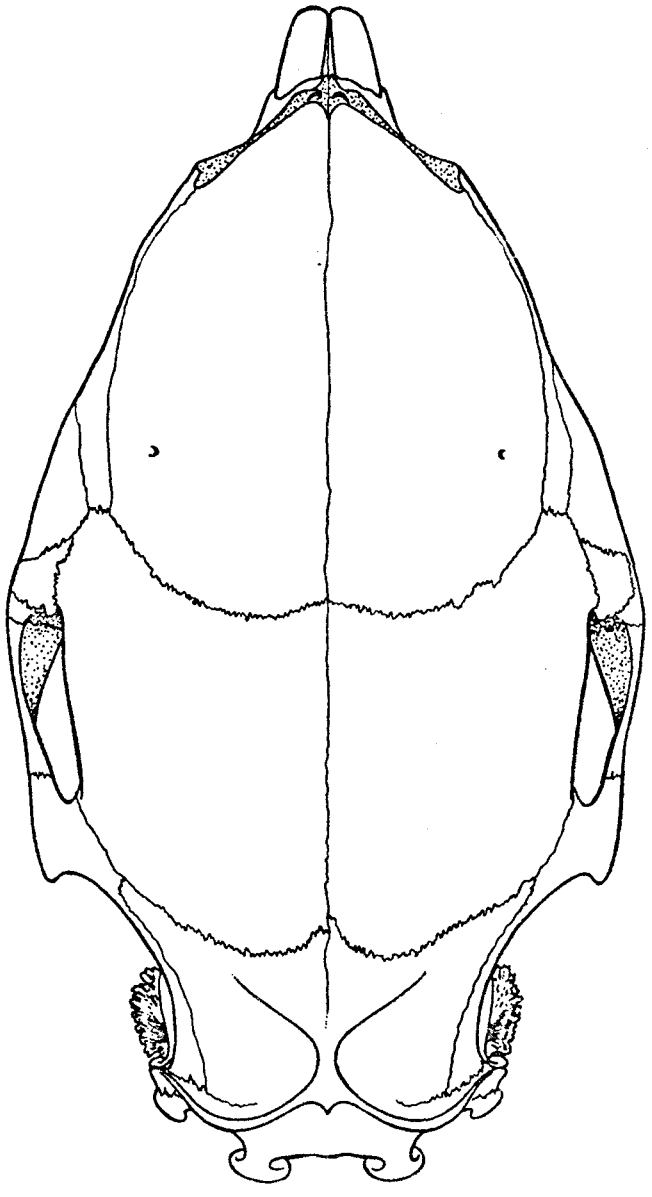


Fig 33

Dorsal view of the cranium of Hystrix africaeaustralis Peters drawn from skull TM 594 (x 1)

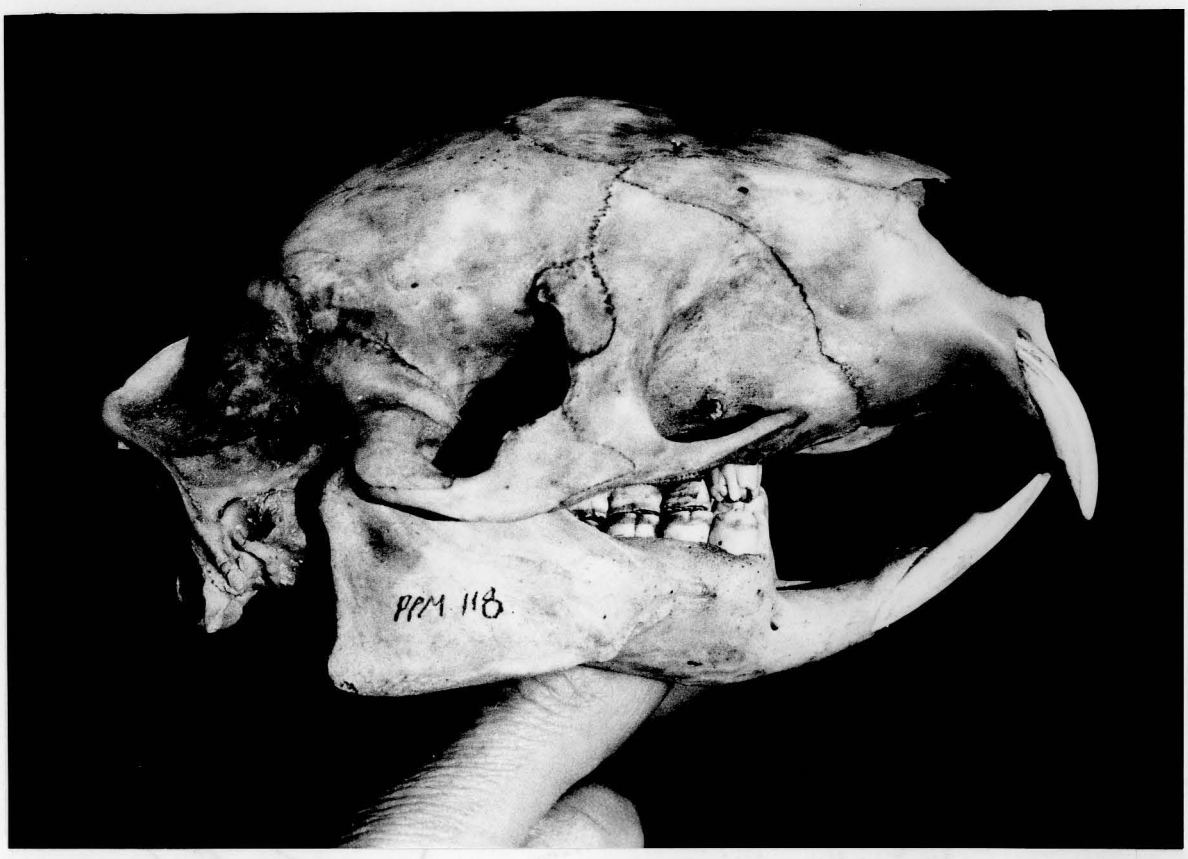


Fig 34

Lateral view of the cranium and mandible of Hystrix (H.) africaeaustralis Peters, approximately natural size

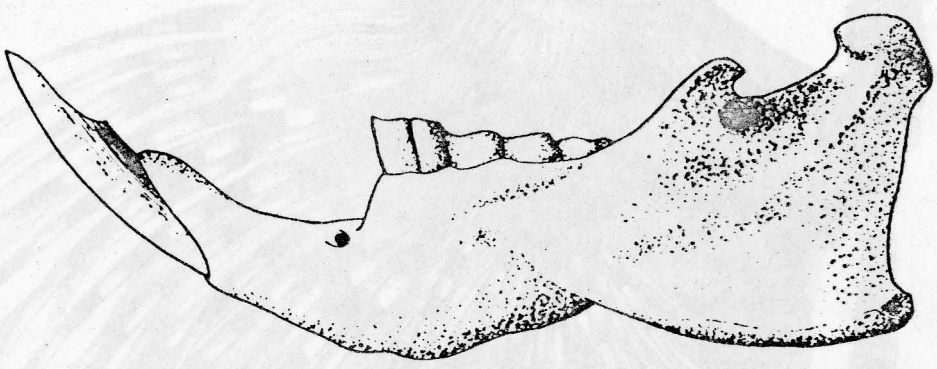


Fig 35

Lateral view of the mandible of Hystrix (H.) africaeaustralis Peters drawn from mandible TM 594 x 1



Fig 36

Illustration of Hystrix (H.) cristata Linn. re-photographed from Shaw Pl. 122

vii) Body covered with highly developed quills, subgenus Hystrix has long crest of quills on back of head and nape

viii) Caudal rattle-quills hollow open-ended capsules, highly developed

ix) Body size large, larger than Thecurus, Atherurus or Trichys

An examination of the distinctive criteria of the four genera, of the published illustrations of their crania, dentitions and external appearances, has indicated that the following adaptive or evolutionary trends have taken place from Trichys, the most generalized genus to Hystrix, the most specialized:

1) General increase in body size

2) Shortening of the tail, increase in the specialization and effectiveness of the caudal rattle quills (Fig. 37)

3) Increase in the effectiveness of the armature of quills

4) Increase in the pneumatization or inflation of skull
This manifests itself in a number of ways:

i) Increase in the width of the rostrum or snout; increase in snout bluntness - apparent shortening of snout region

ii) Increase in the length and/or width of the nasals

iii) Decrease in the length of the frontals, the degree of this depending on the extent to which ii) has taken place

iv) Increase in the width of the nasal process of the premaxilla

v) Increase in the dorsal convexity or arching of the lateral profile of the cranium

vi) Disappearance of the postorbital process

vii) Decrease in the extent of the interorbital constriction

5) Change in the dentition from rooted, brachydont cheek teeth to semi-rooted or rootless molars, the upper dentition apparently achieving the semi-rooted condition ahead of the mandibular dentition

It has previously been noted (Lönnberg 1924, Ellerman 1940) that representatives of Trichys, the least specialized of the 'Atherurus group' and the most generalized porcupines of the family, have a distribution that is strictly confined to the humid, high-rainfall tropical forest regions of South East Asia (the Malay peninsula, Sumatra and Borneo, see distribution map Fig. 38), as have the representatives of

Fig. 37

Quills and caudal 'rattle quills' of the genera of the family Hystricidae (After Lyon 1907 Pl.LVII and Mohr 1965 Fig. 62).

1 a.b Quill and tail bristle of Trichys

2 a,b Quill and tail bristles of Atherurus

3 a,b Quill and caudal rattle-quills of Thecurus

4 a,b Quill and caudal rattle-quill of Acanthion

5 a,b,c Caudal rattle-quill and quills of Hystrix (see also Fig. 152)

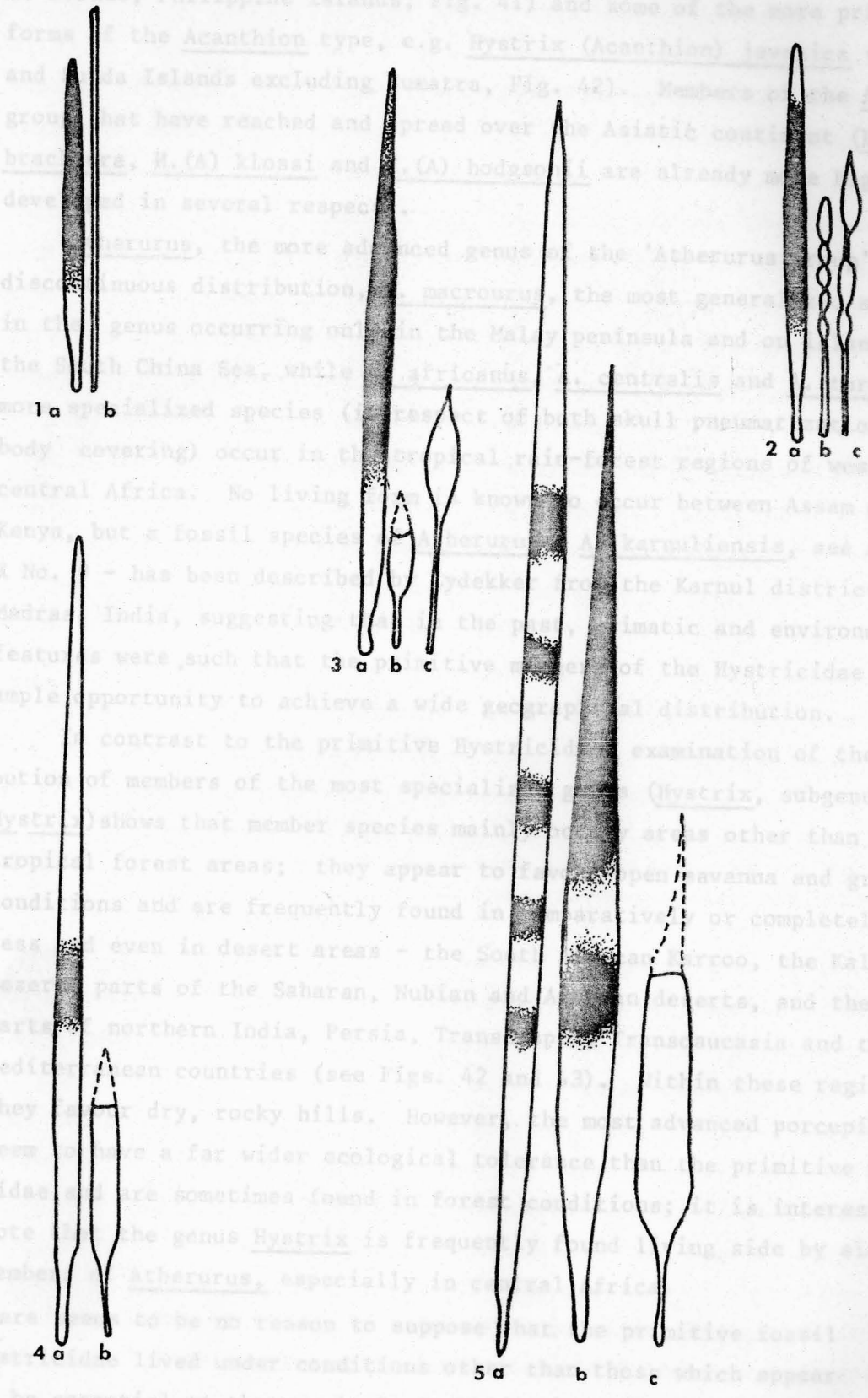


FIG. 37

Thecurus, the least specialized of the 'Hystrix group' (Sumatra, N. Borneo, Philippine Islands, Fig. 41) and some of the more primitive forms of the Acanthion type, e.g. Hystrix (Acanthion) javanica (Java and Sunda Islands excluding Sumatra, Fig. 42). Members of the Acanthion group that have reached and spread over the Asiatic continent (H.(A) brachyura, H.(A) klossi and H.(A) hodgsonii are already more highly developed in several respects.

Atherurus, the more advanced genus of the 'Atherurus group' has a discontinuous distribution, A. macrourus, the most generalized species in the genus occurring only in the Malay peninsula and on islands of the South China Sea, while A. africanus, A. centralis and A. turneri, the more specialized species (in respect of both skull pneumatization and body covering) occur in the tropical rain-forest regions of west and central Africa. No living form is known to occur between Assam and W. Kenya, but a fossil species of Atherurus - A. karnuliensis, see Appendix X No. 9 - has been described by Lydekker from the Karnul district near Madras, India, suggesting that in the past, climatic and environmental features were such that the primitive members of the Hystricidae had ample opportunity to achieve a wide geographical distribution.

In contrast to the primitive Hystricidae, examination of the distribution of members of the most specialized genus (Hystrix, subgenus Hystrix) shows that member species mainly occupy areas other than moist tropical forest areas; they appear to favour open savanna and grassland conditions and are frequently found in comparatively or completely treeless and even in desert areas - the South African Karroo, the Kalahari Desert, parts of the Saharan, Nubian and Arabian deserts, and the drier parts of northern India, Persia, Transcaspia, Transcaucasia and the Mediterranean countries (see Figs. 42 and 43). Within these regions they favour dry, rocky hills. However, the most advanced porcupines seem to have a far wider ecological tolerance than the primitive Hystricidae and are sometimes found in forest conditions; it is interesting to note that the genus Hystrix is frequently found living side by side with members of Atherurus, especially in central Africa.

There seems to be no reason to suppose that the primitive fossil Hystricidae lived under conditions other than those which appear to be essential to the survival of their modern representatives, i.e. wet, humid, tropical-forest conditions. The present day occurrence of species of Atherurus in the tropical forests of west and central Africa separated by vast tracts of treeless and desert

country from the atherurines of S.E. Asia can only be interpreted if one postulates that a tropical forest once connected the two regions, although such a connection need not have been indefinitely continuous. During this time, the forest-loving primitive porcupines had an opportunity of spreading, presumably from a south-east Asiatic centre where present-day primitive forms are concentrated to the Asiatic and ultimately the African continents. At some later period, the climate must have changed causing the forested areas to shrink and in some places to disappear; at this time the forest-loving porcupines would have either succumbed to the changed conditions or retreated to regions where the forests survived; on the other hand, some may have become adapted to suit the new and drier conditions.

It has been demonstrated that the primitive Hystricidae are mainly confined to high-rainfall humid tropical forest regions whereas the highly-developed forms (members of the subgenus Hystrix) are associated with grasslands, open savannas and desert conditions. The latter forms are in all probability the result of adaptation to these conditions.

If this is the case, an assessment of the degree of specialization exhibited by fossilized porcupine remains should give some clue as to the climatic and environmental conditions under which the animals lived. In this connection Lönnberg (1924) has noted that:

> It is no uncommon thing, that, if one of two related animals lives in the forest and the other in the open country, the latter is the more specialized and more highly developed. (p. 6)

All the features of the more specialized porcupines should therefore be explicable in terms of adaptation to lower rainfall conditions and a savanna habitat. Increase in body size and in the effectiveness of the armature of quills would be an obvious advantage in the hazardous and exposed environment of an open savanna. The increased effectiveness of the caudal rattle-quills and the sound they produce could possibly be explained in terms of an increased signalling distance on account of a more widely dispersed population, the degree of dispersal depending on the natural resources of the territory. Shortening of the tail was probably associated with the increase in effectiveness of sound production. The increased pneumatization of the skull could be explained in terms of the need for a more effective olfactory organ: this would be advantageous if the animal had to go in search of subterranean bulbs, tubers and roots at those times of the year when superficial

fresh green vegetatation was difficult to obtain. The increased hypsodonty of the teeth is explicable if it is considered that the diet of savanna-dwelling porcupines must be harder and more fibrous than that of the forest-living forms; their teeth would be subjected to a greater degree of wear, and therefore open-rooted or almost permanently-growing hypsodont teeth would obviously be an advantage.

In view of the fact that degree of specialization seems to be a valid indicator of past climate and environment, it is unfortunate that fossil porcupine remains are often limited to isolated teeth and small dentigerous jaw fragments, leaving degree of dental specialization as the only guide.

The way in which the evidence of the Old World fossil porcupine remains support these views has been discussed in a subsequent chapter (Chapter 13, CONCLUSION AND DISCUSSION).



Fig 38

Map of south-east Asia, showing the distribution of the genus Trichys

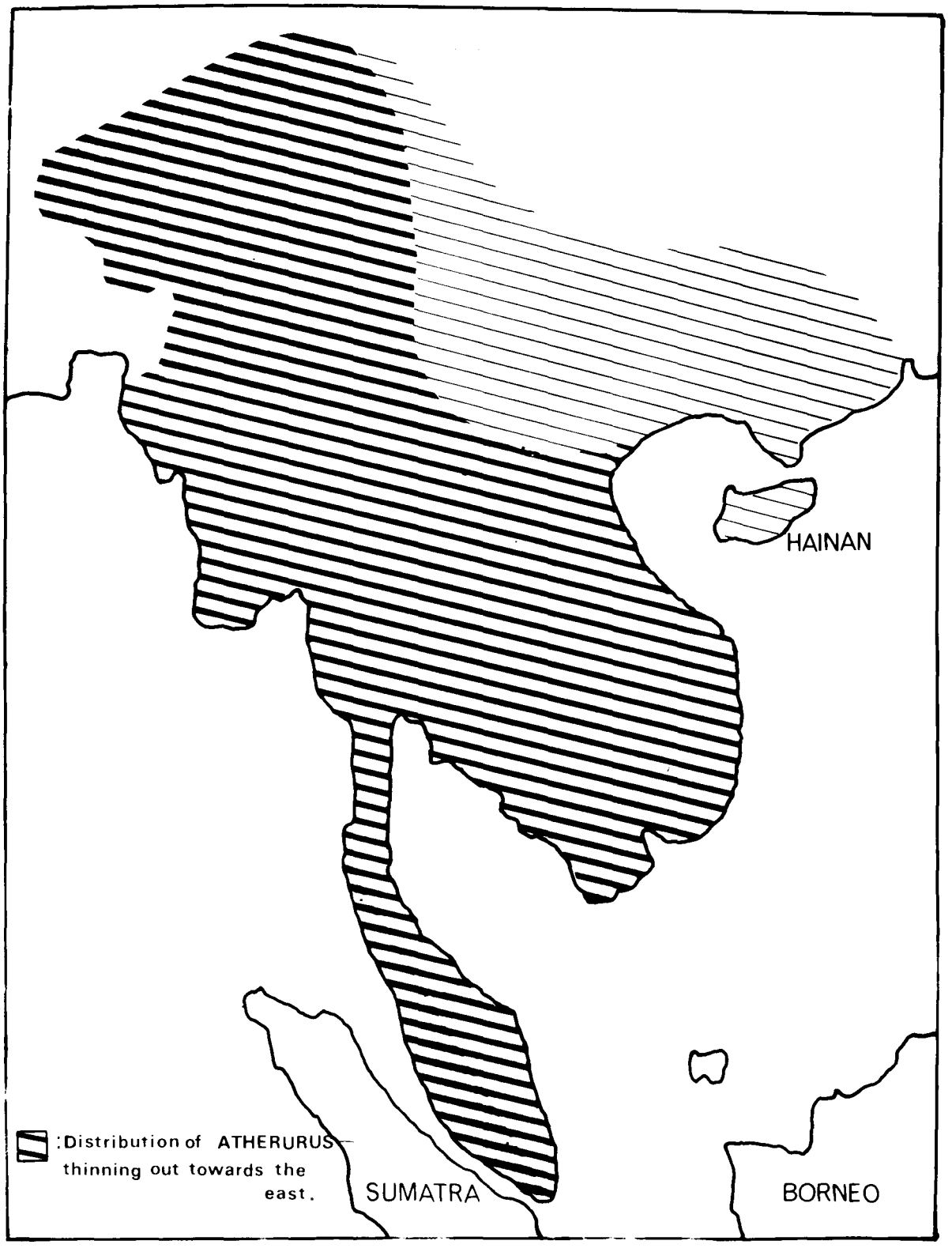


Fig 39

Map showing the distribution of the brush-tailed porcupines (genus Atherurus) in Asia, re-drawn from Mohr 1965 p. 100 fig. 74

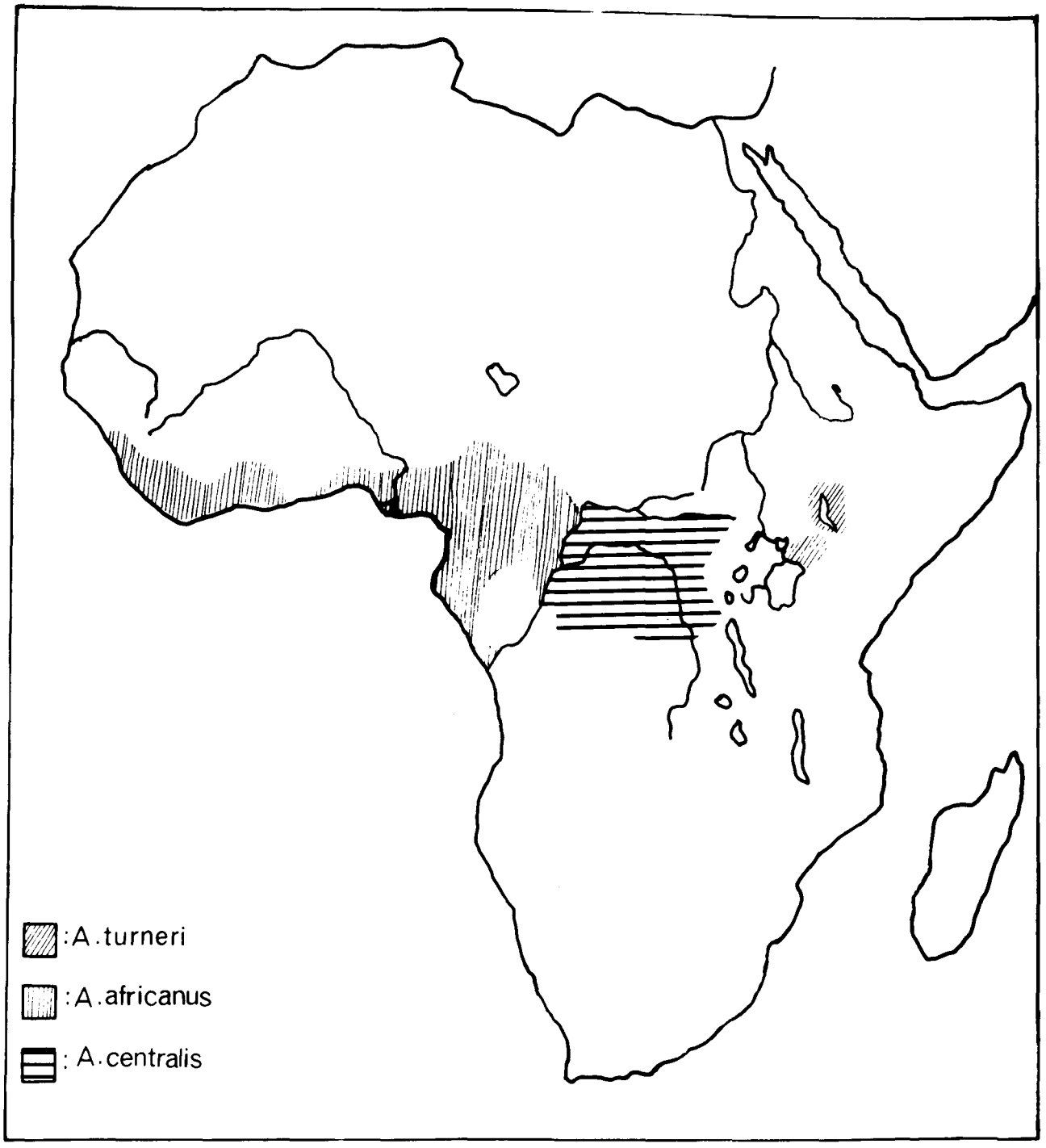


Fig 40

Map showing the distribution of the brush-tailed porcupines (genus Atherurus) in Africa, re-drawn from Mohr 1965 p. 109 fig. 81

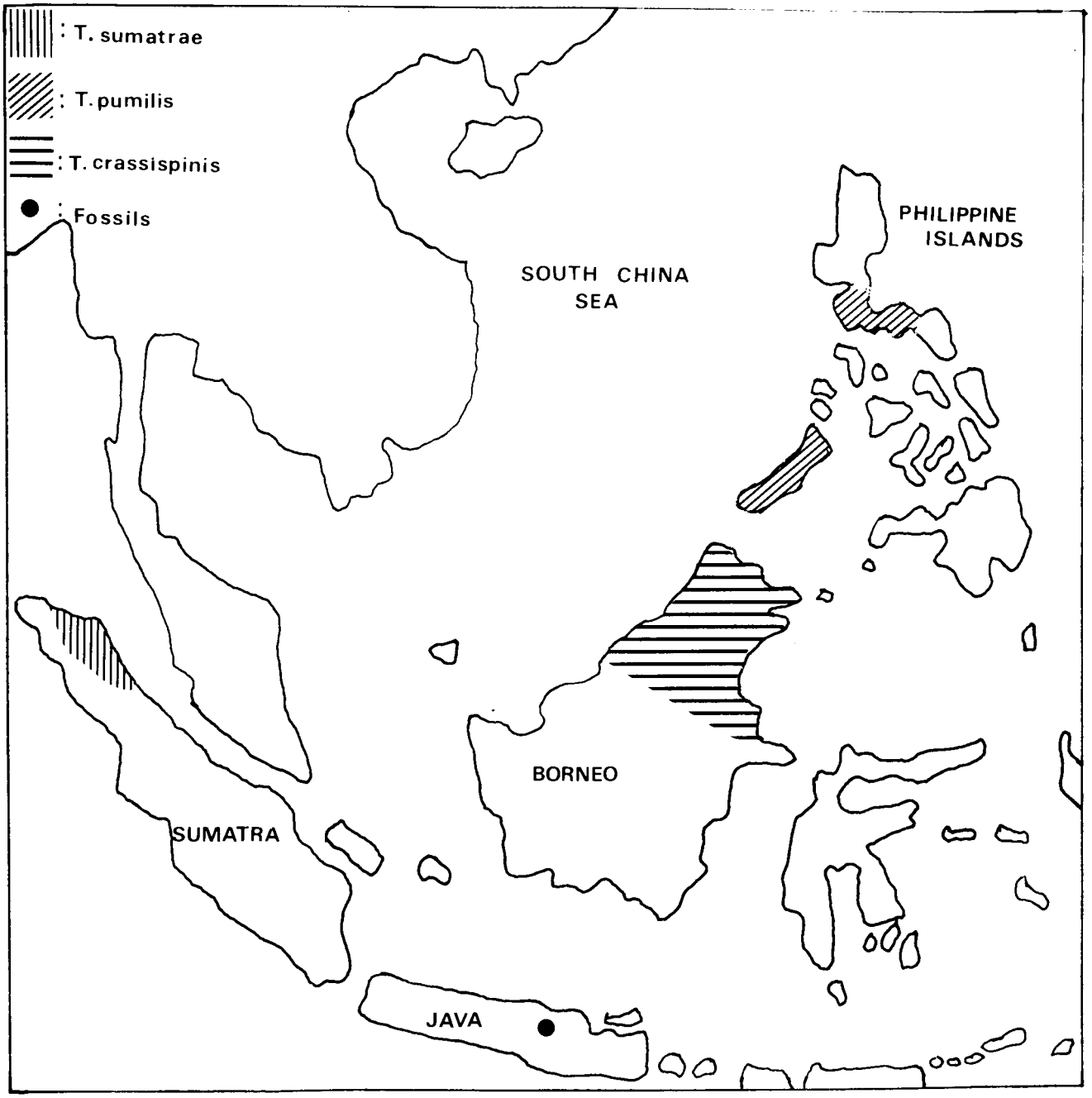


Fig 41

Map showing the distribution of the genus Thecurus, re-drawn from Mohr 1965 p. 115 fig. 87

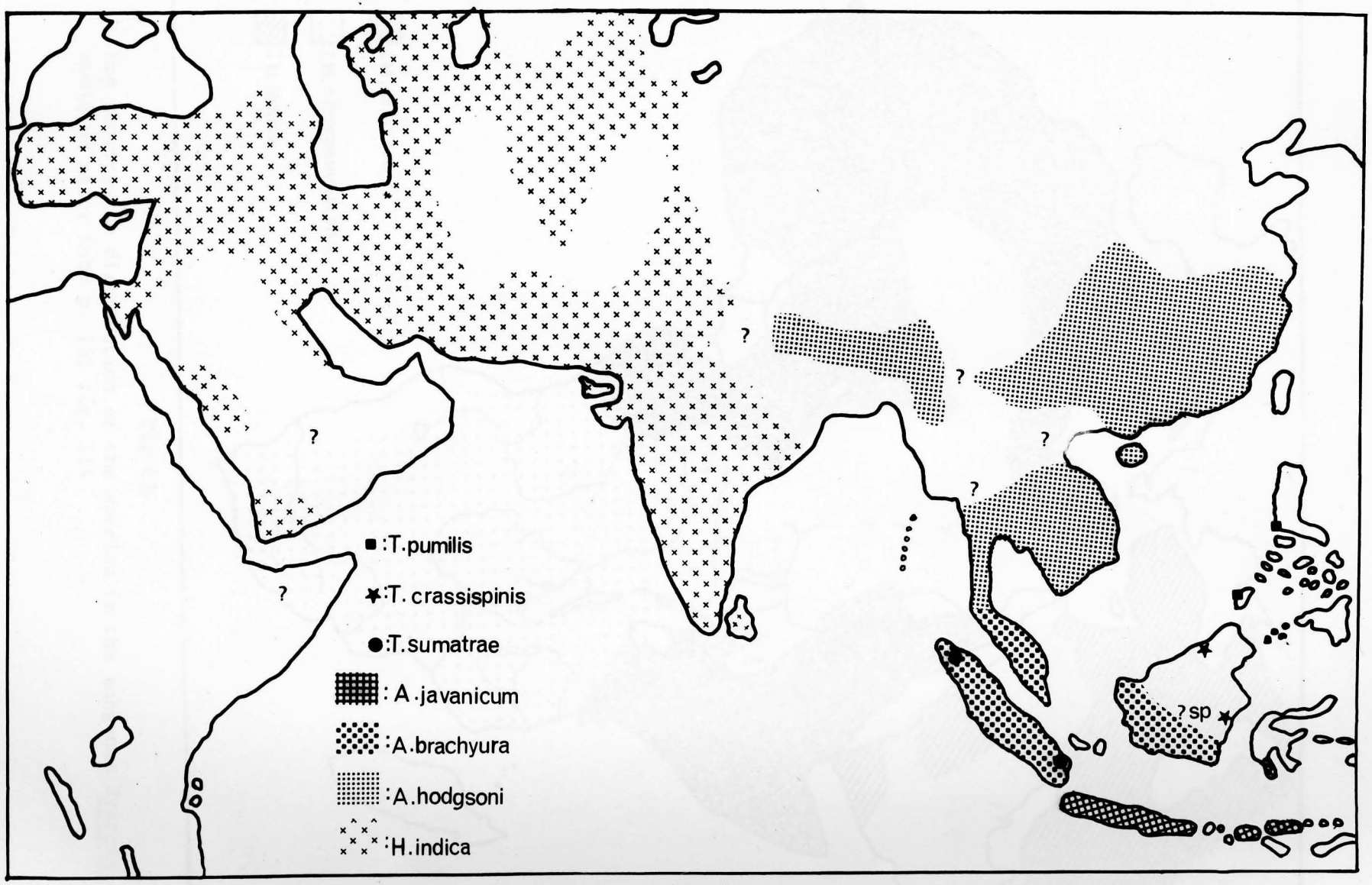


Fig 42

Map showing the distribution of the species in the genus Thecurus and in the subgenus Acanthion and of Hystrix (H.) indica, modified after Mohr 1965 p. 152 fig. 115

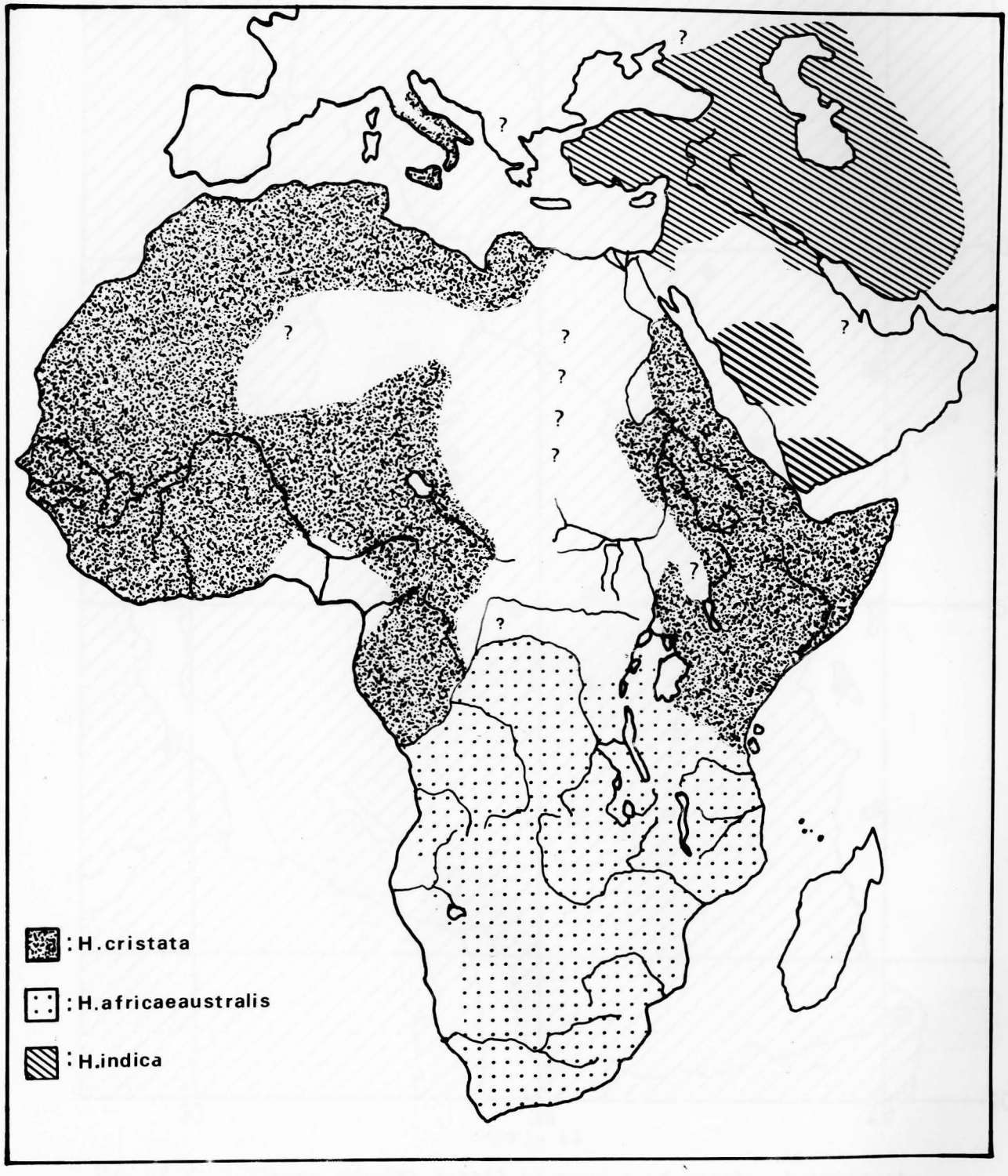


Fig 43

Map showing the distribution of the species in the subgenus Hystrix, modified after Mohr p. 151 fig. 114

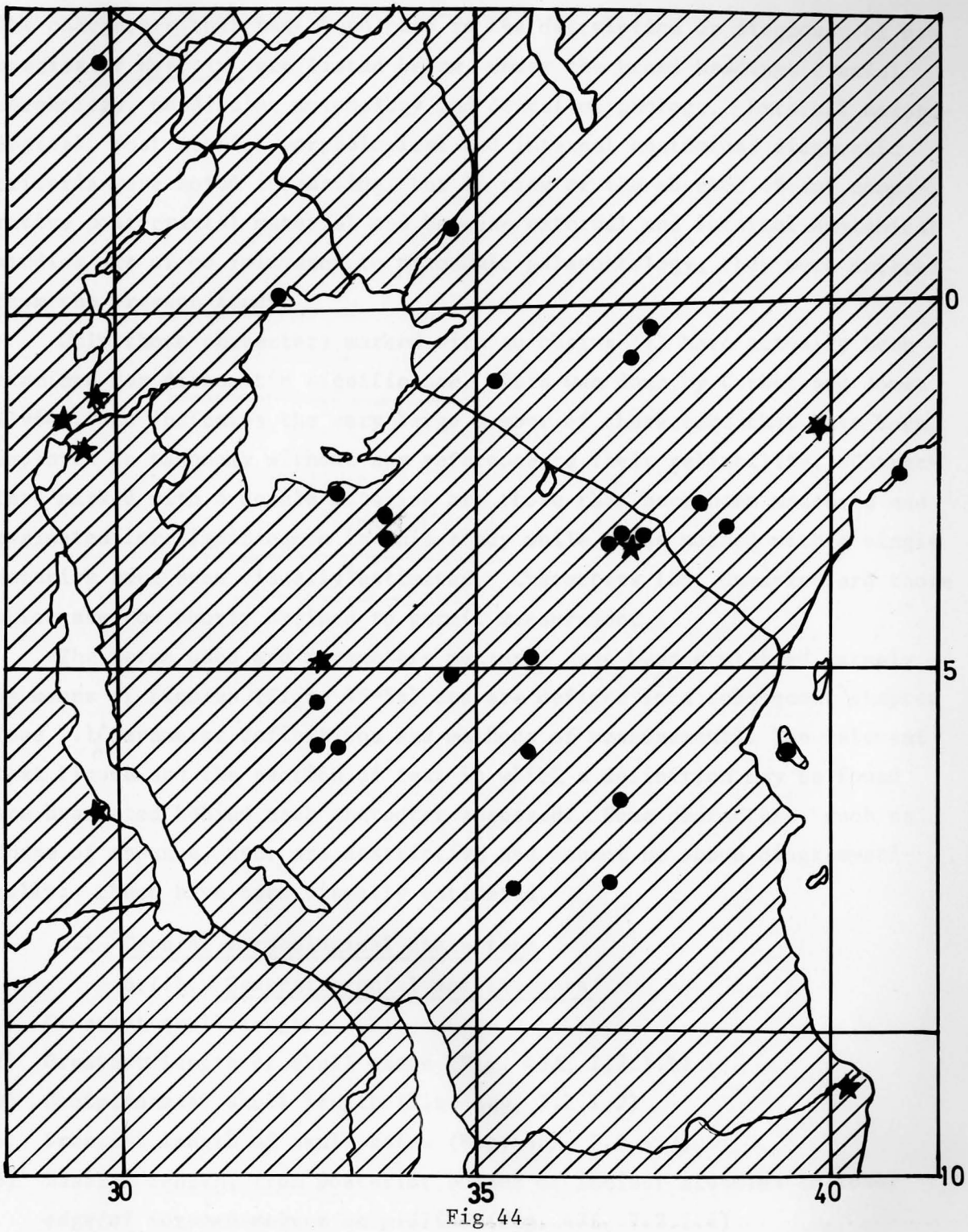


Fig 44

Map of East Africa showing detail of region of overlap between the species Hystrix (H.) cristata (dots) and Hystrix (H.) africaeaustralis (stars), after Corbet and Jones 1964 p. 287 fig. 2

6 LIST OF CRITERIA USED IN THE DIAGNOSES OF NEW SPECIES OF HYSTRIX

The characters that have been used in the description or diagnoses of new species of Hystrix are listed below, under the broad headings cranial morphology, mandibular morphology and dental morphology. External morphological, post-cranial morphological and internal anatomical diagnostic criteria were noted in passing, but in view of the absence of any comparative post-cranial material and because external and internal anatomical studies are of no relevance to taxonomic palaeontology, they were omitted from the present study.

Only those characters marked with an obelus (†) have actually been examined for diagnostic significance. This was done by Corbet and Jones (1964), and indicates the very large number of characters that have been employed in taxonomy without any reference to their reliability. Characters marked with a double asterisk are those that have been measured and evaluated for significance in this study while those marked with a single asterisk have been visually estimated. Characters left unmarked are those which are too poorly defined to permit measurement.

The terms used and parameters measured have been explained largely by means of figures (Figs. 45-56) and are defined in a subsequent chapter (see 7.1 Parameter definitions and methods of measurement). The relevant text figure and the section of text in which a definition may be found are bracketed behind each character assessed. Some characters, such as shape of choanae, etc. are descriptive and cannot be shown diagrammatically: these have been visually estimated.

6.1 Cranial morphological characters

6.1.1. General cranial measurements

1) Greatest skull length

**2) Greatest length of skull above (Fig. 46A, 7.2.1.1)

†**3) Occipitonasal skull length (Fig. 46B, 7.2.1.2)

**4) Greatest length of skull below (Fig. 48R, 7.2.1.3)

**5) Basilar length, from posterior border of incisor alveolus to lower edge of foramen magnum on midline (Fig. 47S, 7.2.1.4)

**6) Greatest width of skull above (Fig. 46C, 7.2.1.5)

**7) Greatest width of skull below (= Char. 6, since this measurement above and below is apparently the same, Fig. 46C, 7.2.1.5)

8) Breadth between outer corners of infraorbital foramen

9) Width of skull at orbit

**10) Width of skull at zygoma (apparently = Chars. 6, 7, Fig. 46C, 7.2.1.5)

11) Width of skull between jugals

12) Width of skull between parietals

**13) Smallest skull breadth behind zygomatic, i.e. least postorbital breadth (Fig. 46D, 7.2.1.6)

**14) Skull width at condyles (Fig. 46E, Fig. 54 A^2, 7.2.1.7)

**15) Zygomatic breadth at the level of the back of the nasals (apparently = Chars. 6, 7, 10, Fig 46C in the case of H. africaeaustralis)

16) Zygomatic breadth at the level of the back of the parietals (Zygomatic does not extend as far back as this in the case of H. africaeaustralis)

**17) Interorbital distance at lachrymal edge (Fig 46F, 7.2.1.8)

**18) Interorbital distance at rudimentary post-orbital process (Fig. 46G 7.2.1.9)

19) Interorbital breadth anteriorly

20) Interorbital breadth posteriorly

**21) Height of skull from palate to posterior end of nasals (Fig. 50E 7.2.1.10)

**22) Height of skull from palate between M^1 (Fig. 50 F^1, 7.2.1.11)

23) Height of skull from processus alveolaris

**24) Least breadth of bony bridge between orbit and foramen interorbitale (sic) (= foramen infraorbitale) (Fig. 50 G^1, 7.2.1.12)

**25) Breadth of choanae (Fig. 52 P^1, 7.2.1.13)

26) Breadth of mesopterygoid opening

**27) Length of sagittal crest (Fig. 46H, 7.2.1.14)

*28) Prominence and breadth of sagittal crest (Fig. 45, 7.2.1.15)

*29) Prominence and breadth of lambdoid or occipital crest (Fig. 45, 7.2.1.16)

30) Size, antero-posterior length of bullae

31) Size of condyles

32) Braincase breadth

33) Length of rostral portion of cranium

34) Compression (narrowness) of muzzle (rostrum)

35) Shape of infraorbital foramen

36) Development of intertemporal constriction

37) Convexity of cranium in frontal region

38) Inflation of skull

39) Position of pterygoid fossa

**40) Position of sphenopalatine foramen (Fig. 47, 7.2.1.17)[i)]

6.1.2 Premaxillary (intermaxillary) morphology

**41) Length of nasal process of premaxilla (Fig. 50 H^1, 7.2.21)

**42) Breadth of nasal process of premaxilla at fronto-premaxillary suture (Fig. 46P, Fig. 50 I; 7.2.2.2)

†**43) Breadth of nasal process of premaxilla at a point on its lower margin midway between the maxillo-frontal suture and the masseteric ridge of the maxilla (Fig. 50J^1, 7.2.2.3)[ii)]

**44) Mesial sutural length of premaxilla ventrally (Fig. 48T, 7.2.2.4)

**45) Palatal length of premaxilla medially, in front of foramen incisiva (Fig. 48U, 7.2.2.5)

*46) Posterior extent of premaxillary process (7.2.2.6)

*47) Shape of nasal process of premaxilla and its termination, i.e. square, rounded, triangular, truncated, etc. (7.2.2.7)

48) Excavation or prominence of anterior border of cranium, i.e. of premaxilla

6.1.3 Nasal morphology

**49) Length of nasals (Fig. 46 I; 7.2.3.1)

**50) Length of nasal suture (Fig. 46J, 7.2.3.2)

**51) Maximum width of nasals (Fig. 46K, sometimes L, 7.2.3.3)

**52) Width of nasal at anterior end of naso-premaxillary suture Fig. 46M, 7.2.3.4)

**53) Anterior width of nasals (= Char. 52, Fig. 46M, 7.2.3.4)

**54) Width of nasal at posterior end of naso-premaxillary suture (Fig. 46K, 7.2.3.5)

**55) Posterior width of nasals (=Char. 54, Fig. 46K, 7.2.3.5)

**56) Posterior extent of nasals behind fronto-premaxillary suture (Fig. 46N, 7.2.3.6)

*57) Posterior extent of nasals in relation to lachrymals (nasal does not extend beyond lachrymal in H. africaeaustralis) (7.2.3.7)

*58) Posterior extent of nasals in relation to orbits (7.2.3.8)

*59) Shape of posterior margin of nasals (7.2.3.9)

**60) Shape of nasals (= combination Chars. 121 and 122, Fig. 46K : I &

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i) As defined by Sulimski (1960) Plate I fig. 1
ii) See Corbet and Jones (1964) p.289 fig. 3

M:K),i.e. relative width, narrowing or shape of nasals (7.2.11.3, 7.2.11.4)

*61) Size and shape of nasal orifice (= Char. 25 in part, Fig. 52P^2, 7.2.3.11)

62) Anterior termination of nasals in relation to incisor

6.1.4 Frontal morphology

**63) Length of frontal along median suture (Fig.46 O, 7.2.4.1)

**64) Length of fronto-premaxillary suture (= Char. 42, Fig. 87, Fig. 46P, Fig. 50 I^1,7.2.2.2, 7.2.4.3)

65) Greatest breadth of frontals

**66) Breadth of frontals across rudimentary post-orbital process (= Char. 18 Fig 46G, 7.2.1.9, 7.2.4.3)

6.1.5 Parietal morphology

67) Median sutural length of parietal (7.2.5.1)

**68) Fronto-occipital distance (Fig. 46Q, 7.2.5.2)

69) Breadth of parietals

6.1.6 Occipital morphology

70) Height of occiput

**71) Distance from upper edge of foramen magnum to occipital crest along median line (Fig. 54S^1, 7.2.6.1)

**72) Distance from lower edge of foramen magnum and occipital crest along median line, maximum height of occiput (Fig. 54T^1,7.2.6.2)

73) Breadth of occiput

74) Greatest breadth of occiput above foramen magnum (Fig. 54U^1, 7.2.6.3)

75) Least breadth of occiput above foramen magnum (Fig. 54V^1, 7.2.6.3)

76) Upper occipital breadth

77) Lower occipital breadth

**78) Greatest occipital breadth at paroccipital processes (Fig. 54W^1, 7.2.6.4)

**79) Length of paroccipital processes (Fig. 54X^1, 7.2.6.5)

**80) Distance between paroccipital processes (Fig. 54Y^1, 7.2.6.6)

**81) Maximum width of occipital condyles between external edges (Fig.54Z^1, 7.2.6.7)

82) Inter-condylar distance

*83) Orientation of long axis of condyles (7.2.6.8)

6.1.7 Palatal morphology

**84) Diastemic length: distance from posterior border of incisor to the anterior alveolar border of P^4 (Fig. 48V, 7.2.7.1)

**85) Median sutural length of palate (Fig. 48W, 7.2.7.2)

86) Length of palate to gnathion (probably = Char. 85, Fig. 48W, 7.2.7.2)[i)]

87) Length of palatine bone measured along median length (= Char. 85, Fig. 48W, 7.2.7.2)[ii)]

**88) Median sutural length of maxillary (Fig. 48X, 7.2.7.3)

**89) Width of palate between dp^4 or P^4 (Fig. 48Y, 7.2.7.4)

**90) Width of palate between M^1 (Fig. 48Z, 7.2.7.5)

**91) Width of palate between M^2 (Fig. $48A^1$, 7.2.7.6)

**92) Width of palate between M^3 (Fig. $48B^1$, 7.2.7.7)

*93) Shape of palate behind (Fig. 48, 7.2.7.8)

*94) Shape of palatal incision (palatine opening of some authors = Char. 93) (Fig. 48, 7.2.7.8)

*95) Anterior extent of palatine incision (Fig. 48, 7.2.7.9)

96) Stoutness of posterior processes of palatines

**97) Length, breadth, shape and position of foramina incisiva (Fig. 48, 7.2.7.10)

6.1.8 Morphology of the zygomatic region

†**98) Zygomatic width (= Chars.6,7,10,15, Fig. 46C, 7.2.1.5)

**99) Greatest width of zygomatic arches (= Chars. 6,7,10,15,98, Fig. 46C, 7.2.1.5)

100) Width of lower edge of zygoma

†**101) Width of vertical zygomatic process of maxilla (probably = Char. 24) (Fig. $50G^1$, 7.2.1.12)

**102) Minimum width of vertical zygomatic process of maxilla (= Chars. 24, 101) (Fig. $50G^1$, 7.2.1.2

**103) Least vertical diameter of lower anterior zygoma root (Fig. $50K^1$, Fig. $50Q^1$, 7.2.8.1)

104) Upper and lower zygoma bar shape

105) Position of base of zygomatic root

**106) Jugal height at maxillo-jugal suture (Fig. $50L^1$, 7.2.8.2)

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i) 'Gnathion' is Lönnberg's (1923) term

ii) Used by Frenkel (1970 p.60). From the measurements (op. cit.Table III) it seems obvious that median sutural length of palate is meant.

**107) Jugal height at jugal-squamosal suture (Fig. 50M[1], 7.2.8.3)

**108) Length of jugal along orbital rim (Fig. 50N[1], 7.2.8.4)

**109) Distance from lower edge of zygoma to median suture dorsally (Fig. 52R[1])

6.1.9 Morphology of lachrymals

110) Distance between lachrymal and the zygomatic suture at the orbital rim (Fig. 50 O[1];7.2.9.1)

**111) Approach of the jugal to lachrymal (= Char. 110, Fig. 50 O[1], 7.2.9.1)

**112) Extent of facial surface of lachrymal (7.2.9.2)

6.1.10 Miscellaneous cranial characters

**113) Molar tympanic distance (Fig. 48D[1], 7.2.10.1)

114) Stoutness of posterior processes of pterygoids

115) Distance of entopterygoid from tympanic

116) Shape of entopterygoid

6.1.11 Cranial relationships (proportions, ratios and percentages)

117) Length of nasal bones as a proportion of total skull length (basically the same as Char. 118)

†**118) Length of nasal bones: occipitonasal skull length (Fig.46 I:B, 7.2.11.1)

**119) Length of nasal bones: length of frontal suture (Fig.46 I:O) or more usually length of frontals: length of nasals (Fig.46 O:I, 7.2.11.2)

**120) Length of frontals % nasal length (= Char. 119, 7.2.11.2)

**121) Relative width of nasals; greatest width: greatest length (Char. 60 in part; Fig. 46K:I, 7.2.11.3)

†**122) Width of nasals anteriorly: width of nasals posteriorly narrowing, shape (= Char. 60 in part; Fig. 46M:K 7.2.11.4

**123) Breadth of premaxilla in relation to greatest nasal width (= Char. 124 below)

**124) Width of nasal process of premaxilla in relation to the greatest width of nasal (Fig. 50J[1]: Fig. 46K, 7.2.11.5)

**125) Maximum width of occiput: maximum height of occiput (Fig. 54U[1]:S[1] and Fig.54U[1]:T[1] , 7.2.11.6)

**126) Maximum width of occiput: maximum width of condyli (Fig. 54U[1]:Z[1] 7.2.11.7)

**127) Height of skull as a % of basilar length (Fig. 50E[1] % Fig. 48S, 7.2.11.8)

**128) Zygomatic breadth: basilar length (Fig. 46C: Fig. 48S, 7.2.11.8)

**129) Length of molar series: molar-tympanic distance (Fig. 48C[1]:D[2])

6.2 Mandibular morphological characters

**130) Length of mandible (greatest length) (Fig. 56B[1], 7.2.12.1)

**131) Length of mandible from posterior border of lower incisor alveolus to tip of angular process (Fig. 56C[1], 7.2.12.2)

**132) Height of mandibula (ascending ramus) from condyle to processus angularis (Fig. 56D[1], 7.2.12.3)

**133) Depth of ramus (= height) below P4 (Fig. 56F[1], 7.2.12.4)

**134) Height of ramus below M1 (Fig. 56F[1], 7.2.12.5)

**135) Height of ramus below M2 (Fig. 56G[1], 7.2.12.6)

**136) Alveole of P4 to foramen mentale (Fig.56H[1], 7.2.12.7)

**137) Position of foramen mentale (7.2.12.8)

**138) Length of diastema from posterior border of alveolus of I1 to anterior border of the alveolus of P4 (Fig.56 I, 7.2.12.9)

**139) Curvature of diastema (7.2.12.10, Fig. 5)

140) Shape of coronoid process

141) Breadth of processus coronoideus

142) Extent of coronoid process above condyle (does not occur in H. africaeaustralis)

*143) Presence or absence of a slanting, dorsally thickened crest on coronoid process, as in Thecurus (7.2.12.11)

**144) Position of ascending ramus in relation to alveolar plane of molars (Fig.56J, i.e. distance from X^2X^2 to top of condyle, 7.2.12.12)

**145) Position of top of mesial symphysis in relation to alveolar plane of molars (Fig. 56K, 7.2.12.13)

146) Foramen mandibulare to symphysis[i)]

147) Foramen mentale to condylus[ii)]

**148) Extent of development of muscle attachments (7.2.12.14)

*149) Position of muscle attachments (7.2.12.14)

150) Foramen mentale to condylus/foramen mandibulare to mesial symphysis[iii)]

151) Height ramus under M_1/height ramus under M_2[iv)]

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i),ii),iii),iv) Frenkel (1970) uses these characters but gives no definition for them; neither from her measurements is it possible to determine where they have been taken and they have therefore not been considered.

6.3 Dental morphological characters[i)]

**152) Degree of divergence from the parallel of maxillary tooth row, i.e. the difference between palatal breadth between M^3 (= Char. 92, Fig. 48B^1) and palatal breadth between M^4 (= Char. 89, Fig. 48Y) (7.2.13.1)

**153) Degree of divergence from the parallel of mandibular tooth rows, i.e. the difference between distance left and right M_3's lingually (= Char. 155) and the distance between left and right P_4's lingually (Char. 154) (7.2.13.2)

**154) Distance between left and right P_4's lingually (7.2.13.3)

**155) Distance between left and right M_3's lingually (7.2.13.4)

**156) Width of palate in relation to width of teeth, i.e. average width of palate (Fig. 48 (Y + Z + A^1 + B^1) ÷ 4: average width of teeth at alveolar rim (7.2.13.5)

**157) Length of maxillary tooth row, measured at the occlusal surface (7.2.13.6)

**158) Length of maxillary tooth row, measured at the alveolar rim (7.2.13.7)

**159) Length of mandibular tooth row, measured at the occlusal surface (7.2.13.6)

**160) Length of mandibular tooth row, measured at the alveolar rim (7.2.13.7)

†161) Length of maxillary tooth row (character investigated by Corbet and Jones, probably measured at the occlusal surface and therefore = Char. 157)

*162) Colour of enamel on upper and lower incisors (7.2.13.8)

*163) Presence or absence of groove on upper incisors (7.2.13.8)

**164) Upper incisor width (i.e. MD diameter): Lower incisor width (7.2.13.9)

**165) Curvature of incisors (Figs. 109, 110) (7.2.13.10)

**166) Height of teeth, i.e. the extent of hypsodonty or of brachydonty (7.2.13.11)

**167) Curvature of maxillary and mandibular teeth (7.2.13.12)

*168) Development and divergence of roots (7.2.13.13)

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i) The terms MD, BL and LL refer to the mesio-distal tooth diameter (length) and bucco-lingual or labio-lingual tooth diameter (breadth) respectively

*169) Number and position of roots (7.2.13.13)

*170) Cross-sectional shape of incisors (7.2.13.14)

*171) Cross-sectional shape of cheek teeth (7.2.13.14)

**172) The nature of the crown enamel pattern, the order of closure of enamel folds and the number of enamel islands (7.2.13.15)

**173) The downward extent of the external enamel fold on the lower teeth, especially on the P_4; i.e. the relationship of the base of the external enamel fold to the level of the divergence of the roots (7.2.13.16)

**174) The MD diameter (length) of I^1 (7.2.13.17)

**175) The LL diameter (breadth) of I^1 (7.2.13.18)

**176) The crown occlusal area of I^1 (7.2.13.19)

**177) The crown shape index of I^1 (7.2.13.20)

**178) The MD diameter (length) of the maxillary teeth, measured at the occlusal surface (7.2.13.21)

**179) The MD diameter (length) of the maxillary teeth measured at the alveolar rim (7.2.13.22)

**180) The BL diameter (breadth) of the maxillary teeth, measured at the occlusal surface (7.2.13.23)

**181) The BL diameter (breadth) of the maxillary teeth, measured at the alveolar rim (7.2.13.24)

**182) The crown occlusal area of the maxillary teeth, measured at the occlusal surface (7.2.13.25)

**183) The area enclosed by the alveolar rim of each of the maxillary teeth (7.2.13.26)

**184) The crown shape index of the maxillary teeth, measured at the occlusal surface (7.2.13.27)

**185) The crown shape index of the maxillary cheek teeth, measured at the alveolar rim (7.2.13.28)

**186) The MD diameter (length) of I_1(7.2.13.17)

**187) The LL diameter (breadth) of I_1 (7.2.13.18)

**188) The crown occlusal area of I_1 (7.2.13.19)

**189) The crown shape index of I_1 (7.2.13.20)

**190) The MD diameter (length) of the mandibular cheek teeth, measured at the occlusal surface (7.2.13.29)

**191) The MD diameter (length) of the mandibular cheek teeth, measured at the alveolar rim (7.2.13.30)

**192) The BL diameter (breadth) of the mandibular cheek teeth measured at the occlusal surface (7.2.13.31)

**193) The BL diameter (breadth) of the mandibular teeth, measured at the alveolar rim (7.2.13.32)

**194) The crown occlusal area of the mandibular teeth, measured at the occlusal surface (7.2.13.33)

**195) The area enclosed by the alveolar rim of each of the mandibular teeth (7.2.13.34)

**196) The crown shape index of the mandibular teeth, measured at the occlusal surface (7.2.13.35)

**197) The crown shape index of each of the mandibular teeth measured at the alveolar rim (7.2.13.36)

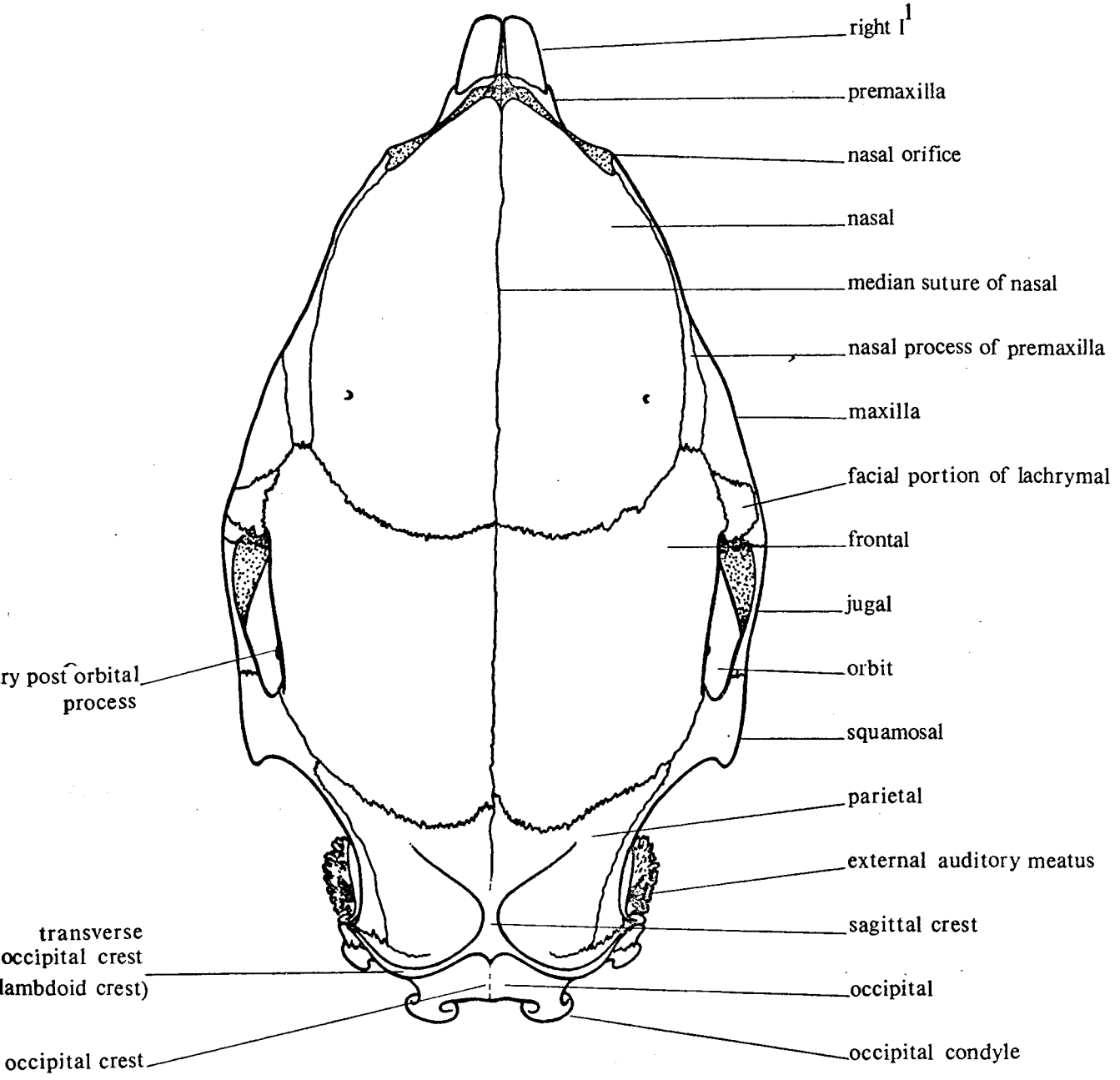


FIG 45

Dorsal view of the cranium of Hystrix africaeaustralis showing cranial morphology. x1

Fig. 46

Dorsal view of the cranium of Hystrix africaeaustralis showing characters measured.

A = Greatest length of skull above, from tip of premaxilla to tip of occipital crest

B = Occipitonasal length

C = Greatest width of skull above; width of skull at zygoma; zygomatic breadth at the level of the back of the nasals and greatest width of skull below

D = Smallest skull breadth behind zygomatic, least postorbital skull breadth

E = Width of skull at condyles

F = Interorbital distance at lachrymal edge

G = Interorbital breadth at rudimentary post-orbital process; breadth of frontals across rudimentary post-orbital process

H = Length of sagittal crest

I = Length of nasals

J = Length of nasal suture

K = Maximum width of nasals, width of nasals at posterior end of naso-premaxillary suture, posterior width of nasals

L = Occasional location of greatest width of nasals

M = Width of nasals at anterior end of naso-premaxillary suture, width of nasals anteriorly

N = Posterior extent of nasals behind fronto-premaxillary suture

O = Length of median frontal suture

P = Length of fronto-premaxillary suture

Q = Fronto-occipital distance

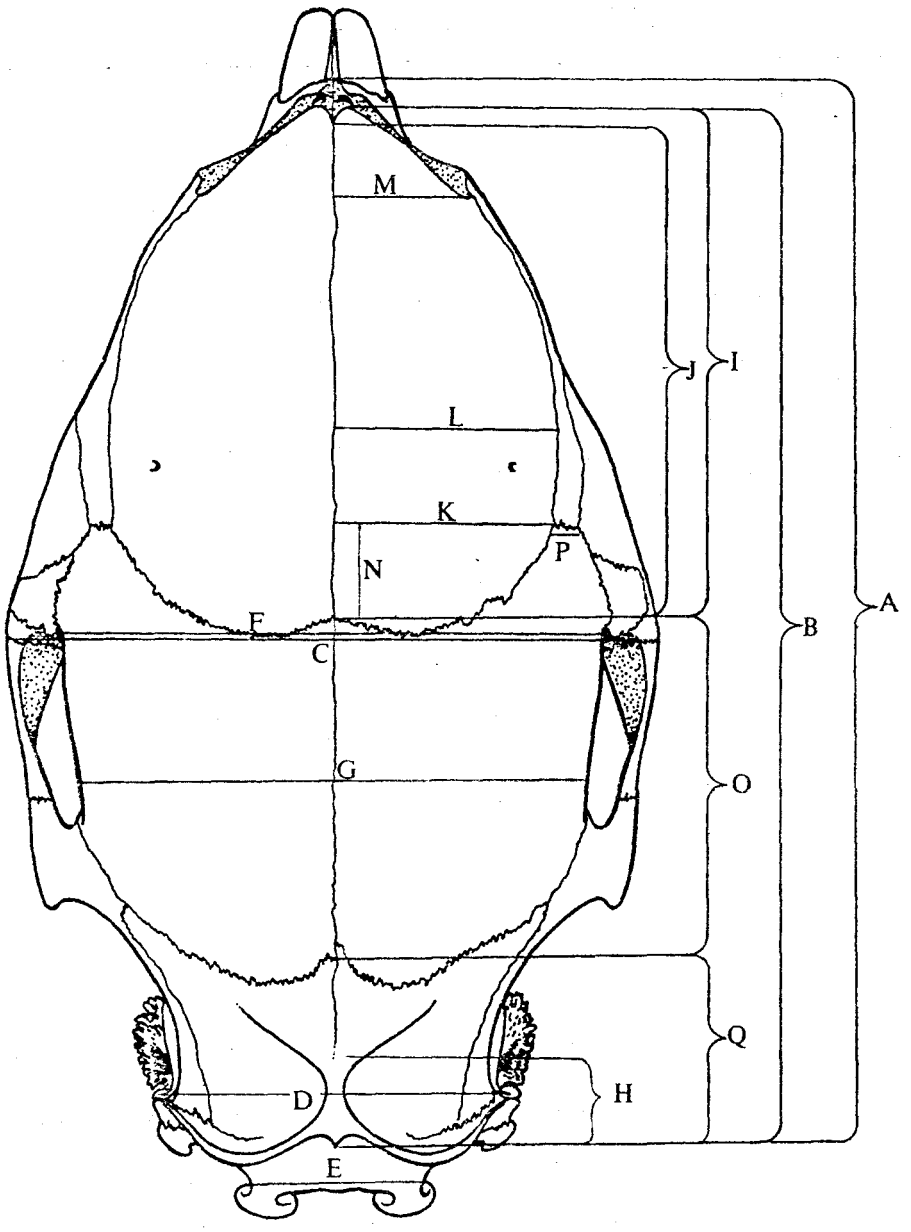


FIG 46

Dorsal view of the cranium of Hystrix africaeaustralis showing characters measured. x1

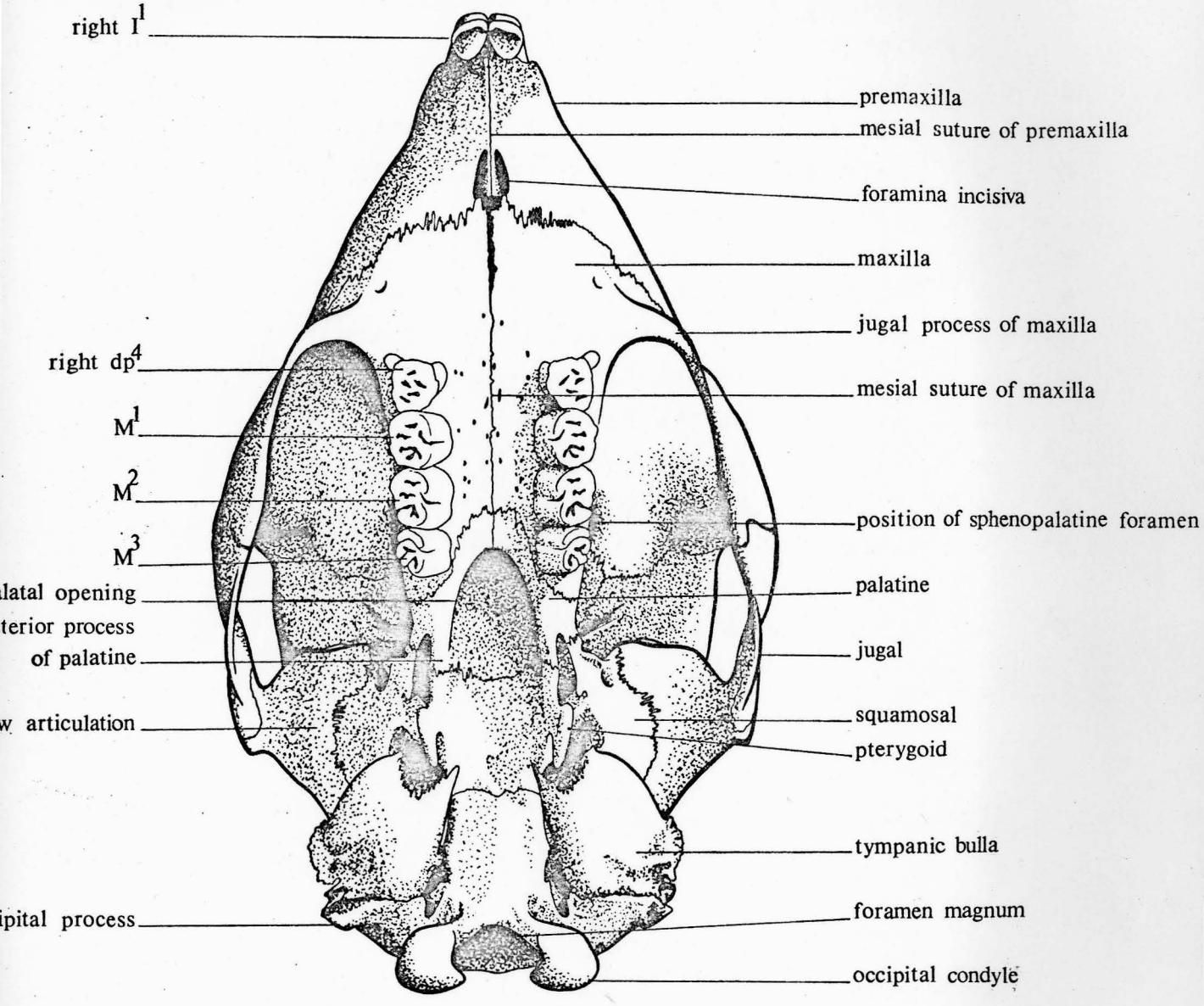


FIG.47

Ventral view of the cranium of Hystrix africaeaustralis showing cranial morphology. x1

Fig. 48

Ventral view of the cranium of Hystrix africaeaustralis showing characters measured

R = Greatest length of skull below, condylo-incisive length

S = Basilar length

T = Median sutural length of premaxilla ventrally

U = Palatal length of premaxilla medially, in front of foramina incisiva

V = Diastemic length

W = Median sutural length of palate

X = Median sutural length of maxillary

Y = Width of palate between dp^4 or P^4

Z = Width of palate between M^1

A^1 = Width of palate between M^2

B^1 = Width of palate between M^3

C^1 = Length of upper cheek tooth row, measured at the alveoli

D^1 = Molar-tympanic distance

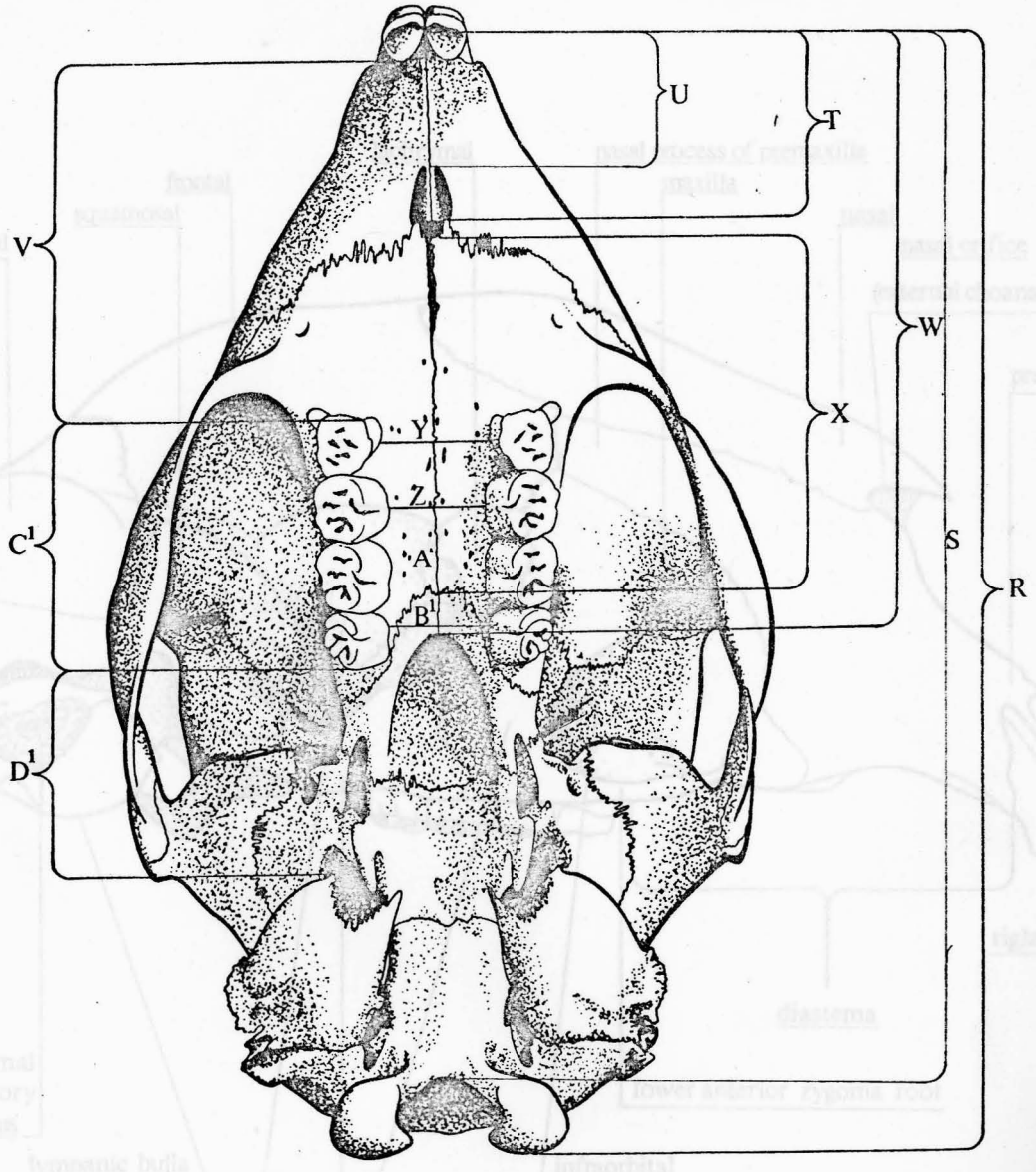


FIG 48

Palatal view of the cranium of Hystrix africaeaustralis showing characters measured. x1

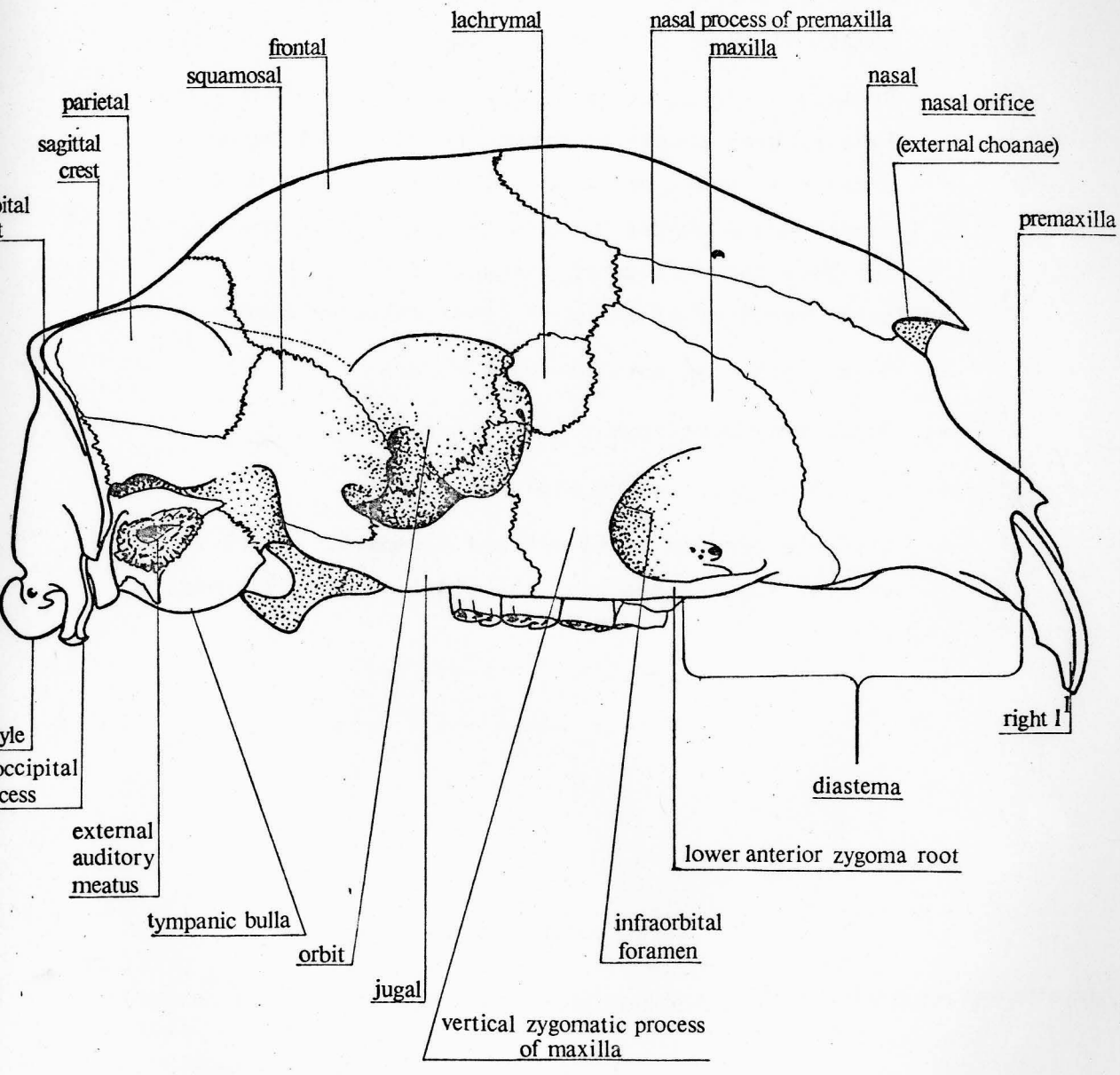


FIG 49

Right lateral view of cranium of Hystrix africaeaustralis showing cranial morphology. x1

Fig. 50

Lateral view of the cranium of Hystrix africaeaustralis showing characters measured

E^1 = Height of skull from palate to posterior end of nasals

F^1 = Height of skull from palate between M^1

G^1 = Least breadth of bony bridge between orbit and foramen infraorbitale, width of vertical process of maxilla, minimum width of vertical zygomatic process of maxilla

H^1 = Length of nasal process of premaxilla

I^1 = Breadth of nasal process of premaxilla at fronto-premaxillary suture, length of fronto-premaxillary suture

J^1 = Breadth of nasal process of premaxilla at a point on its lower margin midway between the maxillo-frontal suture and the masseteric ridge of the maxilla

K^1 = Least vertical diameter of lower anterior zygoma root

L^1 = Jugal height of maxillo-jugal suture

M^1 = Jugal height at jugal-squamosal suture

N^1 = Length of jugal along orbital rim

O^1 = Distance between lachrymal and zygomatic suture at the orbital rim, approach of the jugal to the lachrymal

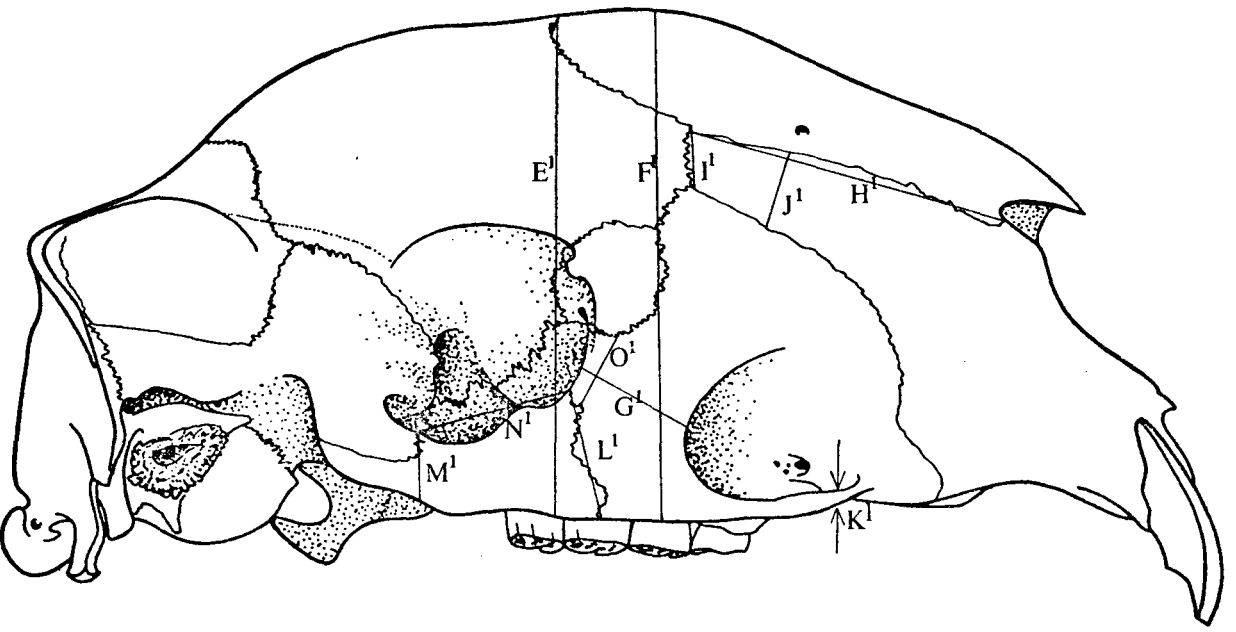


FIG 50

Right lateral view of the cranium of Hystrix africaeaustralis showing characters measured. x1

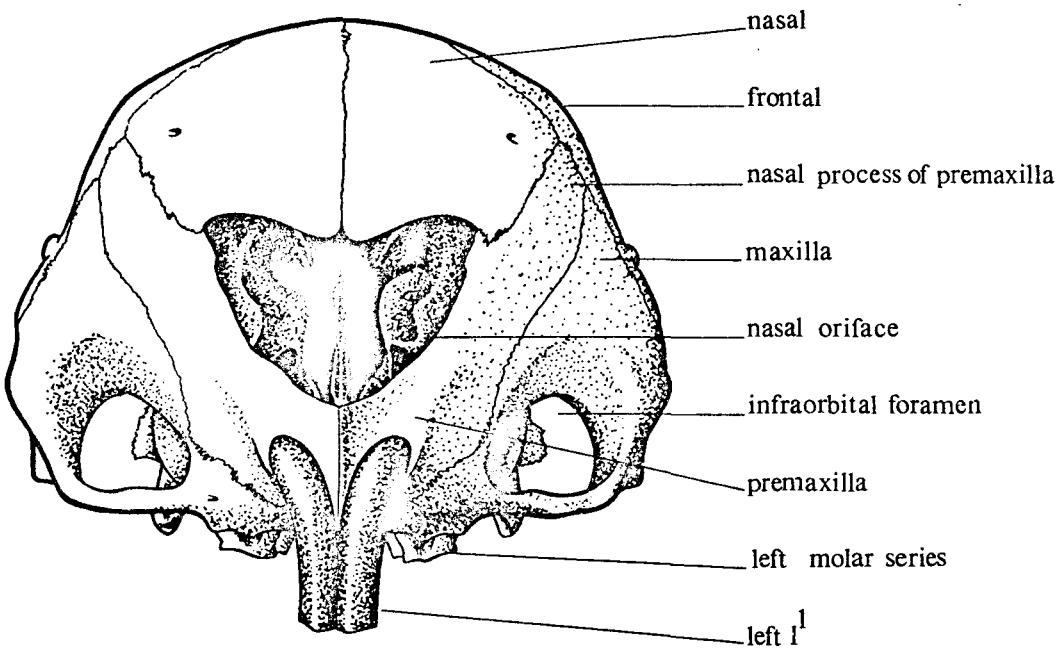


FIG 51

Anterior (facial) view of the cranium of Hystrix africaeaustralis showing cranial morphology. x1

Fig. 52

Anterior view of the cranium of Hystrix africaeaustralis showing characters measured

P^1 = Breadth of choanae

Q^1 = Least vertical diameter of lower anterior zygoma root

R^1 = Distance from lower edge of zygoma to central (mesial) suture

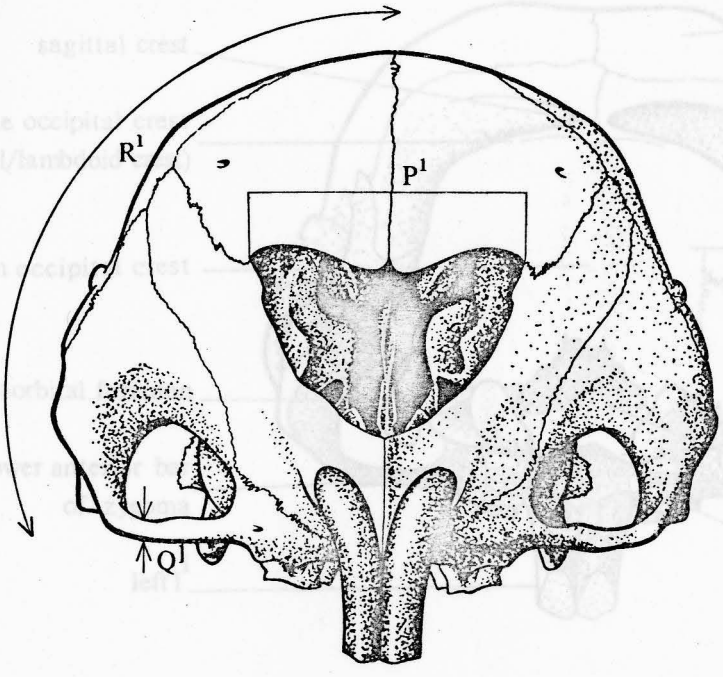


FIG 52

Anterior view of cranium of Hystrix africaeaustralis showing characters measured. x1

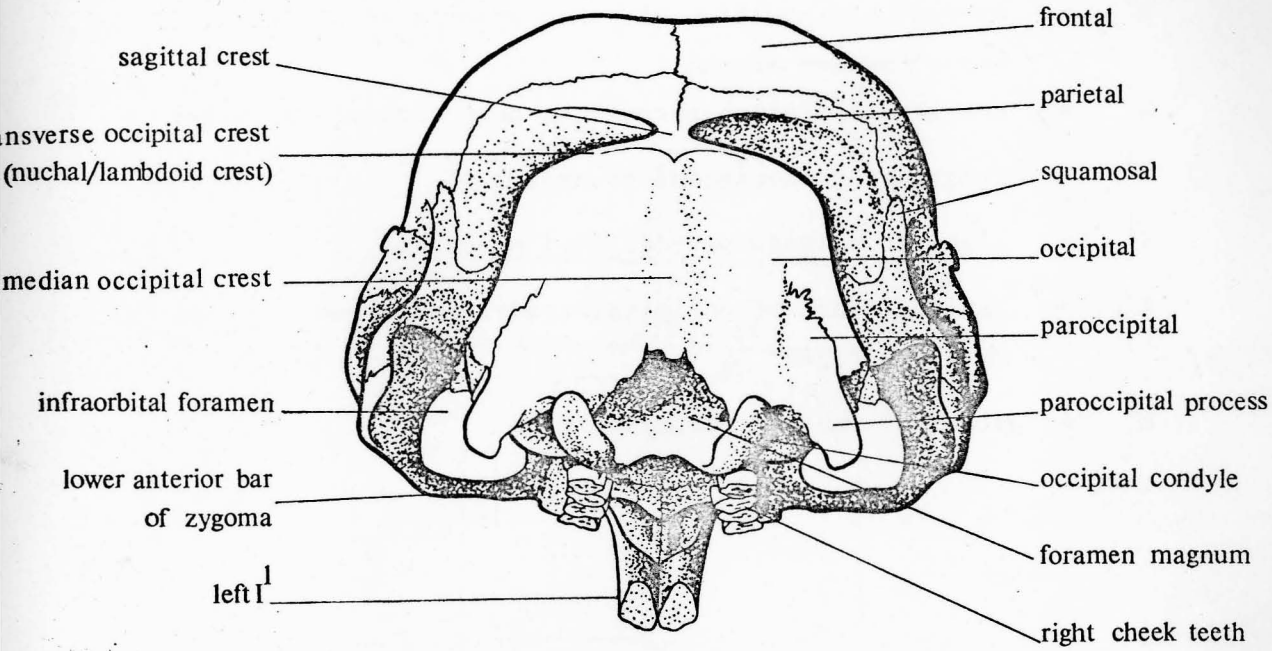


FIG 53

Posterior (occipital) view of cranium of Hystrix africaeaustralis showing cranial morphology. x1

Fig. 54

Posterior (occipital) view of cranium of Hystrix africaeaustralis showing characters measured

S^1 = Distance between upper edge of foramen magnum and occipital crest along midline

T^1 = Distance between lower edge of foramen magnum and occipital crest along midline

U^1 = Approximate position of greatest breadth of occiput above foramen magnum; maximum width of occiput

V^1 = Approximate position of least breadth of occiput above foramen magnum

W^1 = Greatest occipital breadth at paroccipital processes

X^1 = Length of paroccipital processes

Y^1 = Distance between paroccipital processes

Z^1 = Maximum width of occipital condyles between external edges

A^2 = Width of skull at condyles

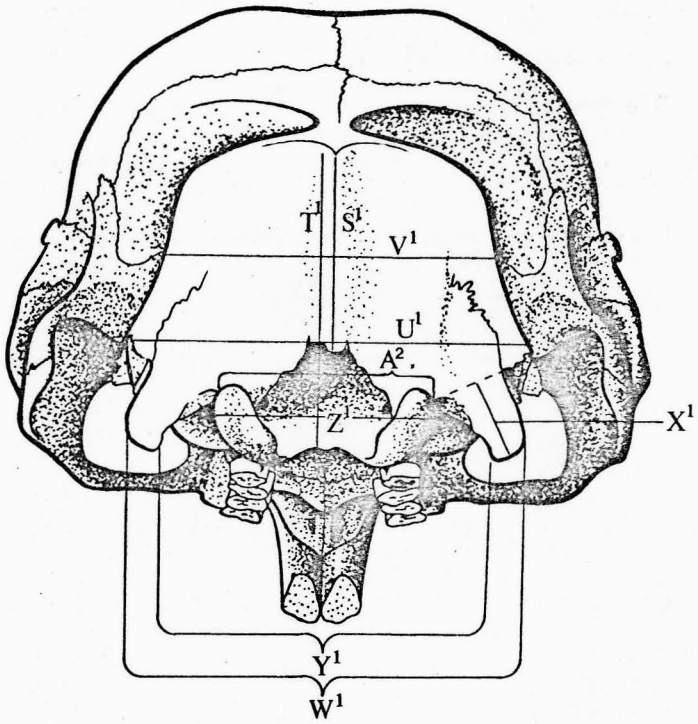


FIG 54

Posterior occipital view of the cranium of Hystrix africaeaustralis showing characters measured. x1

Fig. 55

Lateral views of the left mandible of Hystrix africaeaustralis showing mandibular morphology

a showing bony structures

b showing attachment of muscles

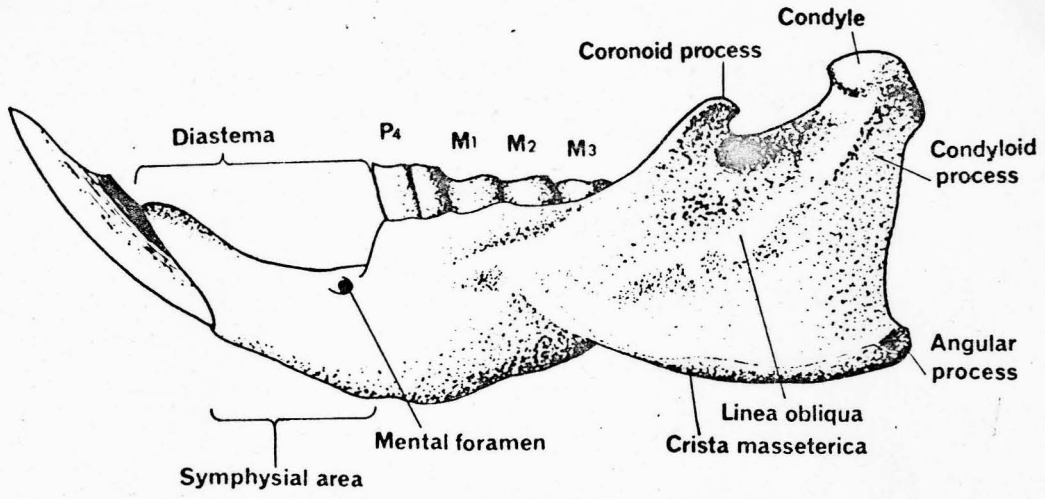


FIG 55a

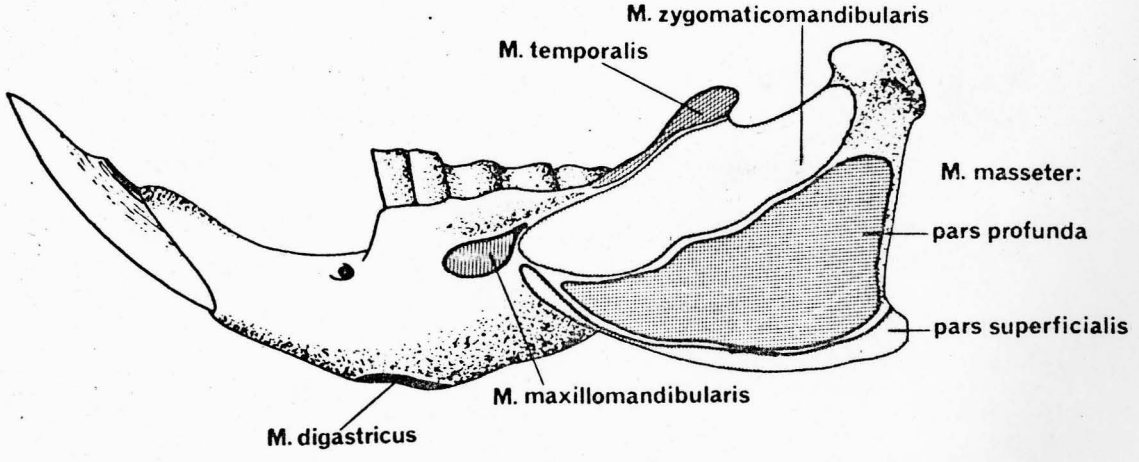


FIG 55b

Fig. 56

Lateral view of left mandible of Hystrix africaeaustralis, showing parameters measured

B^2 = Greatest length of mandible

C^2 = Length of mandible from posterior border of I_1 alveolus to tip of processus angularis

D^2 = Height of mandibula

E^2 = Depth of ramus below P4 (or dp4)

F^2 = Depth of ramus below M_1

G^2 = Depth of ramus below M2

H^2 = P4 (or dp4) alveolus to foramen mentale

I^2 = Diastemic length

J^2 = Height of ascending ramus above alveolar plane of molars

K^2 = Height of mesial symphysis above alveolar plane of molars

XX^2 = Alveolar plane of molars

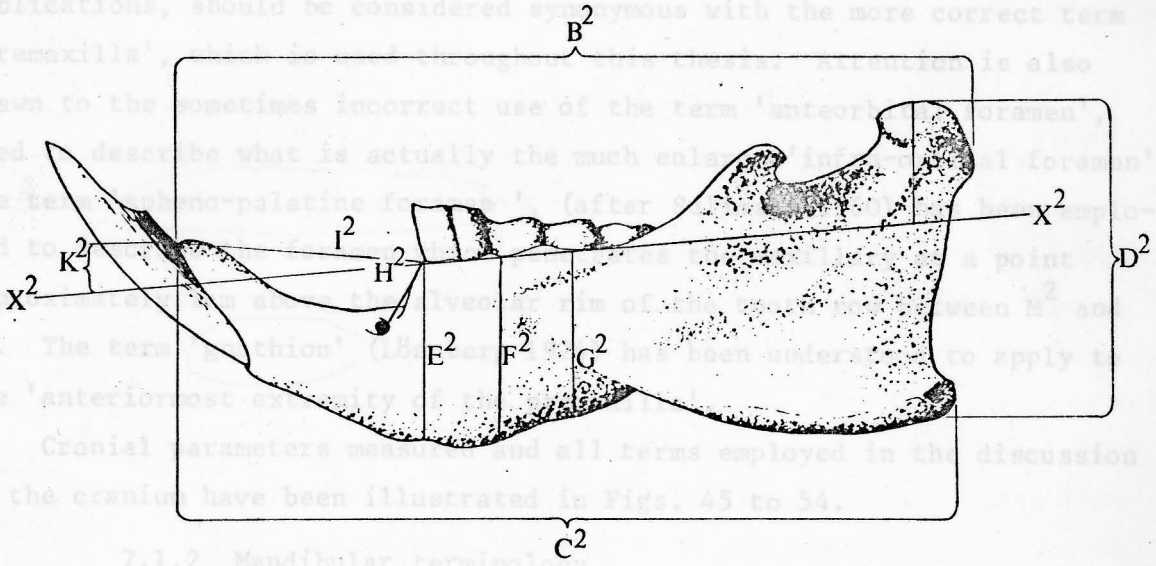


FIG 56

Lateral view of left half-mandible of Hystrix africaeaustralis showing parameters used. x1

7 THE CRANIAL MANDIBULAR AND DENTAL MORPHOLOGY OF HYSTRIX AFRICAEAUSTRALIS

7.1 Terminology

The terminology used in the definition of parameters and in the description of the cranial, mandibular and dental morphology are explained below. Terms which are neither defined below nor illustrated in Figs. 45-56 of this chapter are dealt with in the Glossary (Appendix XI).

7.1.1 Cranial terminology

No special terminology has been employed in the discussion of the various hystricid crania and dentitions. The terms used, with the possible exception of those mentioned below, are those found in most current text books on mammology. The term 'intermaxillary', frequently encountered in earlier publications, should be considered synonymous with the more correct term 'premaxilla', which is used throughout this thesis. Attention is also drawn to the sometimes incorrect use of the term 'anteorbital foramen', used to describe what is actually the much enlarged 'infra-orbital foramen'. The term 'spheno-palatine foramen ', (after Sulimski 1960) has been employed to describe the foramen which penetrates the maxillary at a point approximately 1cm above the alveolar rim of the tooth row between M^2 and M^3. The term 'gnathion' (Lönnberg 1924) has been understood to apply to the 'anteriormost extremity of the premaxilla'.

Cranial parameters measured and all terms employed in the discussion of the cranium have been illustrated in Figs. 45 to 54.

7.1.2 Mandibular terminology

No special terminology has been used except when describing attachment areas of the various masticatory muscles on the lateral mandibular surface. The latter terms have been taken from Turnbull (1970).

The term 'curvature of diastema' has been taken to refer to the degree of curvature occurring over the diastemic length. Its method of measurement has been discussed in section 7.2.12.10. The 'alveolar plane of tooth row (Niveau des Alveolarrandes der Zahnreihe) as suggested by Mottl (1967, pp. 306-308) is here defined as the best fitting straight line that can be drawn through the alveolar rims of the four cheek teeth.

The mandibular parameters measured and all terms used in the discussion of Hystrix mandibles have been illustrated in Figs. 55 and 56.

7.1.3 Dental nomenclature

In order to avoid a proliferation of terms, the terminology applied to the dentitions of various mammalian groups, e.g. Primates, Equids, Bovids, Suids and particularly Rodents, was investigated in order to ascertain how many commonly-used terms could be employed in the description of porcupine dentitions. However, on account of the hypsodont nature and complex crown enamel structure of porcupine teeth, as well as certain other structural differences, no one set of dental terms proved suitable. Apart from the terms referring to the five surfaces of the teeth which are common to all mammalian groups, most other terms required re-definition or defining 'from scratch'. Figs. 59 and 60 contrast sections of a human molar (brachydont, bunodont tooth) and a porcupine molar (hypsodont), to show how the terminology applied to the two differs.

As in all mammalian teeth, each porcupine maxillary or mandibular tooth has four vertical surfaces, the term for each surface having reference to its position relative to the tongue, lip, cheek and median line. The median line passes perpendicularly through the centre of the face and mouth, through the suture uniting the maxillary bones, between the central incisors of both upper and lower jaws and through the mesial suture uniting the left and right mandibular rami. The four surfaces are:

a) Mesial - closest to the median line (or the mesial suture) of the dental arch and following its curve. Note that in rodents, the dental arcade takes the form not of an arch but of an inverted 'v' - see Figs. 57 and 58

b) Distal - farthest away from the median line or mesial suture

c) Lingual - closest to the tongue

d) Labial or Buccal - closest to the lips (labial surface, applied to incisors) or to the cheeks (buccal surface, applied to premolars and molars)

and hence the mesio-distal (MD), labio-lingual (LL) and bucco-lingual (BL) diameters.

The horizontal or grinding surface is termed the occlusal surface. In incisors, the place of the occlusal surface is taken by an oblique chisel-shaped cutting wedge formed by the convergence of the lingual with the labial surface.

The terms mesial, distal, lingual, labial and buccal provide an unambiguous means of naming various roots, no matter what position these may take, e.g. mesio-lingual root, mesio-buccal root, disto-lingual root, etc. see Fig. 58.

The terms mesio-distal diameter (MD) and bucco-lingual diameter (BL) (labio-lingual (LL) in the case of the incisors) have been used throughout this thesis in preference to the terms 'length' and 'breadth' respectively, because the meanings of the latter terms are ambiguous in a number of ways. For example, 'length of tooth' is sometimes used in the sense of 'tooth height' that is, to describe the distance from the occlusal surface to the apex of the longest root. The terms 'length' and 'breadth' also become confusing when teeth, and particularly the almost cylindrical teeth of porcupines, become compressed through the pressure exerted by adjacent teeth until their width exceeds their length. In the latter instance, the terms 'length' and 'breadth' may be confusing if such teeth are found in isolation. The terms 'length' and 'breadth' are particularly confusing when describing incisors, For example Greenwood (1955, Tables 6 and 7) defines length as 'greatest antero-posterior diameter' and 'breadth' as 'greatest labio-lingual' diameter - for the incisors it can be seen that this definition implies that 'length' and 'breadth' are one and the same measurement. The use of the somewhat lengthier but unambiguous terms MD diameter and BL diameter for length and breadth respectively therefore seems justified.

Adjacent teeth are in contact with one another at the proximate contact. In porcupines the latter usually takes the form of a small roughly triangular to semicircular flattened facet at the contact point, the enamel in this region being flattened and thinner due to the pressure and friction exerted by the adjacent tooth, and possibly some enamel resorption. Throughout this thesis such contact areas have been referred to as pressure facets. The enamel covering of the pressure facets is frequently subjected to such a degree of pressure that the dentine becomes exposed.

These surfaces, diameters and roots have been illustrated in Figs. 57 and 58.

The use of the terms crown, root and neck as defined for most other mammalian dentitions had to be modified or alternative terms

provided for description of the porcupine dentition. Usually the term crown refers to that part of the tooth which is covered with enamel or to that part which protrudes above the alveolar bone, whereas the term root refers to the portion of the tooth that is embedded in the bony wall of the alveolus and is covered with cementum. The term neck refers to the junction between 'crown' and 'root', this junction usually coinciding with the junction between enamel and cement. In many mammalian dentitions, the 'neck' is apparent as a constriction of the tooth near the alveolar rim, where the tooth disappears into its socket (Fig. 59).

The hypsodont teeth of Hystrix are, however, almost entirely covered with enamel, as are the hypsodont teeth of some other mammalian groups, e.g. equids. The enamel extends under the outer sheath of cementum (which initially entirely covers the tooth, the enamel becoming exposed with wear) down to the level of divergence of the papillate rootlets deep within the alveolus. The actual termination area proved variable in the teeth examined, in some cases the enamel was found to extend into the rootlets themselves. The extent of the enamel covering is shown in Fig. 60 and is apparent as the palest (least exposed) areas in the X-ray (Fig. 111), being the densest and therefore least X-ray-penetrated material present.

According to the terminology mentioned above, the entire enamel-covered portion of a porcupine tooth would be classed as 'crown'; however, in porcupine teeth more than two-thirds of this 'crown' is embedded within the alveolus during the greater part of the lifetime of the animal. In terms of the above nomenclature, the intra-alveolar portion of a tooth is classed as 'root'. Clearly, the terms 'crown', 'root' and 'neck' require special definition and supplementation for use in the description of porcupine dentitions.

The terms apparent crown and embedded crown have thus been used in this thesis to distinguish the supra-alveolar and intra-alveolar portions of the enamel-covered part of the tooth (the 'crown') respectively. In newly-erupted porcupine teeth, the cementum entirely ensheathes the enamel and covers the tuberculate occlusal surface, progressive wear exposes the enamel and ultimately the dentine. The terms 'apparent crown' and embedded crown' therefore apply whether these enamel covered parts still have their cementum sheath or not. In the

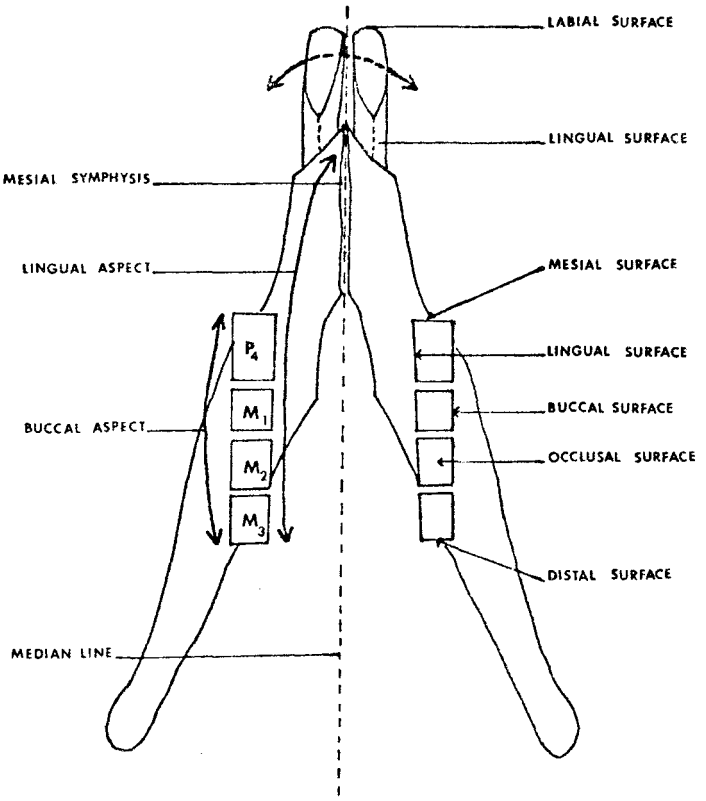


FIG 57

Diagrammatic representation of the mandible of H.africaeaustralis showing terms used

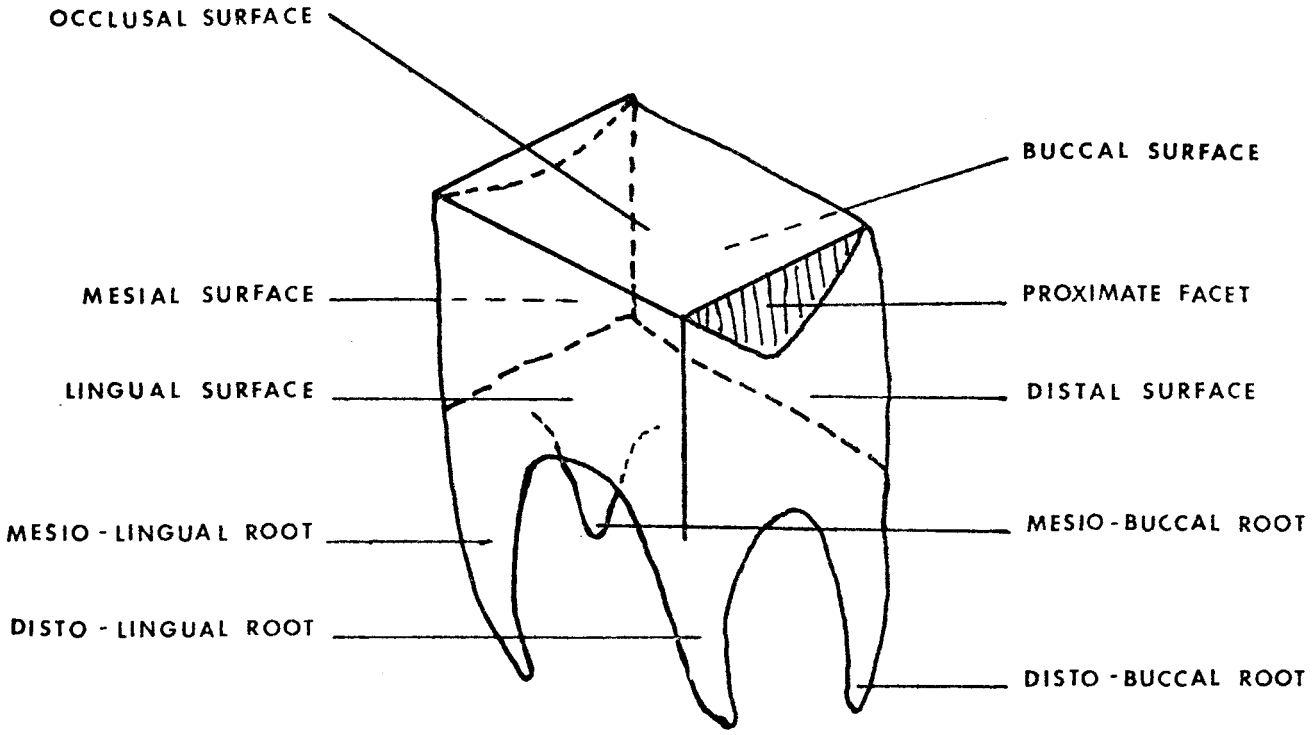


FIG 58

Diagrammatic representation of right M_1 showing dental terms employed

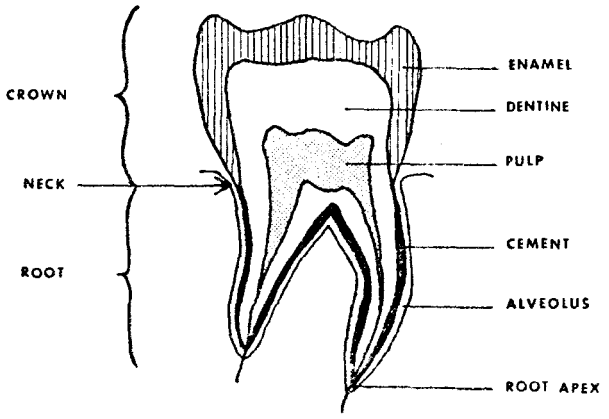


FIG 59
L/S Through human lower molar showing terms used

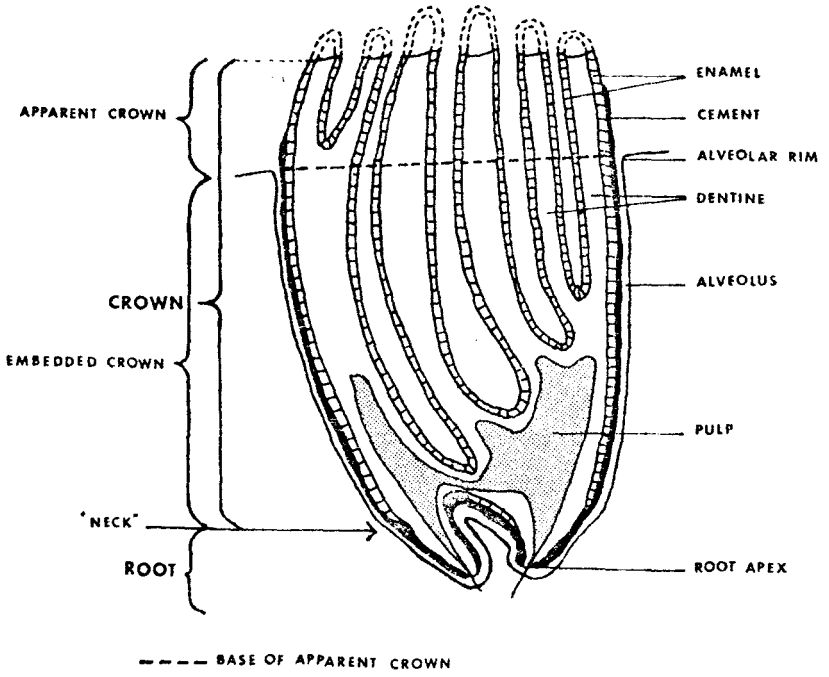


FIG 60
L/S Through Hystrix lower molar showing terms used

in situ teeth of many modern *Hystrix* specimens the cementum sheath is frequently found worn to a level halfway between the occlusal surface and alveolar rim, but in most isolated teeth, the cementum seems to separate from the enamel so that only the papillate rootlets are covered with it. In isolated teeth, the term 'crown' applies to the entire enamel-covered portion, i.e. all but the papillate rootlets.

'Root' as implied by the usual definition cannot be applied to the *Hystrix* dentition since most of the tooth within the bony wall of the socket constitutes cementum-ensheathed, enamel-covered 'embedded crown': furthermore, as explained in the preceding paragraph, the cementum extends beyond the alveolar rim in *in situ* teeth, covering part of the 'apparent crown'. In the descriptions of porcupine dental morphology in this thesis, 'root' therefore refers only to the cementum-covered papillate protuberances from the main body of the tooth (and in some fossil forms to the divergent rootlets), whether these have a small amount of underlying enamel or not.

The term *neck* has been taken to refer to the junction between embedded crown (in *in situ* teeth) or crown (in isolated teeth) and the rootlets, although in *H. africaeaustralis* this junction is by no means obvious. In *Hystrix*, the 'neck' is embedded well within the socket and no actual constriction occurs either here or at the alveolar rim. An alternative term is thus required to refer to that part of the crown which abuts on the latter region (to replace the term 'neck' as applied e.g. in Primate nomenclature), and the term *base of apparent crown* (for *in situ* teeth) has been used. This area cannot be detected in isolated teeth and has to be estimated. The use of the above terms is illustrated in Figs. 57-60.

Discussion of the terminology relating to the complicated system of enamel folds and islands which form the crown enamel patterns of the premolar and molar teeth is difficult without prior reference to tooth morphology. However, the terminology referring to the crown enamel pattern will be briefly mentioned in passing, the significance of the crown enamel pattern and a detailed description of tooth morphology will be discussed in a later section (7.5).

Because of the cuspate appearance of unworn hystricid teeth, Hooijer (1946) and Fields (1957), among others, attempted to apply the tritubercular system of cusp nomenclature to the occlusal pattern of

unworn and worn porcupine teeth, as Stirton (1935) has done in the case of beavers. However, it appears that the arrangement of the cusps and crests of the Hystrix dentition exhibits complications and secondary changes so that the cusp pattern is far removed from the original tritubercular pattern, and the homologies of the cusps are no longer clear. Consequently, a standard nomenclature for the crown enamel structures of hystricid teeth is not yet available.

The various parts of the occlusal pattern have been variously referred to as enamel folds, enamel loops, valleys, inflections, anticlines and synclines, lobes, lophs, sulci, cristae, striae, grooves, lakes, islands, flexids and fosettes. Since the tritubercular nomenclature is widely familiar, Stirton's (1935) terminology has been used throughout this thesis to describe crown enamel structures. However, this use of his terms does not imply homology with the originally-named structures in the beaver dentition he describes. Rather, the terms have been used as a matter of convenience in accordance with the topographic proximity of the structures they name to similar features in the beaver dentition. The presence of an additional inflection in Hystrix teeth (this extra fold is also present in other genera of the Hystricidae) has made it necessary to supplement Stirton's terminology with the additional terms entoflexus and entoflexid (for maxillary and mandibular dentitions respectively) to name this fold, and the terms entofosette and entofossettid (for maxillary and mandibular dentitions respectively) for the circlet of enamel which the extra fold encloses when a tooth is sufficiently worn. These terms are as suggested by Fields (1957). Again, homology with tritubercular structures is not implied.

In moderately worn maxillary teeth, three and sometimes four external (buccal) enamel folds or loops as well as one very deep lingual fold or loop are present. After Stirton (1935), the four buccal folds are termed, from anterior to posterior, the paraflexus, mesoflexus, metaflexus and entoflexus. The single lingual fold has been termed the hypoflexus (Fig. 61a). Once attrition has caused these enamel loops to become 'closed' (the 'neck' of the fold 'fuses') the resulting enamel islands are termed the parafossette, mesofossette, metafossette and entofossette respectively (Fig. 61b). On the buccal and lingual surfaces of moderately worn teeth in which the enamel loops have not yet become 'closed' the loops are manifested as deep grooves

and are respectively termed the parastria, mesostria, metastria, entostria and hypostria, in accordance with the enamel loop they represent (Fig. 61c)

In the mandibular teeth, the system of enamel folds is opposite to that occurring in the maxillary teeth, with three and sometimes four internal (lingual) enamel folds or loops and one very pronounced external (buccal) enamel fold. The four lingual folds are termed the paraflexid, mesoflexid, metaflexid and entoflexid from front to back, while the deep buccal fold is termed the hypoflexid (Fig. 62a). The circlets of enamel which the 'closed' folds isolate are termed the parafossettid, mesofossettid, metafossettid, entofossettid and hypofossettid respectively (Fig. 62b). The grooves which indicate the enamel loops on the lingual and buccal surfaces are termed the parastriid, mesostriid, entostriid and hypostriid respectively (Fig. 62c).

If more than four enamel loops are present, the above terms have been suffixed a, b, etc. as required.

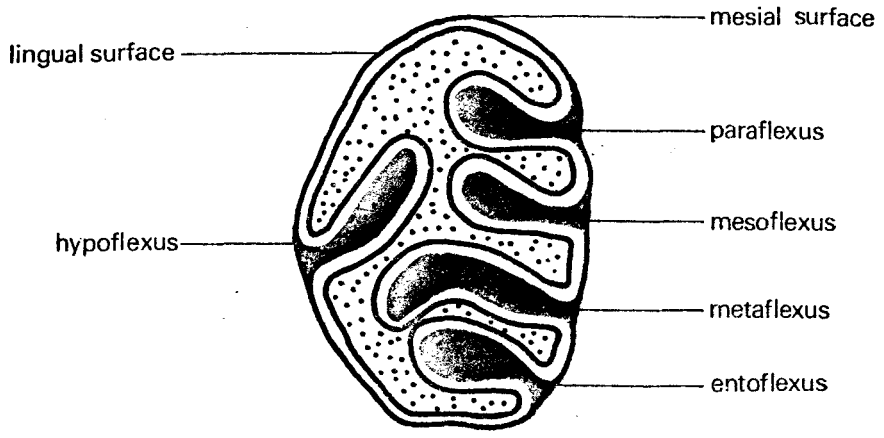
Fig. 61

Hypothetical left maxillary permanent premolar illustrating terminology employed in the description of the crown enamel pattern

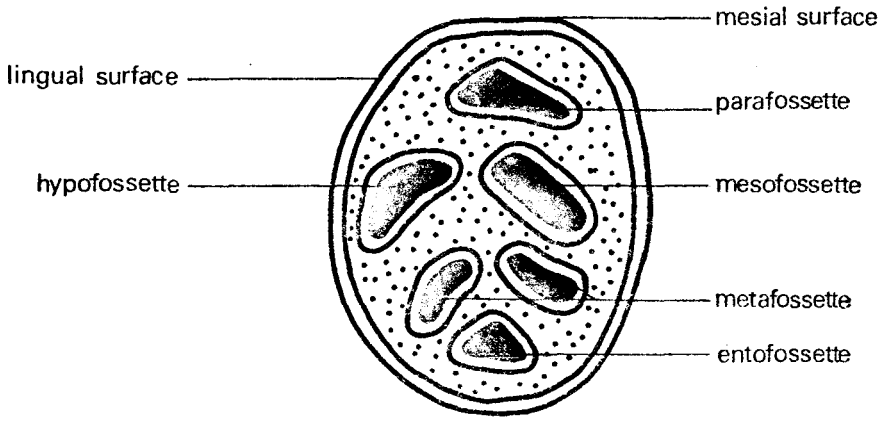
a = slightly worn tooth

b = well-worn tooth

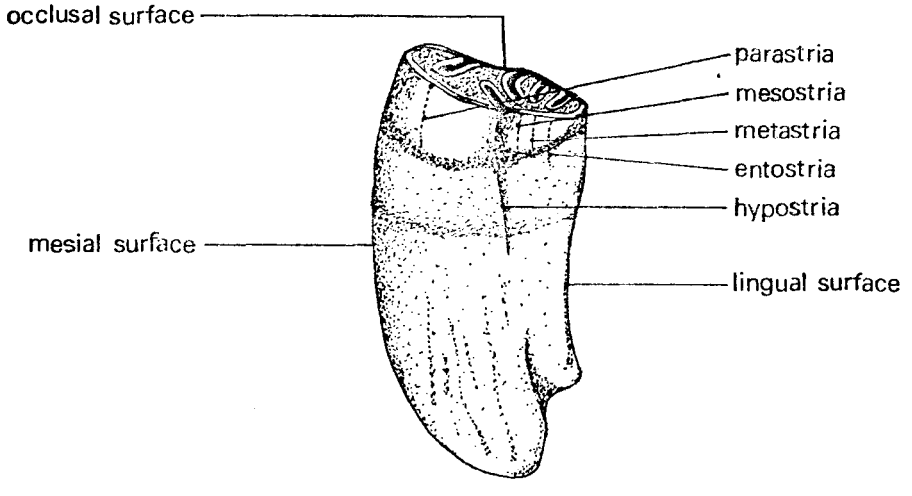
c = lingual view of same tooth at stage a, mesial surface to left


mesial surface
lingual surface
paraflexus
hypoflexus
mesoflexus
metaflexus
entoflexus

a.


mesial surface
lingual surface
parafossette
hypofossette
mesofossette
metafossette
entofossette

b.


occlusal surface
parastria
mesostria
metastria
entostria
hypostria
mesial surface
lingual surface

c.

FIG 61.

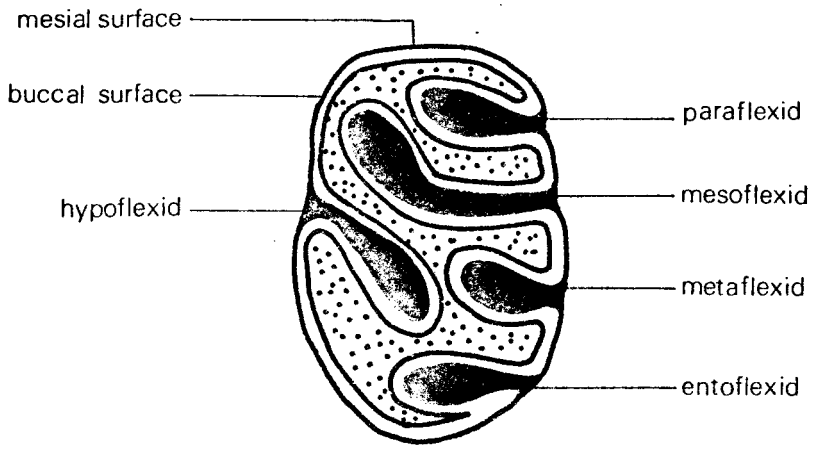
Fig. 62

Hypothetical left mandibular permanent premolar illustrating terminology employed in the description of the crown enamel pattern

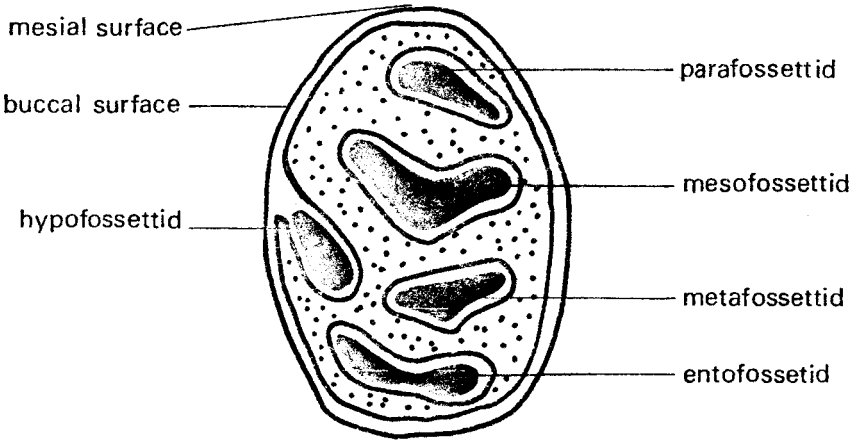
a = slightly worn tooth

b = well-worn tooth

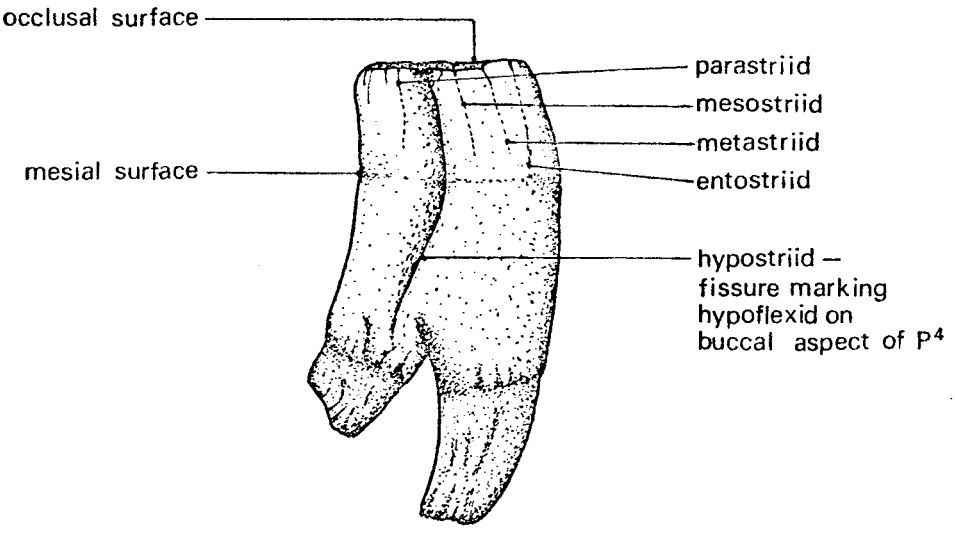
c = buccal view of same tooth at stage a, mesial surface to left


mesial surface
buccal surface
hypoflexid
paraflexid
mesoflexid
metaflexid
entoflexid

a.


mesial surface
buccal surface
hypofossettid
parafossettid
mesofossettid
metafossettid
entofossetid

b.


occlusal surface
mesial surface
parastriid
mesostriid
metastriid
entostriid
hypostriid — fissure marking hypoflexid on buccal aspect of P4

c.

FIG 62.

7.1.4 The sequence of tooth eruption and replacement and age - class subdivision based on dental maturity

Most characters measured (cranial, mandibular and dental) appear to vary considerably with age. For this reason the comparative sample of H. africaeaustralis was divided into a series of age classes within each of which the natural variation of all diagnostic characters could be assessed, the range occurring within a single age class being more restricted than for the whole sample. By comparing maturity of the dentition and crown enamel patterns with the modern material, fossil material, including isolated teeth, and published teeth illustrations could be referred to an appropriate age class. In this way more significant comparisons were facilitated. The age class divisions were based on those proposed by Corbet and Jones (1964) who suggest six, based on the stage of tooth eruption. Before discussing these age-class subdivisions, the sequence of tooth replacement will be explained.

This follows the same order in both maxillary and mandibular dentitions although occasionally eruption may be at a slightly more advanced stage in the mandible than in the upper jaw; it rarely happens that the maxillary dentition is more advanced than that of the mandible. In some specimens, the teeth in one half of the maxilla or mandible may be at a more advanced stage than those of the opposite side, but in general left and right, upper and lower dentitions are in phase with one another. It has therefore been considered sufficient to illustrate tooth eruption of the maxillary dentition only, although both have been discussed.

Briefly, the order of tooth eruption and replacement is as follows: the incisors erupt first, followed by the deciduous premolars (dp^4) followed by the first molars (M^1); then the second molars (M^2) and finally the third molars (M^3). Some time after the third molars attain a well-worn state, the temporary dp^4 is shed and is replaced by the permanent premolar (P^4): the dp^4 is the only tooth which is replaced, therefore Hystrix is partially diphyodont. This replacement seems to occur late in life in H. africaeaustralis, judging by the fusion of the cranial sutures, and as reported by Roberts (1951). However, there appear to be no records of the period over which the teeth of any of the Hystrix species erupt.

From the Hystrix sample at hand it would seem that the rate of eruption slows after the appearance of the M^2. The original three molars

and replacement premolar seem to suffice for a potential lifetime of 20 years, as reported by Labuschagne and Van der Merwe (1968).

The sequence of tooth eruption has been illustrated in Figs. 63 to 72 and may briefly be described as follows: the incisors, followed by the deciduous premolars, probably erupt several days after birth. The mandibular teeth, particularly (the) M_2 and M_3 erupt very obliquely, so that just prior to eruption, and for a while afterwards, the root causes a conspicuous protuberance on the lateral mandibular surface, directly below the coronoid process. Although the maxillary teeth erupt less obliquely, a similar tubercle is sometimes visible in the vicinity of the rootsof erupting and newly-erupted teeth, because their marked buccal curvature places the root in a lateral position. After erupting obliquely, the mandibular teeth begin their cycle of wear at the mesio-buccal corner; as eruption continues they assume a more vertical position, after which wear occurs more or less evenly over the entire occlusal surface. In the maxillary dentition, wear proceeds evenly from the start. In the mandible, the tooth in eruption always lies near the coronoid process, where the tooth-bearing part of the mandible narrows and terminates, so that the jaw has to lengthen before there is room for another tooth to erupt. In the upper jaw, tooth eruption occurs at the posterior extremities of the maxillaries where they abut on the palatines; again, elongation of the palatal region has to take place before additional teeth can erupt. Tooth eruption seems to be associated with an increased degree of vascularity, as is evident from the fine 'sponginess' or porosity of the alveolar bone in the vicinity of erupting teeth. This, according to Henderson-Scott (1967), is because bone is resorbed at sites of increased pressure (for example, at the centre of pressure exerted by an erupting tooth) and for resorption to take place, a certain degree of vascularity is required. Resorption occurs to the extent that an opening is formed through which the tooth erupts (Figs. 63, 65 and 68).

With the eruption of M^2, the dp^4 is in its 'prime' (Figs. 64 and 65); thereafter, increasing attrition and continued eruption rapidly reduce the latter to a stump. It is often worn to the level of the divergence of the rootlets (Fig. 67) or beyond; in the latter case the tooth separates into several pieces. The dp^4 is shed when the M^3 reaches full wear (Fig. 68). The permanent premolar slowly erupts to take its place (Figs. 69, 70), the pattern of root alveoli of the dp^4 persisting

for some time after the eruption of the former. P^4 grows to become noticeably the largest of the teeth. This is particularly evident in the maxillary dentition (Figs. 70, 71 and 72). With the pressure of the expanding P^4 in front and with the developing M^2 behind, the M^1 (the oldest tooth in the jaw apart from the incisor) becomes compressed until its mesio-distal diameter (length) and bucco-lingual diameters (breadth) are sub-equal or the breadth exceeds the length (Figs. 70 and 71), at which stage the condition of the tooth begins to deteriorate. This deterioration is probably due to the combined effects of prolonged wear and increasing pressure. A similar condition eventually awaits the M^2 (Fig. 72). Again, the effects of pressure are more noticeable in the upper jaw. This feature makes the use of dental dimensions such as length unreliable for comparative purposes.

The age-grouping suggested by Corbet and Jones (1964) on the basis of tooth eruption was as follows:

Group 1	(Juvenile Stage 1)	dp^4 only	
Group 2	(Juvenile Stage 2)	$dp^4 + M^1$	
Group 3	(Juvenile Stage 3)	$dp^4 + M^1 + M^2$	
Group 4	(Sub-adult)	$dp^4 + M^1 + M^2 + M^3$	
Group 5	(Adult)	$P^4 + M^1 + M^2 + M^3$	(P4 and M^3 unworn)
Group 6	(Mature adult)	$P^4 + M^1 + M^2 + M^3$	(P4 and M^3 worn)

On attempting to divide the H. africaeaustralis sample according to the above age-grouping, it was noticed that the M^3 becomes worn long before the dp^4 is shed, i.e. during the sub-adult stage in Group 4. The validity of Corbet and Jones' definitions of Groups 5 and 6 are therefore questionable - although the sample studied by them included a large number of specimens from Southern Africa. In no instance was an unworn M^3 found to occur simultaneously with an unworn (or worn) P^4 in the available sample of H. africaeaustralis. Geographical variation can therefore not be cited as a reason for the discrepancies between their definitions for Groups 5 and 6, and the findings of the present author. The age grouping by Corbet and Jones (1964) has therefore been modified as follows:

Group 5	(Adult)	$P^4 + M^1 + M^2 + M^3$	(P4 unworn)
Group 6	(Mature adult)	$P^4 + M^1 + M^2 + M^3$	(P4 worn)

These growth stages, with the exception of Growth Stage 1, are illustrated in Figs. 63 - 73

In dividing the sample, a tooth has only been counted when it has erupted to the extent of protruding above the level of the alveolar rim; for example, the specimen shown in Fig. 63 would be included in Group 2 and not Group 3.

A problem arose when specimens were encountered in which the mandibular teeth were more advanced than in the maxillary. It was therefore decided to group the mandibles separately.

For compiling crown enamel pattern series for each age group, each tooth row has been considered individually.

The above procedure was considered logical in view of the fact that left and right maxillary tooth rows and left and right mandibular rami are rarely found joined in the fossil remains, and even more rarely are the upper and lower dentitions of the same individual found in close association.

The age grouping of the sample arrived at is shown in Table IV.

7.1.5 Growth stage segregation based on the crown enamel pattern

The above method (7.1.4) of segregating specimens into growth stages is only applicable to maxillary and mandibular specimens which have at least some *in situ* teeth and/or well-preserved alveoli. Since most fossil Hystricid material seems to comprise semi-isolated or isolated teeth, a need arose to devise a method for referring such teeth to an appropriate growth stage. Crown height (which reflects degree of wear and hence indirectly, age) as used in studies of the equidae and canidae, could not be used in this instance, because of the differing degrees of hypsodonty encountered amongst living and fossil Hystricidae. Furthermore, differences in relative size, for example between the giant *Xenohystrix* and the small *Hystrix africaeaustralis* make crown heights unsuitable for defining growth stages. An attempt has therefore been made to define the range of crown enamel pattern and degree of enamel fold closure characteristic for each growth stage.

This was done by dividing the *H. africaeaustralis* comparative material into six growth stages according to tooth eruption criteria

Fig. 63

Photograph showing the maxillary dentition of Hystrix africaeaustralis (x 2)

dp^4 and M^1 are fully worn, M^2 is in the process of eruption, but still embedded within its crypt. Note the 'sponginess' of the alveolar bone in the vicinity of the erupting tooth. Specimen TM 5662, Growth Stage 2.

Fig. 64

Photograph showing the maxillary dentition of Hystrix africaeaustralis (x 2)

The palate in front of the maxillary-palatine suture has enlarged enabling the eruption of M^2. Note that the paraflexus and entoflexus of the P^4, open in Fig. 63, have become closed to form parafossette and entofossette respectively. Specimen TM 12698, early Growth Stage 3.

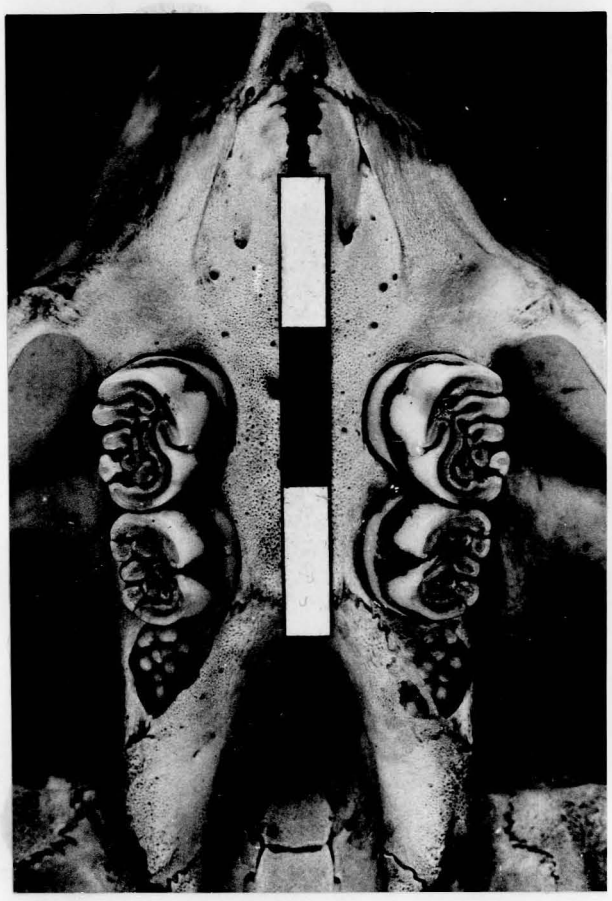


Fig 63

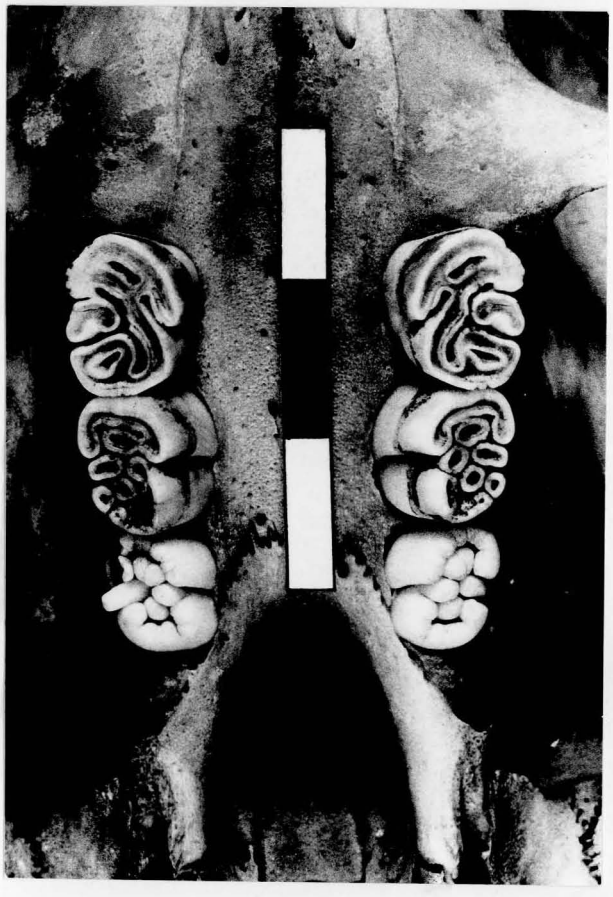


Fig 64

Fig. 65

Photograph showing the maxillary dentition of Hystrix africaeaustralis (x 2)

M^2 is fully worn and a small opening in the alveolar bone behind it indicates the imminent eruption of M^3. The P^4 and M^1 show signs of more advanced wear than in the preceding figure. Specimen TM 12697, late Growth Stage 3.

Fig. 66

Photograph showing the maxillary dentition of Hystrix africaeaustralis (x 2)

The M^3 is in the process of eruption. The specimen is unusual in that its teeth show less wear than those of the preceding figure, despite its more advanced dental maturity. This discrepancy is probably due to environmental considerations ; specimen TM 12697 above comes from the Kaokoveld (SWA), which is a desert area, so presumably the teeth would be subjected to more rigorous wear on account of a harder diet - whilst the specimen shown in Fig. 66 was retrieved from a lush bushveld environment in the vicinity of Rustenburg. Specimen TM 9F F, early Growth Stage 4.

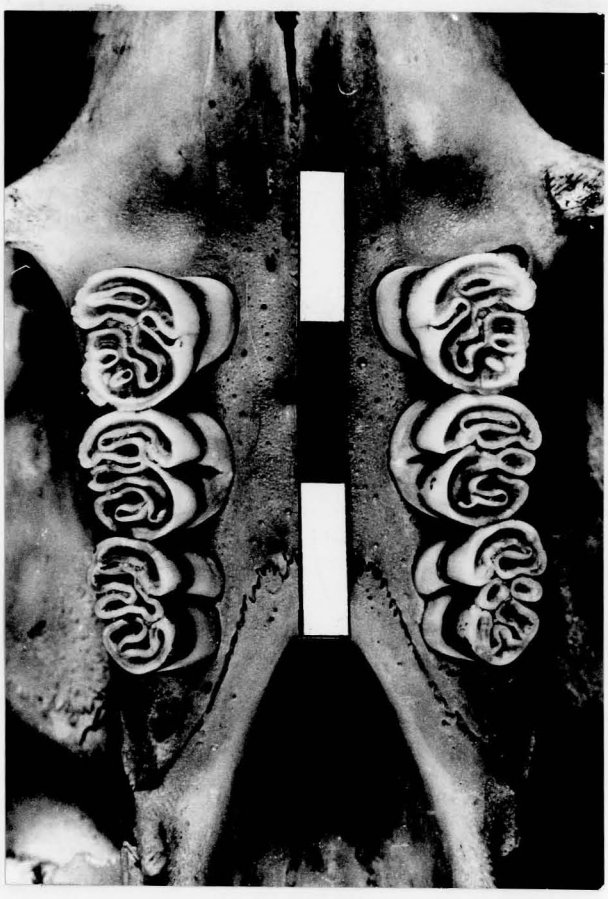


Fig 65

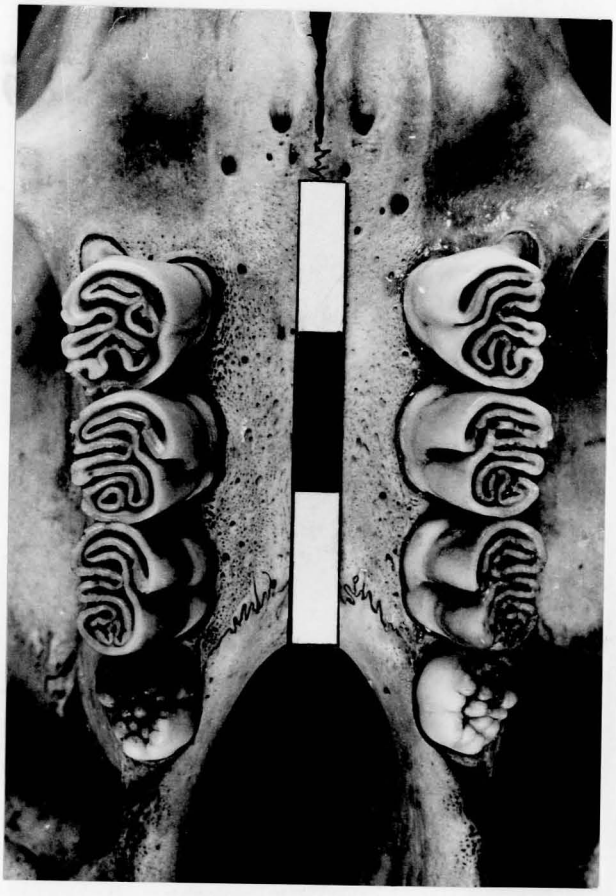


Fig 66

Fig. 67

Photograph illustrating the maxillary dentition of Hystrix africaeaustralis (x 2)

M^3 is fully erupted and is evenly worn. The P^4 shows signs of deterioration and is worn to the level of divergence of its roots. The M^1 and M^2 show more advanced wear than in Fig. 66. Specimen TM 594, late Growth Stage 4.

Fig. 68

Photograph illustrating the maxillary dentition of Hystrix africaeaustralis (x 2)

The permanent P^4 is visible through openings caused by resorption of the alveolar bone of the dp^4. M^3 is fully worn. Specimen BPI/C 682, late Group 4.

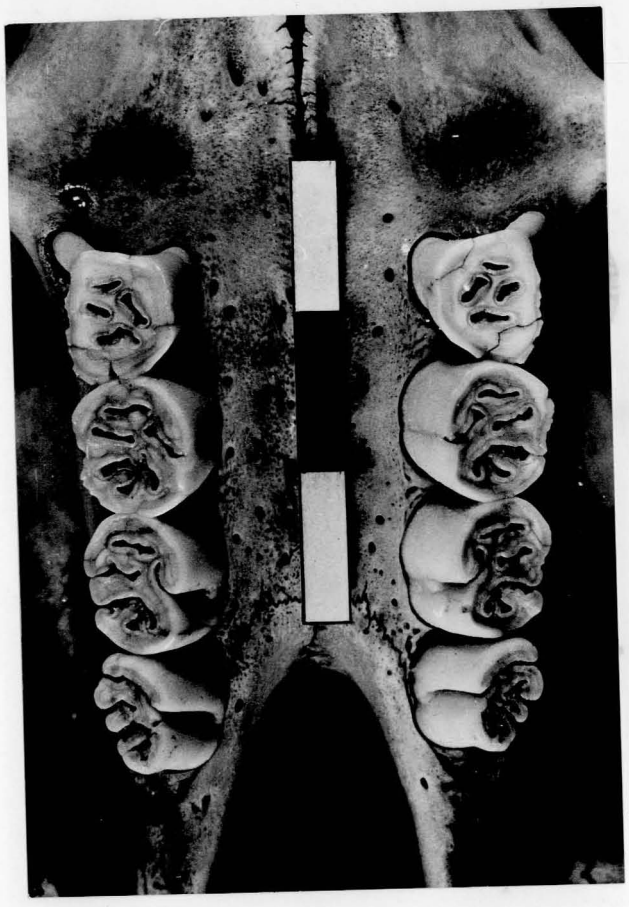


Fig 67

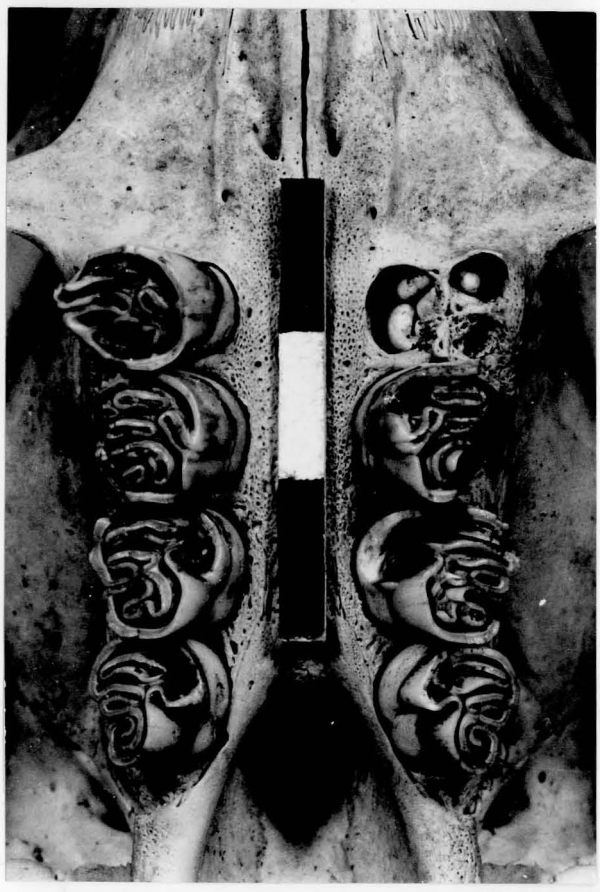


Fig 68

Fig. 69

Photograph illustrating the maxillary dentition of Hystrix africaeaustralis (x 2)
The permanent premolar is in the process of erupting into position. The positions occupied by the roots of the recently shed deciduous premolar are still evident. Specimen TM 12165, early Growth Stage 5.

Fig. 70

Photograph illustrating the maxillary dentition of Hystrix africaeaustralis (x 2)
The permanent premolar has fully erupted and shows a slight amount of wear. It is very evidently the largest tooth in the row. All the flexuoses of the M^1 have 'closed' to become fossettes and only the hypoflexus is still open in the M^2 and M^3. The specimen therefore has a more mature crown enamel pattern than that illustrated in Fig. 69. Specimen TM 866, early Growth Stage 5.

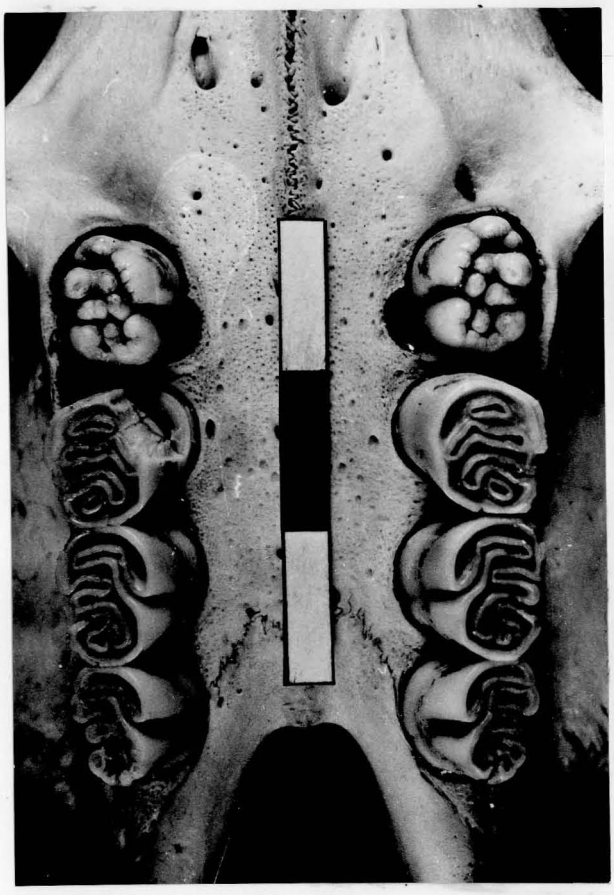


Fig 69

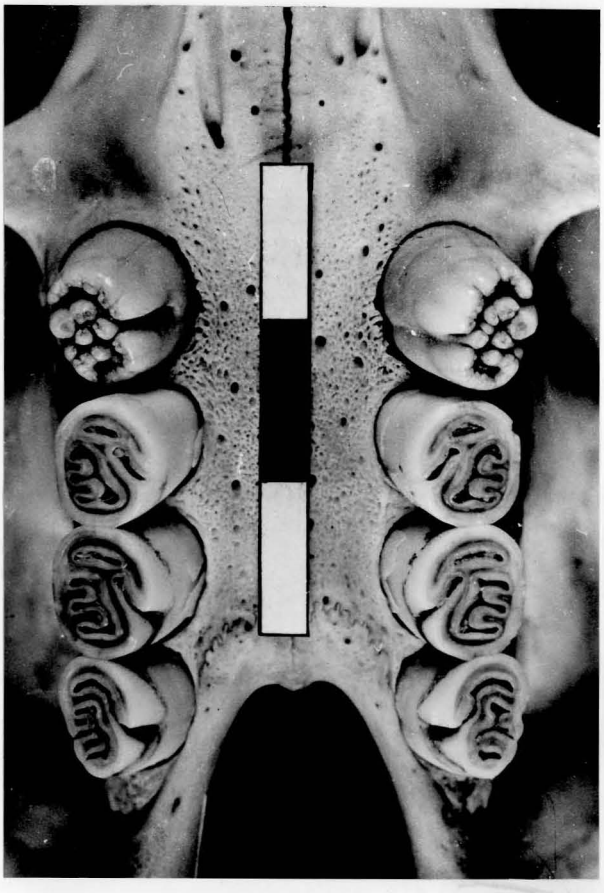


Fig 70

Fig. 71

Photograph illustrating the maxillary dentition of Hystrix africaeaustralis (x 2)

A typical 'mature adult' dentition. The permanent premolar is fully erupted and worn. The pressure exerted by its development is causing the M^1 to become antero-posteriorly compressed, so that its length (mesio-distal diameter) is shorter than its breadth (bucco-lingual diameter). On all teeth, all the flexuoses have closed to form fossettes. Note the differing crown enamel patterns on the second and third molars. Specimen TM 657, Growth Stage 6.

Fig. 72

Photograph illustrating the maxillary dentition of Hystrix africaeaustralis (x 2)

The first molars, the oldest teeth in the upper jaw, now show signs of deteriorating condition, due to prolonged wear and continued pressure. The specimen is interesting in that the flexuoses of the M^3 are open, despite the fact that in other respects the specimen is more mature than the specimen in Fig. 71. This may be due to a difference in the angle of the third molar in the two specimens. Specimen TM 623, Growth Stage 6.

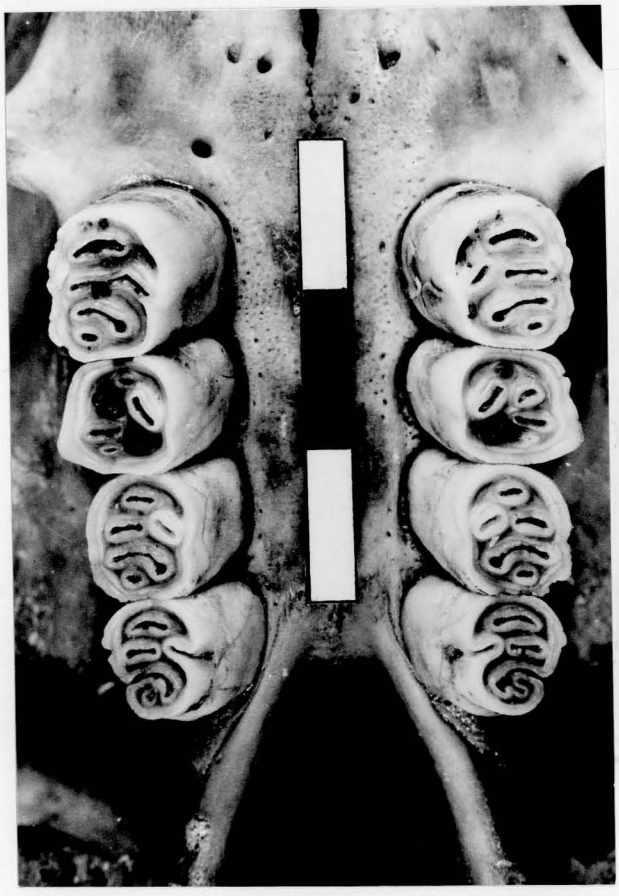


Fig 71

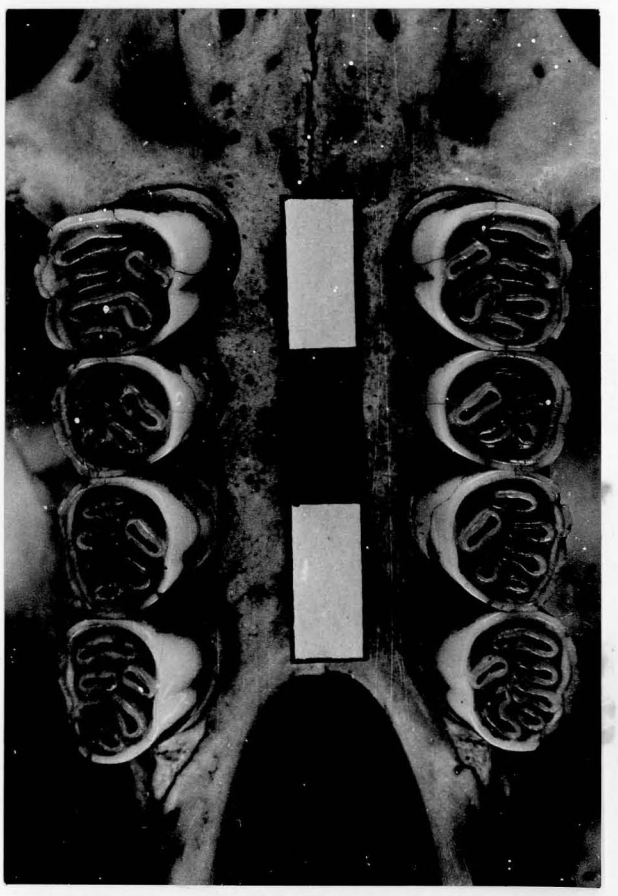


Fig 72

Fig. 73

Photograph showing the maxillary dentition of Hystrix africaeaustralis (x 2)

'Senile' dentition. The permanent premolars can be identified as the youngest teeth as they still retain several enamel fossettes. The alveoli of the second molars have become so shallow that they no longer suffice to hold the roots that anchor the teeth. The right M^2 has worn to a level below the enamel fossettes and hence the surface of the tooth is entirely dentine. Specimen TM 6066, late Growth Stage 6.

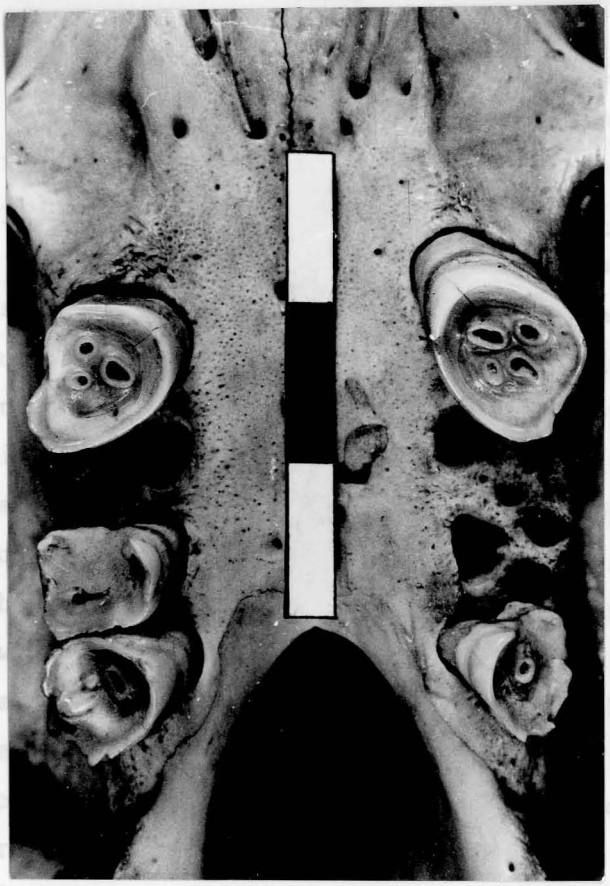


Fig 73

as described in the preceding section, and examining the series of crown enamel patterns displayed at each stage. The whole problem has been complicated by the fact that the H. africaeaustralis 'growth series' does not come from a single locality nor even a restricted area, but from desert as well as tropical localities. This has meant that some specimens (usually the 'tropical' ones) show relatively immature crown enamel patterns for the growth stage as indicated by their tooth eruption; the converse is true for specimens derived from drier environments, where a considerable amount of natural wear is suffered by dentitions due to the hardness of the diet available to the animal. Alternatively tooth eruption may be delayed so that the teeth already in place may suffer considerable wear - such a specimen would be placed in a 'young' growth stage, but its occlusal wear pattern will suggest the opposite, particularly if these worn teeth are found in isolation.

As mentioned above, the left and right tooth rows of both upper and lower jaws were on occasion found to differ in both advancement of tooth eruption and in crown enamel configuration - some animals seemed to display a marked tendency for chewing on one side. Hence each of the four tooth rows has been considered as a separate entity in the initial segregation into age classes. This has meant that sometimes left and right tooth rows of the same specimen may have been referred to different growth stages, e.g. PPM118 left upper = growth stage 3, PPM118 right upper = growth stage 4, or that the maxillary and mandibular dentitions may have been placed in different growth stages.

To make examination of the crown enamel patterns more feasible, each tooth row was photographed and printed to a magnification of x 4. To facilitate comparison the photographic negatives of the right tooth rows of both maxillary and mandibular dentitions were reversed in order to make them appear as left dentitions when printed. The photographs of the tooth rows were then divided into 6 growth stages according to tooth eruption and the crown enamel patterns characteristic of each growth stage examined. A set of enamel pattern tracings was made for each tooth at each growth stage and, arranged serially in order of maturity of their patterns as evidenced by the 'closure' of the flexuoses, transferred onto a single sheet. Identical enamel patterns were naturally not duplicated, so that each figure shows the different patterns evident at that particular growth stage. Every angle of wear

will produce a slightly different wear pattern; this factor will partially explain the wide variety of patterns apparent at any one growth stage.

The results of this investigation are illustrated in Figs. 74-90 (maxillary dentition) and Figs. 91-107 (mandibular dentition) and the conclusions are discussed briefly below. The abbreviations used in the figures are as follows:

	Maxillary dentition		Mandibular dentition
a	= paraflexus	=	paraflexid
b	= mesoflexus	=	mesoflexid
c	= metaflexus	=	metaflexid
d	= entoflexus	=	entoflexid
e	= hypoflexus	=	hypoflexid
A	= parafossette	=	parafossettid
B	= mesofossette	=	mesofossettid
C	= metafossette	=	metafossettid
D	= entofossette	=	entofossettid
E	= hypofossette	=	hypofossettid
*	= fossette or fossettid which has become secondarily penetrated from the inside by a still open flexus or flexid		

The enamel patterns characteristic of each growth stage in Hystrix africaeaustralis may not be identical to those of other species of Hystrix or to those of other genera, such as Xenohystrix (in fact, in most cases they differ) but, especially when using the degree of enamel fold 'closure', the growth stage divisions proposed below were on the whole found to be effective for the South African fossil material including the giant genus Xenohystrix, with the exception of growth stages 3 and 4, which for some teeth are easily confused.

Obviously there is a prior need to be able to identify the positional source of an isolated tooth (i.e. whether premolar or one of the molars), as the wear patterns of the premolar and each of the molars differ from each other at any one growth stage. Methods by which such identification may be made have been described in Chapter 13. By examining the wear pattern and degree of closure of flexi or flexids, such an

identified isolated tooth may be referred to an appropriate growth stage using the criteria outlined below.

The order of closure of the enamel folds and the taxonomic significance of the crown enamel pattern has been discussed in more detail in subsequent sections (10.3.1 and 10.3.2 and Chapter 12).

7.1.5.1 The crown enamel pattern of the maxillary dentition

In some instances it was impossible to define mutually exclusive 'diagnoses' which would effectively distinguish the crown enamel patterns of two or more growth stages divided on the basis of tooth eruption - growth stages 3 and 4 were particularly easily confused. An absolute segregation of growth stages on the basis of crown enamel pattern appears to be impossible on account of the problems referred to above, especially if the latter are to correspond to the growth stages suggested by tooth eruption. If the 'diagnoses' provided below did not enable the isolated tooth in question to be placed in a single growth stage or if it seemed possible to place the tooth in more than one stage, its occlusal pattern was compared directly with the illustrations provided. In this way it has usually been possible, when working with isolated fossil teeth, to refer them to a definite growth stage or at least to give only one alternative.

a) dp^4 or P^4

Growth stage 1 (no figure)

All premolars (deciduous at this growth stage) are unworn and show their original tuberculate cusp pattern.

Diagnosis: Surface of tooth unworn, cuspate pattern still apparent

Growth stage 2 (Fig. 74 Nos. 1-4)

Some crown enamel patterns may be only partially established in early growth stage 2, (the) dp^4 is incompletely worn (Fig. 74 No. 1). Usually only one flexus - the posteriormost or entoflexus - is 'closed' to form a fossette, the entofossette (Fig. 74 No4D). In tooth No. 3, the hypoflexus has rather prematurely become closed to form the hypofossette (E), due to an excessive amount of wear on this (the lingual) side of the tooth. The tooth cannot be confused with the next growth stage because all the external enamel folds (a,b,c, and d) are still open.

Diagnosis: Surface of tooth partially or fully worn, external folds a-d open or at most one external fold (d, the entoflexus) closed (Fig. 74 No.4D). If a hypofossette is present, then all four external folds open (Fig. 74 No.3).

Growth stage 3 (Fig. 75 Nos.1-7)

Some crown enamel patterns, especially those of teeth 6 and 7 which are excessively worn for this growth stage, are barely distinguishable from terminal growth stage 4, and would probably be included in the latter if found in isolation.

Diagnosis: Surface of tooth fully worn, usually at least two external enamel folds (the entoflexus and the paraflexus) 'closed' to form the entofossette (D) and parafossette (A) respectively - teeth numbers 1,2 and 3. If the paraflexus is still open, then a hypofossette (E) and entofossette (D) are present - tooth number 4. The hypoflexus begins and usually completes its closure in this growth stage. The entofossette (D) becomes smaller (tooth number 4), then secondarily penetrated by a branch of the meso- or metaflexus (tooth number 5) and finally disappears in the course of this growth stage. The meso- and meta- flexi are often contiguous.

Growth stage 4 (Fig. 76A Nos.1-6, Fig. 76B Nos.1-6)

Fig. 76, tooth no. 1 shows a somewhat immature wear pattern for this growth stage. Tooth number 2 is the corresponding tooth from the opposite side of the maxilla of the same specimen, and shows a 'normal' wear pattern for this growth stage. The animal obviously favoured chewing on one side (the right) leading to this discrepancy of patterns.

Diagnosis: Surface of tooth fully worn, hypoflexus almost invariably 'closed'. The entofossette (D) usually absent, or if present, perforated by fold of metaflexus (c), Fig. 76A, teeth numbers 1 and 2. Mesoflexus (b) and metaflexus (c) apparently never contiguous, unlike g/s 3. All folds closed to form

fossettes by the end of this growth stage, so that the outer enamel is continuous. Fossettes 3 to 5 in number. It is highly probable that any deciduous premolar with continuous outer enamel is at late growth stage 5.

Note: Fig. 75 Nos.6 and 7, actually in g/s 3 according to their stage of eruption, show particularly advanced crown enamel patterns for their tooth eruptive stage and would be placed in the above growth stage if found in isolation.

Growth stage 5 (Fig. 77 Nos.1-5)

Growth stage 5 is characterised by the replacement permanent P^4 in the unworn state.

Diagnosis: Any unworn or incompletely worn permanent premolar is at growth stage 5.

Growth stage 6 (Fig. 78 Nos.1-12)

Diagnosis: Any permanent premolar which has a fully worn surface is at growth stage 6.

b) M^1

Growth stage 1

M^1 has not yet erupted at this growth stage

Growth stage 2 (Fig. 79 Nos.1-5)

Diagnosis: Surface of tooth completely unworn, partially worn or completely worn. If surface fully worn, then at least 6 lightly worn 'turrets' representing the initial stages of wear of the tuberculate cuspules present. Paraflexus (a) may 'close' buccally toward terminal phase of this stage (tooth number 5);if so, then remaining three buccal folds open. Paraflexus or incipient parafossette always confluent with hypoflexus.

Growth stage 3 (Fig. 80 Nos.1-9)

Teeth numbers 1 and 2 are rather aberrant - number 1 has a rather unusual posterior enamel fold (marked with a query in the Figure) and number 2

has an immature wear pattern for growth stage 3. Both teeth would almost certainly be included in growth stage 2 if found in isolation although number 1 has two 'closed' external folds.

No satisfactory means of separating growth stages 3 and 4 by means of the crown enamel patterns could be defined - some teeth, for example Fig. 80 No.7 (growth stage 3 according to tooth eruption) and Fig.81 No.4 (growth stage 4, using tooth eruption) are practically identical. Hence no formal diagnosis has been given; the tendencies of the crown enamel pattern have simply been listed:

1. Never more than one completely closed fossette present, usually the parafossette; the isolation of the latter from the hypoflexus occurring late in growth stage 3 (teeth numbers 7 and 8). Often no completely closed fossettes present, although the incipient para-, meso- and entofossettes may be closed buccally.

2. The parafossette frequently confluent with the hypoflexus and with the mesoflexus.

3. Hypoflexus apparently never closed.

Growth stage 4 (Fig. 81 Nos.1-11)

No mutually exclusive diagnosis could be devised which could effectively differentiate the crown enamel patterns of this growth stage from those of the preceding and following stage, hence the tendencies of the patterns have been listed below:

1. With the exception of teeth numbers 1 and 2 at early growth stage 4, all crown enamel patterns show one and usually two or more completely sealed fossettes - the parafossette followed by the entofossette are the first to appear.

2. Hypoflexus frequently closed to form hypofossette.

3. Buccal enamel folds usually closed by the end of this growth stage.

4. Occlusal outline of tooth usually oval, long axis anteroposteriorly orientated.

Note: Teeth numbers 1 and 2 would undoubtedly be included in growth stage 3 and teeth numbers 6, 10 and 11 in growth stage 5 if found in isolation. Isolated teeth suspected of belonging to one of these three growth stages were therefore visually compared with the crown enamel patterns of all three and a decision was reached in this way.

Growth stage 5 (Fig. 82 Nos.1-6)

Diagnosis: Hypoflexus never confluent with parafossette; completely sealed parafossette always present. Hypofossette always closed or very nearly closed. Except for tooth number 1 all external enamel folds closed or nearly closed, little or in some cases no dentine intervening between outer enamel and enamel surrounding fossettes. Fossettes large in relation to area occupied by dentine, their surrounding enamel often contiguous with that bounding the tooth. If one fold remains open this is usually the metaflexus. Unlike growth stage 3 mesofossette (b) and metafossette (c) very rarely confluent, if so, then their buccal outlets closed. Occlusal outline of tooth approximately round.

Growth stage 6 (Fig. 83 Nos.1-8)

Diagnosis: All enamel folds closed, outer enamel continuous with dentine intervening between it and the enamel surrounding the nearest fossette. Fossettes four to six in number, small in relation to area occupied by dentine. Occlusal outline of tooth oval, long axis transversely orientated

c) M^2

Growth stage 1

At growth stage 1, the M^2 has not yet erupted.

Growth stage 2

At growth stage 2, the M^2 has not yet erupted

Growth stage 3 (Fig. 84 Nos.1-8)

Diagnosis: Surface of tooth either unworn, partially worn or fully worn. No completely isolated fossettes present, although the paraflexus, and in the terminal stages the entoflexus, may be closed buccally. If paraflexus closed buccally, then hypoflexus confluent with metaflexus (and incipient parafossette). Six to nine slightly worn 'turrets' representing the initial stages of wear of the cusps, may be present.

Growth stage 4 (Fig. 85A Nos.1-6; Fig.85B Nos.1-7

Growth stage 5 (Fig. 86 Nos.1-6)

Tooth No. 1, Fig. 85A (belonging to specimen PPM116) has erupted late and hence illustrates a very immature crown pattern for this growth stage, and would undoubtedly be included in growth stage 3 if found in isolation. The corresponding tooth row has been placed in growth stage 3. It has thus been excluded from considerations of growth stage 4 crown patterns. Growth stages 4 and 5 appear to be inseparable, probably because the eruption of M^3 (the criterion for inclusion in g/s 4) is rapidly followed by eruption of P^4 (the criterion for inclusion in g/s 5), so that the crown patterns are often similar or identical. The characteristic features of the C.E.P.s of these two growth stages are listed below:

1. Parafossette almost invariably completely isolated; if not, hypoflexus never communicating with metaflexus, unlike g/s 3
2. One to three completely isolated fossettes present
3. At least one flexus still open, this is usually the metaflexus but may be the hypoflexus. Usually two or three flexi open
4. Outer enamel never continuous, unlike g/s 6.

Growth stage 6 (Fig. 87 Nos.1-7)

Diagnosis: With the exception of one tooth (No. 1) all enamel folds closed and outer enamel continuous. Four to six fossettes present

d) $\underline{M^3}$

Growth stages 1, 2 and 3

At growth stages 1, 2 and 3 the M^3 has not yet erupted.

Growth stages 4 and 5 (Fig. 88 Nos. 1-9; Fig 89 Nos. 1-7)

The M^3s at growth stages 4 and 5 appear to be inseparable on crown enamel pattern alone, presumably because the eruption of M^3 (the criterion for inclusion in g/s 4) is rapidly followed by the eruption of the P^4 (the criterion for inclusion in g/s 5) so that the wear patterns shown are often at a similar stage of development. However, any unworn or incompletely worn M^3 may safely be placed in g/s 4 because the M^3 is apparently always fully worn prior to the eruption of the permanent premolar. The characteristics of the C.E.P.s of teeth at growth stages 4 and 5 are listed below:

1. The hypoflexus is almost invariably still open, unlike g/s 6; if 'closed' lingually (rare) then at least two external enamel folds still open.
2. Completely separate hypofossette, i.e. not confluent with parafossette, never present. Parafossette rarely present.
3. Usually at least two external enamel folds 'open', the entoflexus followed by the paraflexus being the first to 'close'. The metaflexus closes last.
4. Hypoflexus and paraflexus frequently confluent, unlike g/s 6.
5. Outer enamel never forms an uninterrupted circle, unlike g/s 6.

Growth stage 6 (Fig. 90 Nos. 1-10)

Diagnosis:

(With the exception of tooth No. 1 Fig 90 which could easily belong to g/s 5) Parafossette almost invariably present, seldom confluent with hypofossette. Hypoflexus usually 'closed' lingually; if not, never confluent with parafossette and only one external enamel fold 'open'. Never more than one e.e.f. 'open'.Hypofossette usually present (never in g/s 4 or 5); outer enamel forms continuous circle, unlike g/s 4 and 5. Two to six fossettes present.

7.1.5.2 The crown enamel pattern of the mandibular dentition

a) dp_4 or P_4

Growth stage 1 (no figure)

All premolars (deciduous at this growth stage) are unworn and show their original tuberculate cusp pattern.

Diagnosis:

Surface of tooth unworn, cuspate pattern still apparent

Growth stage 2 (Fig. 91 Nos. 1-5)

Diagnosis:

Occlusal surface partially to fully worn, hypoflexid never closed buccally, usually confluent with meta- and entoflexids. Mesoflexid often still open. Apparently never more than one completely 'closed' fossettid.

Growth stage 3 (Fig. 92 Nos. 1-7)

Diagnosis:

Occlusal surface always fully worn, hypoflexid never confluent with meta- or entoflexids but separated from them lingually. In mature C.E.P.s, hypoflexid may be completely 'closed' to form hypofossettid (Nos. 4, 7). Never more than one internal (lingual) enamel fold (usually the metaflexid) open lingually. Outer enamel never forming an uninterrupted regular circle or ellipse. At least three to six fossettids present.

Growth stage 4 (Fig. 93 Nos. 1-10)

The deciduous premolar at this growth stage is characterised by deterioration of its condition: it has erupted far out of its socket and its three divergent roots are usually apparent even in *in situ* specimens, its occlusal surface is marked by the loss of enamel chips from the outer encircling enamel and by the reduction in size and number of the occlusal fossettids (see Nos. 7, 8, 9 and 10). It is shed by the end of this growth stage, usually when the occlusal surface has worn down to a level beyond the point of divergence of the roots (Nos. 9 and 10).

Diagnosis:

Except for Nos. 1 and 2 which could be confused with g/s 3, all deciduous premolars at g/s 4 have a continuous ellipse of encircling enamel, all the flexids are closed to form fossettids, and the enamel encircling these is separate from the outer encircling enamel. In mature g/s 6 C.E.P.s the fossettids are reduced in size and number (Nos. 9 and 10).

Growth stage 5 (Fig. 94 Nos. 1-4)

Diagnosis:

All the premolars (permanent at this g/s) show an unworn cuspate C.E.P.

Growth stage 6 (Fig. 95 Nos. 1-5)

The permanent premolars can be distinguished from the deciduous premolars by their larger size, more cylindrical shape and non-divergent or less divergent root system (see 13.2.8).

Diagnosis:

Any fully worn permanent premolar is at g/s 6. The hypoflexid is the last flexid to become 'closed'.

b) M_1

Growth stage 2 (Fig. 96 Nos. 1-4)

The M_1 erupts during this growth stage, thus any newly-erupted, unworn or partially worn M_1 can be referred to g/s 2.

Diagnosis:

Surface of tooth unworn, partially worn or slightly worn all over. Original cuspate pattern still apparent, evidence of at least ten distinct cusps being visible (see tooth, Nos. 3, 4).

Growth stage 3 (Fig 97 Nos. 1-7)

No satisfactory means of separating the crown enamel patterns of the M_1 at growth stages 3 and 4 could be defined; some of the C.E.P.s at growth stage 3 being identified with some of those at growth stage 4 (e.g. Fig 97 No. 1 g/s 3 and Fig. 98A No. 1, g/s 4). The tendencies of the M_1 growth stage 3 C.E.P.s are listed below, as no formal 'diagnosis' can be given:

1. Hypoflexid almost always confluent with entoflexid, which may be 'closed' lingually; if hypoflexid not confluent, then entofossettid not completely isolated, in that its surrounding enamel is still contiguous with the enamel surrounding the tooth, usually at a point where it adjoins the still-open hypoflexus.
2. Often at least two lingual flexids 'open'.
3. Apparently never more than two completely isolated fossettids present and usually only one.

Growth stage 4 (Fig. 98 Nos. 1-9)

The crown enamel patterns of the M_1 at this growth stage are often not distinguishable from those at growth stage 3, whilst some of the more mature g/s 4 patterns are not distinguishable from those at g/s 5. Again, the tendencies of the crown enamel patterns are discussed, as no mutually exclusive diagnosis could be devised:

1. Hypoflexid usually not confluent with entoflexid, completely isolated entofossettid usually present.
2. Usually only one, or no, lingual (internal) flexids 'open'.
3. Usually more than one fossettid which is completely isolated; up to five may be present.
4. Except for one tooth (Fig. 98B No. 5) hypoflexus never closed to form hypofossettid.

Growth stage 5 (Fig. 99 Nos. 1-5)

By the time this growth stage has been reached, the pressure exerted by the large erupting permanent premolar immediately anterior to the M_1, causes the condition of the latter to deteriorate. From this growth stage onward, the enamel at the contact point between these two teeth becomes worn away by pressure and friction so that the dentine is exposed anteriorly (teeth Nos. 2, 4 and 5). Once again, some of the crown enamel patterns of the M_1 at this growth stage cannot be distinguished from those of the M_1 at g/s 4, e.g. Fig. 99 tooth No. 5 (g/s 5) and Fig. 98B tooth No. 5 (g/s 4). The tendencies of the M_1 g/s 5 crown enamel pattern are listed below:

1. Dentine often exposed anteriorly at pressure facet.
2. All lingual (internal) flexids 'closed'.

3. Hypofossettid usually present, but its encircling enamel is frequently contiguous with the outer enamel which encircles the tooth at the point where the hypoflexus normally penetrates the tooth (see tooth Nos. 3 and 4).
4. Fossettids large in relation to total occlusal area, with little dentine intervening between them and outer encircling enamel.

Growth stage 6 (Fig. 100 Nos. 1-5)

At this growth stage, the pressure exerted on the M_1 by the now fully-erupted permanent premolar is so great that the enamel at the posterior contact point is affected, and may be worn away, eventually exposing the dentine posteriorly. The dentine is exposed anteriorly as early as g/s 5.

Diagnosis:

No flexids still 'open', four to six fossettids present. Fossettids small in relation to occlusal area, so that the dentine occupies a greater proportion of the occlusal surface than it did in g/s 5. Fossettids separated from outer encircling enamel by substantial width of dentine. Anterior and posterior pressure facets well developed, dentine may be exposed at both.

M_2

Growth stages 1 and 2 (no figure)

The M_2 is not yet present at these growth stages.

Growth stage 3 (Fig. 101, Nos. 1-6)

The M_2 erupts during the course of this growth stage, therefore any unworn or incompletely worn M_2 may be referred to g/s 3.

Diagnosis:

Surface of tooth unworn, partially worn or slightly but fully worn, original pattern of cusps still apparent in the form of up to eleven unworn cusps or slightly worn 'turrets' (see tooth Nos. 1-6). Paraflexus, and in mature g/s 3 C.E.P.s the entoflexus, may be 'closed' lingually, but no completely isolated fossettes present. Usually three lingual flexids still open.

Growth stage 4 (Fig.102 Nos. 1-12)

Diagnosis:

Except for tooth Nos. 1 and 2, never more than two flexids open lingually. Apparently always at least one internal flexus 'open', the last to close being the metaflexus. Entofossette seldom completely isolated, if so, then metaflexus still open lingually. Usually not more than one completely isolated fossette.

Growth stage 5 (Fig. 103 Nos. 1-6)

Diagnosis:

All internal flexids closed lingually, hypoflexid is only open flexid. Often two or more completely isolated fossettids present. The closed lingual flexids distinguishes g/s 5 C.E.P.s from those of g/s 4, while the open hypoflexid distinguishes them from g/s 6.

Growth stage 6 (Fig. 104 Nos. 1-6)

Diagnosis:

All flexids, including hypoflexid, closed, outer enamel an uninterrupted ellipse. Four to six completely isolated fossettids present.

M_3

Growth stages 1, 2 and 3 (no figure)

The M_3 has not yet erupted.

Growth stage 4 (Fig. 105 Nos. 1-9)

The M_3 erupts during the course of this growth stage, thus any unworn or partially worn M_3 may be referred to growth stage 4. The crown enamel patterns of some of the fully worn teeth, however, (particularly tooth No. 8 and 9) could easily be confused with the C.E.P.s of M_3s at a more advanced growth stage - some of the C.E.P.s of lower third molars at g/s 5 (Fig.106 Nos. 1-6) appear considerably less mature than these of tooth Nos. 8 and 9, Fig. 105. For this reason, no mutually exclusive diagnosis effectively separating the C.E.P.s of growth stages 4 and 5 can be given, and frequently encountered characteristics are merely listed below:

1. Occlusal surface frequently unworn or only partially worn, tooth markedly triangular in outline.

2. Entofossettid never completely isolated; hypoflexid usually confluent with lingually sealed entoflexid.
3. Completely isolated fossettids of any nature rare; if present, not more than one, usually the combined para- and mesofossettids.

Growth stage 5 (Fig. 106 Nos. 1-6)

Some of the crown enamel patterns of M_3s at this growth stage seem less mature than those at g/s 4, e.g. teeth Nos. 1 and 2, Fig. 106 (g/s 5) compared with teeth Nos. 7, 8 and 9 Fig. 105 (g/s 4). It may be that the latter teeth were subjected to a harder diet and therefore a greater degree of attrition than the former; alternatively, the g/s 5 teeth may have had their eruption delayed somewhat which would account for their immature crown enamel patterns. Another alternative is that the two g/s 4 teeth mentioned (Fig. 105 Nos. 8 and 9) may have erupted earlier than is usual for M_3, and have therefore suffered a longer period of wear, thus developing an unusually mature crown enamel pattern.

Although the C.E.P.s characteristic of g/s 5 are easily distinguishable from those at g/s 6 the M_3 C.E.P.s at growth stages 4 and 5 are easily confused. For this reason, no formal'diagnosis'can be given; the characteristics of the g/s 6 crown enamel patterns are instead listed below:

1. Shape of occlusal surface less triangular than in g/s 4, tending to be oval.
2. Often as many as three and always at least one lingual flexid open (the metaflexid).
3. Hypoflexid never closed buccally (externally) often confluent internally with either the metaflexid or the entoflexid or both.
4. Never more than one completely isolated fossettid present, this being the combined para- and mesofossettid.
5. Entofossettid may be isolated or nearly so.

Growth stage 6 (Fig. 107 Nos. 1-5)

Diagnosis:

All lingual flexids 'closed. Hypofossettid often present, if not hypoflexid not confluent with ento- or metaflexid, three to five completely isolated fossettids present. Outer enamel often forms an uninterrupted oval.

Fig. 74

The crown enamel patterns of a series of upper deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 2. Approximately x 4

1 - TM Nyasaland (left

2 - TM 5662 (right, drawn as left)

3 - TM 5661 (right, drawn as left)

4 - TM 5661 (left)

a	-	paraflexus	A	-	parafossette
b	-	mesoflexus	B	-	mesofossette
c	-	metaflexus	C	-	metafossette
d	-	entoflexus	D	-	entofossette
e	-	hypoflexus	E	-	hypofossette

* - fossette which has secondarily become penetrated from the inside by another flexus or fossette

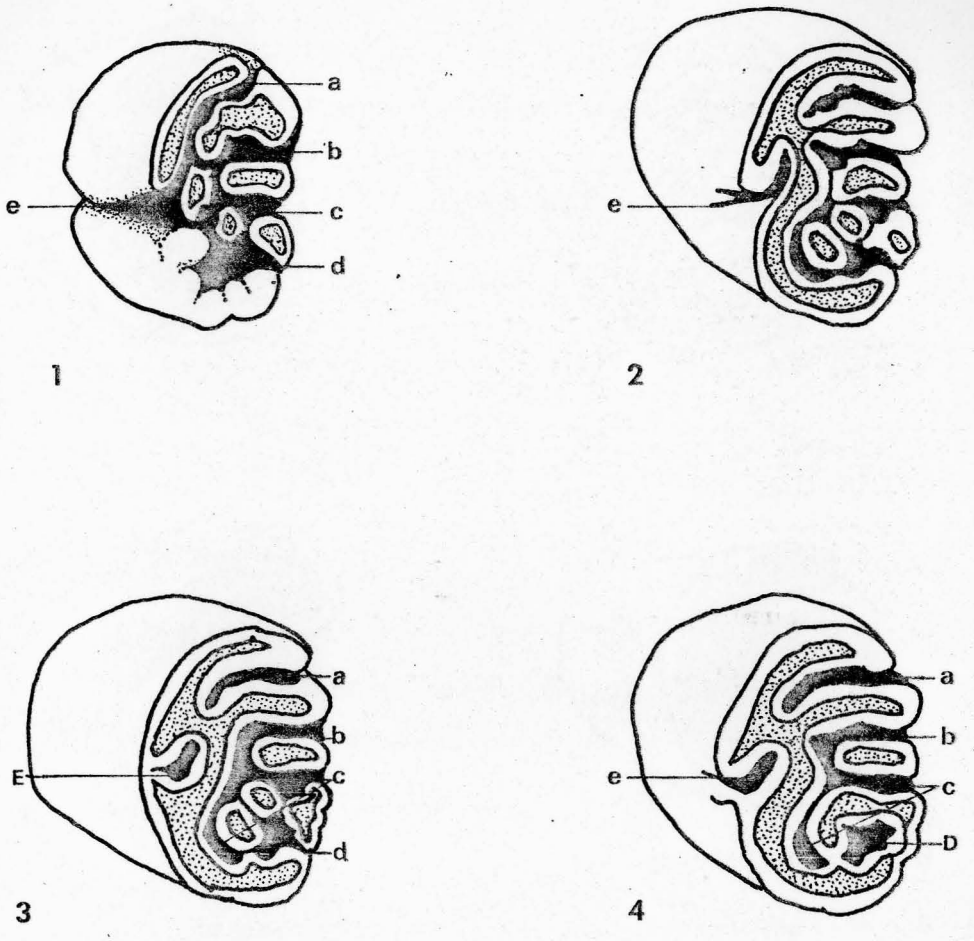


Fig 74

DP^4 GROWTH STAGE 2

Fig. 75

The crown enamel patterns of a series of upper deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 3. Approximately x 4.

1 - TM 12698 (left)

2 - TM 12698 (right, drawn as left)

3 - TM 12697 (right, drawn as left)

4 - PPM 115 (right, drawn as left)

5 - PPM 116 (left)

6 - PPM 114 (left)

7 - PPM 114 (right, drawn as left)

A - parafossette or incipient parafossette

b - mesoflexus

B - mesofossette or incipient mesofossette

c - metaflexus

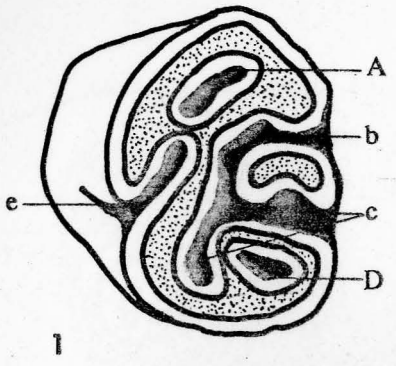
C - metafossette or incipient metafossette

d - entoflexus

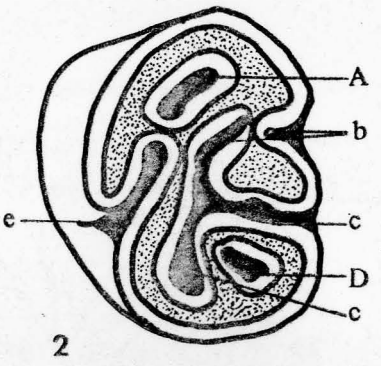
D - entofossette or incipient entofossette

e - hypoflexus

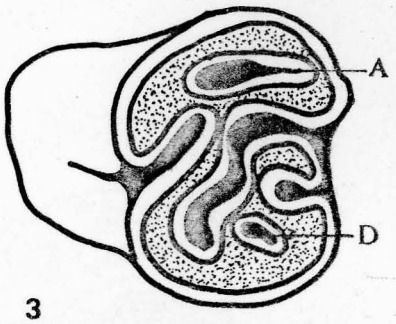
E - hypofossette or incipient hypofossette



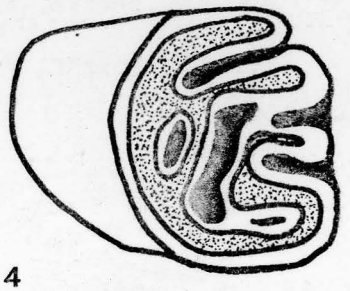
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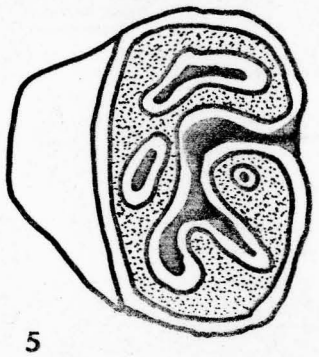
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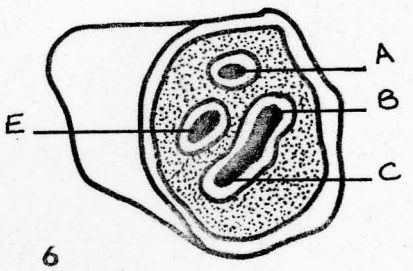
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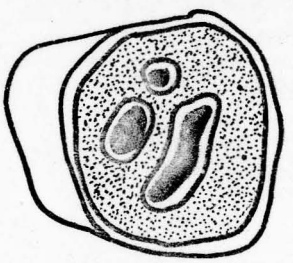
4



5



6



7

Fig 75

DP^4 GROWTH STAGE 3

Fig. 76a

The crown enamel patterns of a series of upper deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Approximately x 4.

1 - TM 94F (left)

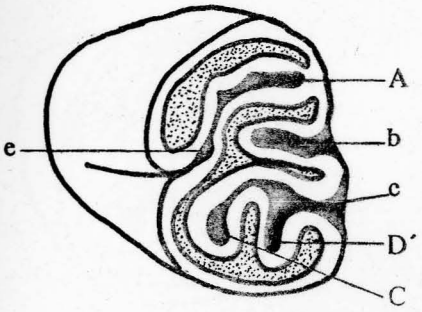
2 - TM 94F (right, drawn as left)

3 - BPI/C 682 (left)

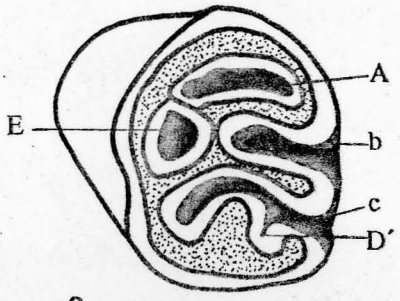
4 - BPI/C 682 (right, drawn as left)

5 - PPM 124 (left)

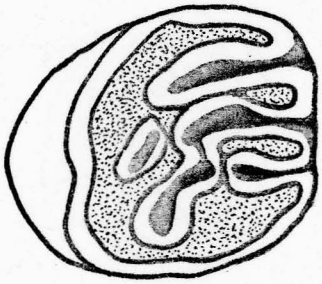
6 - PPM 124 (right, drawn as left)



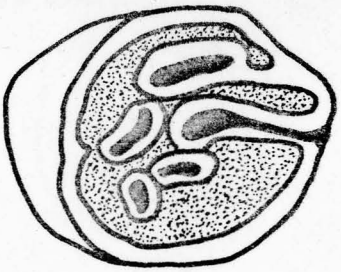
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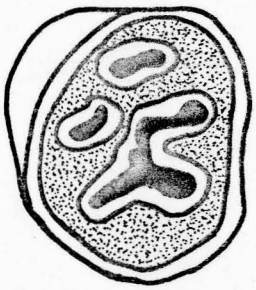
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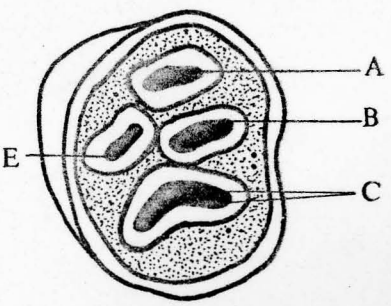
3



4



5



6

Fig 76 A

DP^4 GROWTH STAGE 4

Fig. 76b

The crown enamel patterns of a series of upper deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Approximately x 4.

1 - TM Mountain Zebra Park (left)

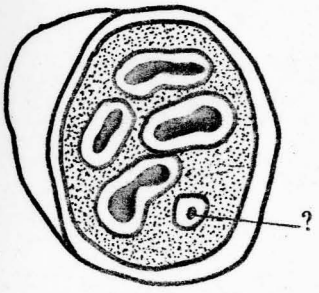
2 - TM 594 (left)

3 - TM 2A (left)

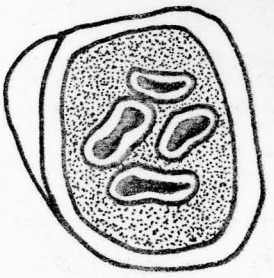
4 - TM 2A (right, drawn as left)

5 - TM 753 (left)

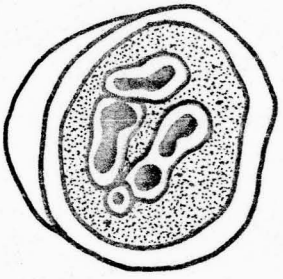
6 - TM 753 (right, drawn as left)



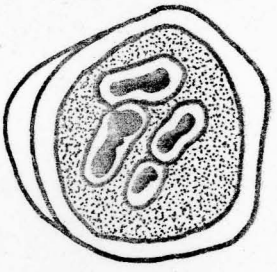
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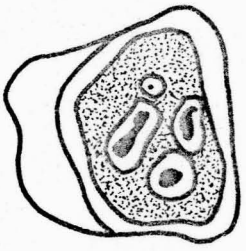
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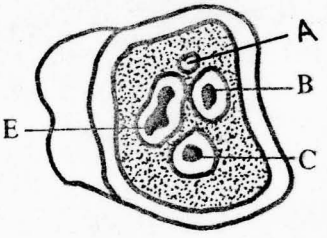
3



4



5



6

Fig 76B

DP 4 GROWTH STAGE 4

Fig. 77

The crown enamel patterns of a series of newly-erupted upper permanent premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Approximately x 4.

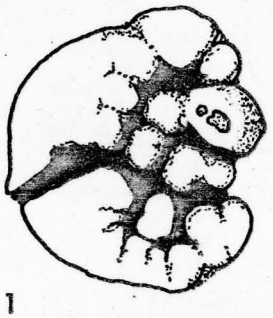
1 - TM 12167 (left)

2 - PPM 117 (right, drawn as left)

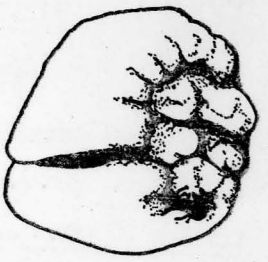
3 - PPM 118 (right, drawn as left)

4 - TM 866 (left)

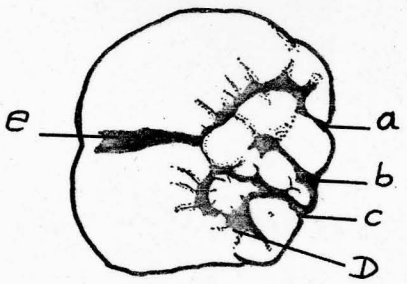
5 - PPM 118 (left)



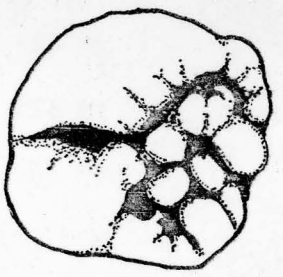
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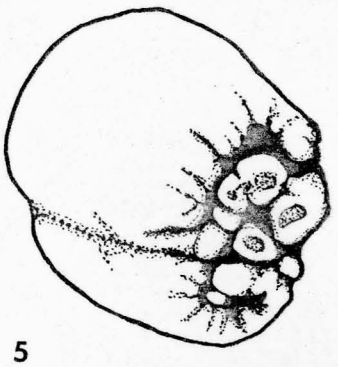
2



3



4



5

Fig 77

P^4 GROWTH STAGE 5

Fig. 78

The crown enamel patterns of a series of upper permanent premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6. Approximately x 4.

1 - TM 8289 (left)

2 - TM 8289 (right, drawn as left)

3 - Za 911 (left)

4 - Za 911 (right, drawn as left)

5 - TM 657 (right, drawn as left)

6 - TM 623 (left)

7 - TM 623 (right, drawn as left)

8 - TM 657 (left)

9 - BPI/C 641 (right, drawn as left)

10 - BPI/C 641 (left)

11 - PPM 122 (left)

12 - PPM 122 (right, drawn as left)

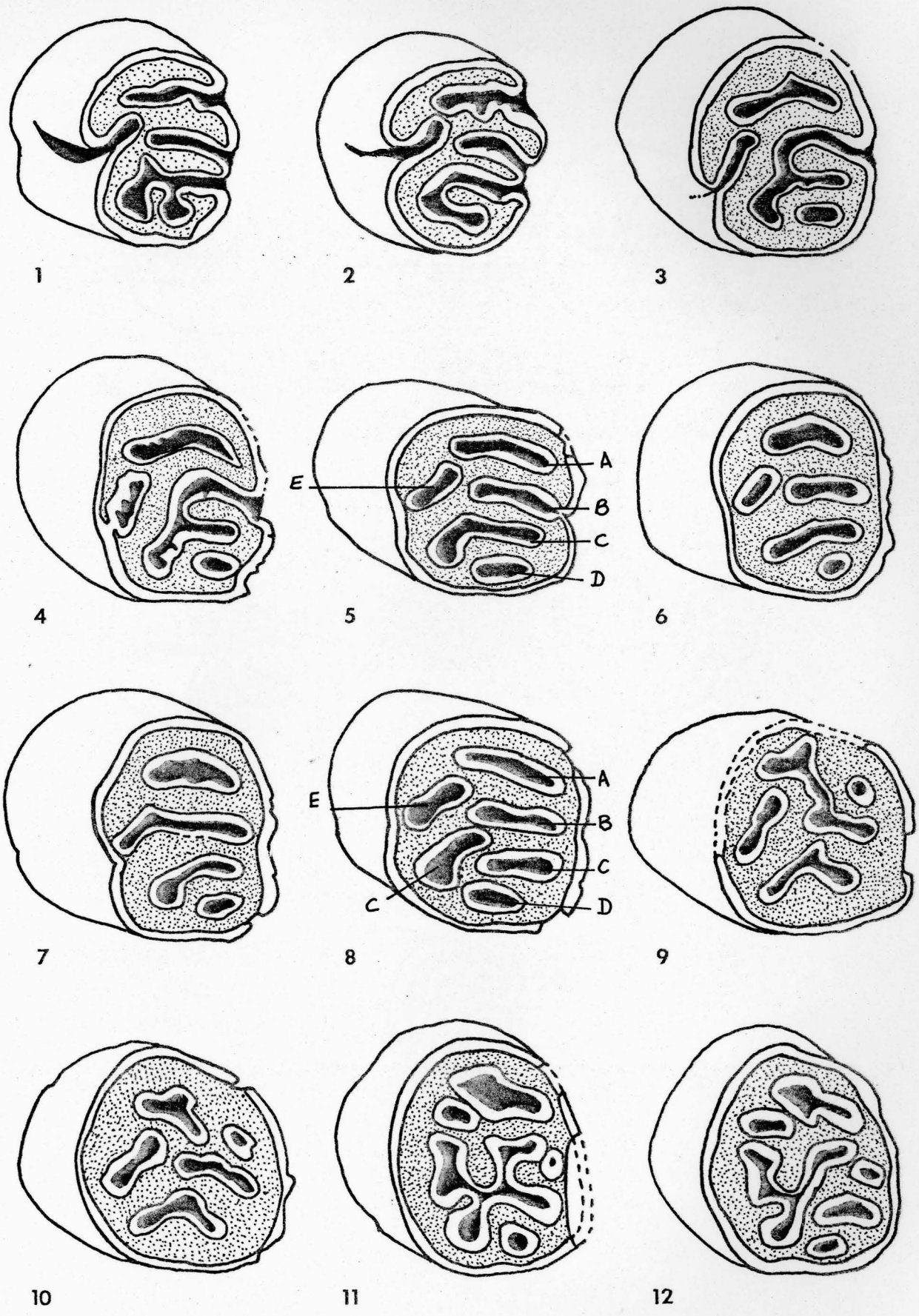


Fig 78

P^4 GROWTH STAGE 6

Fig. 79

The crown enamel patterns of a series of upper first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 2. Approximately x 4.

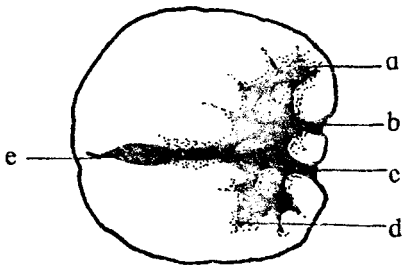
1 - TM NYASALAND (left)

2 - TM 5662 (right, drawn as left)

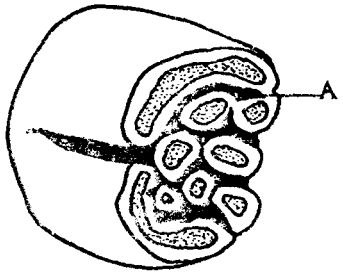
3 - TM 5662 (left)

4 - TM 5661 (right, drawn as left)

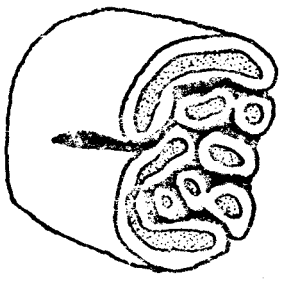
5 - TM 5661 (left)



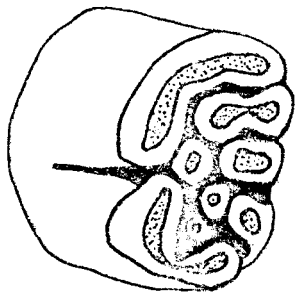
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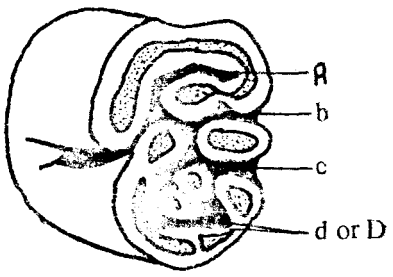
2



3



4



5

Fig 79

M^1 GROWTH STAGE 2

Fig. 80

The crown enamel patterns of a series of upper first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 3. Approximately x 4.

1 - TM 12698 (left)

2 - TM 12698 (right, drawn as left)

3 - PPM 116 (left)

4 - TM 12697 (right, drawn as left)

5 - TM 12697 (left)

6 - PPM 115 (left)

7 - PPM 115 (right, drawn as left)

8 - PPM 114 (left)

9 - PPM 114 (right, drawn as left)

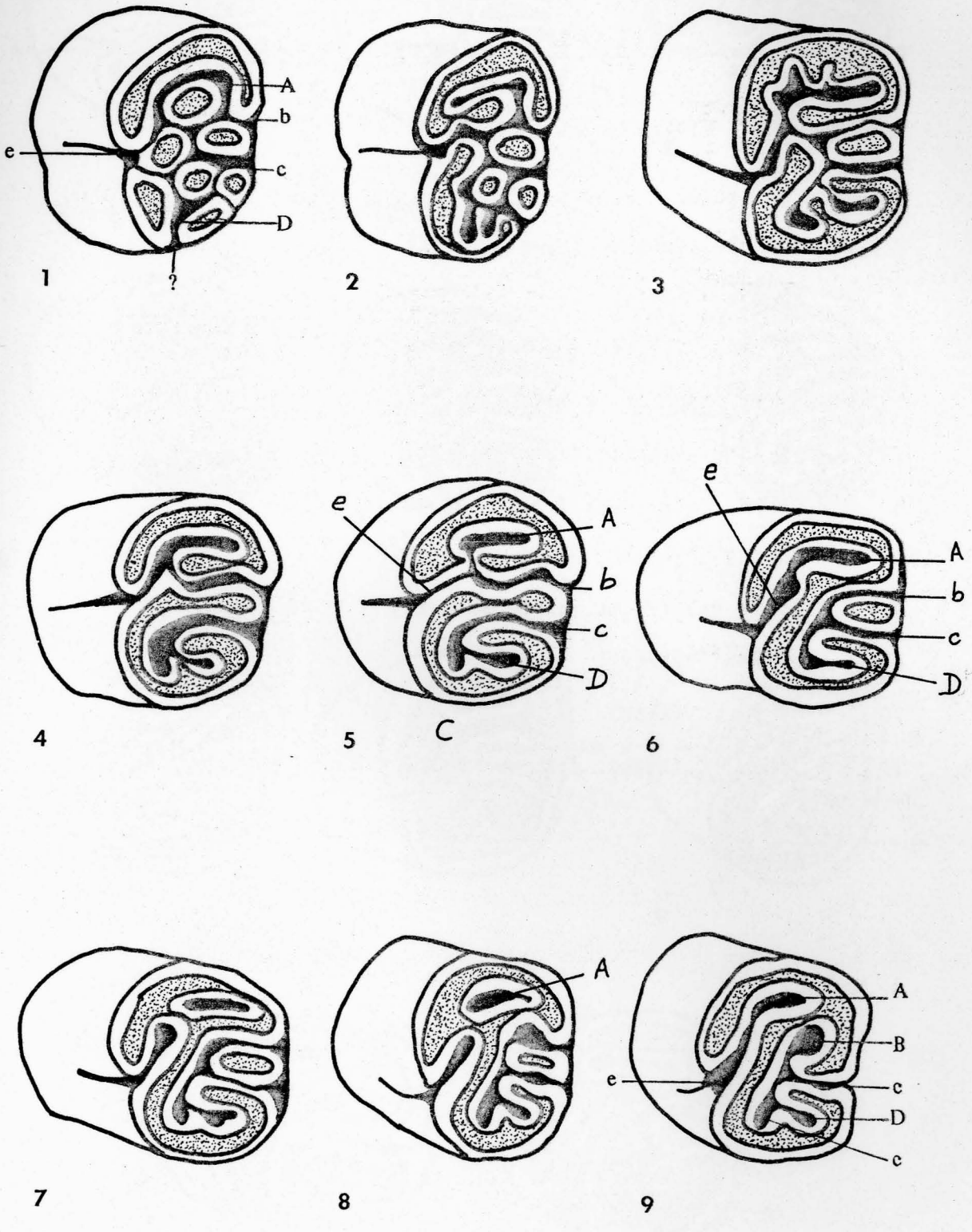


Fig 80

M[1] GROWTH STAGE 3

Fig. 81

The crown enamel patterns of a series of upper first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Approximately x 4.

1 - PPM 116 (right, drawn as left)

2 - TM 94F (left)

3 - TM 94F (right, drawn as left)

4 - TM Mt. Zebra Park (left)

5 - TM 124 (right, drawn as left)

6 - TM Mt. Zebra Park (right, drawn as left)

7 - TM 753 (right, drawn as left)

8 - BPI/C 682 (right, drawn as left)

9 - TM 594 (left)

10 - TM Za (left)

11 - TM Za (right, drawn as left)

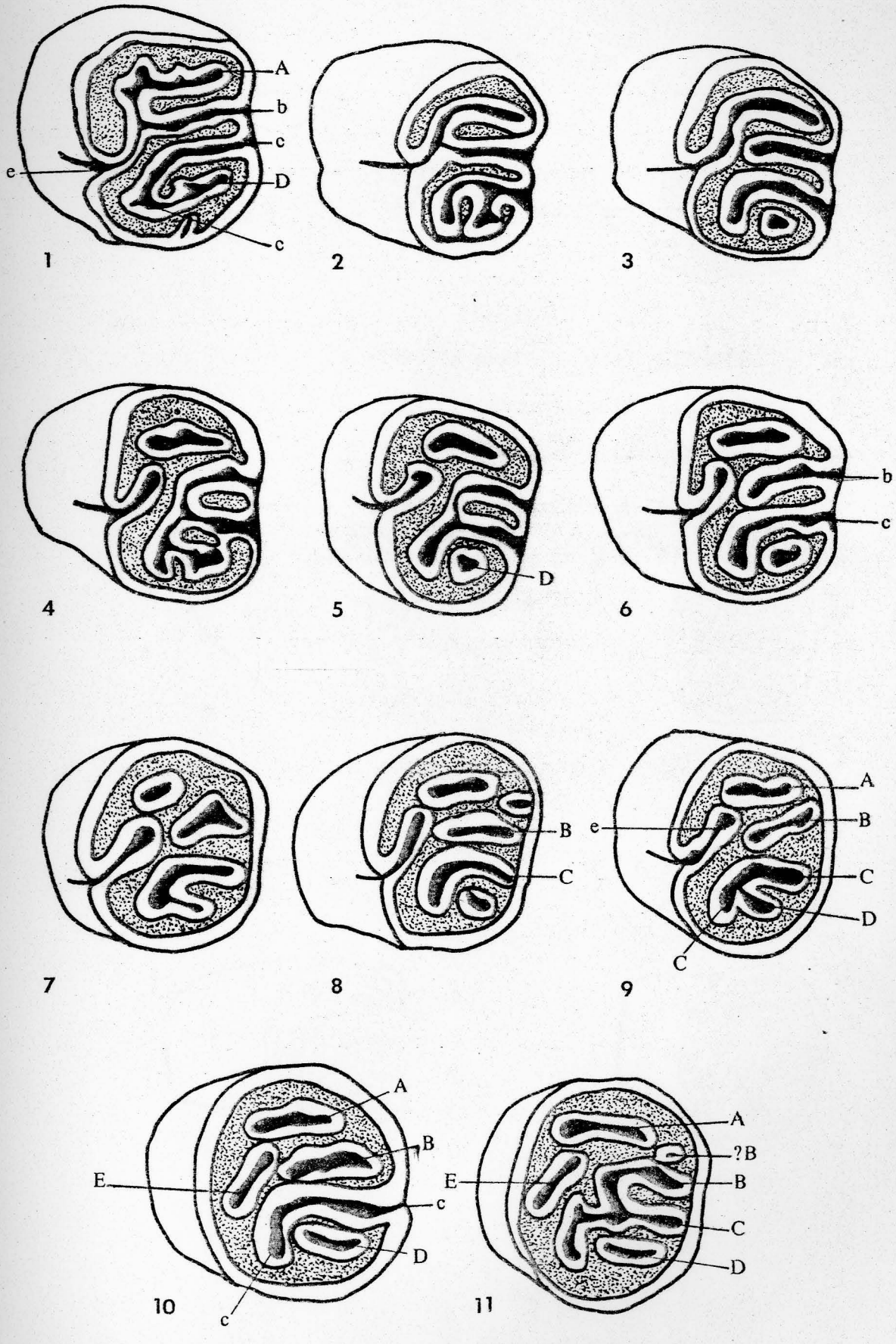


Fig 81

M^1 GROWTH STAGE 4

Fig. 82

The crown enamel patterns of a series of upper first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Approximately x 4.

1 - PPM 117 (right, drawn as left)

2 - PPM 117 (left)

3 - TM 12697 (left)

4 - TM 12697 (right, drawn as left)

5 - PPM 118 (right, drawn as left)

6 - TM 866 (right, drawn as left)

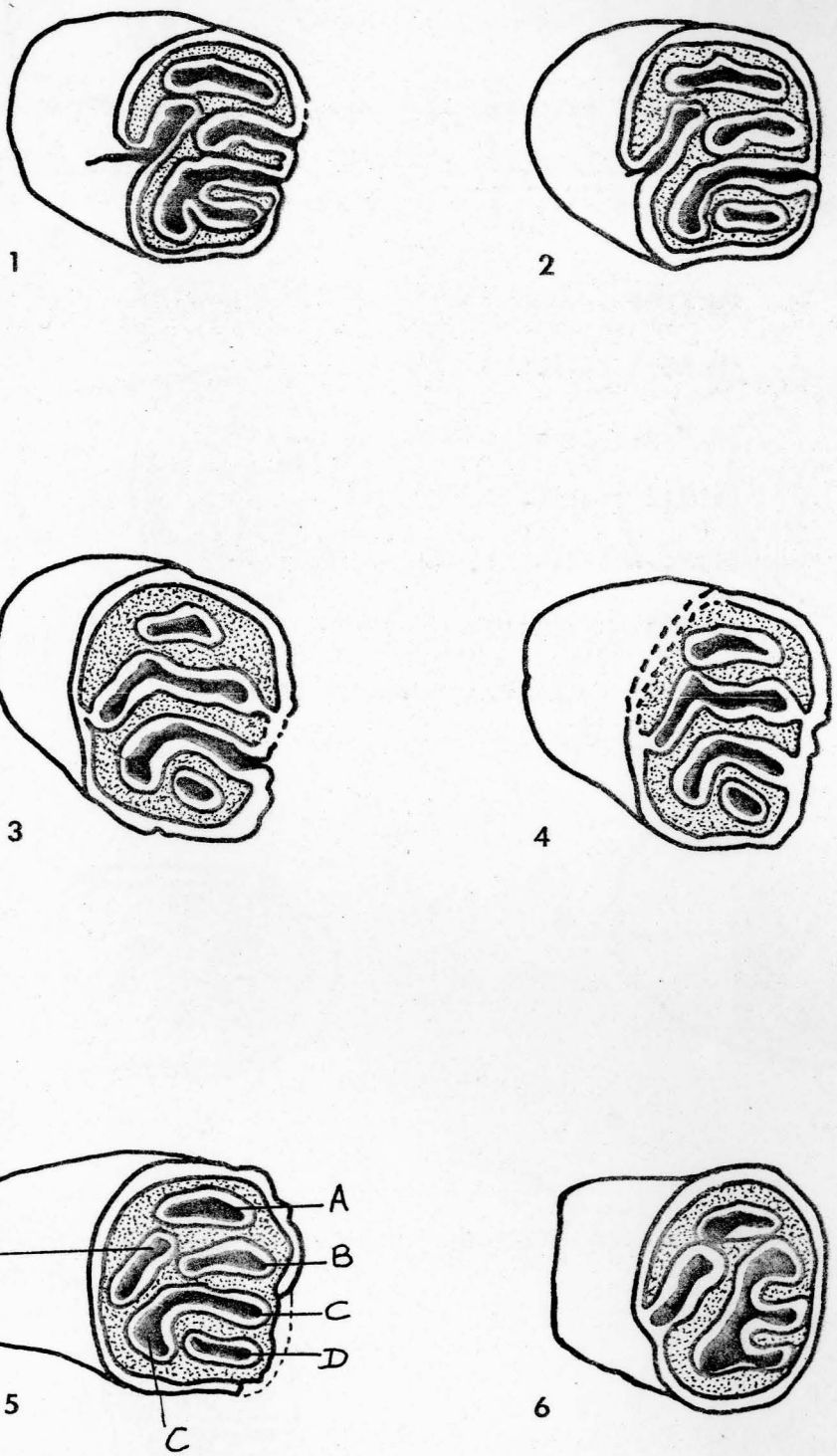


Fig 82

M^1 GROWTH STAGE 5

Fig. 83

The crown enamel patterns of a series of upper first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6. Approximately x 4.

1 - TM 8289 (left)

2 - TM 657 (left)

3 - Za 911 (right, drawn as left)

4 - Za 911 (left)

5 - BPI/C 641 (left)

6 - TM 623 (left)

7 - TM 623 (right, drawn as left)

8 - PPM 122 (left)

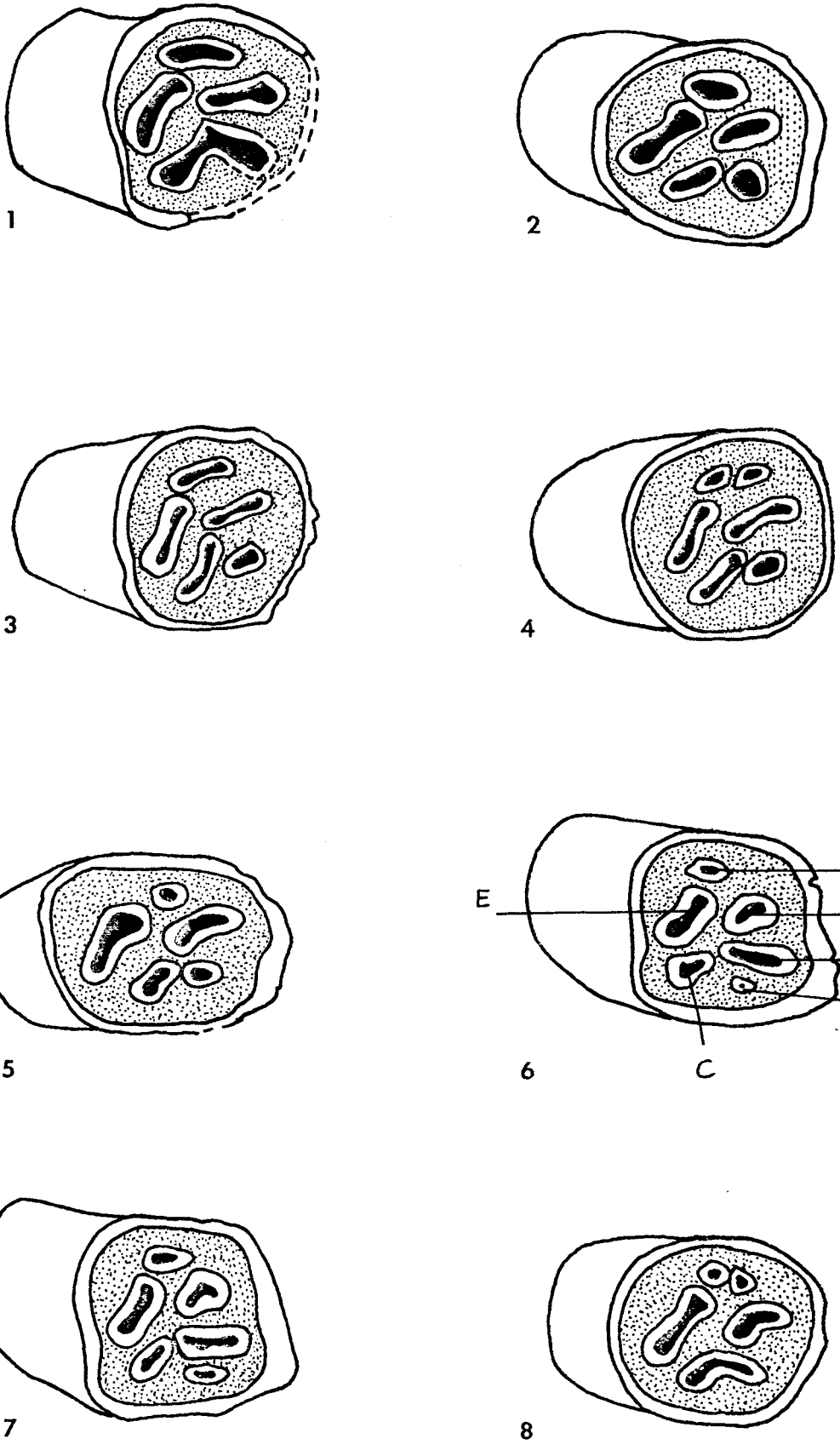


Fig 83

M^1 GROWTH STAGE 6

Fig. 84

The crown enamel patterns of a series of upper second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 3.

1 - TM 12698 (left)

2 - TM 12698 (right, drawn as left)

3 - PPM 114 (right, drawn as left)

4 - PPM 116 (left)

5 - TM 12697 (right, drawn as left)

6 - PPM 115 (right, drawn as left)

7 - PPM 115 (left)

8 - TM 12697 (left)

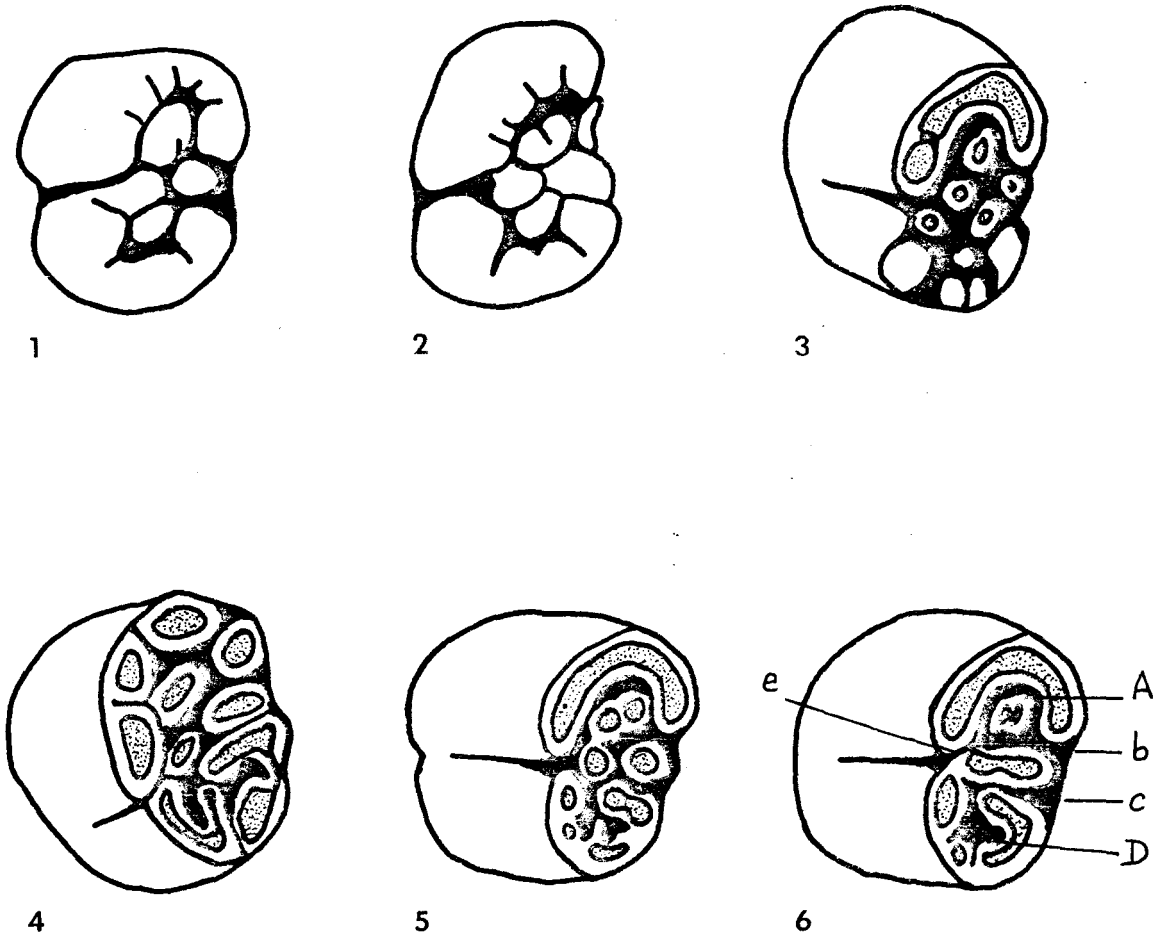


Fig 84

M^2 GROWTH STAGE 3

Fig. 85a

The crown enamel patterns of a series of upper second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Approximately x 4.

1 - PPM 116 (right, drawn as left)

2 - TM 94F (left)

3 - TM 94F (right, drawn as left)

4 - TM Mt. Zebra Park (left)

5 - PPM 124 (left)

6 - PPM 124 (right, drawn as left)

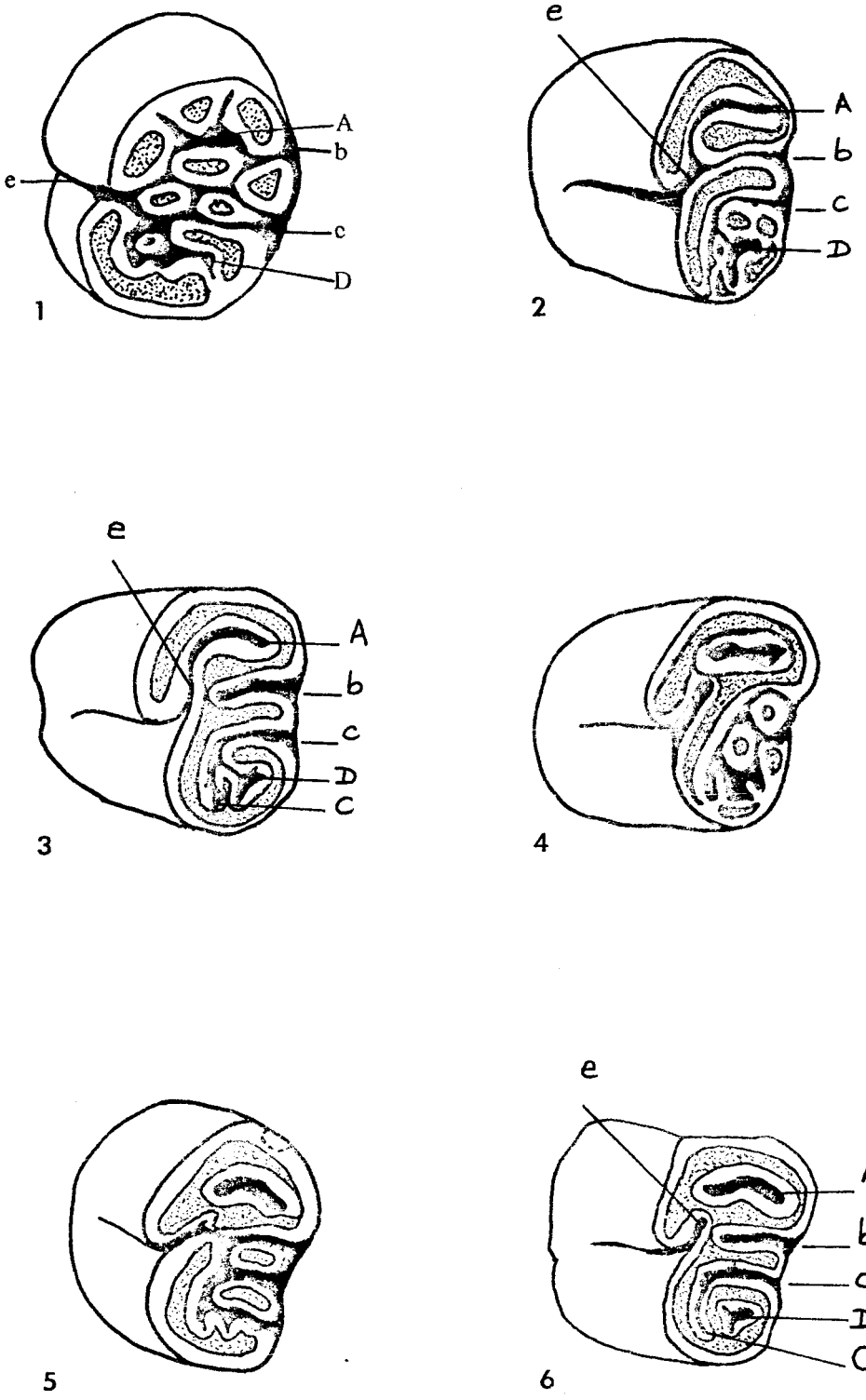


Fig 85A

M^2 GROWTH STAGE 4

Fig. 85b

The crown enamel patterns of a series of upper second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Approximately x 4.

1 - BPI/C 682 (right, drawn as left)

2 - TM 753 (left)

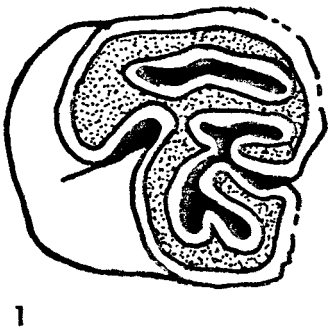
3 - TM 753 (right, drawn as left)

4 - TM 594 (right, drawn as left)

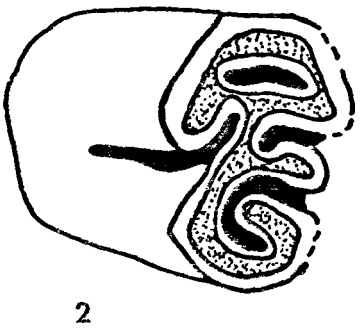
5 - TM 594 (left)

6 - TM 2A (left)

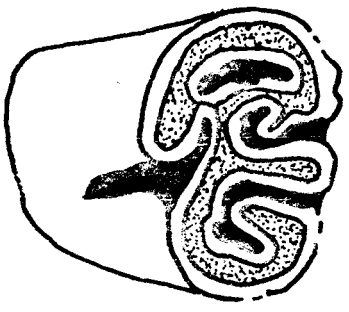
7 - TM 2A (right, drawn as left)



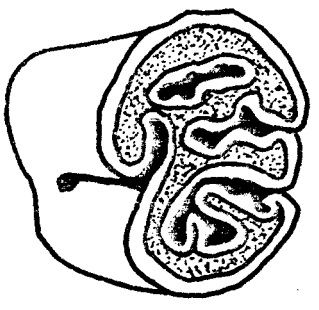
1



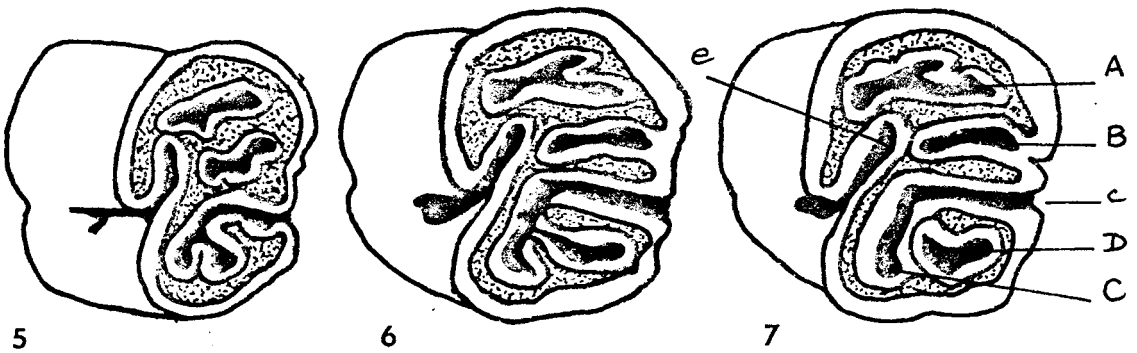
2



3



4



5 6 7

Fig 85B

M^2 GROWTH STAGE 4

Fig. 86

The crown enamel patterns of a series of upper second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Approximately x 4.

1 - PPM 117 (right, drawn as left)

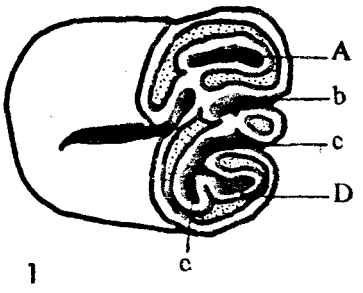
2 - TM 12697 (left)

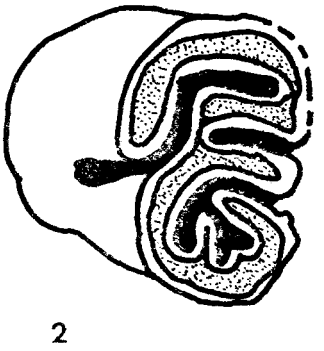
3 - PPM 117 (left)

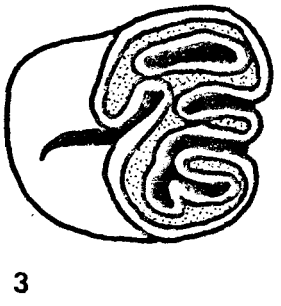
4 - PPM 118 (right, drawn as left)

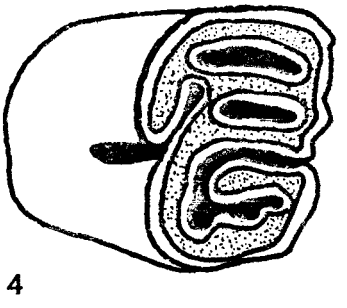
5 - PPM 118 (left)

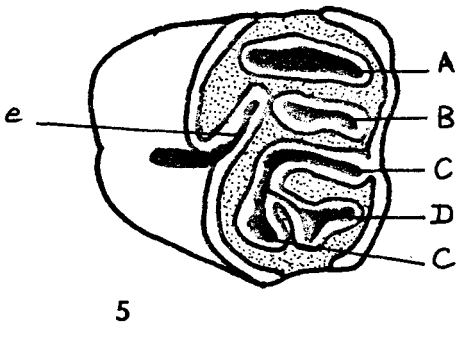
6 - TM 866 (right, drawn as left)











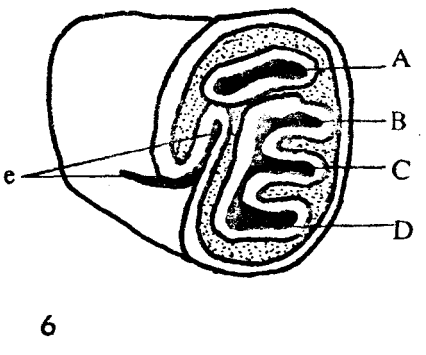


Fig 86

M^2 GROWTH STAGE 5

Fig. 87

The crown enamel patterns of a series of upper second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6.

1 - TM 8289 (right, drawn as left)

2 - TM 657 (left)

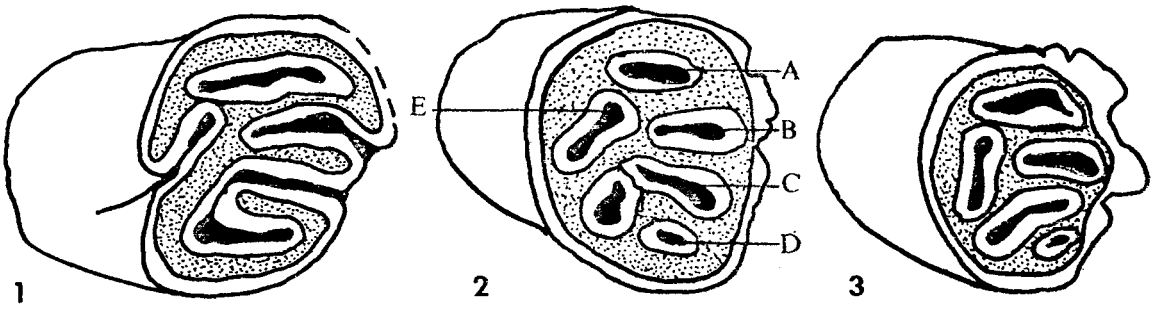
3 - Za 911 (right, drawn as left)

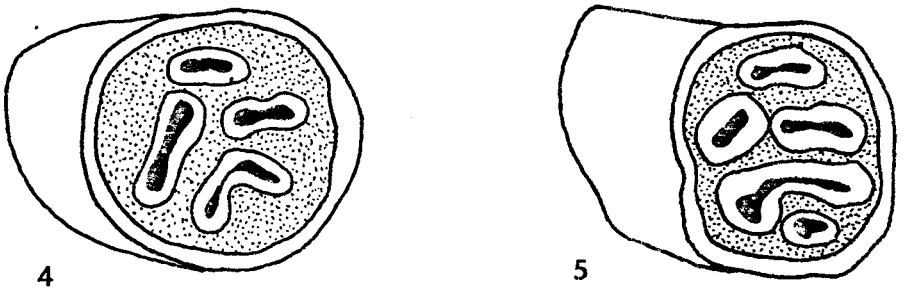
4 - BPI/C 641 (left)

5 - TM 657 (right, drawn as left)

6 - TM 122 (right, drawn as left)

7 - TM 122 (left)





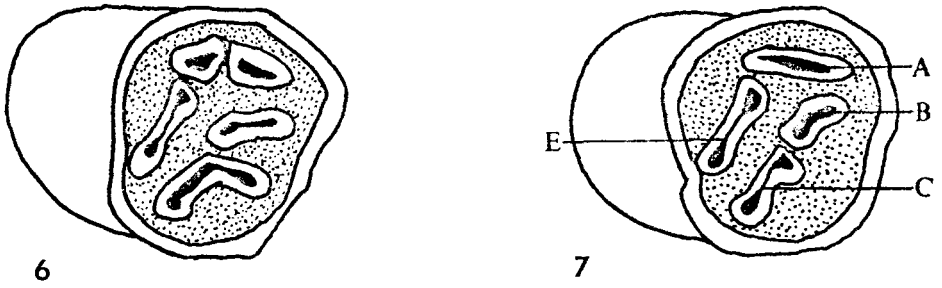


Fig 87

M^2 GROWTH STAGE 6

Fig. 88

The crown enamel patterns of a series of upper third molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Approximately x 4.

1 - TM Za (right, drawn as left)

2 - TM 94F (left)

3 - TM Mt. Zebra Park (left)

4 - PPM 124 (left)

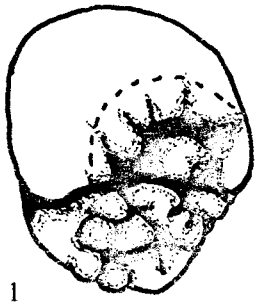
5 - TM 594 (right, drawn as left)

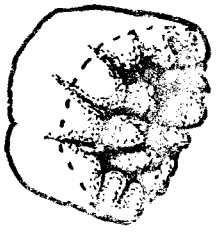
6 - TM 593 (right, drawn as left)

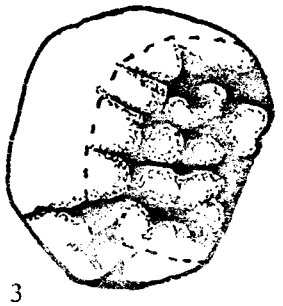
7 - TM 594 (left)

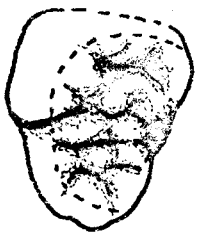
8 - BPI/C 682 (left)

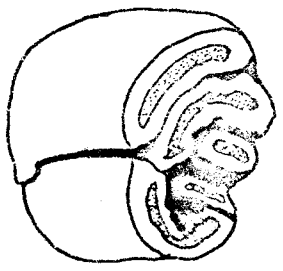
9 - BPI/C 682 (right, drawn as left)

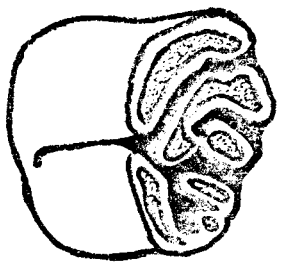

1

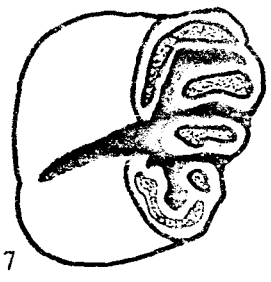

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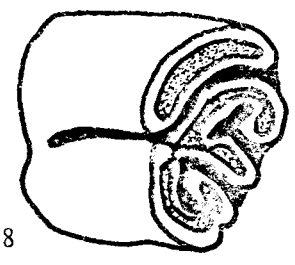

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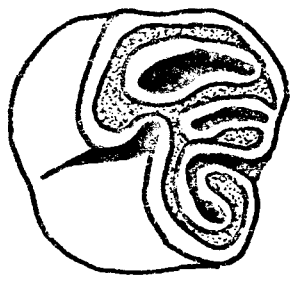

9

Fig 88

M^3 GROWTH STAGE 4

Fig. 89

The crown enamel patterns of a series of upper third molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Approximately x 4.

1 - PPM 117 (right, drawn as left)

2 - PPM 117 (left)

3 - TM 12697 (left)

4 - TM 12697 (right, drawn as left)

5 - PPM 118 (right, drawn as left)

6 - PPM 118 (left)

7 - TM 866 (left)

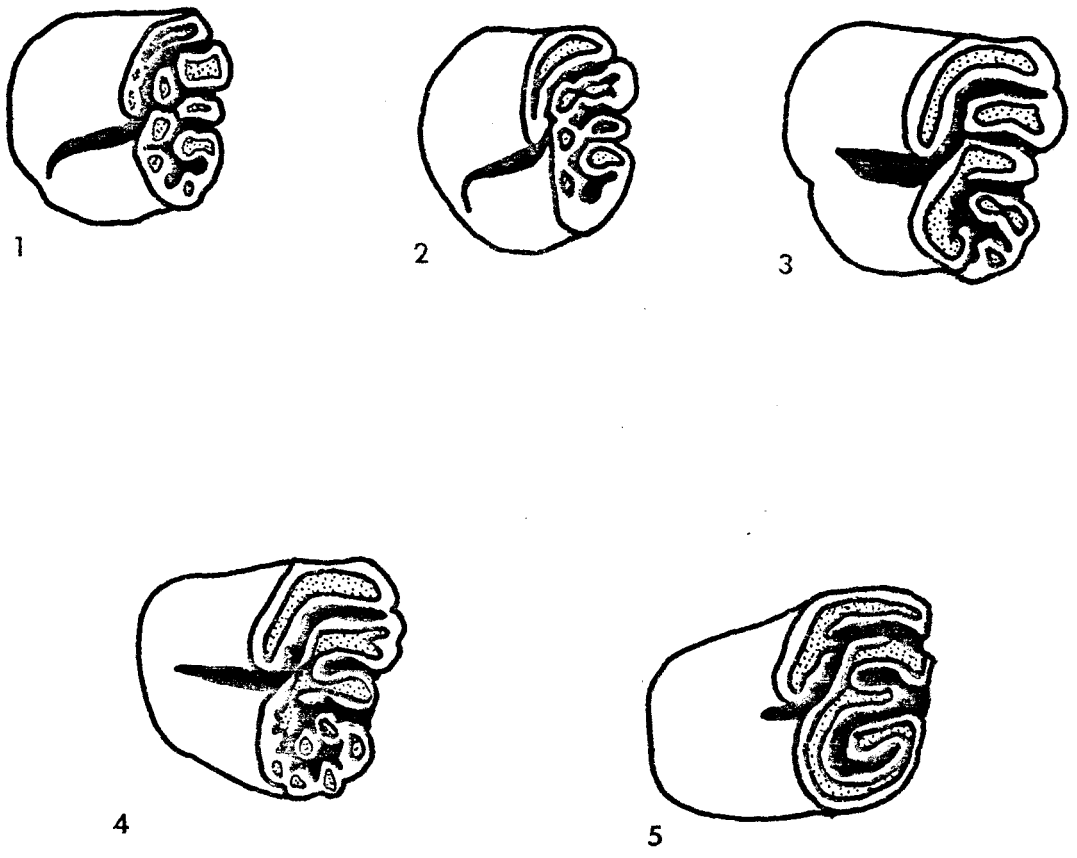


Fig 89

M^3 GROWTH STAGE 5

Fig. 90

The crown enamel patterns of a series of upper third molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6. Approximately x 4.

1 - TM 8289 (right, drawn as left)

2 - TM 623 (left)

3 - TM 623 (right, drawn as left)

4 - TM 657 (right, drawn as left)

5 - TM 657 (left)

6 - BPI/C 641 (left)

7 - Za 911 (right, drawn as left)

8 - Za 911 (left)

9 - TM 122 (right, drawn as left)

10 - TM 122 (left)

? - aberrant flexus, part of either C or D

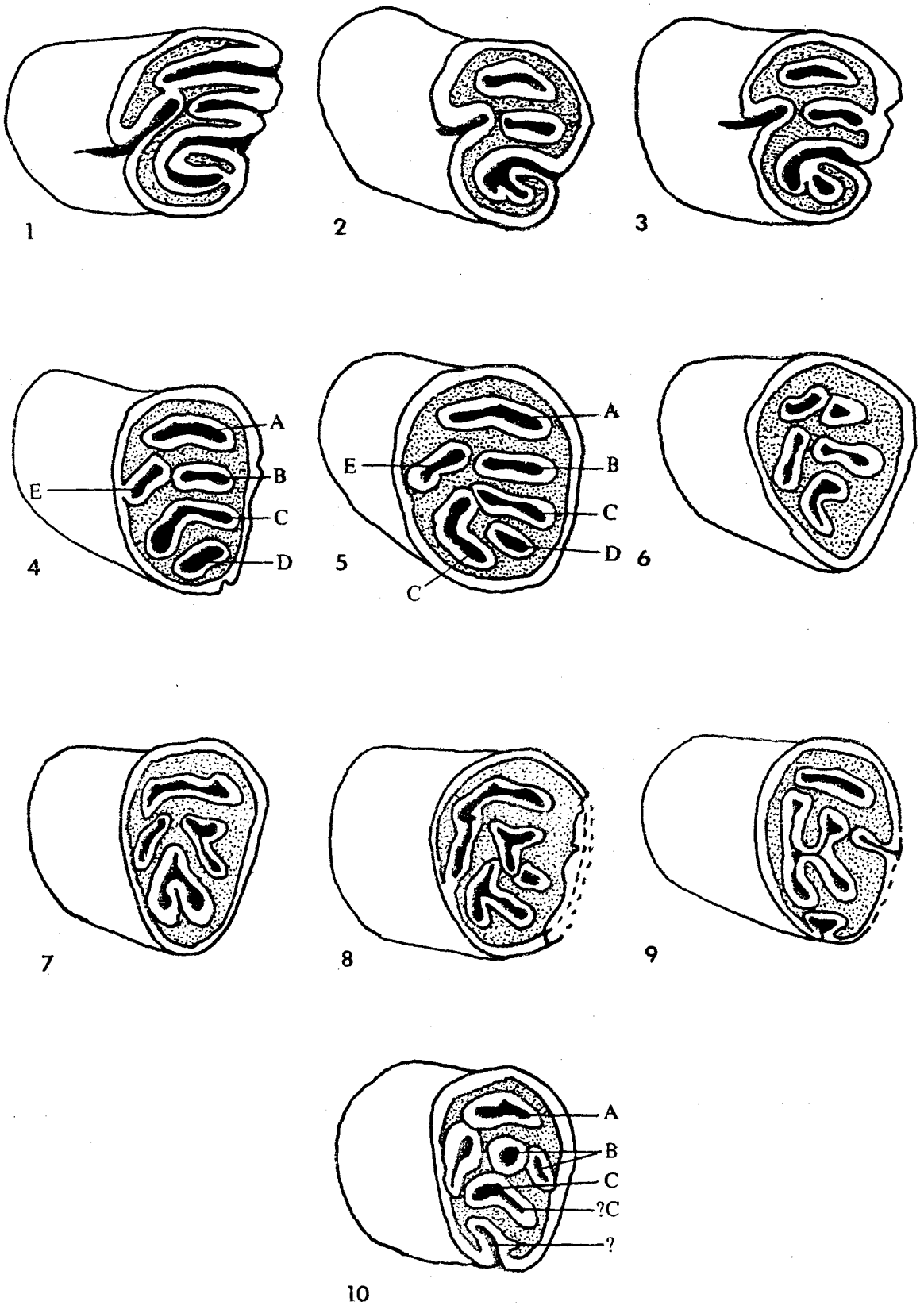


Fig 90

M^3 GROWTH STAGE 6

Fig. 91

The crown enamel patterns of a series of lower deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 2. Slightly less than x 4.

1 - TM Nyasaland (left)

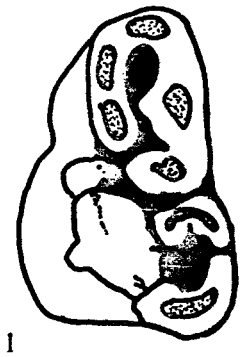
2 - PPM 113 (left)

3 - TM 5661 (right, drawn as left)

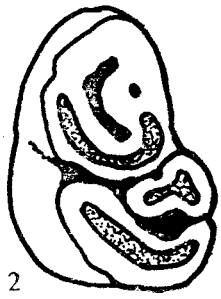
4 - TM 5661 (left)

5 - TM 5662 (left)

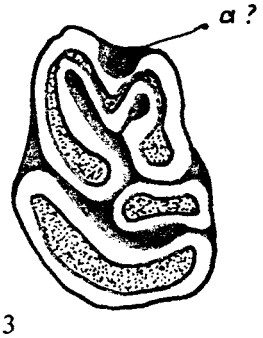
a - paraflexid
A - parafossettid or incipient parafossettid
b - mesoflexid
B - mesofossettid or incipient mesofossettid
c - metaflexid
C - metafossettid or incipient metafossettid
d - entoflexid
D - entofossettid or incipient entofossettid
e - hypoflexid
E - hypofossettid or incipient hypofossettid



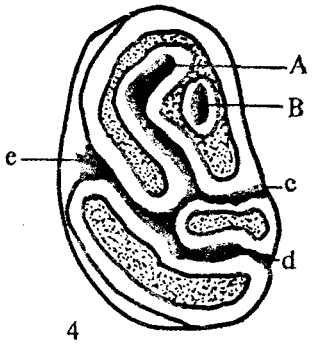
1



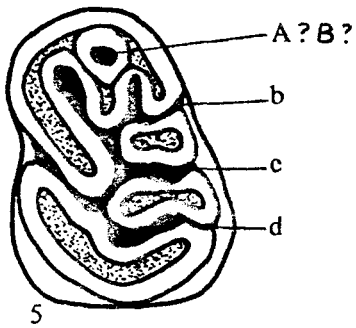
2



3



4



5

Fig 91

DP_4 GROWTH STAGE 2

Fig. 92

The crown enamel patterns of a series of lower deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 3. Slightly less than x 4.

1 - PPM 126 (right, drawn as left)

2 - TM 12698 (left)

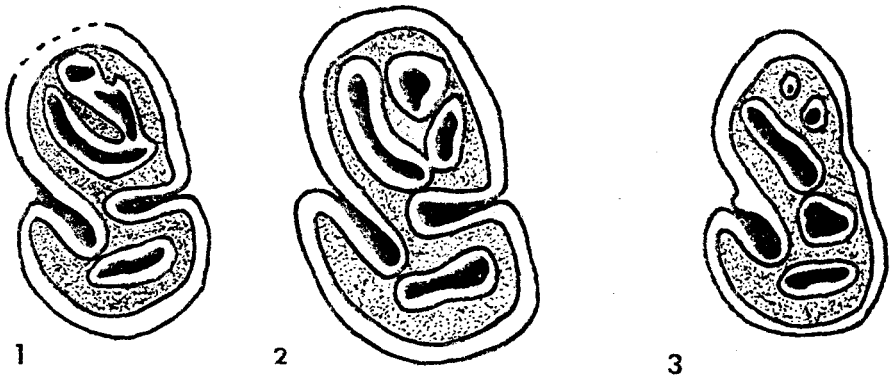
3 - TM 12697 (left)

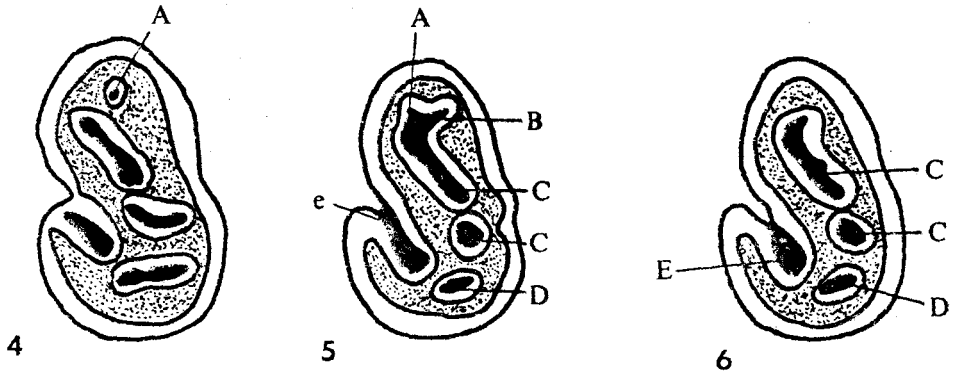
4 - TM 12687 (right, drawn as left)

5 - PPM 115 (left)

6 - PPM 115 (right, drawn as left)

7 - PPM 114 (left)





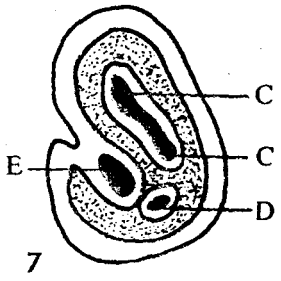


Fig 92

DP4 GROWTH STAGE 3

Fig. 93

The crown enamel patterns of a series of lower deciduous premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Slightly less than x 4.

1 - TM 94F (right, drawn as left)

2 - PPM 116R (right, drawn as left)

3 - TM Mt. Zebra Park (left)

4 - PPM 124 (right, drawn as left)

5 - TM 2A (left)

6 - PPM 124 (left)

7 - TM 753 (left)

8 - TM 2A (right, drawn as left)

9 - PPM 125 (right, drawn as left)

10 - BPI/C 682 (right, drawn as left)

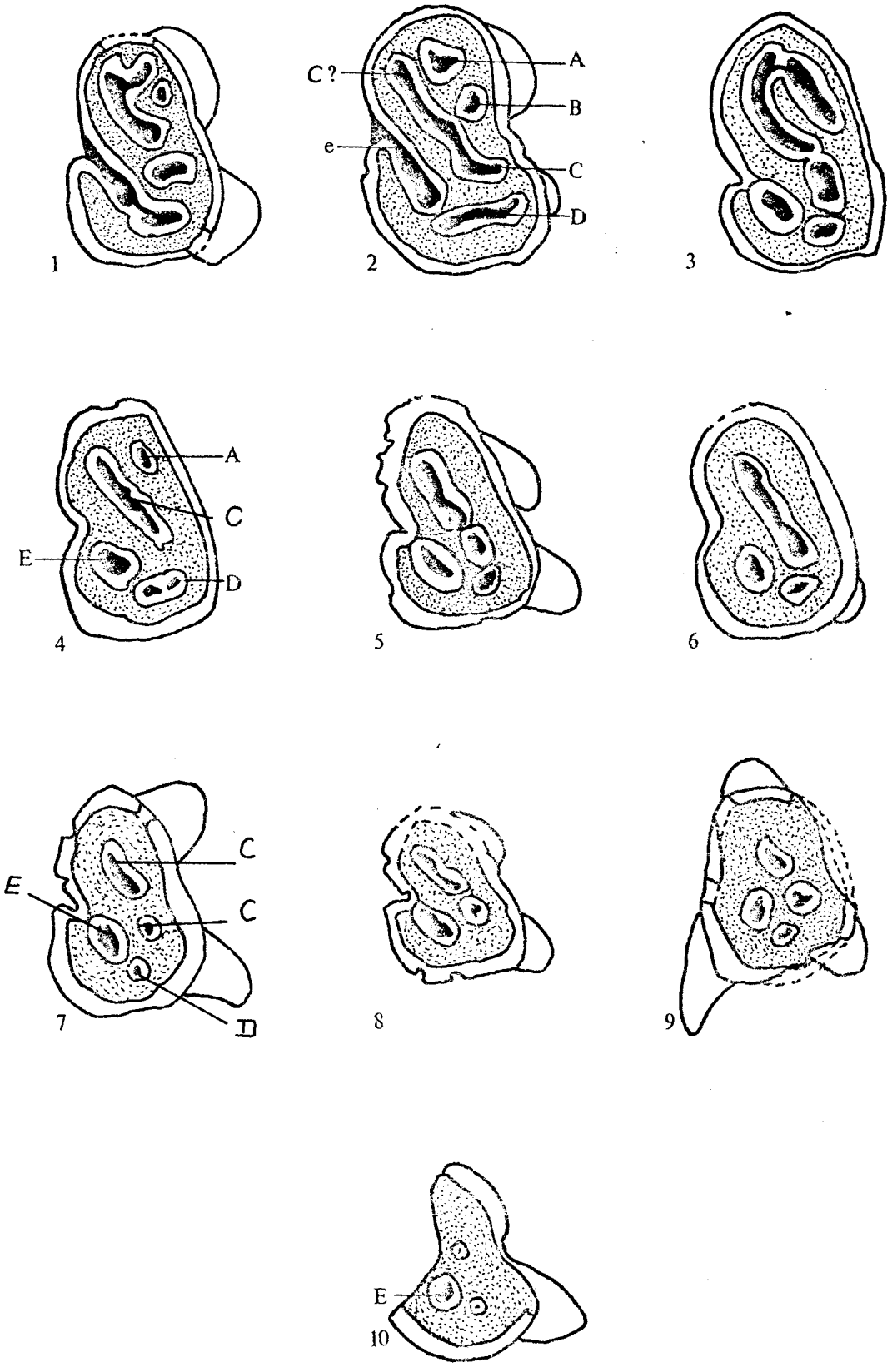


Fig 93
DP4 GROWTH STAGE 4

Fig. 94

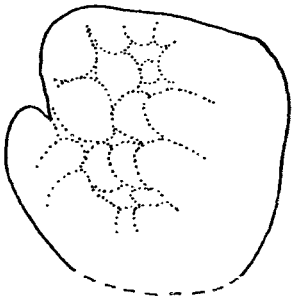
The crown enamel patterns of a series of newly-erupted lower permanent premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Slightly less than x 4.

1 - PPM 118 (left)

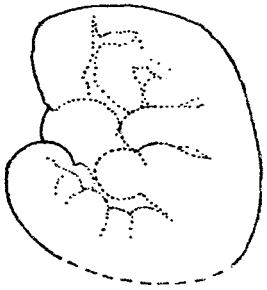
2 - PPM 117 (left)

3 - TM 12165 (left)

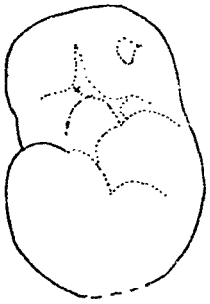
4 - TM 866 (left)



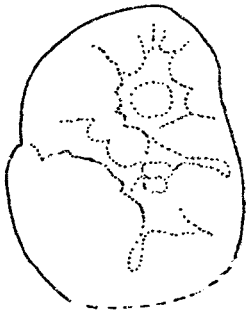
1



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3



4

Fig 94

P_4 GROWTH STAGE 5

Fig. 95

The crown enamel patterns of a series of lower permanent premolars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6. Slightly less than x 4.

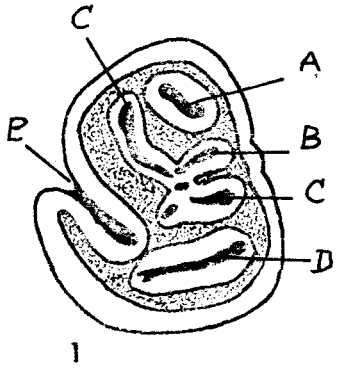
1 - PPM 119 (left)

2 - TM 657 (left)

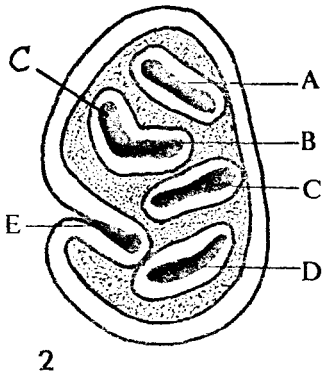
3 - PPM 122 (left)

4 - Za 911 (right, drawn as left)

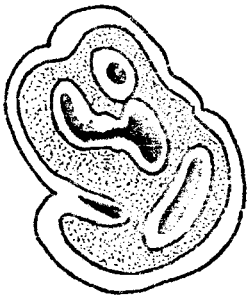
5 - TM 623 (right, drawn as left)



1



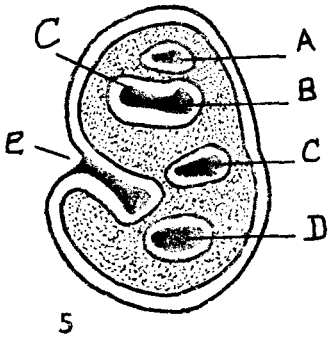
2



3



4



5

Fig 95

P_4 GROWTH STAGE 6

Fig. 96

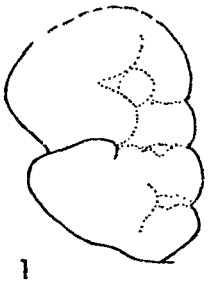
The crown enamel patterns of a series of lower first molars of Hystrix Africaeaustralis Peters 1852 at Growth Stage 2. Slightly less than x 4.

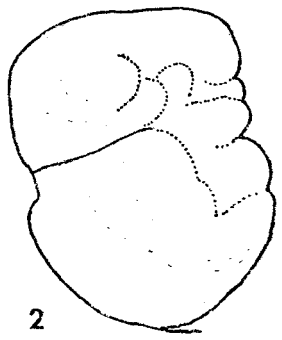
1 - PPM 113 (left)

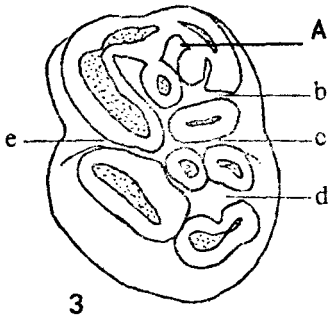
2 - TM Nyasaland (left)

3 - TM 5662 (left)

4 - TM 5661 (left)







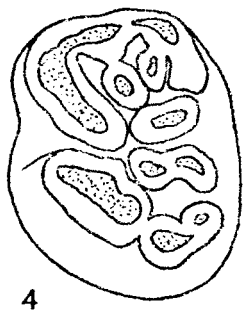


Fig 96

M_1 GROWTH STAGE 2

Fig. 97

The crown enamel patterns of a series of lower first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 3. Slightly less than x 4.

1 - TM 12698 (left)

2 - PPM 126 (left)

3 - PPM 115 (right, drawn as left)

4 - TM 12697 (left)

5 - PPM 114 (left)

6 - PPM 114 (right, drawn as left)

7 - TM 12697 (right, drawn as left)

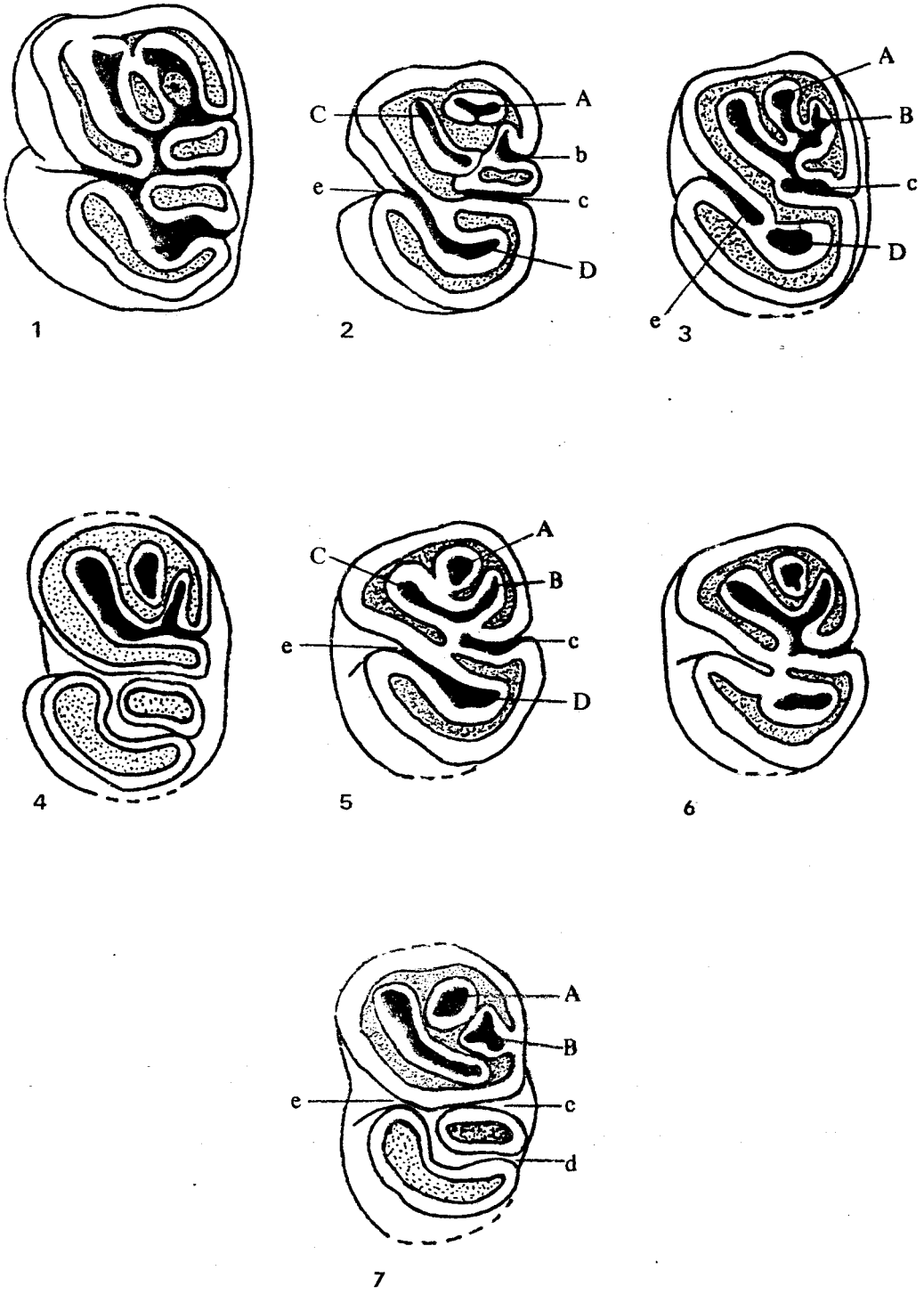


Fig 97

M_1 GROWTH STAGE 3

Fig. 98a

The crown enamel patterns of a series of lower first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Slightly less than x 4.

1 - PPM 116 (right, drawn as left)

2 - PPM 116 (left)

3 - TM Mt. Zebra Park (right, drawn as left)

4 - PPM 124 (left)

5 - TM Mt. Zebra Park (left)

6 - TM 94F (right, drawn as left)

7 - BPL/C 682 (right)

8 - TM 2a (right, drawn as left)

9 - TM 2a (left)

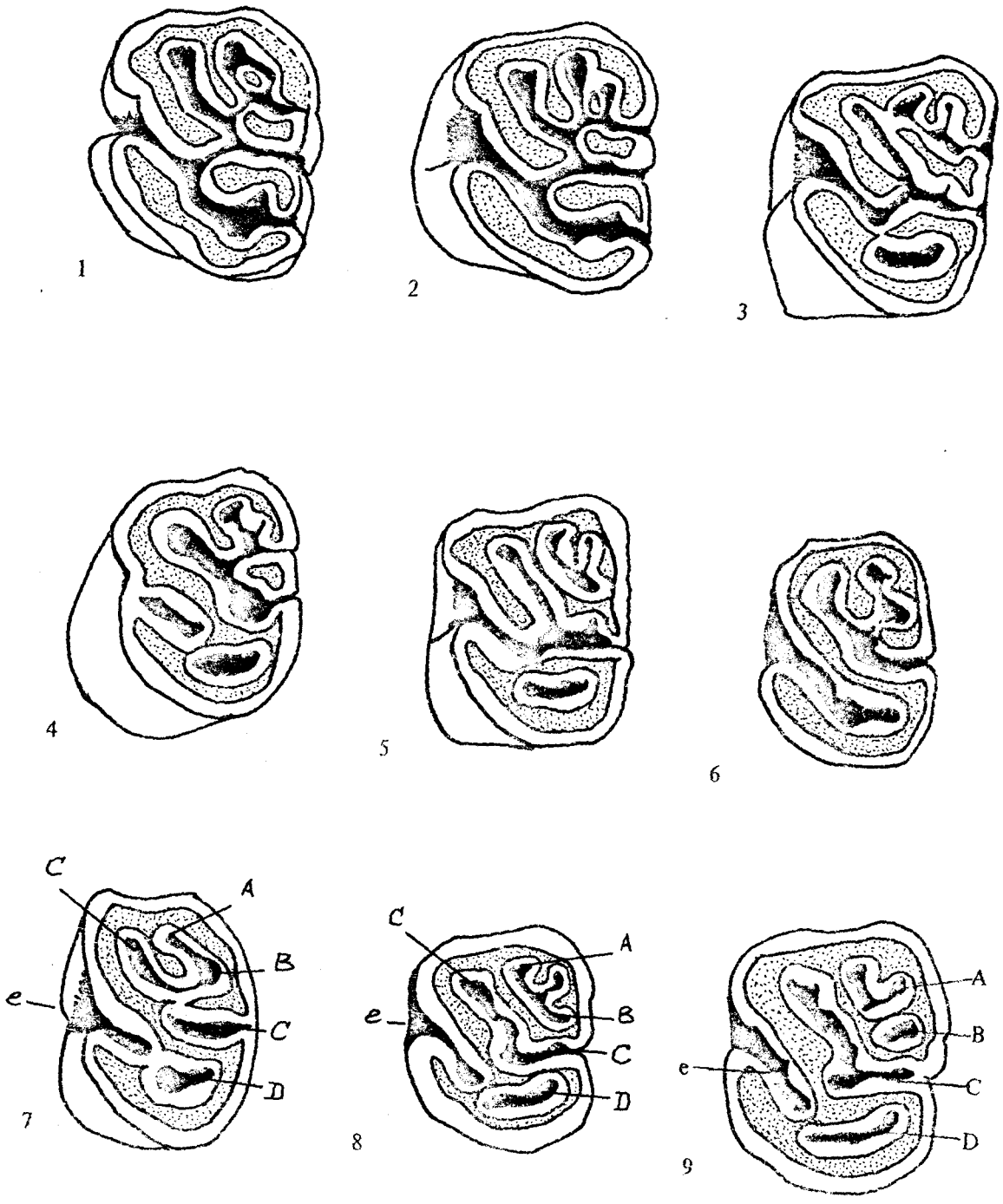


Fig 98A

M_1 GROWTH STAGE 4

Fig. 98b

The crown enamel patterns of a series of lower first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Slightly less than x 4.

1 - TM 789 (left)

2 - TM 594 (right, drawn as left)

3 - TM 753 (left)

4 - TM 594 (left)

5 - PPM 125 (right, drawn as left)

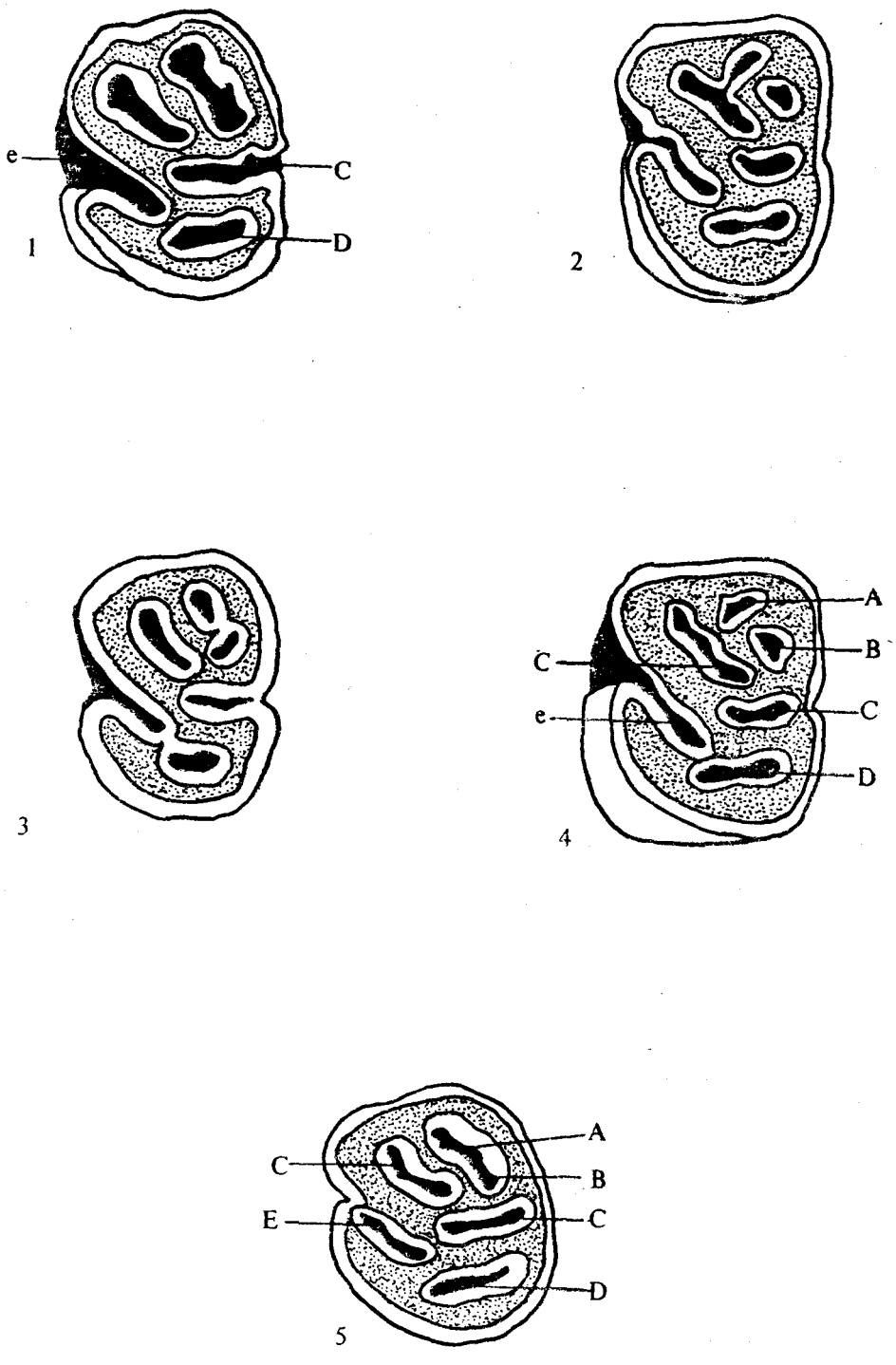


Fig 98B

M_1 GROWTH STAGE 4

Fig. 99

The crown enamel patterns of a series of lower first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Slightly less than x 4.

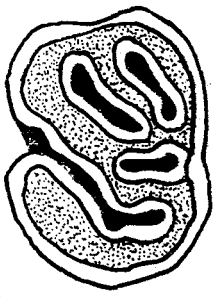
1 - TM 12165 (right, drawn as left)

2 - PPM 117 (left)

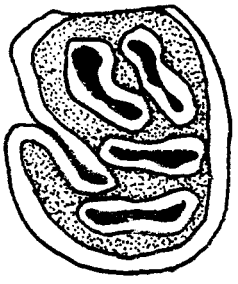
3 - PPM 118 (left)

4 - TM 866 (right, drawn as left)

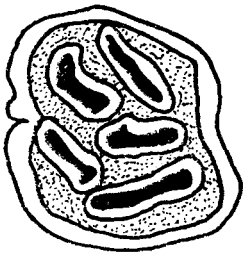
5 - TM 866 (left)



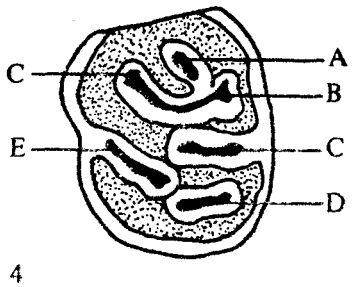
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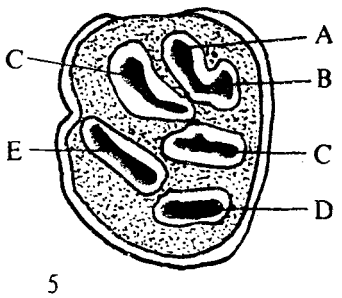
2



3



4



5

Fig 99

M_1 GROWTH STAGE 5

Fig. 100

The crown enamel patterns of a series of lower first molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6.

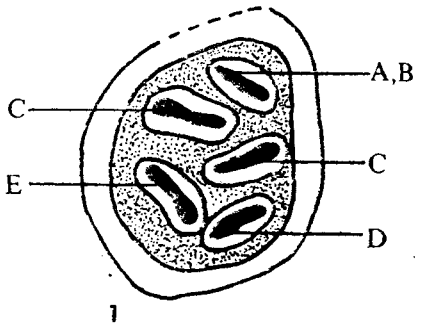
1 - TM 657 (left)

2 - TM 623 (right, drawn as left)

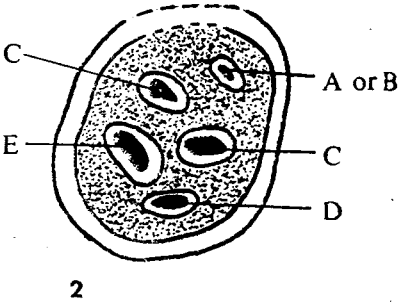
3 - PPM 119 (left)

4 - Za 911 (right, drawn as left)

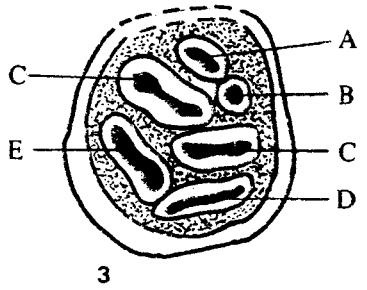
5 - PPM 122 (left)



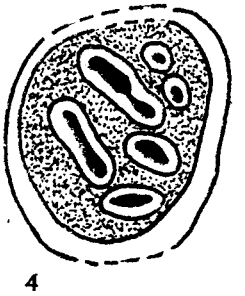
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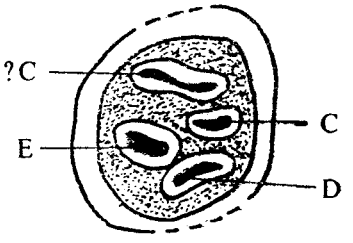
2



3



4



5

Fig 100

M_1 GROWTH STAGE 6

Fig. 101

The crown enamel patterns of a series of lower second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 3. Slightly less than x 4.

1 - TM 12698 (left)

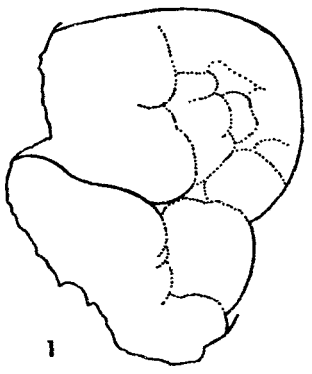
2 - PPM 126 (left)

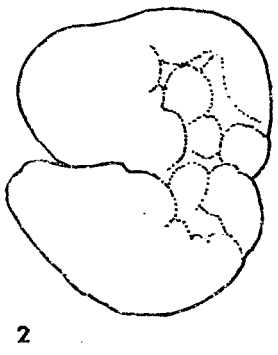
3 - PPM 114 (left)

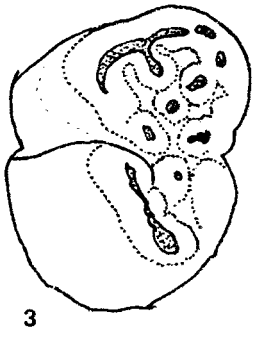
4 - TM 12697 (right, drawn as left)

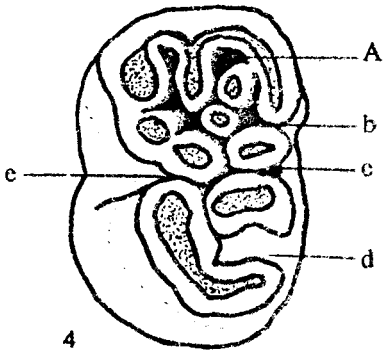
5 - TM 12697 (left)

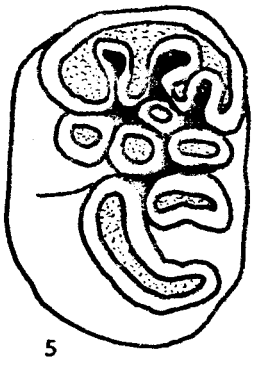
6 - PPM 115 (left)











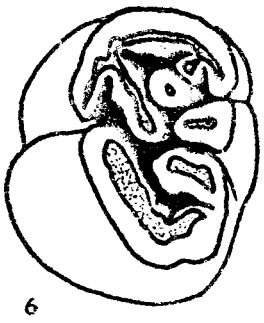


Fig 101

M_2 GROWTH STAGE 3

Fig. 102

The crown enamel patterns of a series of lower second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Slightly less than x 4.

1 - PPM 116 (left)

2 - PPM 124 (left)

3 - TM Mt. Zebra Park (left)

4 - PPM 125 (right, drawn as left)

5 - TM Mt. Zebra Park (right, drawn as left)

6 - TM 2a (right, drawn as left)

7 - TM 2a (left)

8 - TM 789 (left)

9 - TM 95F (left)

10 - TM 94F (right, drawn as left)

11 - TM 753 (left)

12 - BPI/C 682 (right, drawn as left)

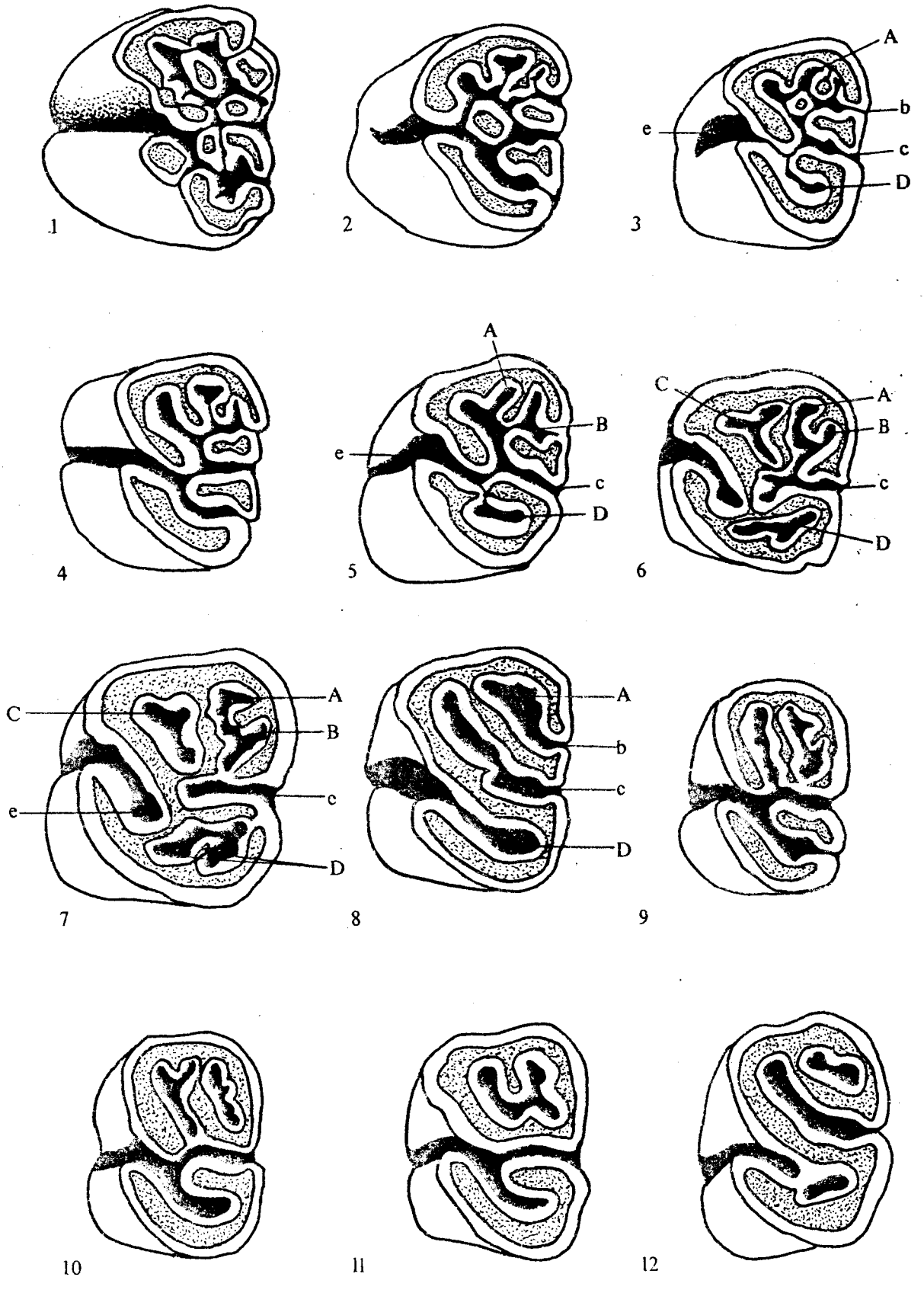


Fig 102

M_2 GROWTH STAGE 4

Fig. 103

The crown enamel patterns of a series of lower second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Slightly less than x 4.

1 - TM 12165 (left)

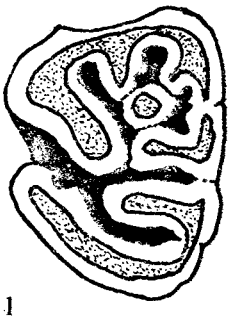
2 - TM 12165 (right, drawn as left)

3 - PPM 117 (left)

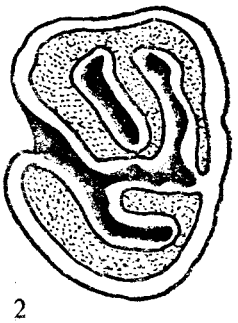
4 - TM 866 (right, drawn as left)

5 - TM 866 (left)

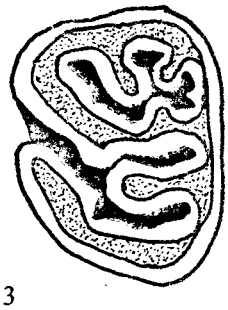
6 - PPM 118 (right, drawn as left)



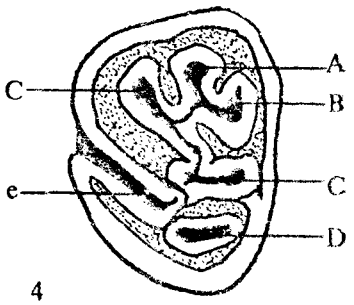
1



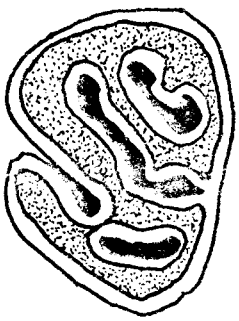
2



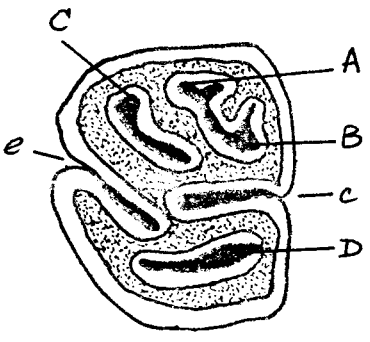
3



4



5



6

Fig 103

M_2 GROWTH STAGE 5

Fig. 104

The crown enamel patterns of a series of lower second molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6.

1 - TM 623 (right, drawn as left)

2 - TM 657 (right, drawn as left)

3 - PPM 119 (left)

4 - TM 657 (left)

5 - Za 911 (right, drawn as left)

6 - PPM 122 (left)

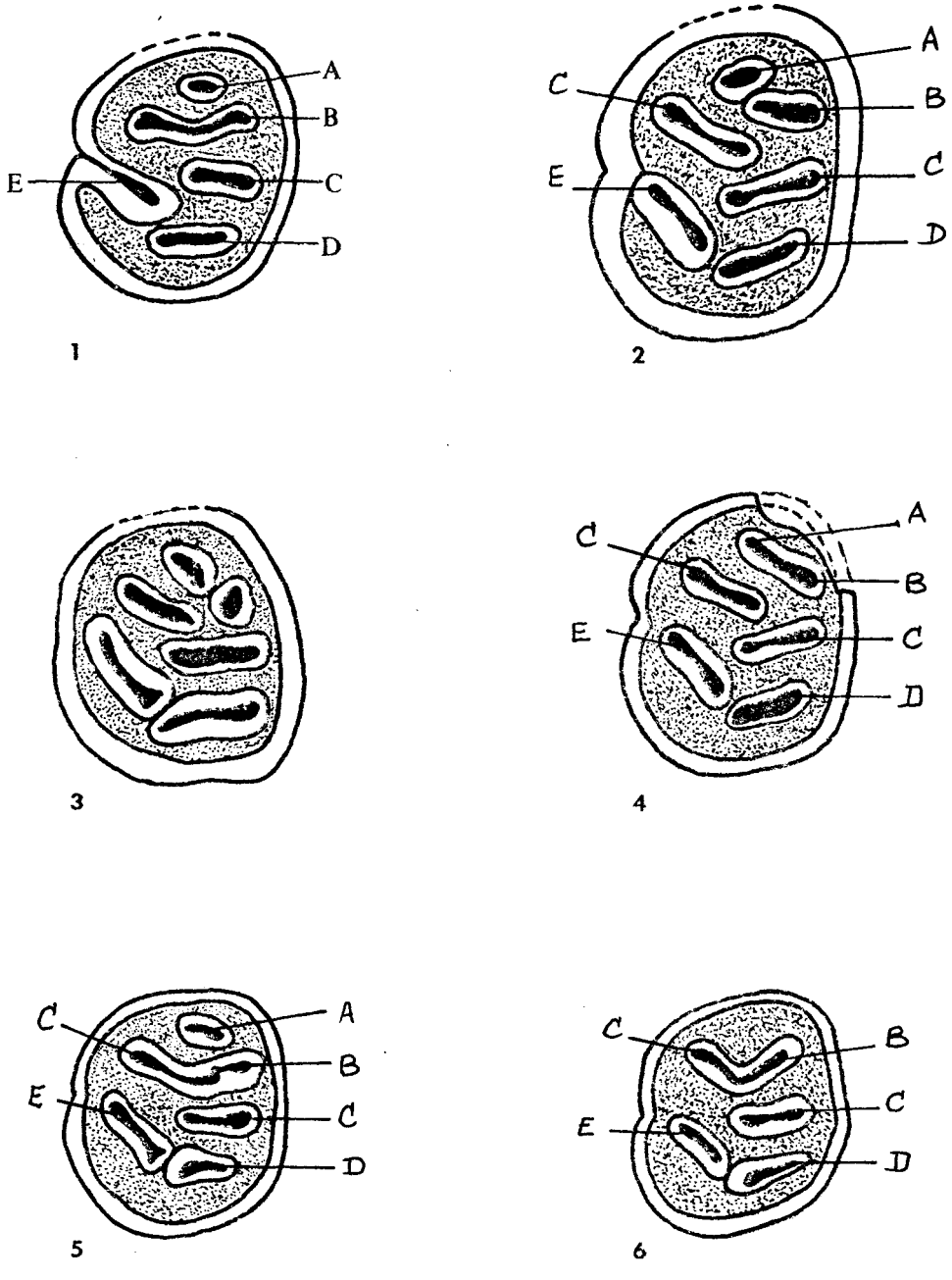


Fig 104

M_2 GROWTH STAGE 6

Fig. 105

The crown enamel patterns of a series of lower third molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 4. Slightly less than x 4.

1 - PPM 116 (right, drawn as left)

2 - TM Mt. Zebra Park (left)

3 - PPM 125 (right, drawn as left)

4 - TM Mt Zebra Park (right, drawn as left)

5 - TM 94F (right)

6 - TM 753 (left)

7 - TM 594 (left)

8 - BPI/C 682 (right, drawn as left)

9 - BPI/C 682 (left)

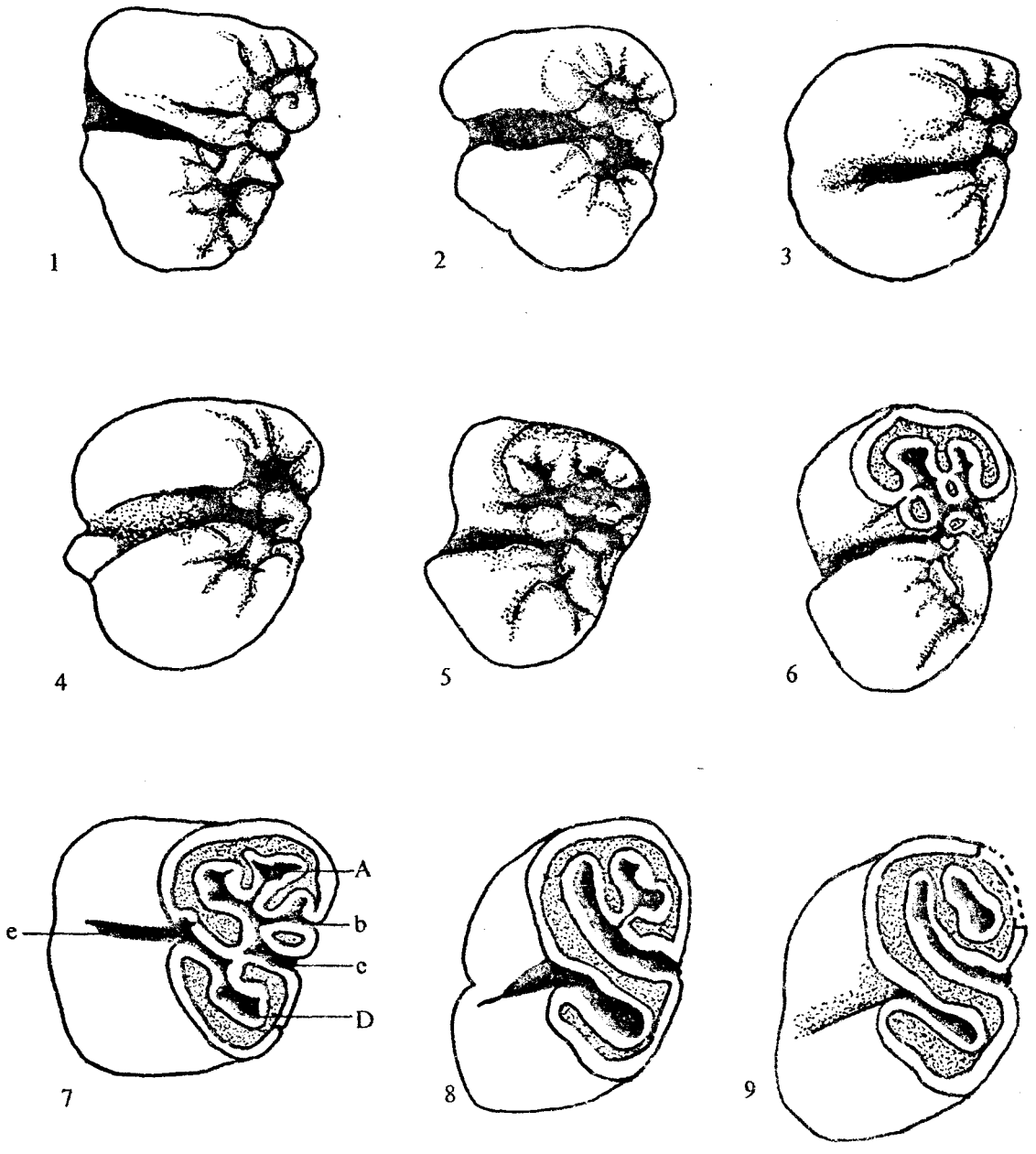


Fig 105

M_3 GROWTH STAGE 4

Fig. 106

The crown enamel patterns of a series of lower third molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 5. Slightly less than x 4.

1 - PPM 117 (left)

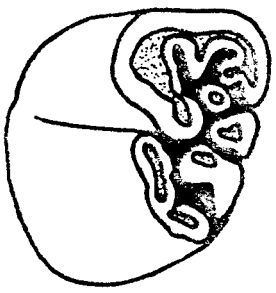
2 - TM 12165 (right, drawn as left)

3 - TM 866 (right, drawn as left)

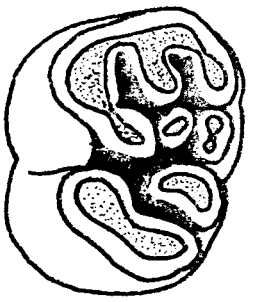
4 - PPM 118 (left)

5 - TM 866 (left)

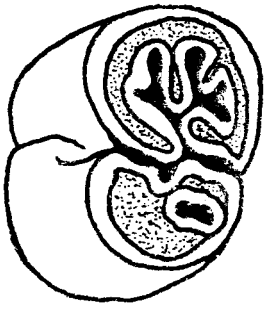
6 - PPM 118 (right, drawn as left)



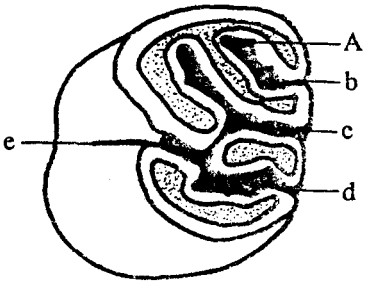
1



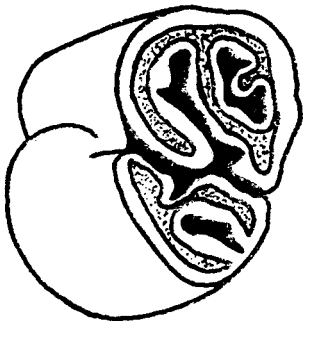
2



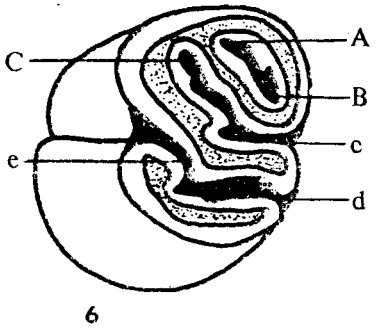
3



4



5



6

Fig 106

M_3 GROWTH STAGE 5

Fig. 107

The crown enamel patterns of a series of lower third molars of Hystrix africaeaustralis Peters 1852 at Growth Stage 6. Slightly less than x 4.

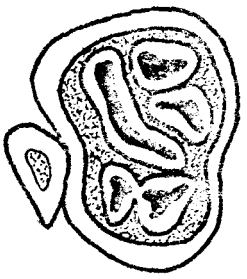
1 - PPM 119 (left)

2 - Za 911 (right, drawn as left)

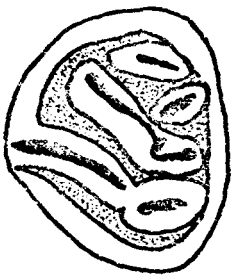
3 - TM 623 (right, drawn as left)

4 - TM 657 (left)

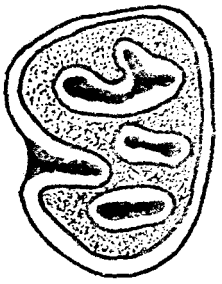
5 - PPM 122 (left)



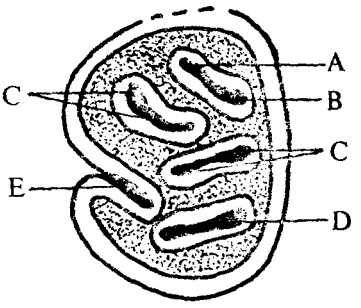
1



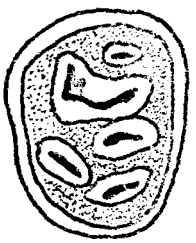
2



3



4



5

Fig 107

M_3 GROWTH STAGE 6

7.2 Parameter definition and method of measurement

This section defines the parameters that have been investigated as part of this thesis (indicated by double asterisks in Chapter 6) and describes the method of measurement, where considered necessary.

Definitions of parameters used were considered essential because the general absence of these in the literature has resulted in a marked lack of consistency in the measurements presented by different authors. For example the vaguely-defined parameter 'greatest width of skull above' may occur between different points on the skull in the three species of the subgenus Hystrix. Furthermore, in any one of the species, the distance may have been measured between entirely different reference points by more than one author. This feature has led to uncertainty as to whether or not certain parameters used and defined in this thesis are the same as those intended and measured, but not defined, by the various authors.

The two points defining the limits of a parameter have been referred to as 'reference points' (abbreviated r.p.); these and the parameters themselves are shown in Figs. 45 - 56. The visual estimation of such characters as 'shape of coronoid process' is obviously subjective and cannot be readily defined, but at least the conclusions reached have been based on the observations of a single observer on an adequate sample.

Measurements are consistently given in millimetres correct to one decimal place, each representing the average of three separate readings. Indices, ratios and percentages are given correct to two decimal places. All cranial measurements were taken from the right side of the skull, except in those cases where the parts normally measured were missing.

Ideally, all measurements should be taken with a single instrument but this was not possible on account of the irregular shape of the skull and teeth of porcupines. Most measurements were taken with a straight-armed 16cm Ahrem's Goodline sliding caliper with one set of measuring points specially sharpened to enable them to be inserted between the teeth and to facilitate the accurate measurement of other awkwardly situated reference points. However, certain reference points could not be reached even with the sharpened points of this instrument; for example, the bucco-lingual diameter (breadth) of the alveolar rim at the base of the curved barrel-shaped *in situ* maxillary teeth, when a Moore and Wright bow-shaped external caliper which could circumvent both the curvature and the bulge of the teeth was used. Unfortunately, this type of instrument does not

have a built-in gauge, so that the measurement had to be read off against a millimetre scale. Such measurements, although given to one decimal place, are strictly speaking correct only to the nearest millimetre. Parameters not measurable by either the Goodline or the external caliper were measured with a large (600mm) purpose-built bow-type sliding caliper with a built-in scale, or with a specially constructed linear scale.

Parameters not accessible to any of the above instruments were measured with a pair of long-pointed Kern dividers, and the measurement read off against a mm scale. As in the case of external calipers, these measurements are correct only to the nearest mm. The accuracy of the purpose-built instruments was checked against the precision Goodline caliper and found to be satisfactory.

7.2.1 General cranial parameters

7.2.1.1 Greatest length of skull above (Fig.46A)(T.I App.V)

The anterior r.p. is the lower anterior margin of the nasal orifice at the midline. In order to avoid confusion, the posterior r.p. has been taken as the posteriormost point attained by the transverse occipital crest on the dorsal midline, a point referred to by Corbet and Jones (op. cit.) as 'top of median occipital crest'.

In some specimens, parts of the crest running from the centre of the upper margin of the foramen magnum to the posterior r.p. defined above (termed by Corbet and Jones 1964, 'median occipital crest') may extend even posterior to this point; such points, however, are more correctly 'occipital'.

The Goodline caliper was used.

7.2.1.2 Occipitonasal skull length (Fig. 46B)(T.I App.V)

The anterior r.p. is the anteriormost tip of the right nasal while the posterior r.p. is the posteriormost point attained by the transverse occipital crest at the midline, alternatively the latter point being defined as the top of the median occipital crest. Note that the anterior r.p. does not fall on the midline so that the line measured is slightly oblique with respect to the midline.

The Goodline caliper was used.

7.2.1.3 Greatest length of skull below; condylo-incisive length (Fig. 48R) (T.I App.V)

In specimens without incisors, the greatest length of the skull below may be defined as the distance between the anteriormost point reached by the

right premaxilla on the ventral midline (anterior r.p.) and the posteriormost point on the right occipital condyle (posterior r.p.), a line which like the last-mentioned parameter is slightly oblique with respect to the midline. In specimens with in situ incisor teeth, the condylo-incisive length as defined above is difficult to measure, because in the ventral view the anterior r.p. is hidden by the incisors. In such specimens an approximate measurement of the parameter may be obtained either by measuring from the anteriormost point of the premaxilla accessible on the lingual side of the incisor, or by using a point on the labial surface of the incisors where the premaxilla disappears between these teeth. The former is difficult to measure because the lingually curving incisors obstruct most measuring instruments. From the published measurements of 'condylo-incisive length' it is not possible to say which alternative has been used for specimens with in situ teeth.

Although it was easier to use the Goodline caliper for specimens in which one or both incisors were missing, the Kern dividers were found to be the only instrument capable of reaching the anterior r.p. in specimens with in situ incisors, as its long points could be inserted between the two teeth. For consistency, the latter instrument was used throughout, each measurement being read off against a millimetre scale.

7.2.1.4 Basilar length (Fig. 48S) (T.I App.V)

The basilar length was measured from the anteriormost point reached by the right premaxilla on the ventral midline to the lower rim of the foramen magnum on the midline.

For the same reason as cited in 7.2.1.3, this parameter was measured with the Kern dividers.

7.2.1.5 Greatest width of skull above; greatest width of skull below (Fig. 46C) (T.II App. V)

Neither of these characters has been adequately defined in print. Theoretically, the skull has only one widest point, differences in the apparent widest point when viewed from above or from below, probably being due to parallax.

In adult specimens, the greatest width of the skull when viewed dorsally appears to be from the upper lateral termination of the jugomaxillary suture at the margin of the orbit on one side of the skull to the corresponding area on the other, although seeming to vary slightly

about this point within the sample. However, because breaks in the slender zygomatic arch more frequently occur along the jugo-maxillary suture, it is more practical to use the definition as given, rather than using a less easily defined reference point some distance posterior to the suture, which may frequently be damaged or missing.

In juvenile specimens, however, up to the stage of eruption (but not wear) of M2, the greatest width of the skull when viewed from above appears to be across the posterior part of the zygomatic arch at a point where the posterior tip of the jugal meets the squamosal, a region frequently missing in specimens because of its fragility. In some specimens, both juvenile and adult, this also appears to be the widest part of the skull when viewed from below, but in the majority of cases the greatest width below appears to be the same as the greatest width above.

The most reasonable solution was to regard the greatest width of skull above and below as the same parameter, with the first definition given as the correct one.

As with the assessment of human cranial material it is clear that the orientation of the skull (plane of view) will affect the apparent points of greatest and least width. In obtaining the measurement of 'greatest width above' the specimen was first placed palatal surface down, and vertical readings then taken on either side of the skull from points lying directly opposite the naso-frontal suture on the midline. In measuring the 'greatest width below', essentially the same procedure was adopted, the specimen being placed dorsal surface down and vertical readings taken from points directly opposite the palatal notch. This parameter is sometimes referred to as the 'zygomatic breadth' in this text. The Goodline caliper was used.

7.2.1.6 Smallest skull breadth behind zygomatic: least postorbital breadth (Fig. 46D) (T.II App.V)

This character has not been adequately defined in publications. In H. africaeaustralis this distance appears to be from the deepest part of the notch on the ventral posterior surface of the squamosal, immediately above the external auditory meatus on the lateral skull surface, on one side, to the corresponding point on the other. In other species of Hystrix, the least postorbital breadth may occur elsewhere, but the distance referred to above is the one that has been employed for H. africaeaustralis in the present study. Measured with the Goodline caliper.

7.2.1.7 Skull width at condyles (Figs. 46E, 54A[2])(T.II App.V)

This was considered to be the width of the occiput between the upper outer articular surfaces of the occipital condyle; this parameter has not been defined in the literature and it could equally well refer to the total width of the occiput at the level of the condyles. The most accurate way of measuring the parameter was with the Goodline caliper.

7.2.1.8 Interorbital distance at lachrymal edge (Fig.46F) (T.II App.V)

This description adequately defines the parameter. It was measured with the Goodline caliper, with the dorsal surface of the specimen facing upwards and the arms of the caliper fitting over the cranium from above.

7.2.1.9 Interorbital distance at rudimentary post-orbital processes (Fig. 46G) (T.II App.V)

The above description suitably defines the parameter, although in H. africaeaustralis the post-orbital process is often rudimentary to the point of being almost absent. The distance was measured as above.

7.2.1.10 Height of skull from palate to posterior end of nasals (Fig. 50E[1]) (T.III App.V)

This has been measured as the distance from the junction of the maxillary with the palatine on the ventral midline to the intersection of the naso-frontal sutures with the dorsal midline. Where the left and right naso-frontal sutures intersect with the midline at different points, the anteriormost intersection has been used as the r.p.

The bow-type sliding caliper was used to measure this parameter because of the awkward position of the r.ps.

7.2.1.11 Height of skull from palate between M^1 (Fig. 50F[1]) (T.III App.V)

This parameter has been measured from the palatal midline at a point opposite the centre of M^1 to a point on the dorsal midline which lies vertically above it. Since there is no specific marking on the dorsal surface of the skull at this point, and since the vertical can only be inferred, the parameter cannot be more accurately defined. The bow-type sliding caliper was used.

7.2.1.12 Least breadth of bony bridge between orbit and foramen infraorbitale (Fig. 50G[1])(T.III App.V)

The above statement adequately defines the parameter, although its position

was found to be variable from the one specimen to the other within the sample. The narrowest part of the bridge was measured by manipulation of the Goodline caliper.

7.2.1.13 Breadth of choanae (Fig. 52P[1])(T.III App. V)

This parameter is defined as the distance from the anterior end of the naso-premaxillary suture on one side of the skull to the corresponding area on the other. It was measured with the Goodline caliper from the front rather than from above because of better visibility.

7.2.1.14 Length of sagittal crest (Fig. 46H)(T.III App.V)

This was measured from the top of the median occipital crest to the point of divergence of the left and right temporal ridges, which together form the sagittal crest. The measurement therefore includes the thickness of the transverse occipital crest. It could not be ascertained whether the published measurements of this parameter incorporate the thickness of the transverse occipital crest. The Goodline caliper was used.

7.2.1.15 Prominence and breadth of sagittal crest (Fig. 45)

This was examined throughout the sample, and assessed against sagittal crests of other species described and figured in the literature.

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

The same procedure as for 7.2.1.15 was followed.

7.2.1.17 Position of spheno-palatine foramen (Fig. 47)(T.III App.V)

The term 'spheno-palatine foramen' as defined by Sulimski (1960), has been used, i.e. the fissure-like foramen penetrating the maxillary bone approximately 10mm above the buccal alveolar rim of M^1, M^2 or M^3. Since its position appears to be variable, the alveolar rims of these teeth have been used as reference points, so that the spheno-palatine foramen may be described as being 13,0mm above the distal end of the alveolar rim of M^2, etc. The anterior margin of the foramen has been used throughout as the r.p. The foramen is very awkwardly placed for measurement, because the zygomatic arch obstructs the placing of measuring instruments. The Kern dividers were used for this measurement.

7.2.2 Measurements of the premaxilla

7.2.2.1 Length of nasal process of premaxilla (Fig. 50H[1])(T.IV App.V)

This has been interpreted as the length of the naso-premaxillary suture. The r.ps. are the anterior and posterior limits of the naso-premaxillary suture

on the right side and the Goodline caliper was used in this measurement.

7.2.2.2 Breadth of nasal process of premaxilla (at fronto-premaxillary suture) (Fig. 50 I^1) (T.IV App.V)

This character is most commonly cited as 'breadth of nasal process of premaxilla' but the point at which is should be measured has not been defined in the literature. Corbet and Jones (1964) have suggested one definite point on the nasal process at which the breadth should be measured (see 7.2.2.3) and as a second measurement of this process, its breadth at its terminal end (the fronto-premaxillary suture) has been considered. The reference points are the extremities of the suture.

7.2.2.3 Breadth of nasal process of premaxilla at a point on its lower margin midway between the maxillo-frontal suture and the masseteric ridge of the maxilla (Fig. 50J^1) (T.IV App.V)

This parameter, its reference points, and method of measurement has been defined and illustrated by Corbet and Jones (op. cit.) and is shown in Fig. 50J^1 of this text. The distance was measured with the Kern dividers.

7.2.2.4 Median sutural length of premaxilla ventrally (Fig. 48T) (T.IV App.V)

This was measured from the anteriormost extremity reached by the premaxilla on the palatal midline to the junction of premaxilla with the maxilla on the midline. In H. africaeaustralis there is frequently a gap or slit in the palatal bones at the latter point, caused by the incomplete closure of the posteriormost extremity of the median premaxillary suture, but more particularly by the incomplete closure of the anterior median maxillary suture. The occurrence of this gap or slit appears to be random and is not characteristic of any particular age group. If this character is present, it is invariably accompanied by a pronounced swelling of the palate along its length (Fig.63); the significance of both slit and swelling are not fully understood. When a gap or slit is present, the parameter has been measured to the posteriormost point reached by the premaxillary on the midline.

As in the case of condylo-incisive length (7.2.1.3) and basal length (7.2.1.4) the anteriormost point reached by the premaxilla on the ventral midline is reached with difficulty in specimens with teeth. The Kern dividers were used to measure this parameter.

7.2.2.5 Palatal length of premaxilla medially in front of foramina incisiva (Fig. 48U) (T.IV App.V)

Because the preceding parameter is frequently difficult to measure on account of the incomplete posterior closure of the median premaxillary suture and frequent breaks in the bone in this region, it was decided that the length of the premaxilla medially, from the anterior margin of the foramina incisiva to the anteriormost point reached by the premaxilla on the palatal midline would be a useful character, as it is more frequently encountered intact in both living and fossil specimens. The distance was measured with the Kern dividers because the anterior r.p. is inaccessible to other instruments.

7.2.2.6 Posterior extent of premaxillary process

This was examined throughout the sample and compared with published descriptions and figures. The reference point used was the anterior border of the lachrymal.

7.2.2.7 Shape of terminal part of premaxillary process

This was examined throughout the sample and compared with published descriptions and figures.

7.2.3 Measurements of the nasal

7.2.3.1 Length of nasals (Fig. 46 I) (T.V App.V)

One r.p. is the anteriormost point reached by the right nasal (slightly lateral to the midline), the other the intersection of the right naso-frontal suture with the median suture. The parameter was measured with the Goodline caliper.

7.2.3.2 Length of nasal suture (Fig. 46J)(T.V App.V)

One r.p. is the anterior termination of the median nasal suture and the other the posteriormost intersection of a naso-frontal suture with the midline. The Goodline caliper was used.

7.2.3.3 Maximum width of nasals (Fig. 46K,L)(T.V App.V)

In most specimens the maximum width of the nasals is across the bone from the fronto-premaxillary suture to the midline, the measurement being made at right angles to the latter, although on some individuals, the greatest width may be anterior or posterior to this line. For convenience, the

greatest width of nasals was measured from the fronto-premaxillary suture to the midline with the Goodline caliper.

7.2.3.4 Width of nasals at anterior end of naso-premaxillary suture (Fig. 46M) (T.V App.V)

One reference point is the anterior end of the naso-premaxillary suture, the other a point on the midline where the line joining the left and right anterior termination of the naso-premaxillary suture crosses it at right angles. The Goodline caliper was used.

7.2.3.5 Width of nasal at posterior end of naso-premaxillary suture (Fig. 46K) (T.V App.V)

The same as 7.2.3.3, maximum width of nasals, in the case of H. africae-australis.

7.2.3.6 Posterior extent of nasals behind fronto-premaxillary suture (Fig. 46N) (T.V App.V)

In most specimens, the posteriormost extent reached by the nasals is at the intersection of the naso-frontal suture at the midline, but in some specimens this point lies lateral to the midline. To avoid confusion, the following reference points have been used when assessing the posterior extent of the nasals: 1) a point on the midline where the line joining left and right fronto-premaxillary sutures crosses it at right angles, drawn in lightly in pencil on specimens prior to measuring: 2) the point of intersection of the naso-frontal suture with the midline. The distance was measured with the Kern dividers.

7.2.3.7 Posterior extent of nasals in relation to lachrymals

The posterior extent of the nasals was visually ascertained for the entire sample, using the lachrymal as a reference point. The findings were compared with published descriptions and figures of this part of the skull for the other two species in the subgenus.

7.2.3.8 Posterior extent of nasals in relation to orbit

The same procedure as for 7.2.3.7 was followed, using the orbit as a reference point.

7.2.3.9 Shape of posterior margin of nasals

The shape of the posterior margin of the nasals was examined in each specimen of the sample and these findings were compared with published

figures and descriptions of H. cristata and H. indica.

7.2.3.10 Shape of nasals (Fig. 46K : I, Fig. 46M : K)(T.XIII App.V)

This has been discussed in subsequent sections (7.2.11.3 and 7.2.11.4).

7.2.3.11 Size and shape of nasal orifice

The measurement of the width of the nasal orifice has already been discussed (7.2.1.13) and the variation of its shape was visually examined for the sample. The findings were compared with published figures for the nasal orifices in H. cristata and H. indica.

7.2.4 Frontal parameters measured

7.2.4.1 Length of frontal suture (Fig. 46 O) (T.VI App.V)

This was measured from the intersection of the right naso-frontal suture with the midline, and from here to the intersection of the right fronto-parietal intersection.

7.2.4.2 Length of fronto-premaxillary suture (Figs. 46P, 50 I^1) (T.VI App.V)

The same as 'breadth of nasal process of premaxilla at fronto-premaxillary suture' (7.2.2.2).

7.2.4.3. Breadth of frontals at rudimentary postorbital processes (Fig. 46G) (T.II App.V)

The same as 'interorbital distance at rudimentary postorbital processes' (7.2.1.9).

7.2.5 Measurements of the parietal

7.2.5.1 Median sutural length of parietals (Fig. 46Q)(T.VI App.V)

The suture between the parietal and occipital is completely fused some time before the eruption of M3, i.e. before growth stage 4 (sub-adult) is reached, so that in most individuals the parietal-occipital junction is very difficult to locate. The present author is therefore convinced that many measurements quoted for this character, particularly those cited for adult specimens, actually refer to the fronto-occipital distance (see below).

7.2.5.2 Fronto-occipital distance (Fig. 46Q) (T.VI App.V)

This was measured from the intersection of the right fronto-parietal suture with the midline to the top of the median occipital crest on the dorsal midline. The Goodline caliper was used.

7.2.6 Measurements of the occiput

7.2.6.1 Distance between upper edge of foramen magnum and occipital crest along midline (Fig. 54S[1]) (T.VIII App.V)

This was measured from the centre of the upper rim of the foramen magnum to the top of the median occipital crest on the midline. The Goodline caliper was used. Some authors may consider this distance to represent the 'maximum height' of the occiput instead of the distance referred to below (7.2.6.2). However, where 'greatest occipital height' has not been accurately defined as being measured from either the upper or the lower margin of the foramen magnum, it is usually impossible to ascertain from the measurements given, so that in the cranial relationship 'maximum width of occiput : maximum height of occiput' both this height (7.2.6.1) and the following (7.2.6.2) have been used in two separate calculations.

7.2.6.2 Distance between the lower edge of foramen magnum and occipital crest along midline, maximum height of occiput? (Fig. 54T[1]) (T.VIII App.V)

Measured from the centre of the lower rim of the foramen magnum to the top of the median occipital crest on the midline, using the Goodline caliper. This distance can also be considered as the 'maximum height of occiput'; however, some authors may consider 7.2.6.1 to represent the true 'maximum height.

7.2.6.3 Greatest and least breadth of occiput above foramen magnum (Fig. 54U[1] and V[1]) (T.VIII App.V)

The size and shape of the foramen magnum and the shape of the occiput itself was found to vary considerably within the sample of H. africae-australis. The distance from the upper margin of the foramen to the top of the median occipital crest was found to be particularly variable. For this reason and because it was impossible to define constant points at which the above parameters should be measured, they were not considered worthy of investigation.

7.2.6.4 Greatest occipital breadth at paroccipital processes (Fig. 54W[1]) (T.VIII App.V)

This is the distance between the outer margins of the paroccipital processes where they attain their greatest lateral expansion. The

distance was measured with the Goodline caliper.

7.2.6.5 Length of paroccipital processes (Fig. 54X[1]) (T.VIII App.V)

This distance was measured along the midline of the process from its distal extremity to a line joining the intersection of the tympanic and paroccipital suture to the top of the notch between the paroccipital process and occipital condyle. In older specimens, the junction of the tympanic-paroccipital suture is difficult to locate on account of its complete fusion, but this point is sometimes marked by a hollow, and occurs at the lower extremity of the transverse occipital crest. The paroccipital processes are frequently missing on account of their fragility. The parameter was measured with the Kern dividers.

7.2.6.6 Distance between paroccipital processes (Fig. 54Y[1]) (T.VIII App.V)

This is the distance between the inner margins of the paroccipital processes at their distal ends. The Goodline caliper was used for this measurement.

7.2.6.7 Maximum width of occipital condyles between external edges (Fig. 54Z[1]) (T.VIII App.V)

This description adequately defines the parameter. The Goodline caliper was used for this measurement.

7.2.6.8 Orientation of the long axis of condyles

This orientation was originally assessed for the whole sample and the findings compared with published figures and descriptions of H. cristata and H. indica.

7.2.7 Measurement of palatal parameters

7.2.7.1 Diastemic length (Fig. 48V) (T.VI App.V)

This was measured from the mesial end of the lingual alveolar rim of I^1 to the lingual end of the anterior (mesial) alveolar rim of dp4 or P4, and is therefore an oblique measurement. The Kern dividers were used.

7.2.7.2 Median sutural length of palate (Fig. 48W) (T.VI App.V)

This was measured from the anteriormost point reached by the premaxillary at the ventral midline to the palatal notch at the median palatal suture. The Kern dividers were used.

7.2.7.3 Median sutural length of maxillary (Fig. 48X) (T.VI App.V)

This was measured from the intersection of the premaxillary-maxillary suture with the median suture, and from the latter to the intersection of the maxillary-palatine suture. As previously mentioned (7.2.2.4) there is frequently a gap or slit in the palate at the junction of the premaxillary, maxillary and median sutures due to incomplete closure. If this is the case, the parameter has been measured to the anterior-most point reached by the maxillary on the ventral midline. The distance was measured with the Kern dividers.

7.2.7.4 Width of palate between dp4 or P^4 (Fig. 48Y)(T.VII App.V)

This is the distance from the centre of the lingual alveolar rim of the left P^4 to the corresponding point on the right alveolar rim. It was measured with the Kern dividers.

7.2.7.5 Width of palate between M^1 (Fig. 48Z) (T.VII App.V)

Same as above, using the centre of the lingual alveolar rim of M^1's as reference points.

7.2.7.6 Width of palate between M^2 (Fig. 48A[1])(T.VII App.V)

Same as 7.2.7.4, using the centre of the lingual alveolar rims of M^2's as reference points.

7.2.7.7 Width of palate between M^3 (Fig. 48B[1])(T.VII App.V)

Same as 7.2.7.4, using the centre of the lingual alveolar rims of M^3's as reference points.

7.2.7.8 Shape of palate behind (Fig. 48)

The shape of the palatal incision was examined throughout the sample and the findings compared with the published descriptions and figures of the same feature in H. cristata and H. indica.

7.2.7.9 Anterior extent of palatal incision (Fig. 48)

The anterior extent of the palatal incision was examined throughout the sample, using the M^3 or its lingual alveolar rim and the maxillary-palatal suture as reference points. The findings were compared with published descriptions and figures of the same feature for H. cristata and H. indica.

7.2.7.10 Length, breadth, shape and position of foramina incisiva (Fig. 48)(T.VI App.V)

The length of the foramina incisiva was measured along its median diameter. Its greatest posterior breadth was measured including both halves. The Kern dividers were used for both measurements. The position of the foramen was assessed with reference to the premaxillary-maxillary suture.

7.2.8 Measurements of the zygomatic region

7.2.8.1 Least vertical diameter of lower anterior zygomatic root (Figs. 50K^1, 52Q^1)(T.IX App.V)

The least vertical diameter of the lower anterior zygomatic root was established by manipulation of the Goodline caliper. This diameter was measured close to the point of origin of the lower zygomatic process of the maxillary, in front of the dp^4 or P^4.

7.2.8.2 Jugal height at maxillo-jugal suture (Fig. 50L^1)(T.IX App.V)

This was taken as the distance from the maxillo-jugal suture at the orbital rim to a point on the lower edge of the zygoma and vertically below it; the latter point in most specimens corresponds to the maxillo-jugal suture on the lower zygoma surface. The uppermost and lowermost extremities of the maxillo-jugal suture have been used as reference points for convenience and because the zygoma frequently fractures along this suture. The Goodline caliper was used.

7.2.8.3 Jugal height at jugal-squamosal suture (Fig. 50M^1)(T.IX App.V)

This has been measured as the distance between the junction of the jugo-squamosal suture at the orbital rim and a point on the lower edge of the zygoma, vertically below it; since there is no clearly defined feature at the latter point the parameter cannot be accurately defined. The distance was measured with the Goodline caliper.

7.2.8.4 Length of jugal along orbital rim (Fig. 50N^1)(T.IX App.V)

This was measured from the maxillo-jugal suture to the jugo-squamosal suture along the orbital rim. The Goodline caliper was used.

7.2.9 Measurement of the lachrymal region

7.2.9.1 Distance of the lachrymal from the zygomatic suture (Fig. 50 O^1)(T.IX App.V)

This is the distance from the maxillo-lachrymal suture to the maxillo-jugal suture on the orbital rim. It was measured with the Goodline caliper.

7.2.9.2 Extent of facial surface of lachrymal

This was visually assessed for the entire sample using the fronto-premaxillary and lower maxillo-jugal suture as reference points, and the extent of the facial surface of the lachrymal compared with those recorded or illustrated for H. cristata and H. indica in the literature.

7.2.10 The measurement of miscellaneous cranial characters

7.2.10.1 Molar-tympanic distance (Fig. 48D^1)(T.IX App.V)

This was measured from the centre of the distal alveolar rim of the right M^3 or the posteriormost erupted tooth to the anterior ventral face of the right tympanic bulla, at a point where the pterygoid almost makes contact with the latter, this point being marked by a cluster of bony papillae. The Kern dividers were used.

7.2.11 The measurement of cranial relationships

7.2.11.1 Length of nasal bones as a proportion of the occipitonasal skull length (Fig.46 I : B) (T.X App.V)

The length of the nasal bone of the right hand side of the cranium, measured as described in 7.2.3.1 (Fig. 46 I) is used as a numerator. The occipito-nasal skull length, measured as described in 7.2.1.2 (Fig. 46B) is used as a denominator. It was found more convenient to express the proportion of the occipito-nasal skull length occupied by the nasal as a percentage, after Corbet and Jones (1964), e.g.

Nasal length TM 12165	7,9mm
Occipito-nasal length TM 12165	14,7mm

$$\text{Nasal: occipito-nasal skull length} = \frac{79}{147} \times \frac{100}{1} \%$$

$$= 53{,}74\%$$

Percentages have been determined to three decimal places and are given correct to two. This character conveys what proportion of the skull

length is occupied by the nasal bone, and hence what degree of 'pneumatization' is present.

7.2.11.2 Length of nasal bones: length of frontal suture (Fig. 46 I : 0) or more usually frontal suture % of nasal length (Fig.46 0 : I) (T.XI App.V)

The proportion frontal length : nasal length is usually given as a percentage (Corbet and Jones, 1964). The median sutural length of the right frontal, measured as described in 7.2.4.1 (Fig. 46 0), is used as a numerator and the median sutural length of the right nasal, measured as defined in 7.2.3.1 (Fig. 46 I) as the denominator, and the fraction expressed as a percentage, e.g.

Frontal length of TM 12165		4,7mm
Nasal length of TM 12165		7,9mm
Frontal % nasal length	$\frac{47}{79} \times \frac{100}{1}$ %	
	= 59,42%	

Since long nasals are correlated with short frontals, lower percentages indicate shorter frontals and hence a greater difference in the lengths of the two bones.

7.2.11.3 Relative width of nasals; greatest width: greatest length (Fig. 46K : I) (T.XII App.V)

The greatest width of the right nasal, as defined in 7.2.3.3. (Fig. 46K) is used as a numerator, and the greatest length of the right nasal, as defined in 7.2.3.1 (Fig. 46 I) as a denominator. The fraction is expressed as a percentage, high percentages representing short, broad nasals and low percentages long, narrow ones, e.g.

Greatest nasal width TM 12165		31,2mm
Greatest nasal length TM 12165		79,0mm
Relative width of nasals	= $\frac{312}{79} \times \frac{100}{1}$ %	
	= 39,49%	

that is, a nasal which is a little over 1/3 as wide as it is long. This character, used in conjunction with the next, should give some idea of the shape of the nasal.

7.2.11.4 Width of nasals anteriorly: width of nasals posteriorly, i.e. narrowing, shape (Fig. 46M:K) (T.XIII App.V)

The anterior width of the nasals as defined in 7.2.3.4 (Fig. 46M) is used as a numerator, with the width of the nasals posteriorly, measured as described in 7.2.3.5 (Fig. 46K) as the denominator. Again, the fraction is more conveniently expressed as a percentage, low percentages indicating nasal bones which are narrow anteriorly and broad posteriorly and high percentages (in excess of 100%) indicating nasals which are broader anteriorly than posteriorly. A nasal giving a 100% reading for anterior : posterior width would have roughtly rectangular nasals, that is, nasals which are as wide in front as they are behind.

7.2.11.5 Width of nasal process of premaxilla in relation to the greatest width of nasal (Figs. 50J ^{1}, 46K) (T.XIV App.V)

In this instance the breadth of premaxilla used is that defined by Corbet and Jones (1964), and was measured as described in 7.2.2.3, Fig. 50J^{1}. The figure obtained is used as a numerator, and the greatest width of the right nasal, measured as described in 7.2.3.3, Fig. 46K as a denominator. Once again, the fraction is expressed as a percentage, small percentages indicating nasals which are considerably wider than the nasal process of the premaxilla and high percentages (in excess of 100%) indicating nasals which are narrower than the nasal process of the premaxilla. Specimens giving a reading of 100% have nasals and premaxillary nasal processes of equal width. The results of this calculation should give some idea of the relative degree of 'expansion' of the rostral bones (nasal and premaxillary) and hence in which areas 'pneumatization' or 'inflation' is occurring.

7.2.11.6 Maximum width of occiput : maximum height of occiput (Fig. 54U^{1} : S^{1}; Fig. 54U^{1} : T^{1})(T.XV App.V)

In some specimens, the maximum width of the occiput was found to occur across the paroccipital processes at their widest expansions, while in others this distance was across the occiput from the terminal point of the transverse occipital crest on the left lateral side of the skull to the termination of this crest on the right. Because the paroccipital processes are frequently absent due to fracture, even in recent specimens the latter greatest width mentioned has been used in the

calculation of the relative height of the occiput. In young specimens, the tympanic suture can be seen to terminate the transverse occipital crest; in older specimens complete fusion obscures the suture, but the transverse occipital crest can be seen to terminate at the point of divergence of the paroccipital process from the occiput. The distance was measured with the Goodline caliper, and the measurement used as the numerator of the fraction. Frenkel (1970), who used this cranial relationship as a species-differentiating character, does not make it clear whether 'maximum height of occiput at midline' (the denominator of the cranial relationship) was measured from the upper or lower margin of the foramen magnum, neither is it clear from her measurements provided (op. cit. Table I). Two separate calculations, using both alternatives (7.2.6.1 from upper margin, and 7.2.6.2 from lower margin) have therefore been made (Fig. $54U^1$: S^1 and Fig. $54U^1$: T^1). The ratio should provide a rough indication of the shape of the occiput. The fraction has been expressed both as a number and as a percentage, a low percentage indicating a high narrow occiput, while a high percentage expresses a broad, squat occiput. Specimens giving percentages of 100% have occiputs which are as broad as they are high, i.e. almost square.

7.2.11.7 Maximum width of occiput : maximum width of condyli (Fig. $54U^1$: Z^1) (T.XVI App.V)

The maximum width of the occiput is the distance as defined above (7.2.11.6, Fig. $54U^1$); this measurement has been used as the numerator; the maximum width of the condyli between external edges as defined in 7.2.6.7. Fig. 54 Z^1 has been used as the denominator, as was done by Frenkel in 1970 (p.56 Table I).

7.2.11.8 Height of skull as a % of (basal) length (Fig. $50E^1$ as a % of Fig. 48S) (T.XVII App.V)

In this instance the height of the skull has been taken as the height from the palate to the posterior end of the nasals as defined in 7.2.1.10 Fig. $50E^1$, though whether this is the height used by all authors employing this character, is doubtful. The basal length has been defined in 7.2.1.4. The character is intended to convey the flatness or roundness of the cranium, and hence some indication of the degree of nasal pneumatization. A low percentage will indicate a long flat cranium, while a high percentage will indicate a short globular cranium.

7.2.11.9 Zygomatic breadth: basal length
Fig. 46C : Fig. 48S) (T.XVIII App.V)

The zygomatic breadth, as defined in 7.2.1.5 (Fig. 46C) has been used as the numerator, and the basal length as defined in 7.2.1.4 (Fig. 48S) as the denominator. The fraction so obtained (more conveniently expressed as a percentage) will give some indication of the shape of the cranium when viewed from above, specimens with low percentage readings having long narrow crania, and those with high percentages short, broad crania.

7.2.11.10 Length of molar series: molar tympanic distance (Fig. $48C^1$: D^1) (T.XIX App.V)

In sub-adult, adult and mature specimens (age groups 4, 5 and 6), the length of the molar series has been measured from the centre of the mesial alveolar rim of dp^4 or P^4 to the centre of the distal alveolar rim of M^3. In juvenile specimens without the full complement of teeth, the distance has been measured to the centre of the distal alveolar rim of the posteriormost erupted tooth. The molar tympanic distance has been measured as in 7.2.10.1.

7.2.12 Measurement of mandibular characters

7.2.12.1 Greatest length of mandible (Fig. $56B^2$) (T.I App.VI)

This was measured from the posterior border of the incisor alveolus at the anterior terminus of the mesial suture to the posteriormost point reached by the condyle. The Goodline caliper was used.

7.2.12.2 Length of mandible from posterior border of incisor alveolus to tip of angular process (Fig. $56C^2$) (T.I App.VI)

The above statement adequately defines the parameter, the 'posterior border of the lower incisor' being taken at the midline. The distance is easier to measure in specimens where the incisors are missing. The Goodline caliper was used.

7.2.12.3 Height of mandibula(ascending ramus) from condyle to processus angularis (Fig. $56D^2$) (T.I App.VI)

This is the maximum height of the mandibula, measured from the most dorsal point attained by the articular condyle to a point on the ventral margin of the processus angularis vertically below. No definite features occur at either reference point so that the measurement is rather

subjective. The Goodline caliper was used.

7.2.12.4 Depth of ramus below P_4 or dp_4 (Fig. 56E[2])(T.I App.VI)

Measured from the anterior outer corner (where the mesial and buccal margins of the alveolar rim meet) of the alveolus of P_4 or dp_4 to the most ventral point reached by the mandible vertically below. There is, in younger specimens, a slight groove in the mandibular bone at the latter point. The Goodline caliper was used.

7.2.12.5 Depth of ramus below M_1 (Fig. 56F[2])(T.I App.VI)

Measured from the midpoint of the buccal alveolar rim of M_1 to the most ventral point reached by the mandible vertically below. The Goodline caliper was used.

7.2.12.6 Depth of ramus below M_2 (Fig. 56G[2])(T.I App.VI)

Measured from the mid-point of the buccal alveolar rim of M_2 to the most ventral point reached by the mandible vertically below. The Goodline caliper was used.

7.2.12.7 Alveole of P_4 or dp_4 to foramen mentale (Fig. 56H[2])(T.II App.VI)

This was measured from the anteriormost point reached by the mesial margin of the alveolar rim of P_4 or dp_4 to the closest approaching point of the circumference of the foramen mentale. It was found that the alveolar rim of the P_4 was frequently chipped away or damaged in fossil specimens, so that the original upper contact with the tooth crown was lost or difficult to locate. The Goodline caliper was used.

7.2.12.8 Position of foramen mentale

This is largely indicated by the measurements of the preceding parameter, but the variability of its position was also visually estimated, using the alveolar rim of the P_4 or dp_4 as a reference point.

7.2.12.9 Length of diastema from posterior border of alveolus of I_1 to anterior border of P_4 or dp_4 (Fig. 56 I[2])(T.II App.VI)

This was measured from the lingual border of the incisor alveolus at the midline, i.e. from the anterior upper termination of the mesial symphysis to the centre of the mesial alveolar rim of the P_4 or dp_4. The Goodline caliper was used.

7.2.12.10 Curvature of diastema (Fig. 108)

The degree of curvature of the diastema was cited by Greenwood (1955) in her generic diagnosis of Xenohystrix but its assessment was of a subjective nature, being simply described as 'sharply curved'. However, the degree of diastemic curvature does seem to be a potentially useful character in distinguishing fossil remains, as the diastema is frequently preserved intact, or almost intact. Because of this, an attempt has been made to quantify it, so that meaningful comparisons can be made.

In a mathematical sense, it is impossible to measure the curvature, as it is irregular over the length of the diastema and there are various practical problems connected with its measurement, but an effort has been made in this text to give an accurate as possible quantitative assessment of curvature for comparative purposes. In practice, it was not the curvature itself that was measured, but a dimension reflecting the degree of curvature:

The diastemic lengths of the hypothetical mandibles A and B illustrated in Fig. 108 are identical (5cm) but their curvature is not; diastema A is almost flat and 'shallower' than that of diastema B which is more strongly curved. A distance which is indicative of their differing degrees of curvature is the distance from the line joining the reference points used in measuring their diastemic lengths (top of mesial suture to anterior alveolar rim of P4) to the deepest point on the diastemic curve, that is, distance X in the case of diastema A, and distance Y in the case of diastema B. This distance has for convenience been termed 'diastemic depth'. It was measured in the following way:

A straight line was drawn on a sheet of paper and the previously measured diastemic length (as defined in 7.2.12.9) of the specimen ~~were~~ marked off. The specimen was then placed over the line so that the reference points used in measuring the diastemic length corresponded with the points marked off. The diastemic curvature was then traced onto the paper. The diastemic depth is the perpendicular distance from the diastemic length line to a second line drawn parallel to it, at a tangent to the deepest point of the diastemic curve, see Fig. 108. This distance, expressed as a percentage of the diastemic length (to eliminate the effect of differing diastemic lengths in different specimens) has been taken as indicative of curvature, high percentages representing short, sharply-curved diastemas, while low percentages represent

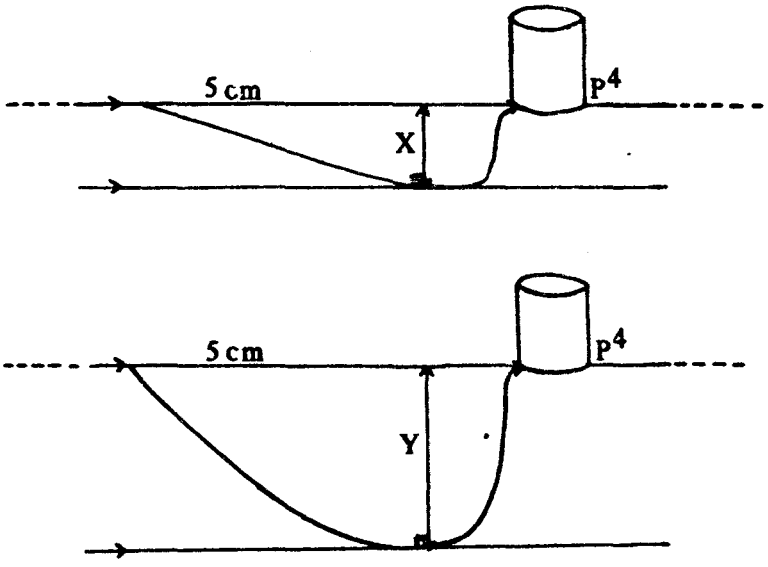


Fig 108

Diagram showing the differing diastemic curvature of two hypothetical mandibles and its method of measurement

long, flat diastemas. Alternatively, a two-dimensional graph comparing diastemic length and depth of specimens at equivalent growth stages (preferably) can be constructed.

7.2.12.11 Presence or absence of dorsally thickened crest on coronoid process

This feature was visually assessed for the whole sample and, where possible, compared with that existing in H. cristata and H. indica, using published data and figures.

7.2.12.12 Position of ascending ramus in relation to alveolar plane of molars (Fig. $56J^2$)(T.II App.VI)

The alveolar plane of the molars (Niveau des alveolarrandes) was a reference point used by Mottl (1967) when comparing the relative heights of the mesial symphysis and mandibular condyle in different species. The term 'alveolar plane of the molars' has already been described (section 7.1.2) as the best-fitting straight line that can be drawn through the alveolar rims of all four mandibular teeth. In measuring the height of the ascending ramus above the alveolar plane, the following procedure was followed: a straight line was drawn on a sheet of paper and the mandible orientated so that the alveolar plane of the molars conformed as closely as possible to the line. Because the coronoid process obscures part of the tooth row, it is easier to orientate the jaw with the lingual surface facing upwards. For various reasons, however, the alveolar plane of the molars will always be an approximation. Once the jaw had been orientated, the highest point reached by the ascending ramus was marked by a pencil point on the paper, and the perpendicular distance between this point and the line measured.

7.2.12.13 Position of top of mesial symphysis in relato alveolar plane of molars (Fig. $56K^2$)(T.II App.VI)

The above procedure (7.2.12.12) was followed, measuring the top of the mesial symphysis instead of the top of the ascending ramus. The latter point may be either above or below the alveolar plane.

7.2.12.14 Extent of development of muscle attachment; position of muscle attachment

The above features were visually examined throughout the sample using the mandibular teeth as reference points in the latter case.

7.2.13 The measurement of dental characters

As mentioned in Chapter 4, numerous isolated teeth and small dentigerous maxillary and mandibular fragments constitute the entire fossil hystricid sample available from South Africa. Other cranial fragments and post-cranial material are conspicuously absent, especially when compared with the abundant bovid post-cranial material. The hystricid maxilla and mandible, and particularly the dentition, therefore assumes an exaggerated taxonomic importance. To date, there have been no standard parameters and no standard dental terminology or methods of measurement. The results obtained by different workers often are not reproducible nor comparable, especially as growth stage is seldom mentioned. Careful attention was therefore given to the latter aspects.

The approach to tooth measurement was at first entirely experimental, no standard procedure for porcupine dentition being available at the time. Because of lack of experience no definite method was devised at the outset, but a suitable procedure gradually evolved as competence increased. This approach meant that the teeth had frequently to be re-measured when faults in one method were discovered and the method abandoned in favour of some improvement. At the same time, suitable parameters for measurement were discovered and defined and the terminology decided upon. The results of this experimentation have been discussed in Roets (1969)[i] and are incorporated below.

Some general problems common to the measurement of several dental parameters are as follows:

(a) Fragments of enamel or dentine are often detached from points required for measurements, particularly in the fossil specimens. If possible, an estimate measurement has been given. Such estimated measurements have been marked in the tables with an asterisk.

(b) The rim of the alveolus is fragile and is often damaged or broken away so that it is difficult to assess the alveolar-crown junction.

(c) In isolated premolars and molars it is often not possible to see the alveolar crown junction. The question arises at which point the measurement should be made.

(d) The only tool suitable for the measurement of BL diameter at the alveolar rim did not have a built-in scale.

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i) 'The dentition of Hystrix africaeaustralis and of the fossil porcupines from the Makapansgat Limeworks deposit.' Unpublished BSc (Hons.) dissertation Department of Palaeontology, University of the Witwatersrand, Johannesburg.

7.2.13.1 Degree of divergence from the parallel of the maxillary tooth rows (T. I, App. VII)

This was assessed as follows: the width of the palate between the fourth upper premolars was measured as described in 7.2.7.4, and the width of the palate between the upper third molars was measured as described in 7.2.7.7., and the former expressed as a percentage of the latter. Specimens giving percentages of 100% have parallel tooth rows, i.e. the inter-upper premolar and inter-upper third molar distances are equal. Specimens with percentages lower than 100% have tooth rows which diverge from front to back, the lower the percentage the greater the degree of divergence from the parallel. Similarly, specimens with percentages in excess of 100% have tooth rows which diverge from back to front.

7.2.13.2 Degree of divergence from the parallel of the mandibular tooth rows (T. I, App. VII)

The same procedure as above was followed, measuring the inter-lower fourth premolar and inter-lower third molar distances as described in 7.2.13.3 and 4 below. This measurement can only be made on specimens which have left and right rami still joined at the symphysis.

7.2.13.3 Distance between left and right lower fourth premolar or deciduous lower premolar (T.I,App.VII)

This can only be measured on specimens in which the mesial suture unites left and right mandibular rami. The inter-premolar distance was measured from the centre of the lingual occlusal rim of the left P_4 or dp_4 to the corresponding point on the right.[i] The Kern dividers were used.

7.2.13.4 Distance between left and right third lower molar lingually (T. I, App. VII)

The same procedure described above was followed, using the centre of the alveolar rims of the third lower molars as reference points.

7.2.13.5 Width of palate in relation to width of teeth (T. II, App.VII)

The width of the palate was taken as the average width and was obtained by averaging the sum of the measurements of the palatal widths between the maxillary teeth, measured as explained in sections 7.2.7.4 to 7. The average palatal width was then expressed as a percentage of the average tooth width, the latter widths being measured as described in section 7.2.13.2. Specimens giving percentages of 100% have palates which are

i) The occlusal rim was measured because the alveolar rim is inaccessible

as wide as the teeth; specimens with low percentages have relatively narrow palates and wide teeth, while high-percentage specimens have broad palates and narrow teeth.

7.2.13.6 Length of maxillary and mandibular tooth rows measured at the occlusal surface (T.III,V,App.VII)

All measurements of this category were taken from the anteriormost point reached by the occlusal surface of the upper and lower premolars or deciduous premolars to the posteriormost point attained by the occlusal surface of the last tooth, which is the upper and lower first molar in growth stage 2, the upper/lower second molars in stage 3, and the third upper/lower molars in stages 4, 5 and 6. The line is not necessarily parallel to the midline of the specimen. The Goodline caliper was used.

7.2.13.7 Length of teeth rows measured at the alveolar rim (T. IV, VI, App. VII)

This is the distance from the anteriormost point attained by the mesial part of the alveolar rims of the fourth premolars to the posteriormost point reached by the distal section of the alveolar rims of the third molars. In fossil specimens the alveolar rim is frequently damaged and estimates of its normal contact with the tooth crown had to be made.

In the maxillary dentition, from early growth stage 4 onwards, the deciduous premolars do not have a single alveolus, as this becomes compartmented to accommodate each of three rather widely divergent rootlets that are present at this stage (see Figs. 67, 68). Likewise, in terminal growth stage 6, the alveolus of the permanent premolar assumes a somewhat similar compartmented form. In the temporary and permanent premolars the mesio-buccal rootlets extend the farthest forward and hence the measurement has been taken from the anteriormost part of the alveoli of the rootlets. The mesial border of the alveolus of the permanent premolar is also variable at the point occupying the anteriormost position, but here too it has been used as the anterior reference point. The distance was measured with the Kern dividers.

7.2.13.8 Colour of enamel on upper and lower incisors, presence or absence of grooves on incisors

These features were visually assessed for the whole sample.

7.2.13.9 Upper incisor 'width': lower incisor 'width', i.e. MDI^1 : MDI_1 (T. VII, App. VII)

The 'width' (MD) of the upper incisor (mesio-distal diameter seems to be implied by the measurements of authors using this parameter), is measured as described in 7.2.13.17. This measurement is expressed as a percentage of the 'width' (MD) of the lower incisor. Specimens with readings of 100% have upper and lower incisors of equal 'width'; specimens with percentages in excess of 100% have broader upper incisors than lower, while specimens with low percentages have broader lower incisors.

7.2.13.10 Curvature of the upper and lower incisors (Figs. 109, 110) (T. VIII, App. VII)

Unlike the diastema, the curvature of the upper and lower incisors is so regular that the curved labial and lingual surfaces of these teeth may be regarded as the arcs of two circles that have the same centre but differing radii. For the incisors, therefore, it was possible to obtain numerical expressions of the degree of curvature (radius of curvature, see section 7.1.6) as the radii of these circles could be measured, the smallest radius indicating the strongest curvature.

Two methods were used, the first being suitable for larger fragments of isolated incisors but not for in situ teeth; while the second method is suitable for both.

The first method utilized is a standard geometrical procedure: the lingual curve of an incisor tooth was traced onto a sheet of paper, placing the specimen with the flat mesial surface downwards for better contact. The lingual curve was used in preference to the labial, because if the latter is used, differences in the 'thickness' (labio-lingual 'thickness') of the teeth compared have to be taken into consideration, as the labial arc will represent a bigger circle than the lingual. Increased tooth thickness would therefore have the effect of increasing the radius of curvature, but if the inner (lingual) curve is used, direct comparisons of the degree of curvature can be obtained.

Two intersecting chords of the circle represented by the arc traced were drawn. The intersection of the perpendicular bisectors of these chords is at the centre (Fig. 109 cc). The radius of curvature is the distance from cc to any point on the arc (Fig. 109 distance rc).

Alternatively, the lingual curve of the incisors can be matched to the circumferences of a series of circles of known radii and an assessment

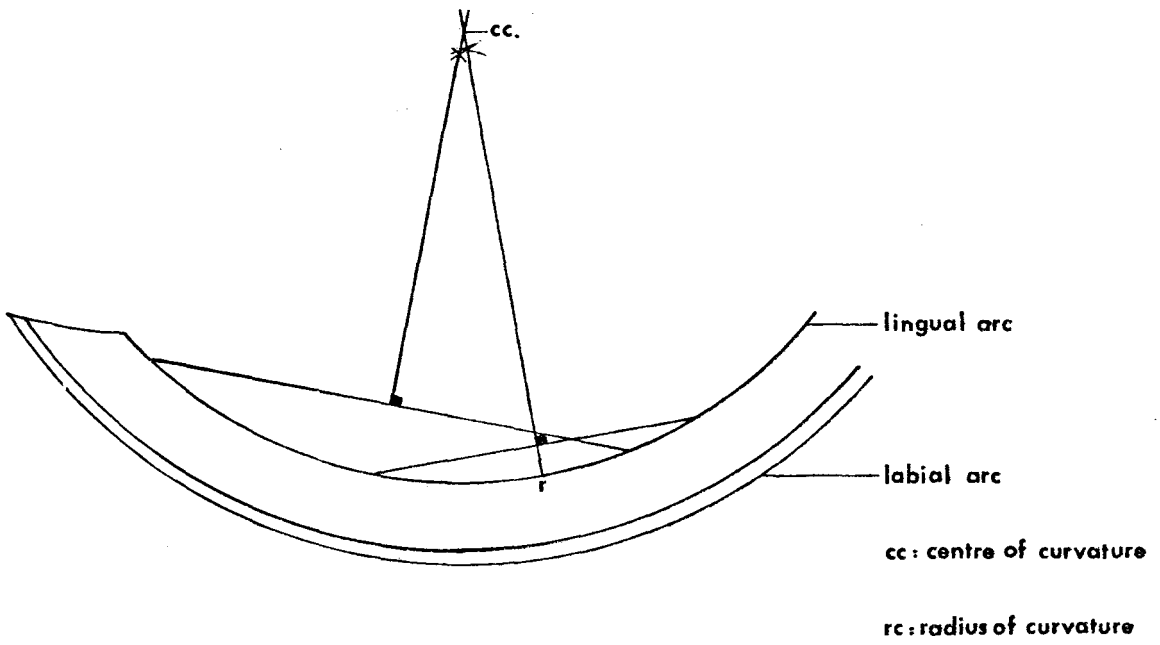


FIG. 109

The construction and measurement of the radius of curvature of the lower incisor of COH 741.

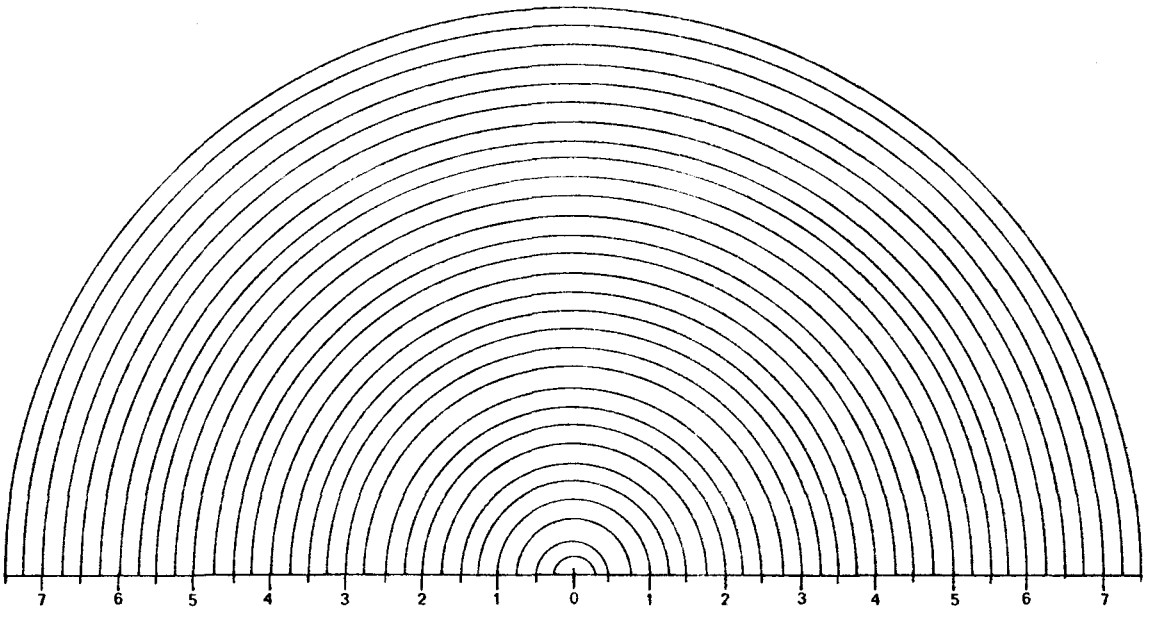


FIG. 110

Series of semi-circles of known radii used to assess degree of curvature.

of the degree of curvature obtained in this way. For this purpose, a series of semi-circles, starting with r = 0,25cm and increasing this by 0,25cm at a time, was constructed (Fig. 110). Curvatures not exactly conforming to the circumferences drawn could be quoted as having a radius of curvature of between 2,25 and 2,5cm etc.

7.2.13.11 Height of teeth, hypsodonty, brachydonty (T.IX,X App.VII)

A fair reflection of the hypsodonty or brachydonty of a tooth is the relationship between crown height and root development. A hypsodont tooth would have a high crown and relatively short rootlets, whereas a brachydont tooth would have a low crown and relatively well-developed, long roots. The ratio root length : crown height would therefore be an ideal means of expressing the degree of hypsodonty. Unfortunately, in the case of porcupines, the crown height is substantially affected with increasing wear, the rootlets are frequently missing in the fossil specimens and the root-crown junction also lies within the alveolus in specimens with in situ teeth. Furthermore, the root-crown junction lies deep within the alveolus and cannot be measured where teeth are in situ. It is therefore difficult to assess hypsodonty numerically.

The measurement of crown height in the various growth stages was considered as a possible way of giving an idea of hypsodonty, but, because Xenohystrix is gigantic when compared with Hystrix, a comparison of crown heights alone does not reveal anything of the brachydonty or hypsodonty of their respective dentitions. Hypsodonty has therefore been assessed visually and by a comparison of root development and divergence (7.2.13.13).

Measurements of crown heights at the various growth stages have been provided for comparative purposes, but do not indicate hypsodonty. Crown height is the maximum distance between the root-crown junction (as defined for porcupine dentitions in the section on dental terminology (7.1.3)) and the occlusal surface. In the maxillary dentition this tends to be on the lingual surface. The points between which greatest crown height can be measured varies from tooth to tooth and from one specimen to the other.

Root length was not considered because in 98% of the fossil specimens the roots are either damaged or completely missing.

7.2.13.12 Curvature of maxillary and mandibular teeth [i]

This was assessed both visually and by comparing the buccal curve of the

i) Most of the teeth in the modern sample of H. africaeaustralis were firmly fixed in their sockets and could not be extracted for this measurement to be made. The data was thus too limited to draw up a table.

maxillary teeth with the circumferences of the circles of known radii shown in Fig. 114. and a quantitative estimate was obtained.

7.2.13.13 Development and divergence of roots, number and position of roots

These features have been examined and described and their variability has been discussed for both modern and fossil samples.

7.2.13.14 Cross-sectional shape of incisors

The cross-sectional shape immediately behind the occlusal surface of the incisors has been considered. It is difficult to draw these sections accurately, only sectioning of the teeth might help.

It has been visually assessed, and camera lucida drawings were made where considered necessary.

7.2.13.15 The nature of the crown enamel pattern, the order of the closure of the enamel folds and number of enamel islands

This was photographically and visually assessed, using the reference drawings for the crown enamel patterns characteristic of each Growth Stage figured in Figs. 64 - 107.

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

This was assessed by measuring the distance from the base of the fold to the termination of the enamel immediately below, at the level of the rootlets.

7.2.13.17 The mesio-distal diameter (MD_1length) of the upper and lower incisors (T. XI, App. VII)

This diameter is often erroneously referred to as 'breadth' by other authors, as explained in section 7.1.3. The mesio-distal diameter of the incisor was found to increase very slightly between the occlusal surface and the apex, but the increase is so slight as to almost make no significant difference as to where the tooth should be measured. However, an attempt was made to measure the MD diameter as closely behind the occlusal surface as possible. If the occlusal surface was missing, the anteriormost intact area of the tooth was measured. The method of orientating short sections of incisors has been explained in a subsequent section (13.1).

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i) See footnote to 7.2.13.12

The MD diameter is the distance from the flat mesial face of the tooth midway between the labial and lingual surfaces to the most distal point reached by the convex distal surface, and measured at a point immediately behind the occlusal surface, or as close to it as possible. The Goodline caliper was used.

7.2.13.18 The labio-lingual diameter (LL_1) breadth of the upper and lower incisors (T.XI, App.VII)

This diameter is frequently erroneously referred to as 'length' by other authors. The reason for this has been explained in 7.1.3. As with the MD diameter, the LL diameter was found to increase slightly between the occlusal surface and the tooth apex, and, as in the above condition, an attempt was made to take the measurement as closely behind the occlusal surface as possible. In broken specimens, the anteriormost intact portion of the tooth was measured. The method of orientating short sections of incisors minus the occlusal surface has been explained in section

The LL diameter is the distance from the labial surface midway between the mesial and distal surfaces to the most lingual point reached by the curved lingual surface of the tooth immediately opposite, and measured as closely behind the occlusal surface as possible. The Goodline caliper was used.

7.2.13.19 The crown occlusal area of the upper and lower incisors (T.XII, App. VII)

This was arrived at by multiplying the measurements of the MD and BL diameters and should provide an idea of the occlusal area of the tooth. Given in square millimetres.

7.2.13.20 The crown shape index of the upper and lower incisors (T. XIII, App. VII)

This index indicates the shape of the tooth - the measurement of the LL (breadth) is expressed as a percentage of the length (MD diameter or the so-called 'breadth of incisor' of other authors). Square teeth will give readings of 100%; long narrow teeth will give low percentages, while percentages in excess of 100% represent short, broad teeth, broader than they are long.

7.2.13.21 The mesio-distal diameters (MD_1 lengths) of the maxillary teeth, measured at the occlusal surface (T. XI, App. VII)

As it has already been pointed out in the section dealing with tooth replacement, the MD diameter of the teeth at the occlusal surface varies according to the amount of wear and pressure to which they have been subjected. The length of the tooth at the occlusal surface is therefore an unsuitable parameter if used by itself or if taken without reference to the growth stage.

The MD diameter at the occlusal surface is defined as the greatest mesio-distal distance measured at the centre of the proximate contacts at the occlusal surface. As the dp^4 (or P^4) and M^3 have no adjacent tooth on one side, they have only one proximate facet; the measurement has thus been made from this to the anteriormost point reached by the occlusal surface in the case of dp^4 (P^4) or to the posteriormost point reached by the distal surface in the case of M^3. It was measured with the Kern dividers.

7.2.13.22 The MD diameter (length) of the maxillary teeth measured at the alveolar rim (T.XVII,App VII)

The teeth grow very closely together and the greatest anterio-posterior length at the alveolar rim occurs between the teeth where one tooth abuts on another. In fossil specimens the interstices between the teeth become matrix-filled and it is often impossible to remove this without damage to the specimen. The anteriormost and posteriormost points of the tooth (except the anteriormost point of the premolar and posteriormost point of M^3) therefore cannot be reached either by the specially sharpened points of the Goodline caliper or by the points of the Kern dividers. The latter instrument, however, proved more successful in the measurement of the modern sample and was therefore used.

The mesio-distal diameter at the alveolar rim is defined as the greatest antero-posterior diameter of the tooth that can be measured at the alveolar rim, and was measured from the buccal side with the Kern dividers held at right angles to the vertical axis of the tooth, with its points inserted as far as possible between the teeth.

In isolated teeth it is often impossible to locate the position

which the alveolar rim occupied. In such cases this has been estimated; one clue to this position is that the enamel is more polished above the rim than below. Such estimated measurements have been marked with an asterisk in the tables.

7.2.13.23 The BL diameter (breadth) of the maxillary teeth measured at the occlusal surface (T.XI, App.VII)

This is the greatest bucco-lingual diameter that can be measured across the occlusal surface of the tooth at right angles to the mesio-distal diameter. The Goodline calipers were manipulated to locate the greatest width and were held vertically, because the teeth in front of and behind the tooth being measured obstruct horizontally held calipers. As with the MD diameter at the occlusal surface (7.2.13.21), the BL diameter at the occlusal surface is dependant on the degree of wear to which the tooth has been subjected, and is therefore unsuitable as a diagnostic character when used in isolation.

7.2.13.24 The BL diameter (breadth) of the maxillary teeth measured at the alveolar rim (T.XVII, App. VII)

This is defined as the greatest bucco-lingual diameter, occurring at the alveolar rim. Because of the marked curvature of the barrel-shaped maxillary teeth, the only instrument which could reach the alveolar rim was the bow caliper. In isolated teeth, it is often impossible to locate the position which the alveolar rim occupied and in such instances this had to be estimated. Such estimated measurements are marked with an asterisk in the relevant tables.

7.2.13.25 The crown occlusal area of each of the maxillary teeth measured at the occlusal surface (T.XII App.VII)

Obtained by multiplying measurements obtained for the MD and BL at the occlusal surface and given in millimetres. This should give an idea of the absolute and relative occlusal surface area provided by each of the maxillary teeth.

7.2.13.26 The area enclosed by the alveolar rims of each of the maxillary teeth (T.XVIII, App. VII)

This was obtained by multiplying the measurements for the MD and BL diameter at the alveolar rim and is useful in the comparative sense

in that vacant alveoli are frequently encountered in the fossil record. The measurements should give an idea of the space occupied by each of the teeth in the jaw. This measurement is given in square millimetres.

7.2.13.27 The crown shape index of the maxillary teeth, measured at the occlusal surface (T.XIII,App.VII)

This index reflects the shape of the tooth - the BL measurement at the occlusal surface (occlusal breadth) is expressed as a percentage of the MD diameter (occlusal length). Teeth which are as broad as they are long will give percentages of 100%. Long narrow teeth will give low percentages and teeth which are wider than they are long will give percentages in excess of 100%.

7.2.13.28 The crown shape index of the maxillary teeth measured at the alveolar rim (T.XIX, App.VII)

The same procedure as above was followed except that the MD and BL measurements were those taken at the alveolar rim. The readings convey some idea of the shape of the alveoli of the different teeth.

7.2.13.29 The MD diameter (length) of the mandibular teeth measured at the occlusal surface (T.XIV,App.VII)

Defined and measured as in 7.2.13.21.

7.2.13.30 The MD diameter (length) of the mandibular teeth measured at the alveolar rim (T. XX, App. VII)

Defined and measured as in 7.2.13.22.

7.2.13.31 The BL diameter (breadth) of the mandibular teeth measured at the occlusal surface (T. XIV, App. VII)

Defined and measured as in 7.2.13.23.

7.2.13.32 The BL diameter (breadth) of the mandibular teeth measured at the alveolar rim (T. XX, App. VII)

Defined and measured as in 7.2.13.24.

7.2.13.33 The crown occlusal area of the mandibular teeth measured at the occlusal surface (T. XV, App. VII)

Measured as in 7.2.13.25.

7.2.13.34 The area enclosed by the alveolar rims of each of the mandibular teeth (T. XXI, App. VII)

Measured as in 7.2.13.26

7.2.13.35 Crown shape index of the mandibular teeth measured at the occlusal surface (T. XVI, App. VII)

Measured as in 7.2.13.27.

7.2.13.36 Crown shape index of the mandibular teeth measured at the alveolar rim (XXII, App. VII)

Measured as in 7.2.13.28.