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1955
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FOSSIL HYSTRICOIDEA FROM THE MAKAPAN VALLEY, TRANSVAAL

By Marjorie Greenwood

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Abstract

In this paper are described three Hystricomorphs from the *Australopithecus prometheus* layer of the Makapan Valley Limeworks Quarry, Transvaal. Besides *Hystrix* cf. *H. africae-australis*, a new genus and species *Xenohystrix crassidens* and a new species *Hystrix major* are recognized.

Introduction

Although remains of small rodents from the Limeworks Quarry of the Makapan Valley, Potgietersrus District, are abundant in certain breccias, they are rarely found in association with the larger mammalian fossils. These "rodent breccias" are apparently formed by the accumulation of fossilized owl pellets. However, large Hystricoidea, which could not have been the prey of owls, occur together with the remains of Primates, Subungulates, Ungulates and Carnivora.

The larger mammalian fauna occurs in three calcified and cemented layers. At the time of writing, the remains of Hystricoidea were confined to the *Australopithecus prometheus* layer, which is both the lowest and the richest zone of the three.

Maxillary and mandibular fragments with teeth still in position as well as isolated teeth are available for study. Some fragments were fossilized in their present imperfect state, whilst others were broken subsequently during quarrying operations. Amongst the large collection of Ungulate bones from the quarry are several bearing evidence of rodent gnawings. These incisor marks, which antedate fossilization, are of different sizes. Obviously, therefore, both large and small rodents frequented the caves as well as being the prey of other inhabitants.

It is apparent from the remains preserved that at least three members of the Hystricomorph group are represented in these Plio-Pleistocene limestone deposits.

Classification

Order RODENTIA
Sub-order HYSTRICOIDEA
Family Hystricidae
Sub-family Hystricinae

Hystrix cf. *H. africae-australis* Peters (1852)

Porcupine material in the collection comprised a fragment of a right lower jaw with an incomplete M_2 and an unworn M_3 (No. M.1000, B.P.I.) and a small portion of an upper incisor (No. M.1001, B.P.I.).

Owing to the fact that fossil material is so meagre, it is not possible to decide with certainty whether or not the Makapan specimens differ specifically from *Hystrix africae-australis.*

The measurements of the teeth preserved lie within the size range of *H. africae-australis.* The enamel pattern of these specimens is closely similar to that in teeth showing a comparable degree of wear in the living porcupine. Since this patttern is known to be a very variable feature, it cannot be considered of any great taxonomic importance.

Broom (1946) remarked on the occurrence at Sterkfontein of a porcupine which differs little from the living species.

Provided that there is sufficient rock or bush cover, the South African Porcupine inhabits country varying from arid mountain areas to thick forest; and the species is present in the Makapan valley today. No information about environmental conditions in any earlier period can be deduced from an animal with such a wide range of tolerance as *Hystrix africae-australis.*

Hystrix major sp. nov.

Specific diagnosis.

An extinct *Hystrix* with cheek teeth approximately one third larger than *Hystrix africae-australis.*

Holo-type:

A left mandibular fragment with a damaged incisor, a perfect P_4 and portion of the M_1 in full wear (No. M.1002, B.P.I. See figures 27 A and B).

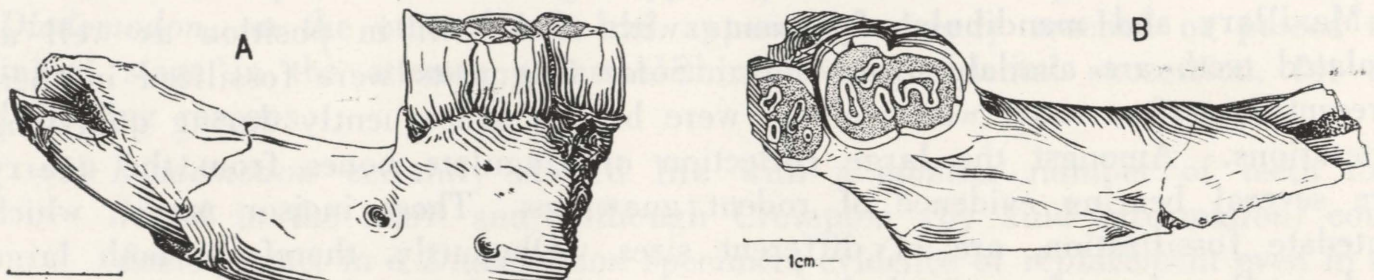


Fig. 27.—*Hystrix major, holotype* (No. M.1002). Left mandibular fragment with I_1, P_4 and M_1 in situ. A, Labial view and B, Occlusal view. Natural size.

Locality:

Limeworks quarry, Makapan Valley.

Horizon:

Australopithecus prometheus zone of the Limeworks quarry.

Discussion of specific characters:

The type specimen, together with a mandibular fragment bearing a well-worn M_3 and a broken M_2, are the only remains of this large porcupine so far recovered from the deposit.

The well-worn surfaces of the teeth of both specimens have the re-entrant folds forming "islands" of enamel completely separated from the surrounding enamel border. At an equivalent stage of wear the pattern formed by these "islands" is similar to that of the living South African species. As in *H. cristata* Linnaeus and *H. africae-australis*, the mandibular teeth are semi-rooted. However, in the new species the roots of the M_3 of specimen No. M.1003 B.P.I. are proportionately more robust and divergent than those of *H. africae-australis* M_3, but compare well with those of *H. cristata*. The apparent brachyodonty is obviously due to wear, but it should be noted that the lower extremity of the external enamel fold almost reaches the junction of the root and crown, unlike that of the hypsodont teeth of the living South African porcupine.

As far as can be determined, the conformation of the lower jaw is identical with that of the living local porcupine, except that the horizontal distance between the anterior aspect of the premolar base and the inner margin of the symphysial surface is shorter, in spite of its larger size.

The first fossil porcupine from Africa, *Hystrix astasobae* (from Abu Hugar on the Blue Nile) was described by Bate 1951, who remarked on the shortness of the snout as one of the senual primitive characters exhibited in the single specimen available. Unfortunately it is not possible to compare *H. major* with *H. astasobae*, since the latter is only known from a cranial fragment.

In size the P_4 agrees closely with *H. primigenia* Wagner, from Pikermi, Greece, but it is manifestly more elongated antero-posteriorly and the curve of the diastemic surface is not as shallow. It exceeds in length and breadth an unnamed specimen briefly described by Colbert, from the Pleistocene of Mogok, Burma. On the other hand the advanced development of the roots is similar to the condition found in the Burmese specimen and to *H. silvalensis* Lydekker, from the Middle Siwaliks of India. Two *Hystrix* fossils, an incisor fragment (B.M.16594) and an isolated M_2 (B.M. 16595) from Olduvai Gorge, Kenya, are apparently from an individual of comparable size. The Olduvai molar is somewhat more hypsodont than that of *Hystrix major*.

For comparison, the dimensions of some correspoding premolars are given below

	Longest diameter in millimeters	
	Anterior-posterior	Transverse
H. africae-australis — mean 5 specimens	9.20	7.35
H. africae-australis — maximum in 5 specimens	10.0	8.0
H. cristata — N. Africa	10.5	7.5
H. cristata — W. Uganda	10.5	8.0
Hystrix (sp. indet.) Burma A.N.S.P. 14646, after Colbert	10.5	8.5
H. primigenia — drawing in Abel	12.0	11.0
H. major — sp. nov	13.0	9.5

The longest antero-posterior dimension of the specimen differs significantly (P.01) from the mean of the dimensions in a sample of five specimens of *Hystrix africae-australis*.

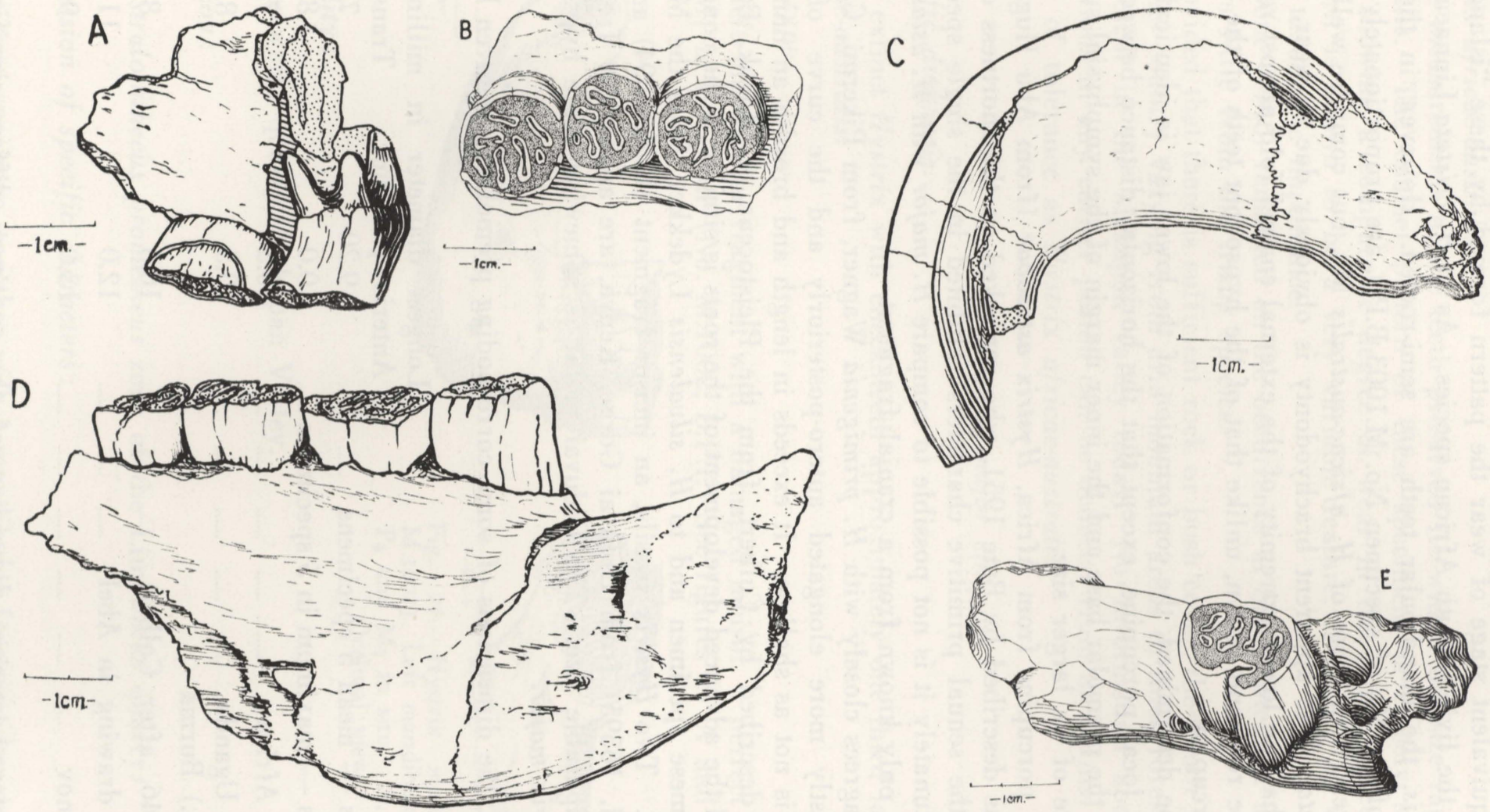


Fig. 28.—*Xenohystrix crassidens*. A, Syntype A, No. M.1004, right maxillary fragment showing M^1 with roots exposed and M^2, labial view. B, Syntype B, No. M.1005, left maxillary fragment, P^4, M^1 and M^2 in situ, occlusal view. C, Syntype C, No. M.1006, portion of left premaxilla and maxilla with I^1 in situ, labial view. D, Syntype D, No. M.1007, left mandibular fragment, P_4, M_1 and M_3 in situ, lingual aspect. E, Mandibular fragment No. M.1008, showing P_4 and alveolus of M_1, dorso-lateral view. All specimens natural size.

XENOHYSTRIX gen. nov.

Generic diagnosis:

A large extinct Hystricoid with rooted upper molars; transverse and anterior posterior diameter of the upper teeth subequal, with occasionally the transverse diameter greater; diastemic portion of the premaxilla and the maxilla strongly arched, and mandibular diastema with corresponding degree of curvature.
Type species: *Xenohystrix crassidens* sp. nov.

Xenohystrix crassidens sp. nov.

Diagnosis:
Teeth of large size: overall length of P^4-M^3 series 40 mm. or more (the mean length of the P^4-M^3 as determined from a sample of eleven *Hystrix africae-australis* is 33.8 mm.).

Syn-type A:
A right maxillary fragment with M^1 and M^2 in position. The roots of the M^1 have been exposed (No. M.1004, B.P.I., see figure 28a).

Syn-type B:

A left maxillary fragment with P^4, M^1 and M^2 in full wear (No. M.1005, B.P.I., see figure 28b).

Syn-type C:

A left diastemic curve of maxilla and premaxilla with an almost complete incisor in position (No. M.1006, B.P.I., see figure 28c).

Syn-type D:

A left mandibular fragment with the intra-alveolar portion of I_1 remaining, P_4 in early wear, M_1, M_2 and a fragmentary M_3 in full wear (No. M.1007, B.P.I., see figure 28d).

Additional material:

Other specimens from the same deposit include a mandibular fragment showing the diasteme and a slightly worn P_4, and the alveolus of M_1 (No. 1008, B.P.I., see figure 28e), and a few isolated cheek teeth and broken incisors. One almost complete left upper incisor shows indentical curvature with that of Syn-type C.

Locality: Limeworks quarry, Makapan Valley.

Horizon: *Australopithecus prometheus* zone of the Limeworks quarry.

TABLE VI

MAXILLARY TEETH		I¹ L.	I¹ B.	P⁴ L.	P⁴ B.	M¹ L.	M¹ B.	M² L.	M² B.	M³ L.	M³ B.	
Hystrix africae-australis	Min.	6·3	6·0	8·2	7·3	7·3	7·0	6·5	7·0	8·0	6·5	
	Max.	8·5	7·4	11·0	10·5	9·5	9·0	9·0	8·5	9·0	7·5	Southern Africa
	Mean	7·4	6·5	9·6	8·5	8·2	8·2	8·5	7·9	8·2	7·5	
	N	7		7		11		10		10		
H. cristata		7·3	7·1	10·5	9·0	8·0	8·0	9·0	8·5	8·5	7·0	N. Africa
H. cristata		8·0	7·0	9·5	9·0	8·0	9·0	8·5	9·0	8·5	7·0	W. Uganda
†*H. primigenia*[1])		—	—	11·0	11·0	9·75	11·0	9·5	10·75	9·5	9·75	Pikermi, Greece
†*H. primigenia*[2])		8·0	—	9·5	—	10·0	—	9·0	—	8·0	—	
†*H. sivalensis*[3])		—	—	—	—	—	—	—	—	—	—	Siwalik Range, India
†*H. sivalensis*[4])		—	—	—	—	—	—	—	—	—	—	Mogok, Burma
†*H. lagrelii*[5])		—	—	6·0	5·5	5·3	5·4	5·3	5·2	4·8	4·3	Honan, China
†*H. sp.* B.M. 16593		9·3	8·0	—	—	—	—	—	—	—	—	Olduvai, Kenya
†*H. sp.* B.M. 16594		—	—	—	—	—	—	11·0	9·5	—	—	Olduvai, Kenya
†*H. sp.*[6])		—	—	—	—	—	—	—	—	—	—	Mogok, Burma
†*H.* cf. *H. africae-australis*	(No. M. 1000, B.P.I.)	—	—	—	—	—	—	—	—	—	—	Makapan, Transvaal
,, ,,	(No. M. 1001, B.P.I.)	8·0	7·5	—	—	—	—	—	—	—	—	,, ,,
†*H. major*	(No. M. 1002, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,,	(No. M. 1003, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
†*Xenohystris crassidens*	(No. M. 1004, B.P.I.)	—	—	—	—	12·5	12·0	13·0	12·0	—	—	,, ,,
,, ,,	(No. M. 1005, B.P.I.)	—	—	12·0	12·0	10·5	12·0	11·5	12·0	—	—	,, ,,
,, ,,	(No. M. 1006, B.P.I.)	11·5	10·5	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1007, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1008, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1010, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1009, B.P.I.)	12·0	11·0	—	—	—	—	—	—	—	—	,, ,,

Measurements in millimeters. [1]) Measurements made on figure in Abel, from Gaudry. [2]) Measurements made on figure by Gaudry.
[3]) Measurements made from Lydekker (spec. G.S.I., No. D. 96). [4]) Measurements made from Colbert (spec. Amer. Mus. No. 19909).
[5]) Measurements made from Lönnberg. [6]) Measurements made from Colbert (spec. Amer. Mus. No. 14646).

TABLE VII

MANDIBULAR TEETH		I¹ L.	I¹ B.	P⁴ L.	P⁴ B.	M¹ L.	M¹ B.	M² L.	M² B.	M³ L.	M³ B.	
Hystrix africae-australis	Min.	6·2	5·0	8·2	6·0	7·5	7·2	8·3	7·0	8·5	6·0	
	Max.	8·0	7·0	10·0	8·0	9·5	8·0	10·5	8·2	10·0	7·75	Southern Africa
	Mean	6·8	6·0	9·2	7·3	8·7	7·4	9·0	7·7	8·9	7·0	
	N	8		5		10		9		10		
H. cristata		6·5	6·5	10·5	7·75	8·5	7·0	9·0	7·75	8·5	7·5	N. Africa
H. cristata		7·5	6·5	9·5	8·0	8·5	7·5	10·0	8·0	9·5	8·0	W. Africa
†*H. primigenia*[1])		8·5	—	12·0	11·0	10·5	11·0	11·0	11·0	10·3	9·0	Pikermi, Greece
†*H. primigenia*[2]		—	—	—	—	—	—	—	—	—	—	
†*H. sivalensis*[3])		—	—	—	—	10·0	7·5	9·2	8·5	—	—	Siwalik Range, India
†*H. sivalensis*[4])		—	—	—	—	9·0	7·5	—	—	—	—	Mogok, Burma
†*H. lagrelii*[5])		—	—	—	—	—	—	—	—	—	—	Honan, China
†*H. sp.* B.M. 16593		—	—	—	—	—	—	—	—	—	—	Olduvai, Kenya
†*H. sp.* B.M. 16594		—	—	—	—	—	—	—	—	—	—	Olduvai, Kenya
†*H. sp.*[6])		—	—	10·5	8·5	—	—	—	—	—	—	Mogok, Burma
†*H.* cf. *H. africae-australis*	(No. M. 1000, B.P.I.)	—	—	—	—	—	—	—	—	—	—	Makapan, Transvaal
,, ,, ,,	(No. M. 1001, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
†*H. major*	(No. M. 1002, B.P.I.)	—	8·0	13·0	9·5	—	9·5	—	—	—	—	,, ,,
,,	(No. M. 1003, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
†*Xenohystrix crassidens*	(No. M. 1004, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1005, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1006, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1007, B.P.I.)	—	—	14·0	12·0	14·0	11·0	14·5	11·5	—	10·5	,, ,,
,, ,,	(No. M. 1008, B.P.I.)	—	—	16·0	12·0	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1010, B.P.I.)	—	—	17·0	13·5	—	—	—	—	—	—	,, ,,
,, ,,	(No. M. 1009, B.P.I.)	—	—	—	—	—	—	—	—	—	—	,, ,,

Where L = Greatest anterior-posterior diameter
Where B = Greatest lingual-labial diameter
When teeth are but slightly worn, the width at its greatest proximally is taken.

Discussion of generic and specific characters:

In July, 1946, an isolated rodent incisor fragment of large size was recovered from the dumps of Limeworks quarry in the Makapan Valley. As the tooth differs only in its robustness from that of the living porcupine, it was assumed that further finds would bring to light an *Hystrix* of considerable size. Later material collected showed that this large rodent differs in several respects from the genus *Hystrix*. The number and nature of the specimens available at the moment limits the description to details of tooth and palate struture only.

The upper premolar and first two molars of the Syn-type B (figure 28B) show a considerable degree of abrasion. Their pattern approximates to that of *Hystrix africae-australis* at the same stage of wear, with the re-entrant enamel folds, prominent in unworn teeth, separated off to form "islands" of enamel within the tooth crown. Further, the upper premolar bears no trace of an external enamel fold — a feature which persists in both *H. cristata* and *H. africae-australis*.

The occlusal surface which has the appearance of a smoothly rounded square, is defined by a continuous band of enamel. The characteristic outline of the occlusal surface in *Xenohystrix crassidens* is related to the subequal antero-posterior and transverse dimensions of the crown. In *Hystrix*, on the other hand, the occlusal surface is more nearly rectangular, with the antero-posterior clearly exceeding the transverse dimension.

A diagnostic character of the genus *Hystrix* is that the upper cheek teeth are rootless or only semi-rooted. In specimens of the living South African and European porcupine examined, the premolar and the molar teeth have papilliform non-divergent rootlets, which are poorly developed in molars M^2 and M^3. *Xenohystrix* has rooted upper molars. The matrix above the base of M^1 of specimen Syn-type A (figure 28A) has been removed exposing lingually a single root, elliptical in section, and two smaller cylindrical roots on the labial side. These three roots are slightly divergent. The enamel sheath of the tooth ends rather abruptly immediately distal to the junction of the root and the crown. From the specimen Syn-type B (figure 28B), which was broken before fossilization, it can be seen that the M^2 is rooted. The M^3 is demonstrably rooted as the well preserved alveolus of the M^3 clearly shows the impressions of a large inner root and the anterior outer root (Syn-type A, No. 1004, B.P.I.).

Apart from its large size, the lower fourth premolar differs little from that of *Hystrix*. So far as can be ascertained from the material available, the degree of development of the roots in the lower cheek teeth is similar to the condition found in that of *Hystrix*. An isolated P_4 (No. M1010) with broken root stumps indicates that, when perfect, the tooth had roots which were similar in proportion to that in the living South African porcupine. The alveolus of the M_1 seen in the mandibular fragment (No. M.1008, B.P.I. see figure 28E) shows that the tooth had shallow roots and that it too might be considered as being semi-rooted, although the roots appear to be more cylindrical in shape and are more divergent than those of the genus *Hystrix*.

For comparison, tooth measurements of some living and fossil Hystrix specics are given in tables VI and VII.

General Discussion

Some fossil bones from the Makapan Limeworks Quarry show large rodent incisor marks predating fossilization. However, the remains of porcupines of a size which would have made these marks are extremely rare. Fragmentary skeletal parts seem to be absent. In *Xenohystrix crassidens*, too, skull and tooth specimens only have been identified. The incisors are far greater in diameter than those which gnawed the bones in the same deposit.

As regards knowledge of the type of environment which existed at the time these Hystricomorphs were preserved, little can be said, as living porcupines have such a wide range of environmental tolerance.

Ellerman, in discussing the Hystricoidea, bases his groupings on external characters only, maintaining that cranial and dental characters alone are unreliable. However, in the case of the Makapan fossils, skull and tooth remains only are available. But it must be borne in mind that though generic and specific identifications are made in this paper, the characters used are those which usually do show such differences in ancestral and generalized forms of a species.

Acknowledgements

My thanks are due to Professor R. A. Dart, Head of the Department of Anatomy, Medical School, University of the Witwatersrand, for placing the material at my disposal; Dr. V. FitzSimons, Director of the Transvaal Museum, Pretoria, for the use of comparative material; to Drs. H.B.S. Cooke, A. T. Hopwood, L. S. B. Leakey, and L. H. Wells for their interest and very helpful criticism; to Messrs. J. W. and B. J. Kitching for their skilful preparation of the specimens, and to Messrs. B. Grobbelaar and A. Pequeux for other technical assistance.

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