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FOSSIL HYAENIDAE FROM THE MAKAPANSGAT LIMEWORKS DEPOSIT, SOUTH AFRICA

by

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ABSTRACT

The remains of three hyaena species have been recovered from the Makapansgat Limeworks deposit. A common small form, *Hyaena hyaena makapani*, and a rare large form, *Pachycrocuta brevirostris*, were recovered from Member 3 (Lower Phase 1 grey breccia). The rare *Crocuta crocuta* was recovered from Member 4 (Upper Phase 1 breccia), and was the only hyaena from this horizon.

Abundant cranial and dental material of *H. h. makapani* facilitated comparisons with extant and fossil forms to confirm its identification as a subspecies of the extant striped hyaena. Despite morphological differences in the skull and teeth, *H. abronia* from Langebaanweg is confirmed as its likely ancestor. Some deciduous teeth of *H. h. makapani* are described and the eruption sequence of permanent cheekteeth deduced. *P. brevirostris* appears to be the largest fossil hyaena from Africa, showing affinities to *P. bellax* from Kromdraai. *C. crocuta* is similar to the extant form and the fossil forms from East Africa. As in the East African deposits, *C. crocuta* appears relatively late in the succession.

The hyaena material has limited value in site faunal correlations for dating purposes, but does not contradict the palaeomagnetic age estimate of more than 2,9 My for Member 3 (grey breccia) (Partridge 1979).

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INTRODUCTION

The family Hyaenidae is well represented in most of the Transvaal cave deposits (Toerien 1952, Ewer 1954, 1955a, Hendey 1974a, Collings *et al.* 1975). The Makapansgat Limeworks deposit is no exception; from there Toerien (1952) described the remains of a small hyaena similar to the extant striped hyaena, *Hyaena hyaena*, which he called *H. makapani*, as well as a large hyaena which he called *Crocuta* cf. *brevirostris*. Since then additional material of both species has been recovered. This material was briefly reported in Collings *et al.* (1975), together with an account of a third species attributed to *C. crocuta*.

The taxonomic and phyletic relationships of the Plio/Pleistocene Hyaenidae have been the subject of many papers (Ewer 1955b, 1967, Kurten 1956, Ficcarelli and Torre 1970, Hendey 1974b, 1978). The close relationship between the Makapansgat small hyaena and the extant striped hyaena is generally acknowledged, and in a review of the African fossil hyaenids Ewer (1967) concluded that they were only subspecifically different. Ewer (1955b) suggested that the Pliocene hyaena *H. namaquensis* might be a possible ancestor of *H. h. makapani*, but this was later considered unlikely (Ewer 1967). The late Miocene/early Pliocene deposit at Langebaanweg has yielded much hyaenid material including the species *H. abronia*, which has been proposed as the likely ancestor of the Makapansgat form and the extant striped hyaena (Hendey 1978).

This paper presents a detailed account of the hyaena material reported in Collings *et al.* (1975), and it covers all the cranial material on hand at the Bernard Price Institute for Palaeontological Research in 1972. The relationships of the hyaenas and their significance is discussed primarily in relation to finds elsewhere in Africa.

MATERIAL AND METHODS

The fossil material was mechanically prepared, mostly by staff preparators at the Bernard Price Institute, using hammer and punch. A few specimens were also prepared by the author using a "Vibro-tool" and emery disc.

With the exception of the carnassials, where additional measurements were taken, two measurements were taken on all teeth. These were the mesiodistal and buccolingual distances, corresponding to the length (L) and breadth (B) respectively. The measurements were taken at the level of the cingulum, and the mean of three measurements was recorded each time. Use was made of ratio diagrams in comparisons between species, and in particular those based upon percentages.

In references to the stratigraphy of the Limeworks the sequence and terminology of Partridge (1979) and Brain (1958) is followed.

RESULTS AND DISCUSSION

Hyaena hyaena makapani

Except for specimen M244 from Member 2 (basal red mud), all *H. h. makapani* specimens were recovered from Member 3 (Lower Phase 1 grey breccia) (J.W. Kitching, pers. comm.).

Skull (table 1; figs. 1, 2)

The skull is morphologically similar to the two extant *Hyaena* species, but is smaller than either *H. hyaena* or the fossil *H. abronia* (table 2).

TABLE 1
Skull measurements of *Hyaena hyaena makapani* from the Makapansgat Limeworks deposit

Dimension	Sample	Mean (mm)	Std. Dev. (mm)	Range (mm)
Condylobasal length	5	200,4	6,5	194,0–210,0
Zygomatic width	1	138,0		
Palate width	4	63,3	3,4	60,3–68,1
Interorbital width	6	45,3	2,9	40,4–47,8

TABLE 2
Comparison of mean skull measurements: *Hyaena hyaena makapani, Hyaena abronia* and extant *Hyaena hyaena*

Species	Condylobasal length (mm)	Zygomatic width (mm)	Interorbital width (mm)
H. h. makapani [a]	200,4	138,0	45,3
H. abronia [b]	217,0	*c.* 145,0	47,7
H. hyaena [b]	211,0	*c.* 146,0	44,0

a = composite reconstruction (figs. 1, 2) based on M 2530, M 299, M 8348
b = Hendey (1974b)

A comparison of *H. h. makapani* with the illustration and description of *H. abronia* in Hendey (1974b) revealed a few cranial differences. In *H. h. makapani* the palate (fig. 2a) is relatively shorter and narrower, and there appears to be a slightly longer precanine diastema. In lateral view (fig. 1a) the angular process of the mandible in *H. h. makapani* is not bulbous as it is in *H. abronia*, and it has a slightly dorsally directed distal end. In all these features *H. h. makapani* is similar to the striped hyaena.

Permanent dentition (table 3)

The dental formula 3/3:1/1:4/3:1/1 = 34 is identical to that in *H. hyaena* and *H. brunnea* (Ewer 1973).

With the exception of the robust caniniform I^3, the incisors are small teeth and are seldom recovered. Of the 28 canines recovered one upper and two lower were still in their alveoli. Upper and lower canines could be distinguished because upper canines are straighter and more elliptical in cross-section. Premolars, both loose and in their alveoli, were the most common hyaenid teeth recovered. Upper and lower premolars could be distinguished because lower premolars have their cusps arranged in a straight line parallel to the jaw ramus, whereas upper premolars have the first cusp offset lingually.

The cusp terminology used for the carnassials is taken from Gromova (1968), and is illustrated in Figure 3. The talonid of M_1 has a mean value of

TABLE 3
Measurements of teeth of *Hyaena hyaena makapani* from the Makapansgat Limeworks deposit

Tooth	Dimension	Sample	Mean (mm)	Std. dev. (mm)	Range (mm)
I^1	length	2	3,1		2,8–3,4
	breadth	2	4,4		
I^2	length	3	4,6		4,1–5,6
	breadth	3	6,6		6,2–7,2
I^3	length	6	7,5	0,4	7,1–8,0
	breadth	6	8,9	0,6	8,2–9,7
C	length	12	13,0	0,5	12,3–14,0
	breadth	12	9,1	0,5	8,3–9,9
P^1	length	5	6,4	0,4	6,0–7,0
	breadth	5	5,9	0,5	5,4–6,6
P^2	length	21	14,6	1,1	12,6–16,1
	breadth	20	9,4	0,5	8,6–10,2
P^3	length	29	19,6	1,1	16,5–21,1
	breadth	31	12,6	0,7	11,0–13,8
P^4	length	28	28,8	1,1	25,8–31,2
	breadth	26	17,1	1,1	15,6–19,5
	length metastyle	26	10,5	0,5	9,3–11,5
M^1	length	16	5,6	0,5	4,7–6,6
	breadth	16	12,8	0,7	12,0–14,1
I_3	length	4	5,6	0,2	5,4–5,8
	breadth	4	6,2	0,1	6,1–6,3
C	length	15	12,9	0,6	11,6–13,9
	breadth	15	9,8	0,5	8,9–10,5
P_2	length	13	13,6	0,7	11,9–14,8
	breadth	14	8,1	0,6	7,2–9,1
P_3	length	20	17,9	0,7	16,7–19,1
	breadth	21	10,8	0,5	9,7–11,5
P_4	length	23	19,2	0,7	17,4–20,4
	breadth	21	10,9	0,5	9,7–12,1
M_1	length	17	20,8	0,9	19,1–22,0
	breadth	19	10,1	0,6	9,3–11,0
	length talonid	15	4,3	0,3	3,7–4,7

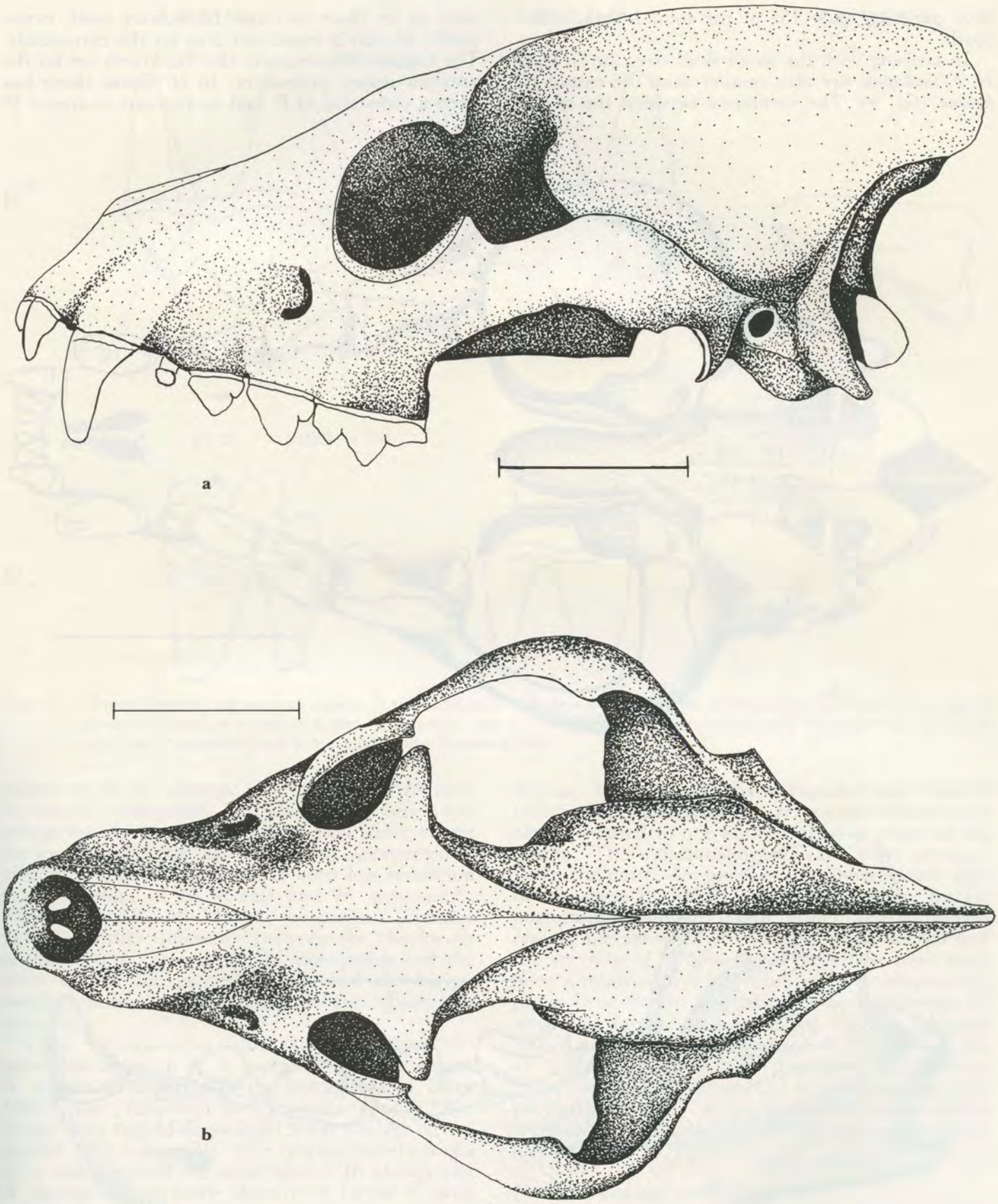

Figure 1. Skull of *Hyaena hyaena makapani* showing (a) lateral and (b) dorsal aspects (scale bar = 5 cm). (Composite reconstruction based mainly on M 2530, M 8348 and M 299.)

20,6 per cent (n = 15) of the total length of the tooth.

In keeping with the small skull size, the teeth of *H. h. makapani* are also smaller than the extant *H. hyaena* (fig. 4). The similarity between the two is seen to be close in terms of various tooth ratios (table 4); this is especially true for the carnassials. The biggest differences in the cheekteeth are for the anterior upper premolars. In *H. hyaena* there has been a reduction of P^1 and an increase in size of P^2

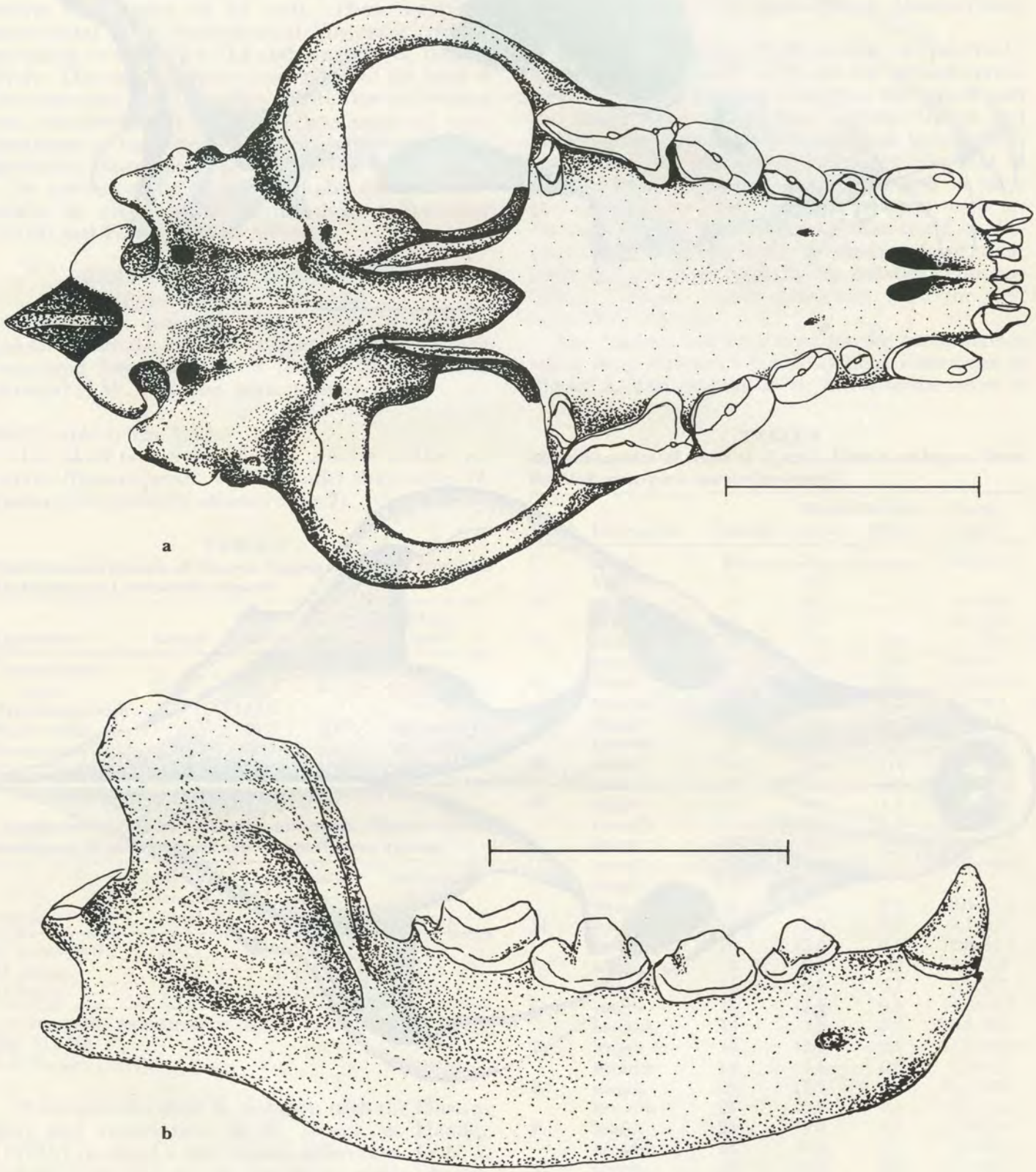

Figure 2. Reconstructed skull and mandible of *Hyaena hyaena makapani* showing (a) ventral aspect of skull and (b) lateral aspect of mandible (scale bar = 5 cm). (Skull reconstruction as in Figure 1; mandible based on M 262.)

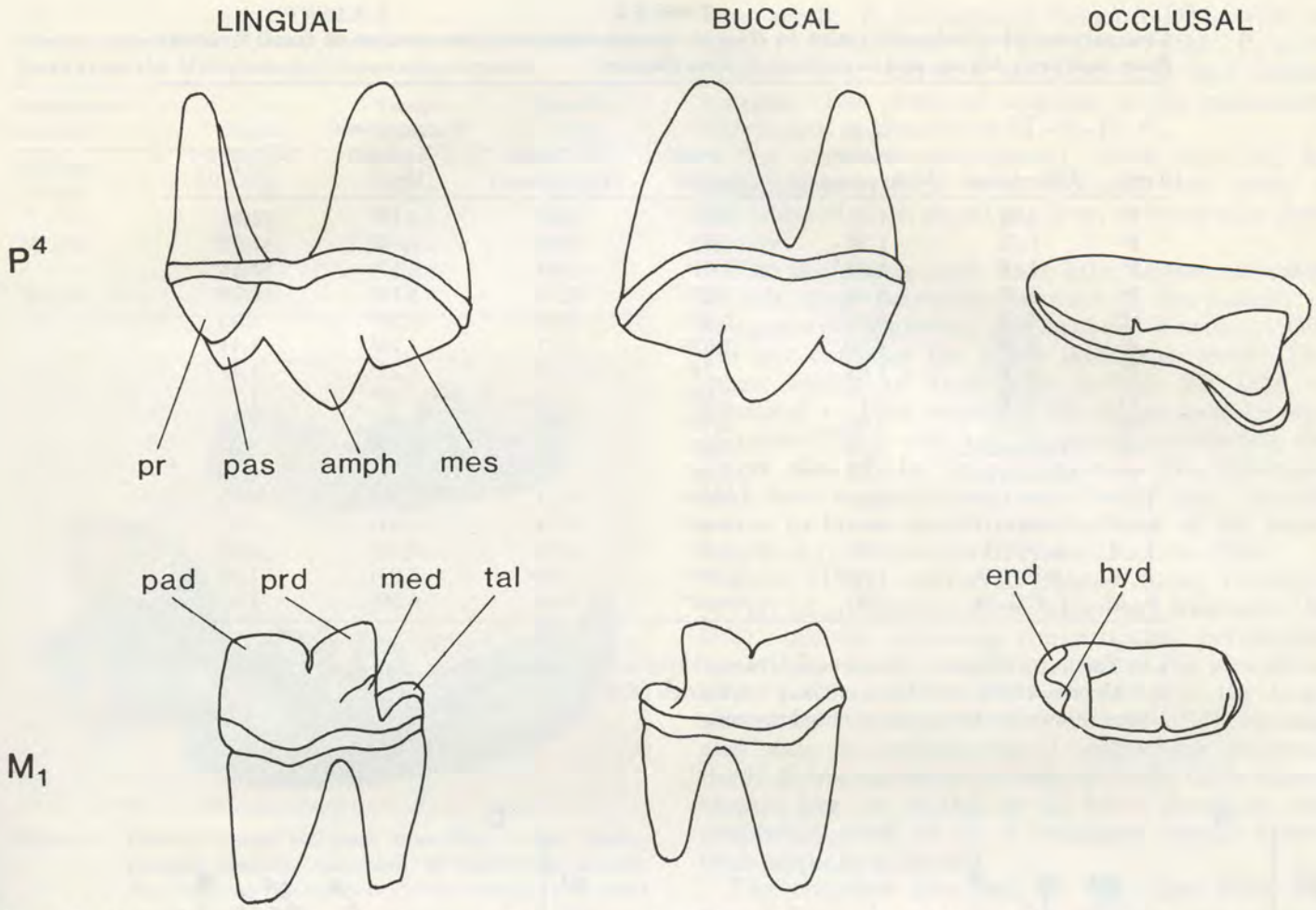

Figure 3. Lingual, buccal and occlusal aspects of the carnassials of *Hyaena hyaena makapani*. Terminology: pr= protocone, pas = parastyle, amph = amphicone, mes = metastyle, pad = paraconid, prd = protoconid, med = metaconid, tal = talonid, end = entoconid, hyd = hypoconid (after Gromova 1968).

relative to *H. h. makapani*. The pattern for *H. abronia* and *H. namaquensis* is similar to the other two except for the upper molar, and to a lesser extent the lower molar (fig. 4). This is not unexpected in view of the fact that there has been less reduction in the molars of *H. abronia* and *H. namaquensis,* where both M^2 and M_2 may be present (Hendey 1978). Another difference between the cheekteeth of the older *H. abronia* and *H. namaquensis* and the other two is the presence of P_1 and the higher length:breadth ratio of most of the cheekteeth (table 4).

These comparisons illustrate the close relationship between *H. h. makapani* and the extant *H. hyaena,* and supports the contention of Ewer (1967) that they are not separate species, but rather that the Makapansgat form should be regarded as a subspecies. The relationship between *H. h. makapani* and the older species *H. abronia* and *H. namaquensis* is more obscure in terms of skull morphology and tooth measurements. Hendey (1978) also noted differences in postcranial elements, where *H. abronia* had relatively longer hind limbs than the extant *H. hyaena*. Hendey (1978) concluded that *H. abronia* was the likely ancestor of *H. hyaena,* with *H. h. makapani* the intermediate form, and *H. namaquensis* the possible ancestor of *H. brunnea*. The comparisons in Figure 4 and Table 4 indicate that *H. abronia* and *H. namaquensis* are more closely related to one another than to either of the others. The relationship appears even stronger when the entire dentition is considered, since they both possess P_1, M^2 and M_2 and have more similar postcranial elements than either of the extant *Hyaena* species or *H. h. makapani*. If *H. abronia* was the ancestor of *H. h. makapani* then there must have been a relatively rapid evolutionary developmental phase between the late Miocene/early Pliocene *H. abronia* at Langebaanweg, dated 4–5 My (Hendey 1978), and the first appearance of *H. hyaena,* dated at 3 My in East Africa (Coppens and Howell 1976). A form from East Rudolf exhibiting the dental characters of *H. hyaena* and many of the cranial features of *H. abronia* may well be an intermediate form (Leakey 1976).

Deciduous dentition (table 5, fig. 5)

The deciduous dentition of hyaenas bears little resemblance to the permanent dentition, and without good comparative material it is unlikely that deciduous teeth would be correctly identified. Fortunately, two specimens from the Limeworks contained deciduous teeth with permanent teeth erupting. By working the surrounding bone away

TABLE 4

Comparison of cheektooth ratios in *Hyaena hyaena makapani*, two species of fossil hyaenas from southern Africa, and two extant hyaena species

Teeth	Dimensions	*H. h. makapani* (Makapansgat)	*H. hyaena* (extant)	*H. abronia* (Langebaan)	*H. namaquensis* (Namaqua-land)	*H. brunnea* (extant)
P^1	L/B	1,09	1,04[a]	1,08[c]	1,18[d]	1,04[a]
P^2	L/B	1,56	1,64[e]	1,82[c]	1,78[d]	1,49[e]
P^3	L/B	1,54	1,61[e]	1,64[c]	1,57[d]	1,43[e]
P^4	L/B	1,69	1,62[b]	1,73[c]	1,70[d]	1,70[b]
M^1	L/B	0,44	0,50[c]	0,62[c]	0,56[d]	0,44
P_2	L/B	1,70	1,55[c]	1,77[c]	1,75[d]	1,41[e]
P_3	L/B	1,65	1,74[e]	1,82[c]	1,77[d]	1,47[e]
P_4	L/B	1,77	1,82[e]	1,90[c]	1,88[d]	1,71[e]
M_1	L/B	2,06	2,00[b]	2,02[c]	2,20[d]	2,05[b]
M_1	Trigonid/L	0,79	0,80[f]		0,75[d]	0,84[f]
P^4	Metastyle/L	0,37	0,36[f]			0,38[f]
P^3, P^4	L P^3/L P^4	0,68	0,68[b]	0,71[c]	0,71[d]	0,65[b]
M^1, P^4	W M^1/L P^4	0,44	0,46[e]	0,54[c]	0,54[d]	0,37[e]
P_3, P_4	L P_3/L P_4	0,92	0,93[b]	0,92[c]	0,92[d]	0,87[b]
P_3, P_4	B P_3/B P_4	1,01	0,99[e]	0,96[c]	0,97[d]	1,04[e]
P_4, M_1	L P_4/L M_1	0,92	0,98[b]	0,90[c]	0,89[d]	1,01[b]

Key:
a = Toerien (1952), b = Ficcarelli and Torre (1970), c = Hendey (1974b), d = Hendey (1978), e = Ewer (1955a), f = Kurten (1956).
Unless otherwise stated = own measurements.

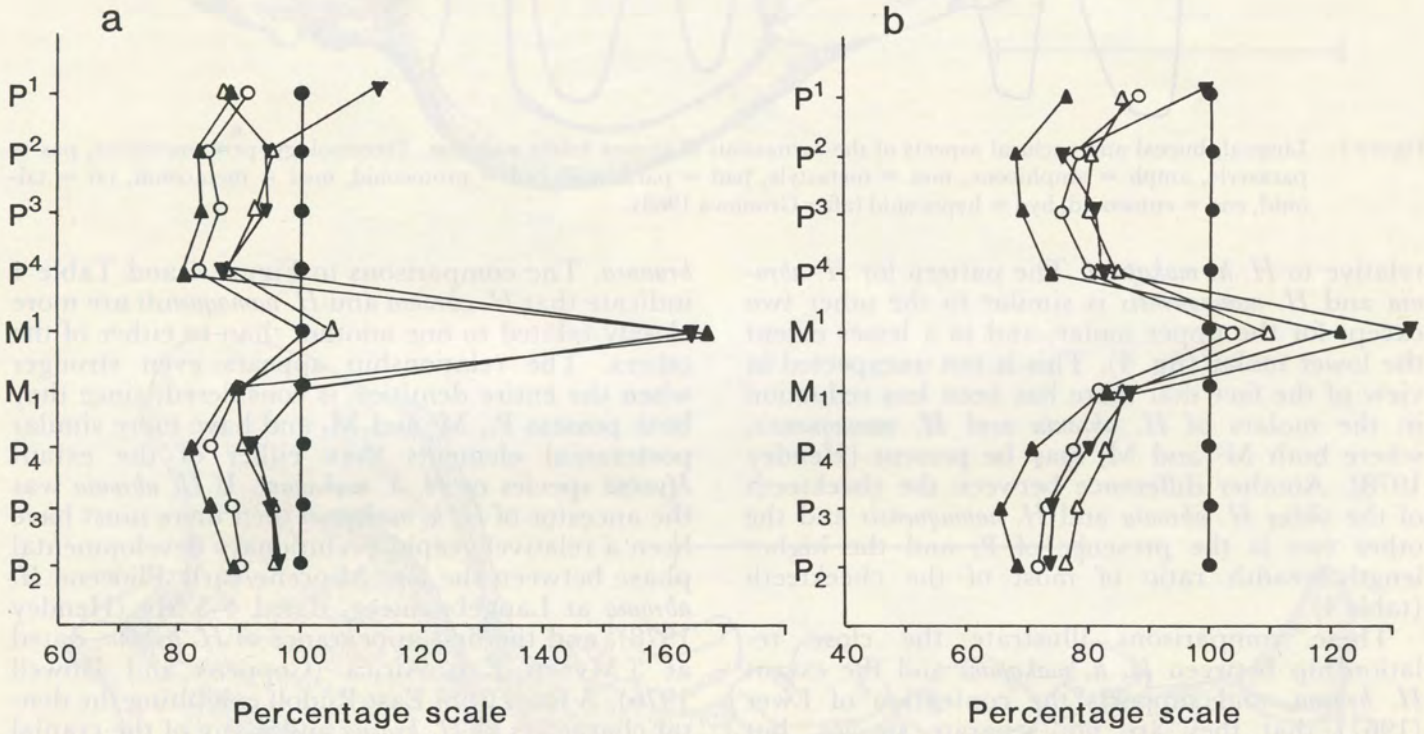

Figure 4. Ratio diagram comparing (a) mean crown lengths and (b) mean crown widths in *Hyaena hyaena makapani* (○), *Hyaena hyaena* extant (△), *Hyaena abronia* (▲) and *Hyaena namaquensis* (▼). Standard of comparison (100 per cent) *Hyaena brunnea* extant (●). Data from Toerien (1952), Kurten (1956), Hendey (1974b, 1978) and own measurements.

with an emery disc and "Vibro-tool" the permanent teeth were exposed and identification as *H. h. makapani* confirmed.

Specimen M 603 is a portion of a right maxilla with DM^3, DM^4 and M^1 *in situ*, with P^4 starting to erupt, and P^3 about to do so. DM^4 resembles M^1 in having a similar crown pattern and being located in a comparable position. Like M^1, it also has a greater breadth (buccolingual axis) than length (mesiodistal axis). DM^3 is a slender shearing tooth functioning as the upper carnassial, and it is comparable to P^4. It has three cusps and a blade arranged roughly in a straight line, meaning that it has one more cusp than P^4, its functional replace-

TABLE 5
Measurements of *Hyaena hyaena makapani* deciduous teeth from the Makapansgat Limeworks deposit

Specimen number	Tooth	Length (mm)	Breadth (mm)
M 2340	DM^3	21,3	
M 603	DM^3	20,2	12,0
	DM^4	7,6	12,3
M 2284	DM_2	*c.* 14,0	*c.* 5,7
	DM_3	15,0	6,3
M 2342	DM_3	14,7	5,8

Figure 5. *Hyaena hyaena makapani* mandibles from Makapansgat showing specimen M 2284 with deciduous teeth, and permanent teeth erupting, and adult paratype (M 252). The mandible of M 2284 was worked away to expose the permanent teeth.

ment tooth. The extra cusp on DM^3 is the paracone which is separate from the metacone, unlike in P^4 where these two cusps have fused to form the amphicone. The DM^3, therefore, has a parastyle, paracone, metacone and metastyle in a line proceeding from the mesial to the distal end. It also has a large protocone situated lingually relative to the paracone and metacone. The amphicone of P^4 was erupting immediately distal to DM^4, and the tip of the protocone of P^4 had erupted anterior to the lingual extension of DM^4. When the permanent premolars were exposed by working away the maxilla, the parastyle of P^4 could be seen erupting immediately lingual to the metastyle of DM^3, and P^3 beneath the paracone and parastyle of DM^3. It appears that P^4 would have erupted before P^3, and the order of eruption of the three hindmost permanent cheekteeth was M^1–P^4–P^3.

Specimen M 2284 consists of the major portion of a right mandible with DM_2 and DM_3 *in situ*, and the permanent teeth C, P_2, P_3 and P_4 about to replace. M_1 had been lost prior to fossilization and DM_4 had either been shed, or like M_1 had been lost. Unlike in the adult, the mandible is short, shallow and comparatively fragile. Both DM_2 and DM_3 are unlike the permanent teeth, being high and narrow. The mandible was worked away on both lingual and buccal sides to expose the permanent teeth. P_2 is erupting beneath DM_2 with its main cusp between the two roots of DM_2. P_3 is replacing DM_3, and P_4 is replacing DM_4 in a similar manner. The order of eruption of the permanent cheekteeth appears to be M_1–P_2–P_4–P_3.

The state of development of the roots of the erupting permanent teeth indicates that many of the isolated teeth found are from animals of a similar age.

The deciduous teeth have little taxonomic value at this stage primarily because of the paucity of comparative material, and because Kurten (1956) did not consider the lower deciduous teeth. The mean length of 14,85 mm (n = 2) for DM_3 is identical to that recorded for the striped hyaena (Kurten 1956), which is surprising considering the larger size of the striped hyaena. The damaged DM_2 has an approximate length of 14 mm, but this seems to be an overestimate in view of the mean length of 11,76 mm for *H. hyaena* (Kurten 1956).

Ewer (1967) expressed doubts about Toerien's (1952) identification of the maxillary fragment (M 603), but by exposing the erupting permanent teeth it has been possible to confirm the identification. Toerien (1952) drew attention to the large size of DM^3 compared to specimens of *H. brunnea*, and also to morphological differences between them. It has not been possible to verify these observations but, in relation to the lower dentition, the deciduous teeth of *H. h. makapani* appear larger than might be expected.

The eruption sequence for the upper teeth deduced from the maxilla (M 603) fits the pattern shown by examples from the families Felidae, Mustelidae and Viverridae (Ewer 1973). In these families the eruption sequence of the lower teeth is M_1–P_2–P_3–P_4, and not M_1–P_2–P_4–P_3 as it appears to be in specimen M 2284.

Pachycrocuta brevirostris

All *Pachycrocuta brevirostris* material obtained came from Member 3 (Lower Phase 1 grey breccia) (J.W. Kitching, pers. comm.).

Since Toerien's (1952) description of the remains of a large hyaena from the Limeworks three additional specimens attributed to the same species have been found. The isolated left lower canine (M 606) described by Toerien fits into the canine alveolus of specimen M 2565, and may be from the same individual. The specimens were mostly fragmentary and the teeth extensively worn, so that accurate measurements could not always be obtained (table 6, fig. 6).

The most noteworthy feature of this form relates to its size, and only *P. brevirostris* has teeth of a comparable size (Howell and Petter 1980). It is principally on this basis that the Makapansgat specimens are assigned to the genus *Pachycrocuta*. The features considered most characteristic of the genus relate to details of M_1, P_4 and P^4 (Ficcarelli and Torre 1970, Howell and Petter 1980). Unfortunately, in the Makapansgat specimens neither M_1 nor P_4 is present, and in neither of the P^4 specimens

TABLE 6
Measurements of *Pachycrocuta brevirostris* teeth from the Makapansgat Limeworks deposit

Specimen number	Tooth	Length (mm)	Breadth (mm)
M 2565	P_2	18,4	13,0
	P_3	23,0	17,1
M 604	P_3	24,9	19,4
M 6010	P^4	42,0	
M 2533	P^3	*c.* 25,2	*c.* 16,1
	P^4	*c.* 44,0	*c.* 20,5
	M^1	*c.* 6,0	*c.* 11,5

Figure 6. *Pachycrocuta brevirostris* mandible fragments from Makapansgat. (a) Specimen M 604 and (b) specimen M 2565.

available can details of the crown pattern be discerned. Nevertheless the Makapansgat form has the robust premolars found in *Pachycrocuta*. In particular, the breadth:length ratios of 0,71 and 0,74–0,78 for P_2 and P_3 respectively are closer to *P. brevirostris* than to other species of *Pachycrocuta* or *Hyaena* (Howell and Petter 1980).

The only hyaena of comparable size from South African Plio/Pleistocene deposits is *Hyaena bellax* from Kromdraai (Ewer 1954). Ewer (1967) concluded that the closest relative of the Kromdraai form was *Hyaena brevirostris* from Europe, a viewpoint supported by Ficcarelli and Torre (1970) when they grouped them as two species under the genus *Pachycrocuta*. Howell and Petter (1980) went further and synonymized the Makapansgat and Kromdraai forms as *P. bellax*. There are, however, differences, notably the larger teeth in the Makapansgat form, particularly P^4. In addition the breadth:length ratios in the Kromdraai form are smaller — 0,67 and 0,72 for P_2 and P_3 respectively. The M^1 is less developed in the Makapansgat form, being considerably smaller in relation to P^4. These differences seem sufficient to warrant separation at the specific level and consequently the Makapansgat form has been assigned to *P. brevirostris*.

Large hyaenas of the *Pachycrocuta* type have therefore twice appeared in southern Africa. As far as can be established the only other site in Africa where these large hyaenas have been recovered is Ain Brimba in Tunisia (Howell and Petter 1980).

Crocuta crocuta

One specimen (M 2567) attributed to *C. crocuta* was obtained from Member 4 (Upper Phase 1 breccia) (J.W. Kitching, pers. comm.) (fig. 7). No other hyaena material has been recovered from this horizon.

Figure 7. *Crocuta crocuta* mandible M 2567 from Makapansgat.

The specimen is the major part of a left mandible with P_2, P_3, P_4 and M_1. Part of the talonid of M_1 was damaged, but otherwise the teeth are well preserved and could be measured (table 7). The trigonid comprises about 87 per cent of the total length of M_1. The damage to the talonid is such that it is impossible to establish if a metaconid was present. Absence of a metaconid would have confirmed identification as *Crocuta,* although its presence would not have excluded the possibility that the specimen belongs to *Crocuta* (Kurten 1956).

TABLE 7
Measurements of *Crocuta crocuta* teeth (specimen M 2567) from the Makapansgat Limeworks deposit

Tooth	Length (mm)	Breadth (mm)	Trigonid (mm)
P_2	14,2	9,1	
P_3	19,3	13,7	
P_4	21,5	13,1	
M_1	*c.* 26,3	11,4	23,0

The teeth are slightly smaller than those of the extant *C. crocuta,* but their similarity is immediately apparent, particularly when compared to the genus *Hyaena* (fig. 8). Ficcarelli and Torre (1970) established several useful dental characters for separating the genera *Crocuta* and *Hyaena,* including two based upon the lower dentition — P_4 length:M_1 length, and M_1 breadth:M_1 length. Both of these ratios for specimen M 2567 fall within the *Crocuta* range (table 8) and outside the *Hyaena* range (table 4).

A comparison of tooth dimensions between the extant *C. crocuta* and the specimens from Makapansgat, East Rudolf, Olduvai, and Swartkrans plus Kromdraai combined shows the similarity between the forms (table 8). The most marked change is seen in M_1, where there has been a trend towards a relative increase in the length up to the extant form. There appears to have been little change in the lower dentition since the earliest occurrence of *C. crocuta.* Leakey (1976) stated that there had been little change in cranial or postcranial morphology of *C. crocuta* for 2 My.

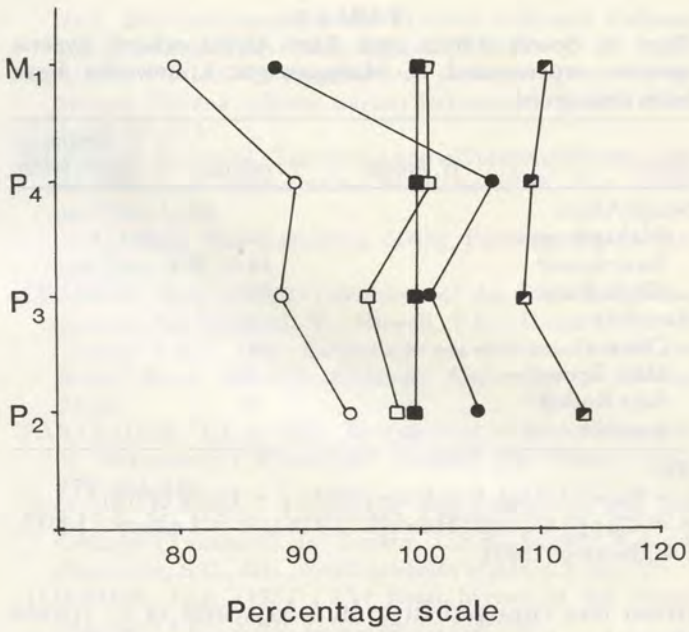

Figure 8. Ratio diagram comparing mean crown lengths in *Crocuta crocuta* from Makapansgat (□), *C. crocuta* from Swartkrans plus Kromdraai (◪), *Hyaena hyaena makapani* (○) and *Hyaena brunnea* (●). Standard of comparison (100 per cent) *Crocuta crocuta* extant (■). Data from Ewer (1954, 1955a), Kurten (1956), Leakey (1976) and own measurements.

TABLE 8
Comparison of cheektooth ratios in *Crocuta crocuta* from several Plio/Pleistocene deposits in Africa, and the extant form

Teeth	Dimension	Makapansgat	East Rudolf [a]	Olduvai [b]	Swartkrans and Kromdraai [c]	Extant [d]
M_1	L/B	2,31	2,26	2,27	2,32	2,39
P_4	L/B	1,64	1,66	1,61	1,72	1,77
P_3	L/B	1,41	1,44	1,44	1,50	1,44
P_2	L/B	1,56	1,41	1,43	1,43	
P_4, M_1	L P_4/L M_1	0,82	0,77	0,76	0,80	0,81
P_3, P_4	L P_3/L P_4	0,90	0,94	0,95	0,94	0,94

Key:
a = Leakey (1976), b = Petter (1973), c = Ewer (1954, 1955a), d = Ficcarelli and Torre (1970).

Correlations and dating

Both *H. hyaena* and *C. crocuta* have been recovered at several sites of Plio/Pleistocene age in East Africa and South Africa (table 9). These include some sites in East Africa for which K-Ar dates have been obtained. The earliest datable deposits at which a small hyaena similar to the Makapansgat form have been recovered are the lower member of the Koobi Fora Formation, East Rudolf (Leakey 1976), and the Usno Formation and Member B of the Shungura Formation, Omo Group (Howell and Petter 1976). The earliest dated deposits containing *C. crocuta* are the lower member of the Koobi Fora Formation, East Rudolf (Leakey 1976) and Member G of the Shungura Formation, Omo Group (Howell and Petter 1976). Dates for these formations are: lower member Koobi Fora 2,61–3,18 My (Fitch and Miller 1976); Usno Formation > 2,97 My, Member B Shungura Formation 2,95–2,97 My, and Member G Shungura Formation 1,83–1,93 My (Coppens and Howell 1976). It must be emphasized that *H. hyaena,* and to a lesser extent *C. crocuta,* occurred in later horizons from both East Rudolf and the Omo Group (Leakey 1976, Howell and Petter 1976). Leakey (1976) drew attention to the fact that the Hyaenidae, especially *H. hyaena,* have little value in site comparisons and correlations because the den-

TABLE 9
Sites in South Africa and East Africa where hyaena species represented at Makapansgat Limeworks have been recovered

Sites	*H. hyaena*	*C. crocuta*	*P. brevirostris and P. bellax*
South Africa			
Makapansgat	x	x	x
Swartkrans[a]		x	
Kromdraai[b]		x	x
East Africa			
Olduvai[c]	x	x	
Omo Group[d]	x	x	
East Rudolf[e]	x	x	
Laetolil[f]	x	x	

Key:
a = Ewer (1955a), b = Ewer (1954), c = Petter (1973), d = Coppens and Howell (1976), e = Leakey (1976), f = Dietrich (1942).

tition has changed little in 3 My, and in *C. crocuta* there has been little cranial or postcranial change in 2 My. Thus, based upon the hyaena material, Member 3 (Lower Phase 1 grey breccia) could be any age up to 3 My and Member 4 (Upper Phase 1 breccia) up to 2,6 My but, because of their conservatism, hyaenas appear to have limited use in correlations for dating purposes. Consequently there is nothing in the hyaena material to contradict the palaeomagnetic age estimate of > 2,9 My for the Makapansgat Limeworks grey breccia (Member 3) (Partridge 1979).

CONCLUSIONS

Cranial and dental characters confirm the identification of the abundant remains of the small hyaena in Member 3 (Lower Phase 1 breccia) as a subspecies of the extant striped hyaena. Comparisons support Hendey's (1978) suggestion that its likely ancestor is *H. abronia* from Langebaanweg. However, the relationship between *H. h. makapani* and extant *H. hyaena* seems to be closer than the relationship between *H. h. makapani* and *H. abronia; H. abronia* seems to be more closely related to *H. namaquensis*.

Fragmentary remains of a large hyaena in Member 3 (Lower Phase 1 grey breccia) are identified as *P. brevirostris*. This large hyaena shows affinities to *P. bellax* from Kromdraai, and these specimens seem to be the only records of these large hyaenas from Africa.

Hyaenas are represented by one specimen from Member 4 (Upper Phase 1 breccia), here identified as *C. crocuta*. This form is similar to the extant form and to fossil Plio/Pleistocene forms from East Africa.

C. crocuta seems to have replaced *H. h. makapani* and *P. brevirostris* in the upper horizons. Kurten (1956) documented replacement of *P. brevirostris* by *C. crocuta* at several deposits in Europe and China, which he believed was due to direct competition. A similar replacement of *H. hyaena* by *C. crocuta* occurred in the Upper Pleistocene of Palestine, with *H. hyaena* only reappearing after the extinction of *C. crocuta* (Kurten 1965). By contrast, in several East African deposits both *H. hyaena* and *C. crocuta* have been recovered from the same horizon (Leakey 1976, Howell and Petter 1976), and the ranges of the extant forms overlap (Kruuk 1976). Consequently the apparent disappearance of *H. h. makapani* in later horizons at Makapansgat is unlikely to be due only to competition with *C. crocuta*.

H. h. makapani and *C. crocuta* are morphologically similar to forms from datable deposits in East Africa. Correlations indicate that the age of Member 3 (Lower Phase 1 grey breccia) could be up to 3,0 My, and Member 4 (Upper Phase 1 breccia) up to 2,6 My. The hyaena material therefore provides general support for the palaeomagnetic age estimate of > 2,9 My for the grey breccia (Partridge 1979). However, because the Hyaenidae, especially *H. hyaena* and to a lesser extent *C. crocuta*, are so conservative they have limited value in site correlations for dating purposes.

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