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NEW EVIDENCE OF THE GIANT HYAENA, *PACHYCROCUTA BREVIROSTRIS* (CARNIVORA, HYAENIDAE), FROM THE GLADYSVALE CAVE DEPOSIT (PLIO-PLEISTOCENE, JOHN NASH NATURE RESERVE, GAUTENG, SOUTH AFRICA)

by

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ABSTRACT

A well preserved cranium which represents the most complete skull of *Pachycrocuta brevirostris* (Carnivora, Hyaenidae) discovered in Africa, and a maxillary fragment from the Gladysvale Cave Deposit (John Nash Nature Reserve, Gauteng, South Africa) are described and compared to other fossil and extant hyaenid specimens from South Africa and Europe. In addition, some aspects of functional morphology in the hyaenid dentition are reconsidered and suggested to be directly related to the palaeoecological role of *P. brevirostris*.

KEYWORDS: Plio-Pleistocene, *Pachycrocuta brevirostris*, morphology, functional morphology, palaeoecology, South Africa, Europe.

INTRODUCTION

In 1954, Ewer described the fairly complete cranium KA-55 from the Kromdraai A Deposit and named the new species *Hyaena bellax* (Ewer 1954b). Sixteen years later the suggestion was made that this specimen be assigned rather to the genus *Pachycrocuta* (Ficcarelli & Torre 1970), known from several sites in Eurasia. At least two species of *Pachycrocuta* are known in Europe, *P. brevirostris* and *P. perrieri* (Werdelin & Solounias 1991; Guérin & Patou-Mathis 1996), and the two taxa are distinguished by metric tooth features (Werdelin & Solounias 1991: 22). Howell & Petter (1980) have pointed out close affinities between *P. bellax* and the comparatively well known Eurasian specimens of *P. brevirostris* and *P. perrieri*. This view was also supported by Turner (1986, 1987, 1988, 1990; Turner & Anton 1996), who had originally postulated close affinities between *Pachycrocuta* and *Hyaena*. Howell & Petter (1980) favored a two-lineage theory: *P. pyrenaica – P. perrieri / P. brevirostris / H. hyaena*. Ficcarelli & Torre had proposed a similar theory in 1970, although their analysis relied on different features. Further studies including all hyaenids (Werdelin & Solounias 1991) led to *H. brunnea* being placed in the new genus, *Parahyaena*, because of the lack of shared synapomorphies with *H. hyaena*.

Currently, research interests have shifted to the question of attributing a palaeoecological role to the giant hyaena *Pachycrocuta* in the Plio-Pleistocene. Turner & Anton (1996) have offered initial concrete conclusions from its fossil record. From this same perspective, an initial comprehensive study of new East African material (Turkana Basin, Kenya) has contributed interesting insights (see Werdelin 1999). On the basis of new material from the Gladysvale Cave Deposit (Gauteng, South Africa) assigned to *P. brevirostris*, we examine and review certain morphological aspects and discuss the palaeoecological implications.

MATERIAL AND METHODS

(List of abbreviations on page xxx)

BPI: GV 3914 *Pachycrocuta brevirostris* (fairly complete cranium with dentition: P^2, P^3, P^4, M^1 sin. et dext.), dump 8, block 1, collected 28.4.1996.

BPI: GV 4264 *Pachycrocuta brevirostris* (left maxillary fragment with dentition: P^2, P^3, fragmentary P^4), dump 8, collected 9.10.1996.

Locality: Gladysvale Cave Deposit (John Nash Nature Reserve, Gauteng, South Africa)

Age: approximately 1.0 million years

Comparative fossil material

NMB: Se 279 *Pliocrocuta perrieri* (Croizet & Jobert 1828) (skull and dentition: P^1, P^2, M^1 dext., P^3, M^1 sin.). St.V. 974 *Euryboas* sp. (cranium, dentition: P^2, P^3, P^4, M^1 sin. et dext., upper C, I^1, I^2, I^3 dext.), V.A. 2005 *Pachycrocuta brevirostris* (*Hyaena robusta* LeVille 1921: cranium, dentition: P^1, P^2, P^3, P^4, M^1 sin. et dext.). V.A. 65 *Pachycrocuta brevirostris* (*Hyaena robusta* LeVille 1921: cranium, dentition: I^3, P^1, P^2, P^3, P^4, M^1 dext., upper C sin. fragmentary, I^3 sin. fragm. P^3 sin. fragm.)

TM: KA 55 *Pachycrocuta brevirostris* (*Hyaena bellax* Ewer 1954b) (left half of a cranium with articulated mandible, right maxillary fragment, dentition).

BPI: M 2530 *Parahyaena brunnea.* M 2567 cf. *Chasmaporthetes.* M 299, M 8348, M 245, M 248, M 254, M 8297, M 8925, M 2560, M 2587, M 8295, M 253 *Hyaena makapani.*

TM: KA 56 *Crocuta spelaea capensis*, KA 58 and KA 60 *Crocuta ultra*, SK 314 *Hyaenictis*, SK 326 *Parahyaena brunnea dispar*, Sts 128 *Crocuta crocuta*, Sts 129 hyaenid indet., Sts 135 *Euryboas silberbergi*, SF 376 *Pachycrocuta brevirostris.*

Comparative extant material

Hyaena hyaena
ZMUZ: 10155, 10156, 10157, 17510. FIS: 1158, 1356, 4273, 4578, 6729, 4644, 4645, 1158, 1356, 15687, 15689, 15690, 15691, 32782, 63952, 15687 (juvenile).

Parahyaena brunnea
FIS: 15684, 6926.

Crocuta crocuta
ZMUZ: 12258, 13096, 13097, 13098. SI: 4579, 16358 (juvenile). MS: ZA 1147M9, 162 (juvenile).

Measurements were taken with calipers to the nearest 0.1 millimeter several times and averaged each time. Where possible, measurements were taken buccally. Terminology follows current literature.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowditch, 1821
Family HYAENIDAE Gray, 1869
Genus *Pachycrocuta* Kretzoi, 1938
Pachycrocuta brevirostris (Aymard, 1846)

Synonymy: see Werdelin & Solounias (1991: 23), Turner & Anton (1996) and Werdelin (1999).

DESCRIPTION

GV 3914 (Figures 1-5, measurements see Table 1)

The cranium

The cranium consists of a large and broad hyaenid skull belonging to a relatively old individual (Figures 1-4). The upper jaws, the anterior portion of the cranium and the left zygomatic arch are preserved. The latter increases considerably in depth and massiveness while projecting dorsolaterally. In ventral view, the zygomatic arch appears trapezoidal in outline (Figure 2). The posterior portion of the frontals and the palate, plus a major part of the left maxilla, including the infraorbital foramen, are penetrated, distorted, shifted or destroyed by calcite crystals containing breccia infill. The original vaulting of the palate cannot be directly observed, but there are longitudinal crevices on the left and right palatine, suggesting that considerable vaulting was originally present and was at least comparable to the condition usually stated for *C. crocuta.*



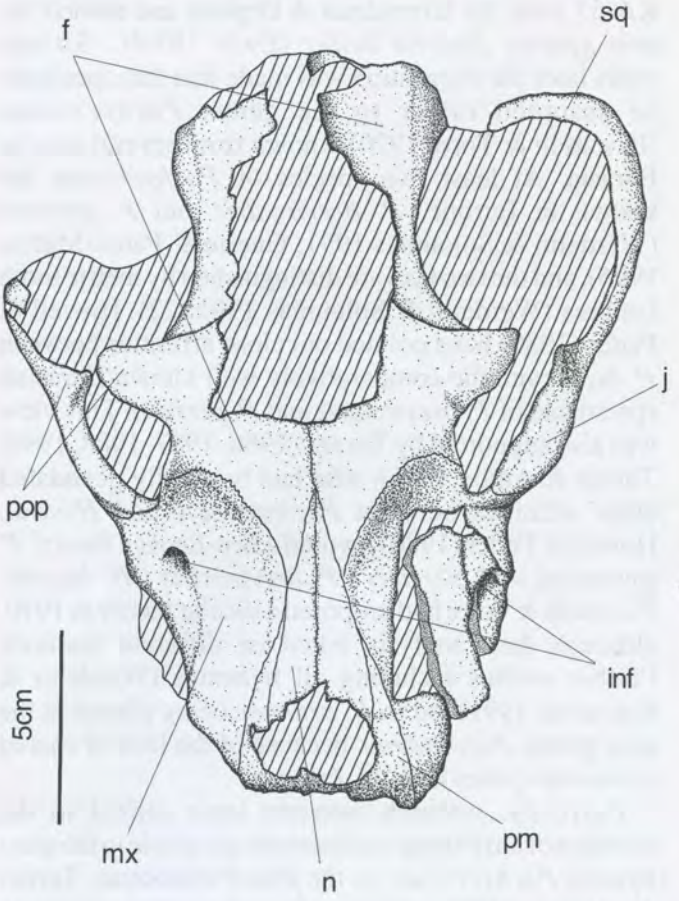


Figure 1A, B. Dorsal view of the skull of *Pachycrocuta brevirostris* (GV 3914). Hatch lines indicate breccia infill. The scale bar equals 5 cm.

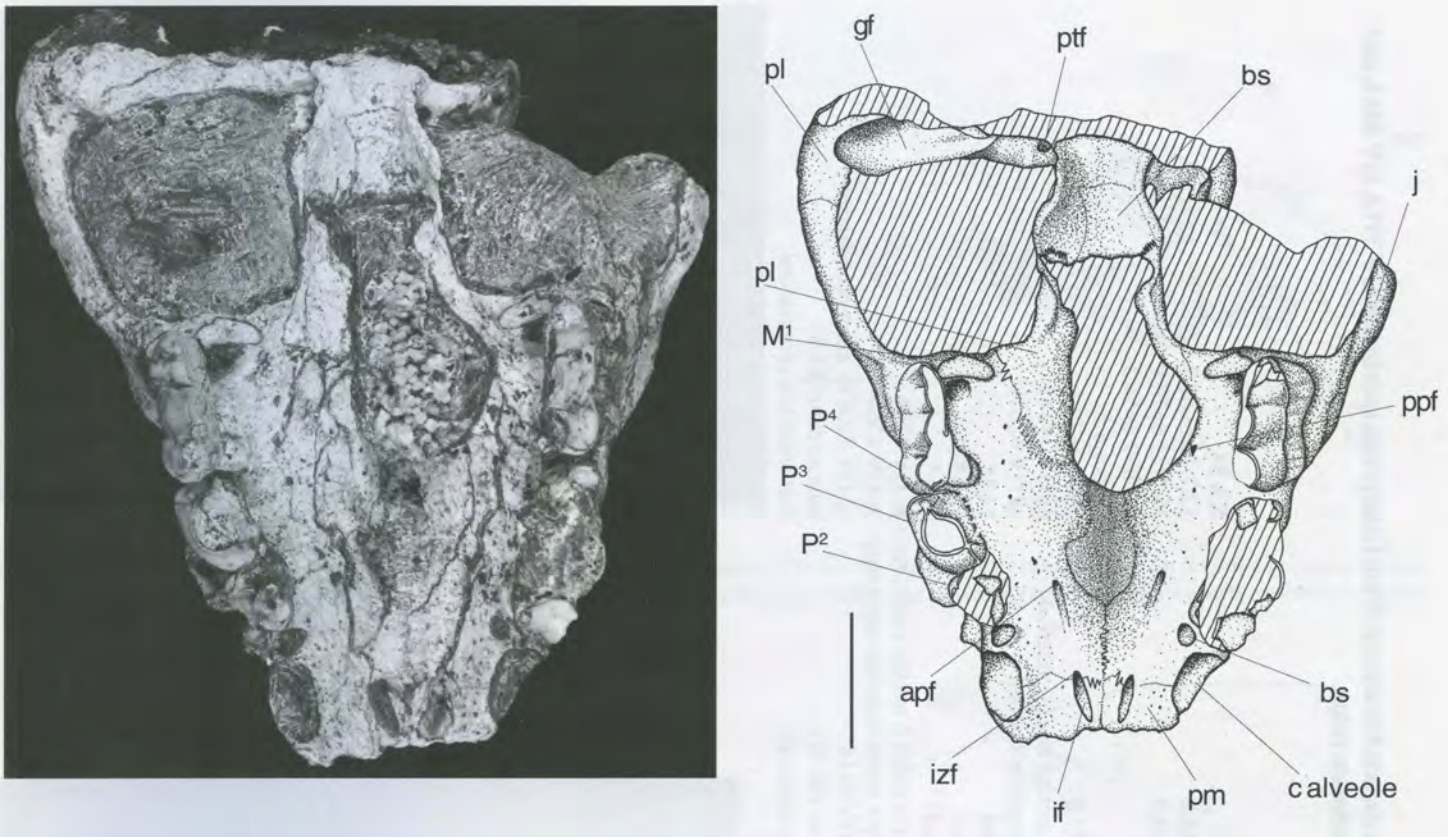


Figure 2A,B. *Pachycrocuta brevirostris* skull (GV 3914) in ventral view. Stippled lines indicate the probable course of the sutures. Wear facets are blank (Figure B). The scale bar equals 5 cm.

The postorbital processes of the jugals are large, oriented vertically and project slightly forwards rather than backwards. Below the orbit, the dorsal border of the jugal is flat and sloped, and reaches far anteroventrally.

All sutures in the specimen differ in accordance with their state of preservation or, in some cases, because of their ontogenetic development. Although some sutures in the forehead can be traced easily, their preservation in the palate is such that it is often impossible to distinguish between bone margins and fine cracks. Nevertheless, we include their most probable courses, using dotted lines (Figure 4). The maxilla-frontal suture reaches further posteriorly than in extant hyaenids. Unfortunately, the nasals are too imperfectly preserved to be measured accurately; they are comparatively long and broad relative to the width of the skull. In lateral view, the frontals slope down less abruptly than in extant hyaenids and the face is characterized by an upwardly tilted forehead.

The posterior portion of the maxilla and the posterior part of the jugal form the well developed cheek region, which bears a conspicuous impression between the roots of the upper P^4 (dented area of at least one square centimetre, compare Qiu 1987: 53).

The incisive foramina lie at the level of the anterior portion of the canine alveole and the incisive fossa reaches almost as far to the posterior as the hindmost point of the root of the second premolar. Premaxilla-maxilla sutures pass near the posterior end of the incisive foramen. The foramen incisivum is narrow at its posterior end, compared to extant *Hyaena* and *Crocuta*. An index of the foramen palatinum anterior length versus fossa palatina length would be advantageous, but cannot be given. Judged from the position of the foramen palatinum anterior, there is greater similarity to the 'crocutoid' than to the 'hyaenid' type (compare Qiu 1987: 62).

The jugal-maxilla suture describes a regular curve some distance from the orbita in the rostral portion. The posterior course is more difficult to trace, but both features seem to be 'crocutoid'.

The dentition (Figure 5)

All teeth are heavily worn. M^1 is placed obliquely rather than perpendicularly in relation to the longitudinal axis of P^4. From P^4 to P^2 the buccal outline describes a regularly curved line. The long axes of the two fourth premolars are almost parallel to each other.

M^1

Three distinct cusps have probably been developed. The upper first molars were worn down to a considerable extent by the talonid of M_1, and their overall state of preservation is too imperfect to allow detailed description.

P^4

The P^4 is relatively broad; the metastyle blade runs just offline from the longitudinal tooth axis. It forms nearly a right angle with the longitudinal axis of the comparatively large protocone. The protocone is large and shorter than the parastyle, which in turn is not as long as the metastyle (see Table 1). The paracone cusp

TABLE 1.

Summary of comparative measurements in the skull and upper dentition (in mm), taken from *Pachycrocuta brevirostris* from Gladysvale specimens GV 3914, GV 4264, and from Kromdraai specimen KA 55. * = approximate value.

	GV 3914	GV 4264	KA 55
P^2 w/l=ratio x100	11.9/19.0=62.8	12.0/17.5=68.6	12.7/18.5=68.7
P^3 w/l=ratio x100	17.9*/26.7=67.0	17.0/26.0=65.0	18.0/25.4=70.9
P^4 w/l=ratio x100	22.5/38.4=58.6	21.9/?	21.4/39.3=54.5
P^4 protocone diameter	at root 6.9	at root 5.7	at root 6.5
P^4 protocone w/l=ratio x100	7.6/9.1=83.5	6.0*/8.0*=75.0	7.0/9.2=76.1
P^4 protocone shape	massive, projecting far anteriad	slender, projecting less far anteriad	as GV 3914
P^4 parastyle	less massive than GV 4264 (wear?)	massive, anteriorly swollen	as GV 4264
P^4 parastyle length	12.0*	not preserved	11.1*
P^4 paracone length	12.4*	not preserved	13.1*
P^4 metastyle length	14.0*	not preserved	15.1*
P^2 anterior cusp	no notch, less prominent than GV 4264	separated by a notch from the main cusp	as GV 4264
P^3 anterior cusp	no notch, more or less incorporated into main cusp	separated by a notch from the main cusp	as GV 4264
P^3 posterior cusp	distinct, but smaller than GV 4264	larger than GV 3914	as GV 4264 or more pronounced
tooth row P^2-P^4 (length)	more curved than GV 4264 (81.2)	faintly curved (80.0*)	intermediate (81.5)
P^2 cingulum lingual	curvature pronounced	curvature pronounced	curvature less pronounced
shape of cingulum in general	intermediate	sharp edged	rounded
distance mx/j - P^4 alveole border	21.0*	30.0*	23.0*
M^1 w/l	6.9/19.9	M^1 ?present	?/16.0*
distance inf - averaged alveole heigth P^3	25.5	26.3*	25
minimum width of snout	at height of P^1	at heigth of P^2	at heigth of P^1
depression above P^4	present	present	not present
position of inf	at height between roots of P^3	at height of posterior part of P^3	at height of posterior part of P^3
anterior vertical edge of P^3	faintly developed, more linguo-posterior	developed more anterior	as GV 3914
cingulum buccally	faintly developed	more prominent	as GV 4264
skull length (P^2 - posterior end of zyg.)	170.0*	?	168
max. canine alveole diameter	21.0*	?	19.5*
distance orbit - alveole P^4	45.0*	?	37.0*
length of orbit (measured parallel to tooth row)	33.9*	?	37.6*

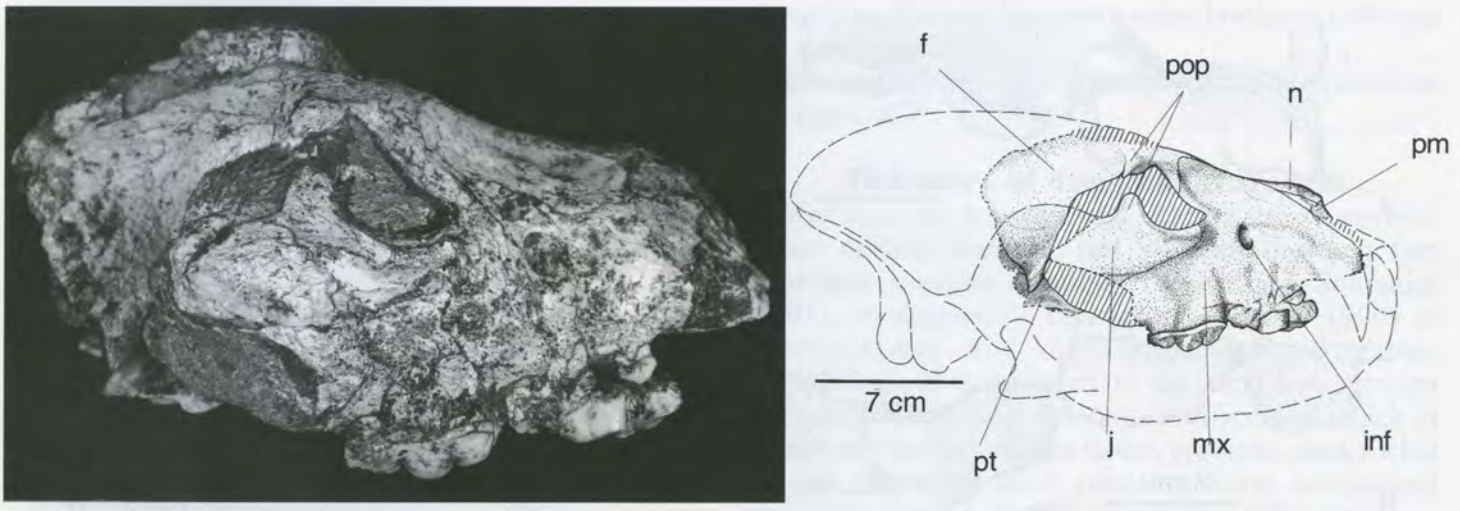


Figure 3A,B. Right lateral view of the skull of *Pachycrocuta brevirostris* (GV 3914). Outline restoration based on recent *Crocuta crocuta* specimens and on Turner & Anton (1996, Figure 2). Note the small orbit, the upwardly orientated face and the relatively short zygomatic arch. The scale bar equals 5 cm.

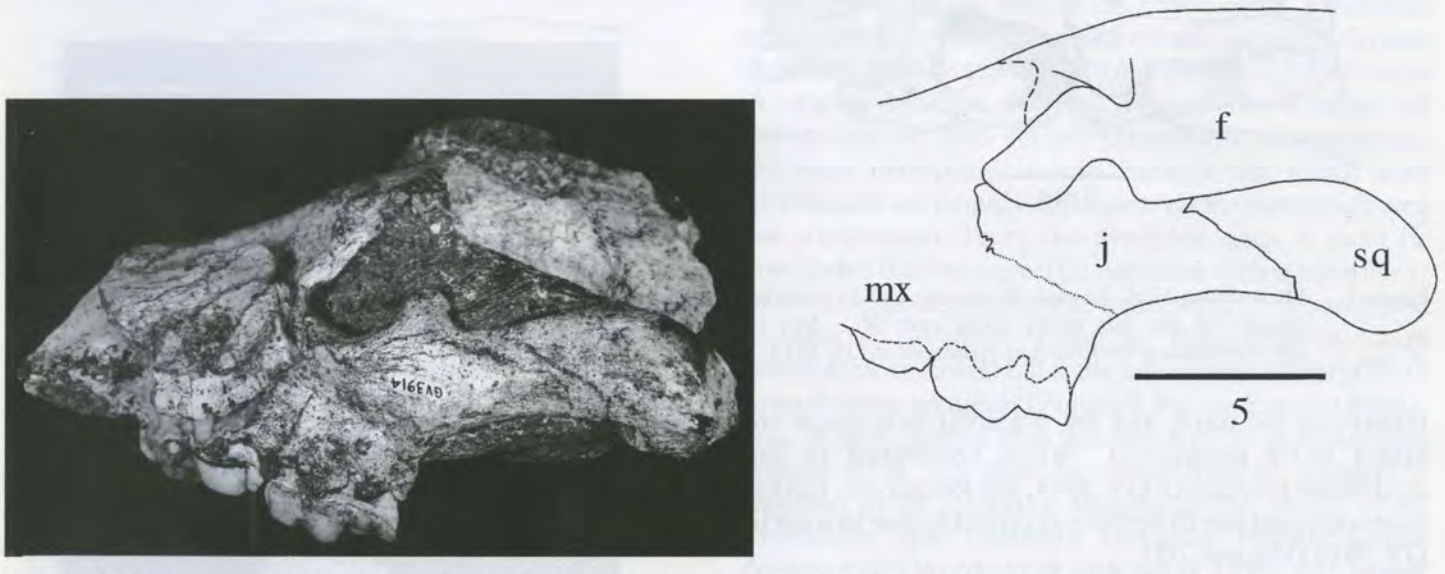


Figure 4A,B. Outline sketch of the skull of *Pachycrocuta brevirostris* (GV 3914) in left lateral view, showing the reconstruction of the sutures on the zygomatic arch (Figure B). The scale bar equals 5 cm.

projects slightly posteriad. On the lingual wall of P^4 the cingulum is weakly developed and, although worn off, appears to have persisted from the protocone to the posterior end of the metastyle. In buccal view the longitudinal grooves on the enamel diverge between metacone and paracone, paracone and parastyle. The anterior wear facet of the paracone of P^4 (as described by Ewer 1954a: 189) is present and very small. The anterior obliquely inclined part of the wear facet of the protocone is worn down considerably by the paraconid and the main cusp of lower P^4 (see Figure 5A,B).

P^3

The P^3 is rather slender, and within the tooth row its longitudinal axis forms an angle of about 25 degrees with the longitudinal axis of P^4. The posterior cusp is clearly separated from the cingulum and moderately large. Between the main and the posterior cusp is a vestigial, oblique groove.

P^2

The P^2 is fairly large and its longitudinal axis within the tooth row forms an angle of about 45 degrees with the longitudinal axis of P^4. The posterior cusp is damaged, whereas the anterior is moderately developed and the lingual cingulum between the two roots is considerably curved (not figured).

Only the alveoli of P^1, not the teeth, are preserved (see Figure 2).

GV 4264 (Figures 6-8, measurements see Table 1)

This specimen consists of a left maxillary fragment belonging to an adult individual, including the infraorbital foramen and part of the dentition with P^2, P^3 and a fragmentary P^4 preserved (Figure 6-8).

On the maxilla above the roots of P^4 is a depression similar to that in GV 3914. The minimum width of the snout is measured more toward the posterior (see Table 1). All teeth are less heavily worn than in GV 3914. Compared to GV 3914, the second premolar is smaller

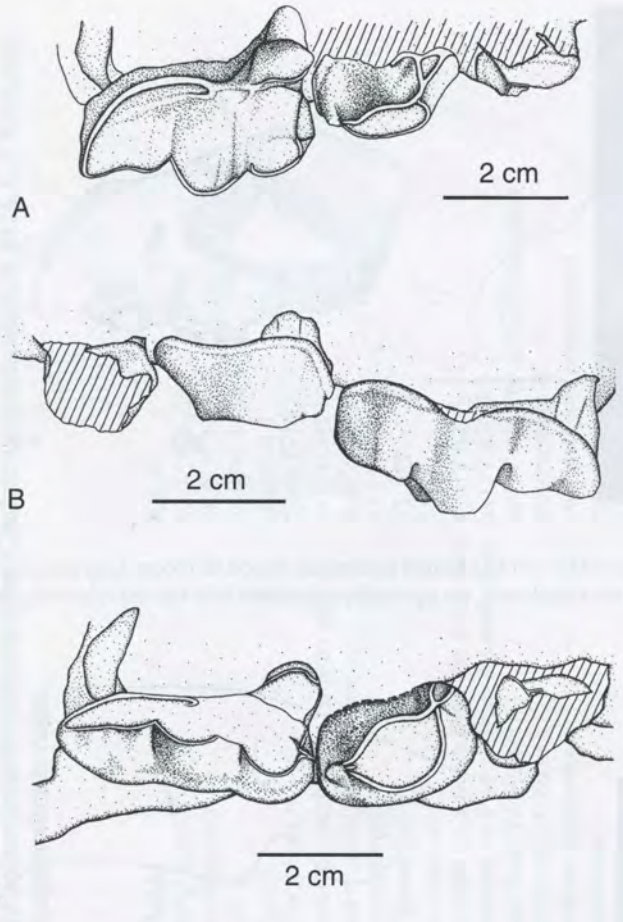


Figure 5. Illustrations of A. lingual, B. buccal, and C. occlusal aspects of the left upper tooth row (P^2 - M^1) of *Pachycrocuta brevirostris* as preserved in GV 3914.

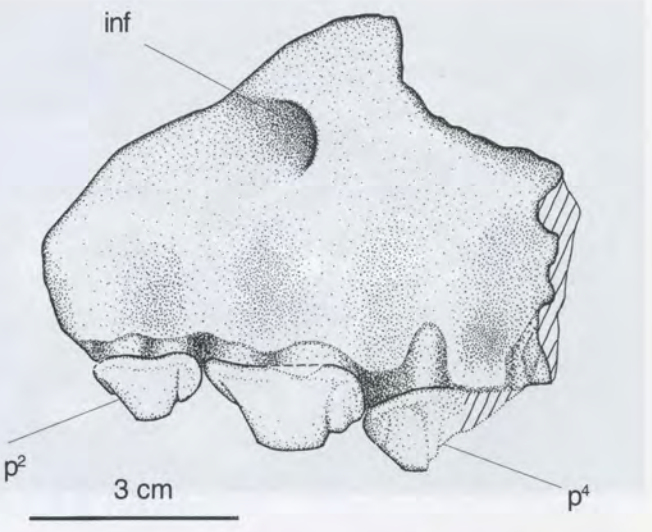


Figure 6. Lateral view of *Pachycrocuta brevirostris* maxillary fragment with P^2, P^3 and anterior portion of P^4 in specimen GV 4264.

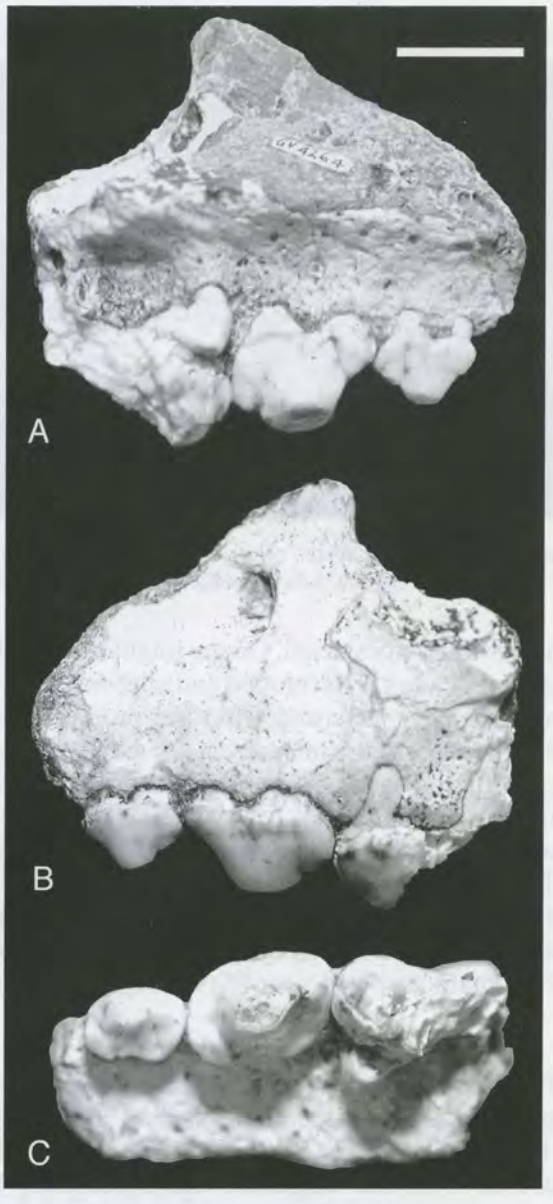


Figure 7. *Pachycrocuta brevirostris* (GV 4264), upper premolar tooth row as preserved in A. lingual, B. buccal, and C. occlusal views. The scale bar equals 2cm

relative to the third, and the premolar side cusps are much more prominent. When compared to the equivalent features in GV 3914, the P4 extends further anteriorly, but this difference is probably due to wear in GV 3914 (Figures 7/8).

In the P^2 and P^3, the lingual cingulum and all accessory cusps are more prominently developed than in GV 3914. The main cusp of the P^3 is more slender and smaller, while the anterior accessory cusp is positioned more anteriorly than mesially compared to GV 3914.

Only the P^4 protocone and parastyle are preserved. The parastyle appears to have been slightly smaller than in GV 3914, although no accurate measurements could be taken. The protocone is considerably smaller than in GV 3914 (see measurements in Table 1). In lateral view the infraorbital foramen lies exactly above P^3, and the minimum width of the snout is measured across the anterior palatine foramina. Unfortunately, the fossae for the inferior oblique muscles are not preserved.

The curvature of the upper tooth row is much less pronounced in GV 4264 than in GV 3914.

In overall size, GV 3914 exceeds GV 4264 slightly.

Additional remarks

We did not observe the kind of wear facet preserved in GV 3914 protocone in any other fossil or extant specimen (Figures 5A and 5B). In KA-55, GV 3914, and GV 4264 the P4 parastyle is worn off in various ways,

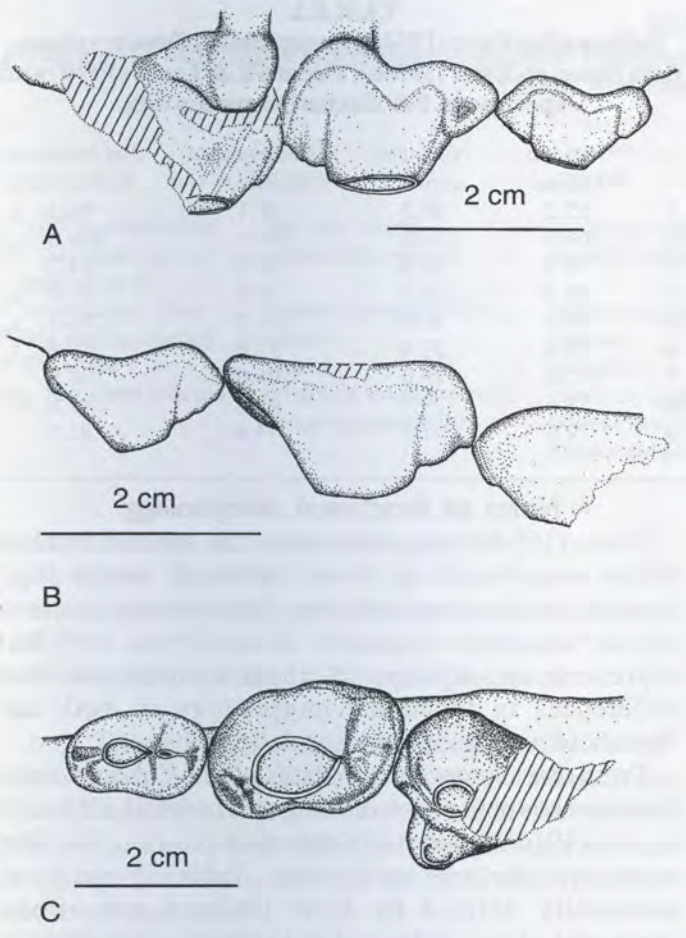


Figure 8. *Pachycrocuta brevirostris*. Line drawings of specimen GV 4264; upper premolar tooth row as preserved in A. lingual, B. buccal, and C. occlusal views. Note the size of the accessory cusps in relation to the main cusps in premolars 2 and 3.

making comparison difficult. In KA-55 the anterior wall is least worn off and therefore gives the impression of a comparatively large parastyle.

Non diagnostic characters in Gladysvale specimens attributed to *Pachycrocuta brevirostris*

There is a wide range of interpretations in the literature concerning the taxon-specific characters in fossil and extant hyaenids (see e.g. Qiu 1987: 59-67). Based on our comparative studies of fossil and extant hyaenids, we would suggest that, among the characters described in the South African specimens assigned to *Pachycrocuta brevirostris*, the following probably represent geographic or individual variation and should not be regarded as diagnostic features at the species level:

1. lingual cingulum is either sharply edged or rounded;
2. buccal cingulum variably pronounced;
3. varying massiveness of P^2 and P^3 posterior side cusps (see Table 1);
4. P^2 and P^3 anterior basal cusps variably distinct from paracones;
5. varying size of P^4 protocone in relation to P^4 parastyle;
6. varying curvature of tooth row;
7. varying distance between ventral border of orbit and alveolus of P^4;
8. absence or presence of maxillary depression between roots of P^4.

Discussion of diagnostic characters

Parahyaena brunnea and *Pachycrocuta perrieri* share certain features, but whether these in fact represent primitive retentions (Werdelin & Solounias 1991) or diagnostic characters (Turner 1990) is controversial, and the significance of certain morphological differences in the dentition remains unclear. Furthermore, taxonomic difficulties, which of course are directly related to this problem, render what would appear to be a simple generic assignment debatable (see e.g. Turner 1986: 208, 1987: 326).

Occasionally, in hyaenid taxonomy it may be a matter of interpretation whether to keep two samples in separate taxa or to unite them within the same taxon on the basis of considering 'only' dental characters. Examples can be found in *Pliohyaena pyrenaica orientalis* Qiu 1987 and *Pliocrocuta perrieri* (Croizet & Jobert, 1828) (see Werdelin & Solounias 1991; Guérin & Patou-Mathis 1996). The wide variety of interpretations also reflect taxonomic discrepancies, because groupings based merely on tooth size differences are heavily dependent on the sample chosen for comparison. From the available data, it must be concluded that intraspecific variation within samples is of considerable importance. Interestingly, if compared to other *P. brevirostris* samples from Eurasia, many South African fossils fall at the lower range of variability in tooth measurements (Figure 8, but see Randall 1981). It is in this context that the status of *P. perrieri* (see Kurtén 1956: 42) must be considered. *P. perrieri* is reported to be changing slightly in the course of its evolution and trending towards *Pachycrocuta brevirostris* (Werdelin & Solounias 1991: 22). Apart from absolute size, the only distinguishing feature between the two species is reported to be in the M_1 metaconid, which is always absent in *P. perrieri* (see Werdelin & Solounias 1991: 63). As already stated by Koufos (1992: 28), the length of the P^4 metastyle is quite variable in *P. brevirostris*. Evidently, the taxonomic importance of what is most probably a polymorphic character has to be questioned in *P. brevirostris*, since this cusp is present in only four out of 29 specimens listed by Turner & Anton (1996); its mere presence therefore may indicate intraspecific variation. The solution to this problem may require reinvestigating the considerable dental variation within all *P. perrieri* samples – a task which is beyond the scope of the present study.

New east African remains from the Turkana Basin in Kenya were reported and compared to some of the known Eurasian *P. brevirostris* samples (Werdelin 1999). Interestingly, measurements of mandibular premolars 2,3 and 4 consolidate the taxonomic view adopted here on the basis of cranial and upper dentition features. Nonetheless, equivalent measurements of the upper premolar dentition in South African specimens

(Figure 9) remain within the extreme range of variability found in the Eurasian samples.

Revised diagnosis of *Pachycrocuta brevirostris* (Aymard, 1846)

Pachycrocuta brevirostris represents the largest known hyaenid, with an estimated skull length of around 300 mm (see Figure 1). According to Thackeray & Kieser (1992), an approximate body weight of 63 kg should be assumed based on lower carnassial length extrapolation. However, this weight appears to be underestimated, considering the fact that limb proportions indicate a shoulder height of 0.9 to 1 m (Turner & Anton 1996: 460). The size of the *Pachycrocuta* cranium presented in this paper suggests a markedly heavier body weight than proposed by Thackeray & Kieser (1992), but a lighter body weight than the approximately 125 kg of extant small female lions.

The skull is massive and broad, and the muzzle is comparatively short. Zygomatic arches are relatively short and broad. The tibia is proportionally shorter than the femur in comparison to extant hyaenids (Turner & Anton 1996: 460).

Not a single autapomorphic feature is currently held to be found in *P. brevirostris*. As a result of our analysis, we propose a group of presumably diagnostic dental characters:

1. P^1 normally present, occasionally small;
2. P^2 and P^3 proportionally similar to *Hyaena* and *Parahyaena*, less similar to *Crocuta*;
3. M^1 present, large and only slightly obliquely positioned in relation to P^4 longitudinal axis.

Apart from its taxonomic weight, the hyaenid dentition reveals important information concerning functional morphology and allows conclusions about palaeoecology. Some suggestions have been brought forward in the literature, and in the following section we comment on some of these aspects concerning *P. brevirostris*.

TABLE 2.
Indices after Ewer (1954a). Comparison of mean values; data based on Ewer (1954a), Ficcarelli & Torre (1970) and specimens. For discussion see the text.

	Hyaena hyaena	*Crocuta crocuta*	*Parahyaena brunnea*	*Pachycrocuta brevirostris*
1.	85.2	95.3	88.1	88.3
2.	104.0	133.0	104	109.8
3.	75.5	89.8	84.2	84.2
4.	33.3	44.7	35.2	37.9
5.	76.8	90.0	81.0	84.5
6.	52.8	72.4	53.8	62.5
7.	102.0	113.0	104.0	108.9
8.	43.5	29.7	47.7	42.6
9.	74.5	81.1	74.4	82.5

Notes on functional morphology

Ewer (1954a) has shown that the spotted hyaena differs considerably in dental functional morphology from its smaller extant relatives. The relevant features are not 'absolutely diagnostic' (Ewer 1954a: 189), but represent an attempt to show tendencies and differences in functional morphology in both the 'hyaenoid' and 'crocutoid' specializations.

From this standpoint, the status of the *P. brevirostris* dentition has never been investigated in detail, although Kurtén (1956) hinted at this important question. We here summarize the relevant features (Tables 2 and 3) as essentially defined by Ewer (indices 1-6 of the carnassial shear, indices 7-9 to show adaptation to crushing).

Comparison and interpretation of indices in Table 2

For the sake of clarifying ambiguity, the indices of functional significance as defined and applied by Ewer (1954a: 190-191) are:

1. P^4 length : combined lengths of P^2+P^3
2. M_1 length : P_4 length
3. Width across protocone : length of paracone + metacone of P^4
4. Metacone length : total length of P^4
5. Blade length of M_1 : total length of M_1

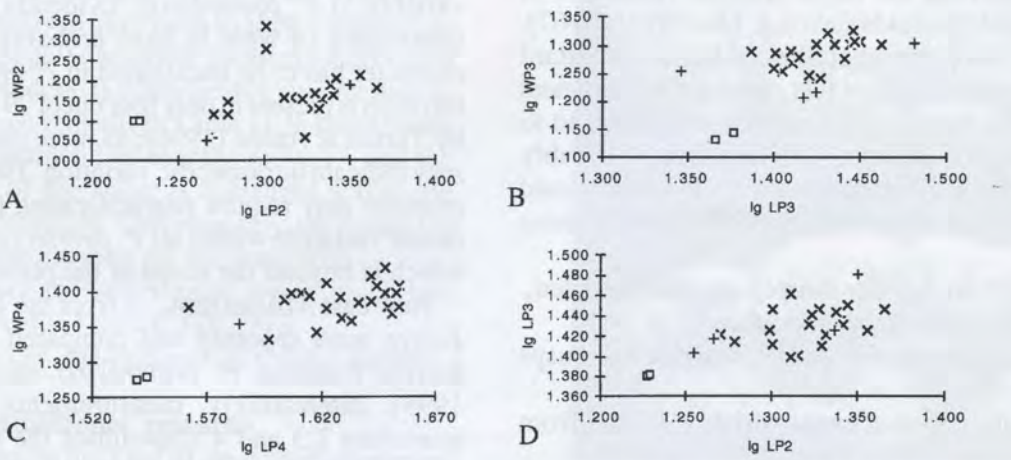


Figure 9 A-C. Bivariate plots of premolar length/width and D. length P2/length P3 ratio in lg (mm) of *Pachycrocuta brevirostris*. Taken from South African specimens (+: our data) and Eurasian specimens (x: from Turner & Anton 1996). Reference data is *Crocuta crocuta* (squares), most of which is omitted for clarity of illustration. See also Werdelin (1999: 162-164).

TABLE3.
Functionally interpreted morphology in the bone-cracking hyaenid dentitions. Based on Ewer (1954a, 1954b) and Kurtén (1988). For discussion see the text.

	Hyaena hyaena	*Crocuta crocuta*	*Parahyaena brunnea*	*Pachycrocuta brevirostris*
P^4 slicing adaptation	less specialized	highly specialized	less specialized	intermediate
M^1 size reduction in relation to P^4	moderately reduced	strongly reduced	reduced	moderately reduced
P^4 orientation: bone	sagittal chewing efficacy	almost sagittal	sagittal	sagittal
P^4/P_4 sliding contact	absent	present	absent	present
P^3/P_4 shear	absent	present	absent	absent or present
M_1: form and function	relatively shorter: tabloid chopping mechanism	relatively longer: talonid functionless, metaconid lost	relatively shorter: talonid chopping mechanism	relatively shorter talonid reduced

6. Blade length of M_1 : total length of P^4
7. P_3 width : P_4 width
8. Parastyle length : length of paracone + metacone of P^4
9. Width of P^3 : width of P^4 across protocone

1-6: These indices characterize efficiency of the carnassial blade. In all these indices *P. brevirostris* comes closest to the condition observed in *P. brunnea*, indicating the double function morphology of the chopping and slicing mechanism involving posterior premolars and molar.

7: The premolar accessory cusps are usually well developed in *P. brevirostris*, but there is also evidence which suggests considerable intraspecific variation. *H. hyaena* and *P. brunnea* show signs of reduction in the anterior accessory cusp of P^4 (Ewer 1954a: 191), whereas *C. crocuta* does not. *P. brevirostris* has an intermediate character in this sense: the P^4 works less efficiently as a crusher compared to *Hyaena* and *Parahyaena*, but more efficiently than in *C. crocuta.*

8,9: These indices reveal that the crushing function of the upper premolar teeth is not as efficient as observed in *P. brunnea*, index 8 being closer to *H. hyaena* but still far from the specialized condition developed in *C. crocuta.* Index 9 reveals an even higher value in *P. brevirostris* than in *C. crocuta.*

Admittedly, indices 7 and 9 are less appropriate for comparison, because the third premolar reflects rather the evolutionary level, as it has not yet reached the 'larger relative width' developed in younger taxa, as recognized by Qiu (1987). In our opinion, this diminishes the functional significance of these two indices. We conclude from the above that *P. brevirostris* was an efficient bone crusher but a less efficient meat slicer, compared to extant bone-cracking hyaenids.

Notes on body size, palaeoecology and behavior

Some morphologies in the carnivore skull and dentition are known to be directly correlated with body size (Kurtén 1973; Werdelin & Solounias 1990) and can reflect its evolutionary changes (Soergel 1936; Kurtén 1965). On the one hand, the body mass of the hyaena has been shown to be closely related to climatic change (Klein & Scott 1989; Thackeray & Kieser 1992), while on the other hand animal size is undoubtedly related to hunting ability and social behavior (Skinner, Davis & Ilani 1980; Hennig 1986). Considering its large size, dental morphology and limb proportions, the feeding habits of *P. brevirostris* may also be reconstructed on the basis of faunal analyses, which mirror the palaeoecological circumstances. Extant hyaenas are, aside from their opportunistic adaptation to scavenging, successful at killing prey. Bagged prey constitutes a variable but considerable percentage of their diet (see e.g. Tilson, Blottnitz & Henschel 1980; Skinner, Henschel & van Jaarsveld 1986; Cooper 1990; Henschel & Skinner 1990; Sillero-Zubiri & Gottelli 1992). Despite the fact that hyaenas are well known as taphonomic agents (e.g. Thenius 1961, 1976; Mills & Mills 1977; Lam 1992; Marean, Spencer, Blumenschine & Capaldo 1992), bones found in hyaena dens can be correlated with high accumulations of ungulate populations (Skinner, Henschel & van Jaarsveld 1986). On the basis of the fossil record, Werdelin (1989: 389) concluded from the relatively short distal limb bones that *P. brevirostris* was not adapted as a pursuit predator, and Turner & Anton (1996) suggested that the behavior of *P. brevirostris* may be comparable to *C. crocuta* of the Late Pleistocene. In this context it is interesting that the Gladysvale D-8 deposits more frequently revealed equid remains than other early hominid-bearing sites in South Africa. This may possibly correspond with the occurrence of a bone-accumulating agent (Berger 1992, 1993), such as *P. brevirostris.*

This hypothesis is speculative at the present time, but it is testable through faunal analysis (see Sutcliffe 1970; Blumenschine 1988; Marean, Spencer, Blumenschine & Capaldo 1992) in a chronological framework provided by ESR-dating. By contrast, carnivore tooth attrition (Lindeque & Skinner 1984: 293) and an encephalization quotient (Sheppey & Bernard 1984) may be regarded as less promising approaches to the task of widening palaeoecological understanding.

ABBREVIATIONS

Institutions

AIUZ Anthropologisches Institut der Universität Zürich (Switzerland)

BPI Bernard Price Institute for Palaeontological

	Research, University of the Witwatersrand, Johannesburg (South Africa)
NMB	Naturhistorisches Museum Basel (Switzerland)
PIMUZ	Paläontologisches Institut und Museum der Universität Zürich (Switzerland)
FIS	Forschungsinstitut Senckenberg, Frankfurt (Germany)
TMP	Transvaal Museum, Pretoria (South Africa)
ZMUZ	Zoologisches Museum der Universität Zürich (Switzerland)

Localities (South Africa)

BF	Bolt's Farm
GV	Gladysvale Cave
KA	Kromdraai
M	Makapansgat .
SK	Swartkrans
Sts	Sterkfontein

Localities (France)

Se	Senèze
St.V.	St-Vallier

Locality (Italy)

V.A.	Val d'Arno

Measurements

l, length; w, width.

Morphology

apf	anterior palatine foramen
bs	basisphenoid
c	canine
dext.	dextra
f	frontal
gf	glenoid fossa
if	incisive fossa
inf	infraorbital foramen
izf	incisive foramen
j	jugal
M	molar
mx	maxillary
n	nasal
P	premolar
pl	palatine
pm	premaxillary
pop	postorbital processes
ppf	posterior palatine foramen
pt	pterygoid
ptf	pterygoid foramen
sin.	sinistra
sq	squamosum
zyg.	zygomatic (arch)

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