

A C T A Z O O L O G I C A
C R A C O V I E N S I A

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Björn KURTÉN

(Helsingfors)

Percrocuta KRETZOI (*Mammalia, Carnivora*), grupa hien
z neogenu

Percrocuta KRETZOI (*Mammalia, Carnivora*) группа гиен
неогена

Percrocuta KRETZOI (*Mammalia, Carnivora*), a group of Neo-
gene hyenas

(With 7 figures in text)

INTRODUCTION

The *Percrocuta* KRETZOI group, here tentatively given the taxonomic rank of subgenus of the genus *Crocuta* KAUP, comprises the dominant hyenas of the Pliocene; one species is even known from the uppermost Miocene. As far as known, its history ends in the upper Pliocene, perhaps even with the close of the middle Pliocene. The number of known and valid species is small, some five or six in my opinion.

The first species to become known was *Crocuta eximia* described by ROTH and WAGNER in 1855 from the lower Pliocene of Pikermi. It is also the most widespread and best-known species in this group. Later discoveries have shown it to be a characteristic element in the lower Pliocene, or Pontian, Hipparion fauna of Europe. It is also recorded from Siberia, and the Chinese *Crocuta variabilis* (ZDANSKY) is clearly con-

specific with the European form. Finally, an Indian form, *Crocuta latro* PILGRIM, appears also to belong to the same species.

Other species of the same group are only known from local records; *Crocuta gigantea* (SCHLOSSER) from China, *Crocuta carnifex* PILGRIM from India, and *Crocuta tungurensis* COLBERT from Mongolia. A new species, *Crocuta grandis* n. sp. from India, is described in the present paper. Finally, a little-known species, ?*Hyaena salonicae* ANDREWS from Greece, may belong to the same group, but its affinities are uncertain.

Most knowledge of these species is summarized and excellently integrated in the two revisions by PILGRIM (1931, 1932). PILGRIM divided the heterogeneous genus *Hyaena* BRISSON into two genera, reviving KAUP's (1828) name *Crocuta* for the spotted hyena and its allies. At the same time he noted that *Crocuta* KAUP, as understood by him, includes two distinct series of species: those in which the protocone of P⁴ is large, and those in which it is considerably reduced. The former group (see KURTÉN, 1956) has only two species, both Quaternary; the latter group is the subject of the present study. PILGRIM hesitated to introduce a new genus for this group, „partly because our knowledge of the species in question is at present deficient and the other differences from the more usual form of *Crocuta* may be too slight to warrant generic separation: partly because ZDANSKY (1924, p. 96) considers that *C. variabilis* shows some variability in regard to the size of the protocone“ (PILGRIM, 1931, p. 115), though he emphasized that it formed „a special precocious evolutionary line“. In such a situation the subgenus grade is a suitable taxonomic tool.

It remained for KRETZOI (1938) to provide the name. His revision of the *Hyaenidae* is, however, completely preoccupied with analysis at the cost of synthesis, and the result was a welter of names, most of which lack taxonomic significance. Out of the generic names proposed by him for this group, *Percrocuta* has line priority (unless the puzzling and at present inadequately characterized forms called *Allohyaena* and *Xenohyaena* also belong here), and was revived on the subgenus level by KURTÉN (1956).

I have had the good fortune to have access to most of the main collections of these hyaenids. The material for this study has been examined in the following institutions:

Austria: The Natural History Museum in Vienna (*C. eximia*); the Paleontological Institute of Vienna University (*C. eximia*).

England: The British Museum (Natural History), London (*C. carnifex*, *C. e. eximia*, *C. e. latro*, *C. gigantea*, ?*H. salonicae*).

Germany: The Institute of Paleontology and Historical Geology, Munich (type material of *C. eximia* and *C. gigantea*; *C. e. variabilis*).

Netherlands: The Geological Institute of Utrecht University (*C. e. variabilis*, *C. gigantea*).

Spain: The Museum of Sabadell (*C. eximia*).

Sweden: The Paleontological Institute of Uppsala University (*C. e. variabilis*).

Finally, casts of *C. tungurensis* were kindly supplied by Dr. E. H. COLBERT, the American Museum of Natural History.

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It was found that certain applications of quantitative methodology gave important addition to the understanding of the forms studied, especially regarding the species question. The methods here used include univariate and bivariate analysis, and application of SIMPSON'S (1941) ratio diagram. Quantitative data on some samples not accessible to me have been culled from the literature, and some measurements have been taken on published photographs. For a discussion of the possibilities and pitfalls of such methods, which require great caution, see KURTÉN (1956).

GENERAL CHARACTERS

The species of the *Percrocuta* group all have the following characters. The upper carnassial is a slicing blade with modally very much reduced protocone, though the reduction never reaches the extreme conditions seen in some machairodonts. In exceptional instances the protocone is fairly prominent. This condition occurs in some specimens of *C. eximia*.

The metastyle blade of P^4 is modally longer than in the genus *Hyaena*, but shorter than in *Crocuta* (*Crocuta*); but these distinctions only hold over a certain range of size. Bivariate analysis (KURTÉN, 1956) has shown that the metastyle length is positively allometric to the crown length of P^4 in both *Hyaena* and *C. (Crocuta)*; the two trend lines are parallel but distinct. The trend line of *Crocuta (Percrocuta)* has a less marked positive allometry and intersects both the *Hyaena* and *C. (Crocuta)* lines (KURTÉN, op. cit., figs. 2—3). For this reason, the relative length of the metastyle is similar to that in *C. (Crocuta)* of equal size for very small species, like *C. carnifex*, and to that in *Hyaena* for very large species, like *C. gigantea*. For forms of intermediate size, like *C. eximia*, the relative metastyle length is intermediate.

P^3 has a relatively well-developed posterior cusp, as in *Hyaena*; as in that genus it intervenes between the main cusp and the posterior cingulum, whereas in *C. (Crocuta)* the cusp is minute and arises directly from the cingulum. P^2 is rather like P^3 in miniature, with a moderately large posterior cusp and a small anterointernal cusp. In occlusal view the anterior premolars of *C. (Percrocuta)* have a square to ovoid outline, sometimes with a pronounced lingual incurvation, and thus contrast with the rhomboidal *Hyaena* teeth. The homodonty of P^2 and P^3 contrasts with the heterodont condition in *C. (Crocuta)*, in which P^2 is lower and has a larger posterior cusp.

M_1 normally lacks the metaconid, but in *C. eximia*, again, a small metaconid may be occasionally present. The talonid is variable in structure with from one to three cusps. P_4 always has well-developed anterior and posterior cusps. The remarks on P^2 and P^3 apply in general also to P_2 and P_3 .

The canine teeth are relatively larger and stouter than

in *C. (Crocuta)*, and this gives the *Percrocutas*, like the *Hyaenas*, more of a „chin“ than *C. (Crocuta)*, the depth of the symphysis being correlated with the size of the canine root.

THE HYENAS OF THE MIDDLE SIWALIKS

Before proceeding to a discussion of the differentiation within the subgenus *Percrocuta*, a preliminary discussion of the forms from the Middle Siwaliks in India is necessary. In most instances it seems to me that the taxonomic units recognized by PILGRIM are natural groups (though not necessarily on the taxonomic level suggested by him). An exception is formed by the hyenas which have been described as *Crocuta gigantea latro* and *Crocuta mordax* (PILGRIM, 1932). Both are known from the Dhok Pathan zone of the Middle Siwaliks, *G. gigantea latro* also from the Nagri zone. My interpretation of the specimens on which these two forms are based differs entirely from PILGRIM's.

The measurements of the cheek teeth of the specimens in question appear in table 1, which is compiled from the data by PILGRIM (op. cit.) and COLBERT (1935), and original measurements; certain emendations of PILGRIM's data are discussed below (see page 380).

Four maxillary fragments are known, all of them from the Dhok Pathan zone. G. S. I. D 205 is the type of *C. mordax* together with the ramus G. S. I. D 204, which belongs to the same individual. It is a juvenile specimen with the permanent dentition emerging (PILGRIM, op. cit., pl. VI, fig. 1). PILGRIM gives the length and width of P³ as approximately 16,5 and approximately 14,4 mm. respectively, dimensions which appear incredibly small. The figure clearly shows that the basal part of the P³ germ had not yet been formed, and the cingulum is lacking; the dimensions of the fully-formed tooth would have been much greater.

G. S. I. D 206 is the type of *C. gigantea latro*. For P³ PILGRIM gives the approximate length 20 mm. According to the figure (PILGRIM, op. cit., pl. VI, fig. 2) the tooth is lacking and the alveolus so badly damaged that it would be impossible

Table 1

Dimensions of cheek teeth in specimens of *Crocota* from the Middle Siwaliks, India. Data from PILGRIM (G. S. I. specimens), COLBERT (A. M. N. H. specimen) and original (B. M. specimen). For some emendations of PILGRIM's see the text.

Specimen	Zone	P ³		P ⁴					
		L	W	L	W				
G. S. I. D 205 Type, „ <i>mordax</i> “	Dhok Pathan	—	—	37,0	17.3				
G. S. I. D 206 Type, „ <i>latro</i> “	Dhok Pathan	—	a18	37.8	17.5				
G. S. I. D 208 „ <i>latro</i> “	Dhok Pathan	21	18	—	—				
A. M. N. H. 19888 „ <i>gigan- tea</i> “	Dhok Pathan	26,0	18.0	41.0	21.0				
		P ₂		P ₃		P ₄		M ₁	
		L	W	L	W	L	W	L	W
G. S. I. D 204 Type, „ <i>mordax</i> “	Dhok Pathan	16.1	10.0	a20.0	a12.0	22.3	13.8	28.0	13.5
G. S. I. D 163 „ <i>mordax</i> “	Dhok Pathan	—	—	—	—	24.0	13.8	—	—
B. M. M 13176 „ <i>mordax</i> “	Middle Siwaliks	—	—	—	—	22.6	12.4	—	—
G. S. I. D 209 „ <i>latro</i> “	Nagri	—	—	—	—	25	15	—	—
G. S. I. D 231 „ <i>latro</i> “	Nagri	a20.4	a14.3	—	—	—	—	—	—
G. S. I. D 162 „ <i>latro</i> “	Dhok Pathan	—	—	—	—	29.5	17.3	a30?	—
G. S. I. D 164 <i>carnifex</i>	Dhok Pathan? (Hasnot)	—	—	—	—	—	—	22.5	11.7

L, length; W, width; a, approximate.

to determine the length. The P⁴ has the same dimensions and morphological characters as that of the *mordax* type.

G. S. I. D 208 is an isolated P³ of medium size, about as large as in *C. eximia* (PILGRIM, pl. VII, fig. 13).

A. M. N. H. 19888 is a maxillary fragment with P³—P⁴ (COLBERT, 1935, fig. 52). It is probably from the Dhok Pathan, certainly not earlier. P³ is much longer than G. S. I. D 208, but of the same width, thus relatively more slender; it is also

more simply built, without the strong incurvation on the lingual side seen in D 208 and some specimens of *C. eximia*. P_4 is larger than in the types of *C. gigantea latro* and *C. mordax*, and more stoutly built, with the protocone shifted farther backward.

Lower dentitions are more numerous. G. S. I. D 204 (PILGRIM, op. cit., pl. VI, figs. 3—4) is with D 205 the type of *C. mordax*, and has a wellnigh complete lower dentition. G. S. I. D 163 (PILGRIM, op. cit., pl. VII, fig. 10), also from the Dhok Pathan, and B. M. M 13176, from the Middle Siwaliks (Nagri or Dhok Pathan), agree with D 204, and were placed in *C. mordax* by PILGRIM.

G. S. I. D 209, classified as *G. gigantea latro* by PILGRIM, is a ramus fragment with complete P_4 and the roots of M_1 (PILGRIM, op. cit., pl. VIII, fig. 1); it comes from the Nagri. P_4 is slightly larger than in the specimens placed in *C. mordax*, but is morphologically very similar to them. The length of M_1 is given by PILGRIM as about 26 mm., presumably the alveolar length; the crown length would be somewhat greater, probably as in G. S. I. D 204. The ramus is relatively shallow and does not indicate an animal larger than *C. eximia*.

G. S. I. D 231 (PILGRIM, op. cit., pl. VIII, fig. 3), also from the Nagri, is a much larger animal. The specimen is a fragment of a deep and heavy ramus, exceeding D 204, and yet this is a very young individual with milk teeth still in position and P_2 concealed in the jaw. This P_2 is much larger than that of D 204, and the milk teeth are also much larger than their homologues in D 204. The specimen was referred to *C. g. latro* by PILGRIM.

G. S. I. D 162 (PILGRIM, op. cit., pl. VII, fig. 11), also *C. gigantea latro* according to PILGRIM, comes from the Dhok Pathan; it is a very large jaw fragment with P_4 and the roots of M_1 . P_4 is much larger than in the specimens discussed above. For M_1 PILGRIM gives the approximate length 29 mm., presumably again for the alveolus; the actual length must have been somewhat greater, perhaps 30—31 mm.

Apart from these forms, there is a record of *C. carnifex* PILGRIM probably from the Dhok Pathan (G. S. I. D 164). The dimensions of this specimen are much smaller, and the

assignment is in my opinion correct. As PILGRIM notes, reference to the Dhok Pathan zone cannot be taken as absolutely certain.

The specimens placed by PILGRIM in the two species *C. gigantea* and *C. mordax* are thus seen to fall into two natural groups: (1) a medium-sized form (G. S. I. D 205, 206, 204, 163, 209; B. M. M 13176) about the size of *C. eximia*; and (2) a very large form (A. M. N. H. 19888; G. S. I. D 162, 231).

The distinctions appear very clearly if the data are plotted in a ratio diagram, comparing the lengths of homologous teeth in different specimens. The method is to select a standard (in this case the European population of *C. eximia*, for which the arithmetic means are used) the dimensions of which are given the value 100 per cent. The dimensions of the other specimens are expressed as percentages of the value for the homologous variate in the standard. The percentages are plotted on a logarithmic scale to give a correct impression of relative variation. If the values for another specimen tend to fall along a straight vertical, this indicates that its relative proportions are similar to those of the standard, regardless of absolute size. Similarly, specimens which depart from the straight vertical, but give identical patterns in the diagram, will be similar to each other in relative proportions, and differ from the standard in homologous features. For the construction of the ratio diagram — a most efficient and easily handled tool in taxonomic comparison — see SIMPSON (1941).

The diagram (fig. 1) shows that the data for the smaller form tend to cluster around the *C. eximia* means. Those for the larger form deviate strongly from the *C. eximia* means and form a pattern resembling that of the Chinese *C. gigantea*, also plotted in the figure.

There can be no doubt that this dichotomy is real. The statistical parameters for P_4 in the smaller form may be obtained with some accuracy, because four specimens are known. The mean length is 23,48 mm., and its standard deviation is 1,26 mm. The P_4 of G. S. I. D 162 deviates from this mean by 6,0 mm., or about 4,8 times the standard deviation. The difference is of the highest order of significance. The mean width is 13,75 mm. and its standard deviation 1,06 mm.; the deviation of D 162

is more than 3,3 times the standard deviation, and probably significant. It may thus be taken as a certain fact that two distinct populations (apart from the small *C. carnifex*) were present in the Nagri and Dhok Pathan. As they occur together, they must have belonged to different species, since two subspecies cannot exist together.

It remains to determine the proper designations of these species. Both the types of *C. gigantea latro* and *C. mordax*

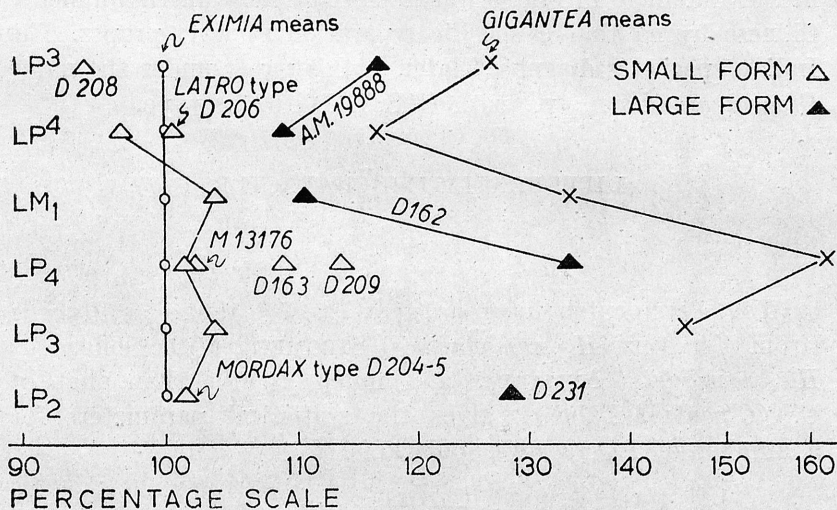


Fig. 1. Ratio diagram, comparing relative lengths in teeth of *Crocuta „gigantea“ latro* PILGRIM and *Crocuta „mordax“* PILGRIM, with means for the European population of *C. eximia* as a standard (100%). For comparison, means for *C. gigantea* from China are also given. The Indian specimens fall into two groups, a „small form“ (including the types of *C. latro* and *C. mordax*) closely resembling *C. eximia*, and a „large form“ approaching *C. gigantea* in general proportions. Data from tables 1 and 2.

belong to the smaller species. Line priority validates the name *latro*, which thus becomes the trivial name of this species, *mordax* becoming a synonym. Naturally, this smaller species has nothing to do with *C. gigantea*; I hope to show that it is actually a local form of *C. eximia*, and the proper designation is therefore *Crocuta eximia latro* (PILGRIM). It is unfortunate that the name *latro* was based on a specimen which does not belong to the *gigantea*-like population.

This leaves the larger species without a name. It evidently is closely affiliated to *C. gigantea*, but it is clear that the size differences between the Chinese and Indian forms were vastly under-estimated by PILGRIM. The mean length of four Chinese M_1 's is 36.40 mm., and its standard deviation 1.19 mm. The length of M_1 in G. S. I. D 162 was probably at most 31 mm, which gives a difference of about 4.5 times the standard deviation; this is highly significant. Similarly, the other dimensions in the Indian form fall so much short of those in the immense Chinese hyena that a specific separation appears proper. The Indian species is diagnosed later in this paper under the name *Crocota grandis* n. sp., with G. S. I. D 162 as type.

DIFFERENTIATING CHARACTERS

Size

The *Percrocotas* have as great a size range as *Hyaena* (from the tiny *H. namaquensis* STROMER to the enormous *H. brevirostris* AYMARD), and much greater than that of *C. (Crocota)*. Table 2 gives the statistical parameters for a number of *Percrocota* populations.

Table 2

Dimensions of cheek teeth in populations of *Crocota (Percrocota)*

		N	M	S. D.	V	S. R.
<i>C. tungurensis</i>	LP ²	1	18.8			
Tung Gur	LP ³	1	21.5			
	LP ⁴	1	40.3			
	WM ¹	1	4.2			
	LM ₁	3	27.1±1.4			
	LP ₄	3	21.7±1.5			
	LP ₃	3	18.8±0.7			
	LP ₂	2	15.0			
<i>C. eximia</i>	LP ²	9	17.70±0.30	0.89±0.21	5.0±1.2	14.8—20.6
<i>eximia</i>	LP ³	11	22.23±0.36	1.19±0.25	5.4±1.1	18.4—26.1
Europe	LP ⁴	18	37.57±0.57	2.40±0.40	6.4±1.1	29.8—45.3
	WM ¹	3	14.1±0.2			
	LM ₁	12	27.12±0.40	1.38±0.28	5.1±1.0	22.6—31.6
	LP ₄	15	21.99±0.27	1.03±0.19	4.7±0.9	18.7—25.3
	LP ₃	14	19.29±0.36	1.35±0.26	7.0±1.3	14.9—23.7
	LP ₂	12	15.88±0.23	0.80±0.16	5.0±1.0	13.3—18.5
	WCi	5	13.95±0.33	0.73±0.23	5.2±1.7	11.6—16.3
<i>C. eximia</i>	LP ²	2	17.4			

		N	M	S. D.	V	S. R.
<i>eximia</i>	LP ³	2	22.0			
Pavlodar	LP ⁴	3	37.6±0.8			
(Siberia)	WM ¹	1	14.0			
	LM ₁	3	28.8±0.6			
	LP ₄	2	22.5			
	LP ₃	2	20.8			
	LP ₂	2	15.6			
	WCi	2	13.5			
<i>C. eximia</i>	LP ²	11	18.29±0.35	1.17±0.25	6.4±1.4	14.5—22.1
<i>variabilis</i>	LP ³	14	22.62±0.34	1.29±0.24	5.7±1.1	18.4—26.8
North China	LP ⁴	8	37.16±0.57	1.60±0.40	4.3±1.1	32.0—43.4
	WM ¹	14	14.70±0.37	1.38±0.26	9.4±1.8	10.2—19.2
	LM ₁	17	27.91±0.25	1.04±0.18	3.7±0.6	24.5—31.3
	LP ₄	19	22.72±0.23	1.01±0.16	4.4±0.7	19.5—26.0
	LP ₃	18	19.92±0.24	1.00±0.17	5.0±0.8	16.7—23.2
	LP ₂	13	16.48±0.22	0.81±0.16	4.9±1.0	13.9—19.1
	WCi	9	13.88±0.23	0.70±0.17	5.1±1.2	11.6—16.2
<i>C. eximia latro</i>	LP ³	1	21			
India	LP ⁴	2	37.4			
	WM ¹	1	14.5			
	LM ₁	1	28.0			
	LP ₄	4	23.48±0.63	1.26±0.44	5.4±1.9	19.4—27.6
	LP ₃	2	20.2			
	LP ₂	1	16.1			
<i>C. carnifex</i>	LP ²	1	17.0			
India	LP ³	1	21.2			
	LP ⁴	1	29.0			
	LM ₁	3	22.0±0.3			
	LP ₄	4	20.58±0.27	0.53±0.19	2.6±0.9	18.9—22.3
	LP ₃	4	16.90±0.40	0.80±0.28	4.7±1.7	14.3—19.5
	LP ₂	1	12.8			
<i>C. grandis</i>	LP ³	1	26.0			
India	LP ⁴	1	41.0			
	LM ₁	1	a30?			
	LP ₄	1	29.5			
	LP ₂	1	a20.4			
<i>C. gigantea</i>	LP ³	2	28.2			
China	LP ⁴	1	44.			
	IM ₁	1	36.40±0.59	1.19±0.42	3.3±1.2	32.5—40.3
	LP ₄	1	35.6			
	LP ₃	2	28.2			

N, number of individuals; M, arithmetic mean; S. D., standard deviation; V, Pearsonian coefficient of variation; S. R., standard range (SIMPSON, 1941a).

The means have been used for the construction of a ratio diagram, comparing the mean lengths (or widths) of homologous teeth in the populations, with the European population of *C. eximia* as a standard, as in fig. 1. To avoid cluttering of the picture, two diagrams were drawn, one (fig. 2) representing the *C. eximia* group, and the other (fig. 3) the remainder of the Percrocutas. The European *C. eximia* is standard in

both, and they might be thought of as superimposed on each other. For comparison, fig. 2B represents some populations of the single species *Crocota crocuta* (ZIMMERMANN).

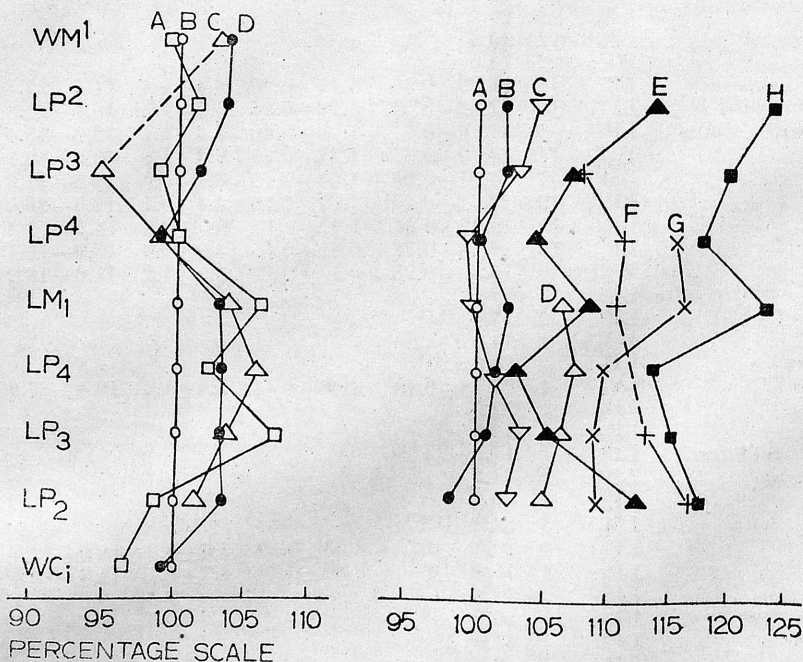


Fig. 2. Left, ratio diagram, comparing relative dimensions of teeth in (A) Siberian population of *Crocota eximia* (data from ORLOV), (B) European *C. eximia* (original data), (C) Indian *C. eximia latro* (data from PILGRIM and original), (D) Chinese *C. eximia variabilis* (original data). Right, analogous diagram, showing geographic differentiation within the single species *Crocota crocuta* (spotted hyena): (A) Recent, Balbal, Tanganyika Territory, (B) Recent, Kenya, (C) Recent, Uganda, (D) Recent, Congo, (E) Recent, South Africa, (F) Latest Pleistocene, Ksar' Akil, Lebanon, (G) Late Pleistocene, Odessa, (H) Late Pleistocene, Eggenburg, Austria; all from original data. The geographic differentiation in *C. crocuta* exceeds that in *C. eximia*, even if only the recent populations (A—E) are taken into account.

The patterns — though not the absolute sizes — of the *Percrocotas* appear to fall into two main groups. One group is represented by the standard population, the European *C. eximia*, and along with it the Siberian population of the

same species; the Chinese *C. e. variabilis*; the Indian *C. e. latro* (all of these in fig. 2); and, finally, the Mongolian *C. tungurensis* (fig. 3). All of these are roughly of the same size. Naturally they do not all give straight vertical patterns; the means for different populations tend to deviate a little from each other. Analysis for significance shows that all of these differences

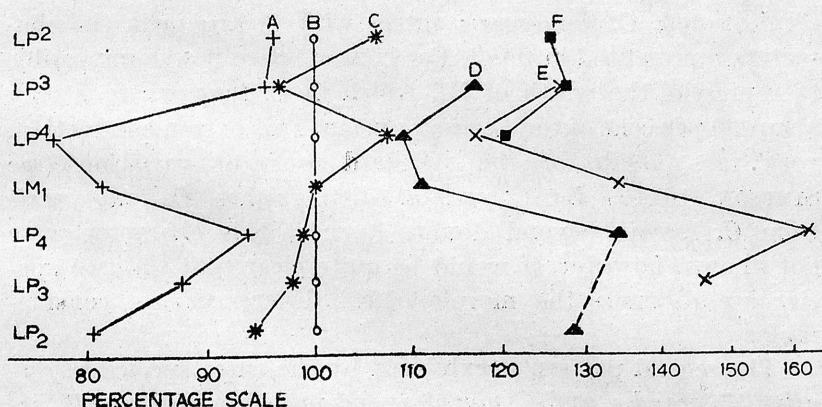


Fig. 3. Ratio diagram, comparing mean lengths of teeth in (A) *Crocuta carnifex* (data from PILGRIM, COLBERT, and original), (B) European *C. eximia* (standard, as in fig. 2), (C) *C. tungurensis* (data from COLBERT), (D) *C. grandis* n. sp. (data from PILGRIM and COLBERT), (E) *C. gigantea* and (F) ? *Hyae-na salonicae* (original data).

may possibly be ascribed to chances of sampling alone, and that no surely significant differentiation in size can be established within this group. It is probable, however, that some of the differences are real (particularly for *C. tungurensis*), though this cannot now be proved. I discuss initially the forms here placed in *C. eximia*, and return to *C. tungurensis* later on.

The range of *C. eximia* appears thus to have covered the Indian region and most of the Palearctic region; the temporal relationship between different populations will be touched on below. The geographic differentiation in size appears to have been remarkably slight. It is apparently inferior to that in the living spotted hyena (fig. 2B), though the range of this species at present is much smaller than the total range of

C. eximia. It may thus be inferred that *C. eximia*, *C. variabilis* and *C. latro* are subspecies of a single species, a result which will be supported later on by morphological analysis. The known species range may appear great, but it is matched or even greatly exceeded by the geographic ranges of many living carnivores: *Vulpes vulpes* (L.), *Canis lupus* L., *Ursus arctos* L., *Hyaena hyaena* (L.), and others.

As noted, *C. tungurensis* agrees with *C. eximia* in the characters represented in fig. 3. For lack of space it was impossible to represent the width of M^1 , which in *C. tungurensis* is only about 30 per cent of the *C. eximia* mean. This extreme reduction, very far outside of the standard range of variation (see SIMPSON, 1941a) for *C. eximia*, distinguishes *C. tungurensis* from *C. eximia* beyond doubt. Even if this character were not known, however, it would be quite clear that the two species are distinct; the morphological differences are considerable.

The second pattern is exhibited by the three species *C. carnifex*, *C. grandis*, and *C. gigantea*, and probably also by ?*H. salonicae*. In spite of the very great size differences in this group (fig. 3), the curves for the three populations resemble each other, as far as the scanty material of *C. grandis* and *C. gigantea* permits comparison. Points of resemblance are seen in the relatively short carnassials and P_3 , and the long P_4 . The size differences appear to be great enough to distinguish the three species from each other. It should be noted, however, that the difference between *C. grandis* and *C. gigantea* is matched by the difference between the two subspecies *C. crocuta crocuta* (ERXLEBEN) and *C. crocuta spelaea* (GOLDFUSS) (fig. 2B). In this latter case we have evidence for specific unity in the presence of intermediate populations linking up the extremes. There is no such evidence for *C. grandis* and *C. gigantea*, but it might of course be thought that they were actually on a cline, connected by a graded series of interjacent populations. Such a great geographic differentiation between the Chinese and Indian populations of one species would however appear improbable, since *C. eximia* does not exhibit anything like this differentiation in the same area. On the other hand, it is quite likely that the two species were not contemporary,

and that we are dealing here with a chronocline; this will be discussed below.

The lengths of P^3 and P^4 of ?*H. salonicae* are almost exactly identical with those for the homologous teeth of *C. gigantea*. The morphological difference seems to preclude reference of the Salonica form to *C. gigantea*.

Dental morphology

M_1 . — This tooth is fairly characteristic for the *Percrocuta* group. As noted above, it almost always lacks a metaconid, with the exception of a few aberrant individuals of *C. eximia*; the population from Siberia described by ORLOV (1941) probably had a local concentration of genes for this character, possibly warranting subspecific recognition.

The talonid is fairly variable. It is extremely small in *C. turgurensis*, almost as small as in *C. crocuta*, with apparently a single trenchant cusp. It is also relatively small in *C. carnifex*, where it has a single cusp, and in *C. gigantea*, where it is bicuspid. In *C. eximia*, which is known from a large material, a variation from unicuspid to tricuspid condition is encountered; the modal condition is bicuspid, with the external cusp somewhat larger. The talonid of this species is relatively longer than in the others.

Mensuration of talonid length is difficult, but a quantitative expression of relative talonid length may be obtained by studying the covariation of trigonid length (from the foremost point of the tooth to the hind edge of the protoconid) and total crown length (see KURTÉN, 1956). The variation and trend lines for different populations are recorded in fig. 4.

The populations occupy different positions in this diagram. The question is whether the trend lines, or regressions, for these populations may be considered identical or no. The problem was studied by means of analysis of variance (see e. g., SNEDECOR, 1946). The result was that there is certainly a significant differentiation in the *Percrocutas* as a whole; all the species are not on a single trend line. This, in turn, means that there was genetic differentiation for this character (relative talonid length) in different species.

The detailed results were as follows. *Crocota e. eximia*, *C. e. variabilis*, and *C. e. latro* do not show any significant differences, and these populations may be considered as identical in the genetic characters determining the relationship. The

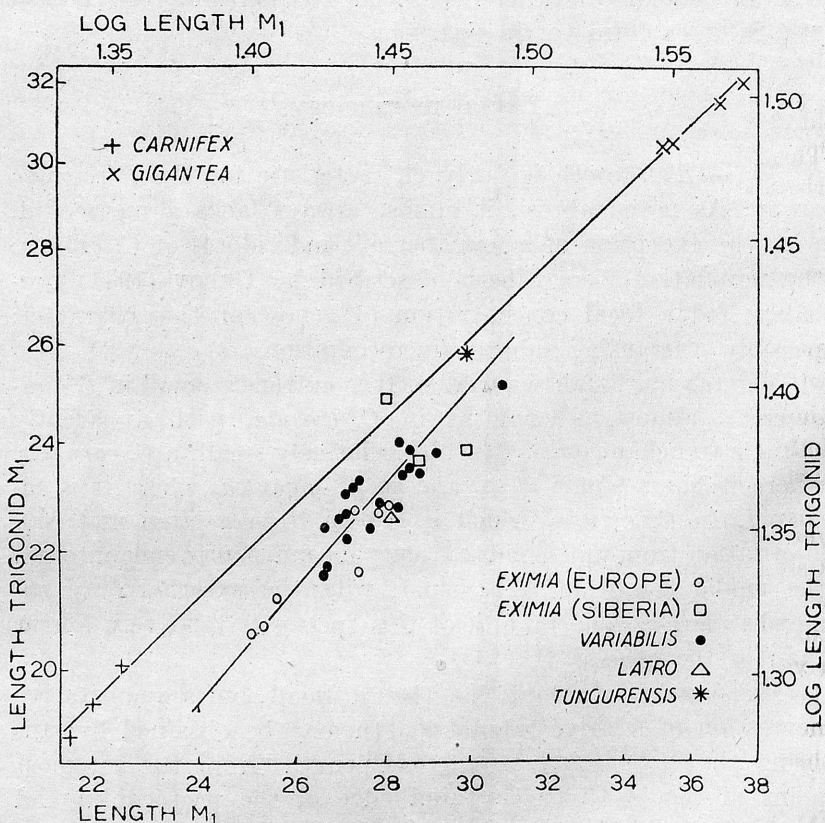


Fig. 4. Covariation between crown length and trigonid length in lower carnassials of *Crocota* (*Percrocota*), as labelled. Regression lines fitted to *eximia* group and *carnifex-gigantea* group. Coefficients of allometry: $k=1.13$ for *eximia* group, $k=0.92$ for *carnifex-gigantea* group.

trend line for *C. carnifex* is significantly different from that for the populations of *C. eximia* ($P<0.01$, that is, the chances that this conclusion is erroneous are less than one in a hundred). The trigonid of *C. carnifex* is relatively longer, and hence the talonid relatively shorter, than in *C. eximia*. *C. gigantea* does

not differ significantly from either *C. eximia* or *C. carnifex*, that is, it may be on the extension of either trend line. Considering the evidently close relationship between *C. gigantea* and *C. carnifex*, it may be that these two were on a common regression. *C. tungurensis* may belong to this same group, but I have only one observation. The M_1 of *C. grandis* is unknown.

The blade of M_1 seems to have a distinct backward rake, such as commonly seen in *Crocuta crocuta* and larger members of *Hyaena*, only in some specimens of *C. eximia* and *C. gigantea*. In *C. carnifex* and *C. tungurensis*, and in some specimens of *C. eximia* (e. g., the type) the hind edge of the protoconid actually slopes somewhat forward.

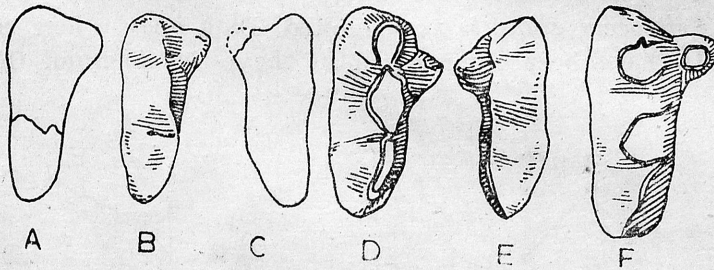


Fig. 5. Upper carnassials of hyaenids in crown view. A. *C. eximia latro*; type, G. S. I. D 206; B. *C. e. eximia*, Pikermi, B.M. M 8969; C. *C. e. latro* G.S.I. D. 205 (type of „mordax“); D. *C. grandis* n. sp., A.M.N.H. 19888, E. *C. tungurensis*, type, A.M.N.H. 26602; F. ? *H. salonicae*, type, B.M. M 11413, A, C, after PILGRIM; D, E, after COLBERT; B, F, original.

P^4 (fig. 5). The upper carnassial shows various stages in the reduction of the protocone. It is small and relatively far forward in *C. eximia* and *C. carnifex*, adjacent to the base of the parastyle. In *C. tungurensis*, *C. grandis* and *C. gigantea* it is shifted backward, to the fore part of the paracone. In ?*H. salonicae* it takes an intermediate position and is more strongly developed. The type of development of the protocone, and of other features in this tooth, suggest *Hyaena* BRISSON

(KURTÉN, 1956), but the specimen may only be a *Percrocuta* with unusually large protocone.

Anterior premolars. — P^3 of the *carnifex-grandis-gigantea* group is more elongate, with a flatter inner wall, than that in *C. eximia* and *C. tungurensis*. In *C. tungurensis* this tooth and the other anterior premolars are exceedingly broad. P_4 of *C. carnifex* and *C. tungurensis* is relatively broader than the modal conditions in *C. eximia*, *C. grandis* and *C. gigantea*; analysis of variance gives a surely significant distinction between *C. eximia* and *C. carnifex*. $P\ 2/2$ are usually little-modified miniature replicas of the succeeding $P\ 3/3$; only in *C. tungurensis* P_2 has become somewhat reduced in height, and the incipient heterodonty is somewhat reminiscent of *C. crocuta*.

Milk teeth. — Our knowledge of the milk dentitions in the *Percrocuta* group is very limited. Data on the lengths of D_2 — D_4 have been summarized in the ratio diagram, fig. 6.

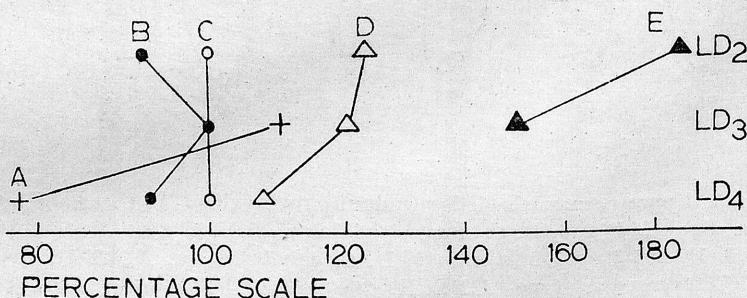


Fig. 6. Ratio diagram, comparing relative lengths of lower milk teeth in (A) *Crocuto carnifex* (after PILGRIM), (B) *C. eximia variabilis*, (C) *C. e. eximia* (original data), (D) *C. e. latro* and (E) *C. grandis* n. sp. (after PILGRIM).

Each of the *C. e. eximia* values is a mean for 2 observations; all the other populations are represented by single specimens. The deviations within the *C. eximia* group are relatively slight. Both *C. carnifex* and *C. grandis* differ sharply from the eximias in absolute as well as relative proportions.

STRATIGRAPHIC OCCURRENCE

The stratigraphic position of all the forms here discussed, except *C. gigantea*, is determinable.

C. tungurensis from the upper Miocene of the Tung Gur formation in Mongol'a is the earliest species. It appears not to have survived into the Pliocene.

Two species, *C. eximia* and *C. carnifex*, appear at the beginning of the Pliocene. In the Palearctic region, the former species appears to survive to the end of the lower Pliocene. It seems to have entered India somewhat later than Europe, and to have survived to a later date in the Indian region. The difficulties of correlation of the Siwalik series are sown by the conflicting views of eminent authorities (PILGRIM on one side, MATTHEW and COLBERT on the other). It now seems quite clear that the immigration of *Hipparion* CHRISTOL at the beginning of the Chinji stage is significant: the Chinji cannot be older than Lower Pliocene, and with this as a datum line the position of the succeeding zones may be approximately determined (COLBERT, 1935). The Chinji stage corresponds roughly to the Vallesian of Spain, and the Nagri stage to the Pikermian, or Pontian sensu stricto. This makes Dhok Pathan middle Pliocene.

C. eximia latro appears in the Nagri, and survives into the Dhok Pathan. The species thus reached India at about the middle of the lower Pliocene, and survived into the middle Pliocene, provided that the Hasnot specimen (G. S. I. D 164) actually came from the Dhok Pathan zone, which is not altogether certain.

The history of *C. grandis* in India is parallel to that of *C. eximia latro*. The species is known both from the Nagri and Dhok Pathan.

C. gigantea has been thought to be Pontian in age (e. g., PILGRIM, 1931), mostly because it was described by SCHLOSSER (1903) together with a sample of indubitably lower Pliocene species in a drugstore collection. It appears then most peculiar that the large LAGRELIUS collection of Pontian Chinese mammals, excavated by competent collectors, does not contain any specimens referable to that species. The only large Pontian hyena from China in the LAGRELIUS collection is *C. eximia*.

A specimen in the British Museum (B M 49998; see KURTÉN, 1956) bears the label, „Pleistocene; caves, China“ It was not collected by competent observers, and the suggested age is almost surely too recent, but at any rate the species seems likely to postdate the Pontian.

The very large size of the Chinese form has been stressed previously, as well as its probable affinity with the lower to middle Pliocene *C. grandis*. It seems not improbable that *C. gigantea* is the end form of a line with continued size increase. This line would seem to have had its origin together with *C. carnifex* at or just before the beginning of the Pliocene; to have been represented by *C. grandis* in the lower Pliocene and the middle Pliocene; and to have culminated in *C. gigantea*, which might then be late middle Pliocene or upper Pliocene.

?*H. salonicae* has been identified in Pontian associations in North Africa and Turkey.

TAXONOMY

Subgenus *Percrocuta* KRETZOI

Percrocuta KRETZOI, 1938, p. 117.

Aderouta KRETZOI, 1938, p. 118.

Type species: *Crocuta carnifex* PILGRIM.

Diagnosis: M_1 almost always without a metaconid; protocone of P^4 much reduced; P^3 with posterior cusp intervening between cingulum and main cone; anterior premolar stout, square to ovoid in outline; M^1 reduced.

Stratigraphic range: Upper Miocene to Pliocene.

Referred species: *Crocuta tungurensis* COLBERT; *Crocuta eximia* (ROTH and WAGNER); *Crocuta gigantea* (SCHLOSSER); *Crocuta grandis* n. sp.; possibly ?*Hyaena salonicae* ANDREWS.

Crocuta (*Percrocuta*) *tungurensis* COLBERT

Crocuta tungurensis COLBERT, 1939, p. 72.

Type: A. M. N. H. 26602, skull and mandible.

Type locality and horizon: „Wolf Camp“ quarry, Tung Gur formation, Inner Mongolia; upper Miocene.

Diagnosis: Carnassials relatively long; M_1 with very small, trenchant talonid; P^4 protocone extremely small; M^1 greatly reduced; P^3 relatively short; P_2 relatively brachyodont; premolars broad and ovoid in outline. Dimensions as in table 2.

Stratigraphic and geographic range: Known from type locality only.

Crocuta (Percrocuta) carnifex (PILGRIM)

Hyaena carnifex PILGRIM, 1913, p. 312.

Crocuta carnifex, PILGRIM, 1932, p. 141.

Type: G. S. I. No. D 172, right mandibular ramus of a juvenile individual with milk dentition and permanent teeth.

Type locality and horizon: East of Chinji and south of Nagri village; upper Chinji, Siwaliks, India: lower Pliocene.

Diagnosis: Very small size (dimensions in table 2); carnassials relatively short; M_1 with short, unicuspid, trenchant talonid; cheek teeth relatively broad; protocone of P^4 adjacent to base of parastyle, farther forward than in most other *C. (Percrocuta)*. Stratigraphic and geographic range: From base of Chinji to upper Chinji, early lower Pliocene; possibly also from the Dhok Pathan zone, middle Pliocene; India.

Crocuta (Percrocuta) gigantea (SCHLOSSER)

Hyaena gigantea SCHLOSSER, 1903, p. 35.

Crocuta gigantea, PILGRIM, 1931, p. 115.

Type (lectotype, here designated): A lower carnassial, figured by SCHLOSSER, 1903, pl. II, fig. 6; in the Institute of Historical Geology and Paleontology, Munich.

Diagnosis: Extremely large size, very robust teeth; carnassials relatively short; M_1 with small, bicuspid talonid; P^4 with protocone adjacent to base of paracone and very much reduced. Dimensions in table 2.

Type locality and horizon: China; locality and horizon unknown.

Stratigraphic and geographic range: Unknown.

New referred specimens of *C. gigantea*. Thanks to the kindness of Prof. Dr. G. H. R. von KOENIGSWALD, I have

had the opportunity to examine some teeth of *C. gigantea* in his collection from China. The source of the material is not known. The material includes P^3 , P_3 and M_1 . Furthermore, a lower carnassial in the British Museum (Natural History), no. 49998, represents the same species. The measurements of these specimens are given in table 3.

Table 3

Measurements of specimens of *Crocota gigantea*

Coll. von	P_3	
	L	W
KOENIGSWALD	28.3	19.5

Coll von	P_3	
	L	W
KOENIGSWALD	28.0	19.3

Coll. von	M_1		L trigonid
	L	W	
KOENIGSWALD	37.0	18.5	31.5
B. M. 49998	35.5	16.0	30.5

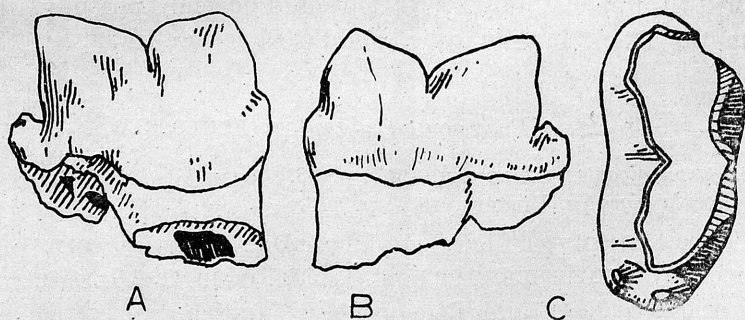


Fig. 7. Lower carnassials of *Crocota gigantea*. A, B, right M_1 in SCHLOSSER's type collection, Munich, external and internal views; C, right M_1 in the von KOENIGSWALD collection, Utrecht, crown view.

The two carnassials show the same characters as those in the type collection. Both are heavily worn. The small talonid, which appears diminutive in comparison with the extremely heavy and high-crowned trigonid, is bicuspid; the two cusps

are about equal in size. In spite of the fact that the blade is deeply worn, the talonid is almost intact, which shows that there was little functional occlusion with M^1 . The anterior and posterior lobes of the blade are of about equal width, in contrast with *C. (Crocuta)* and *Hyaena*, where the posterior lobe is much narrower; in *C. eximia* the condition may be intermediate or as in *C. gigantea*.

Crocuta (Percrocuta) grandis n. sp.

Type: G. S. I. D 162, a fragmentary ramus with P_4 and the roots of M_1 (PILGRIM, 1932, pl. VII, fig. 11).

Type locality and horizon: Nila, Dhok Pathan zone, India; middle Pliocene.

Diagnosis: Size intermediate between *C. carnifex* and *C. gigantea* (dimensions in table 2); carnassials relatively short; protocone of P^4 adjacent to base of paracone; morphology much like *C. gigantea*.

Referred specimens: A. M. N. H. 19888, maxillary fragment with P^3 — P^4 ; G. S. I. D 231, mandible fragment with P_2 and D_2 — D_3 .

Stratigraphic and geographic range: Nagri and Dhok Pathan zones, India; late lower Pliocene and middle Pliocene.

This species is distinguished from *C. gigantea* only by its much inferior size. If future discoveries should reveal that *C. gigantea* and *C. grandis* are on a cline, temporally or spatially, it may be found proper to give *C. grandis* the status of a subspecies of *C. gigantea*.

Crocuta (Percrocuta) eximia (ROTH and WAGNER)

Hyaena eximia ROTH and WAGNER, 1855, p. 396.

Crocuta eximia, PILGRIM, 1931, p. 116.

Type: A right mandibular ramus figured by ROTH and WAGNER (1855, pl. II, fig. 6), in the Institute of Historical Geology and Paleontology, Munich.

Type locality and horizon: Pikermi, Greece, late lower Pliocene.

Diagnosis: Medium size (dimensions in table 2); carnassials long; M_1 with a relatively large, unicuspid to tricuspid talonid; M^1 less reduced than in other *C. (Percrocuta)*, as far as known.

Stratigraphic and geographic range: Lower Pliocene, Europe, Middle East, Siberia, China; lower Pliocene to middle Pliocene, India.

PILGRIM (1931, p. 117) notes that *Hyaena variabilis* ZDANSKY „may hardly be entitled to specific distinction“ from *C. eximia*. In some specimens of the Chinese form the anterior cusps of P^2 and P^3 are much reduced, others agree with the typical European form. Some specimens of *H. variabilis*, moreover, have a somewhat larger protocone than the modal European type, but this variation is matched by *C. e. eximia* specimens. The dimensions are identical. Bivariate analysis of a number of characters has failed to indicate any differences. The geographic distance is great, but living species may have still greater ranges. The two populations are linked up by interjacent records from Siberia, Persia, and India. It may be concluded that *C. e. variabilis* and *C. e. eximia* belonged to a single widespread population, and hence to one species.

PILGRIM also noted the very close affinity between his *Crocuta „mordax“* (= *latro*) and *C. eximia*; he noted the possibility that the Indian form was a local race of „that apparently widely spread and variable species“ (1932, p. 152). In the following characters, PILGRIM notes, *C. latro* („*mordax*“) differs from the usual conditions in *C. eximia*, but all of them are matched in some European specimens: (1) the presence of a metaconid in M_1 ; (2) the absence of $P\ 1/1$; (3) the strong anterior cusp in P_4 . The following points would characterize *C. „mordax“*: (4) the larger M^1 ; (5) the shallower ramus. As to these, M^1 is well within the range of *C. eximia*, and actually smaller than the mean in *C. e. variabilis*, and the depth of the ramus is only known from juvenile or young adult individuals, in which it naturally would be less deep (G. S. I. No. D 163 has P_4 in permanent position, but it is almost unworn). In G. S. I. D 209, which PILGRIM excluded from his „*C. mordax*“, the ramus is as deep as in typical *C. eximia*, and so nothing precludes reference of the Indian form to *C. eximia*.

The named subspecies of *Crocuta eximia* are as follows:

Crocuta (Percrocuta) eximia eximia (ROTH and WAGNER)

The nominate subspecies; type and type locality as for the species. Diagnosis: P² and P³ with anterior cusps fairly well developed; protocone of P⁴ modally much reduced; M₁ occasionally with a metaconid.

Stratigraphic and geographic range: All of the lower Pliocene, Europe; lower Pliocene, Persia, Asia Minor, Siberia.

It is possible that the Siberian population described by ORLOV (1941) may be found to belong to a distinct subspecies, when more material is known. Possibly, the Vallesian and Pikermian forms might also be subspecifically distinct.

Crocuta (Percrocuta) eximia variabilis (ZDANSKY)

Hyæna variabilis ZDANSKY, 1924, p. 93.

Hyæna honanensis pars, ZDANSKY, 1924, p. 103.

Type (lectotype, here designated): The associated skull and mandible figured by ZDANSKY (1924, fig. 11), in the LAGRELIUS collection, the Paleontological Institute of Uppsala University.

Type locality and horizon: Loc. 114 North (Ma-Hua-T'an, Nan-Sha-Wa, Hochü, Shansi, China), lower Pliocene.

Diagnosis: Modally slightly more reduced anterior cusps in P² and P³, and slightly less reduced protocone in P⁴, than in the nominate subspecies; M₁ always without a metaconid.

Stratigraphic and geographic range: Lower Pliocene, northern China.

No character suffices to distinguish more than a part of the Chinese material from the nominate subspecies, but some differentiation on the infraspecific level had clearly occurred, and subspecific distinction appears warranted.

Crocuta (Percrocuta) eximia latro (PILGRIM)

Crocuta gigantea latro, pars, PILGRIM, 1932, p. 146.

Crocuta mordax PILGRIM, 1932, p. 150.

Type: G. S. I. D 206, right maxillary fragment with P⁴ and roots of P³.

Type locality and horizon. Hasnot, Dhok Pathan zone, India; middle Pliocene.

Diagnosis: Anterior cusp of P^2 and P^3 modally somewhat larger than in nominate subspecies; M_1 with metaconid.

Stratigraphic and geographic range: Late lower Pliocene to middle Pliocene, India.

Subspecific distinction of this form is probably warranted, though the distinguishing characters are matched by occasional specimens from other populations.

?Crocota (?Percrocota) salonicae (ANDREWS)

Hyaena salonicae ANDREWS, 1918, p. 540.

Crocota salonicae, PILGRIM, 1931, p. 123.

Type: B. M. M 11413, a right maxilla with P^2 — M^1 and part of C alveolus; sole known specimen.

Type locality and horizon: Dudular, near Salonica, Greece; horizon uncertain.

Diagnosis: Size and general proportions as in *C. gigantea*; P^4 with protocone larger than in other *C. (Percrocota)*, though smaller than in *Hyaena* and *C. (Crocota)*, and at base of partition between paracone and parastyle, at right angles to the long axis of the tooth.

Stratigraphic and geographic range: Lower Pliocene, Europe, Asia Minor, North Africa.

In 1956 I referred this species to the genus *Hyaena*, because its relative metastyle length in P^4 agrees with the *Hyaena* regression and the P^4 protocone is larger than in *C. (Percrocota)*. The possibility that *H. salonicae* is an aberrant *Percrocota* was however noted. Further study makes this even more probable. The anterior premolars have the somewhat ovoid outline typical of *Percrocota*, rather than the rhomboidal shape of the *Hyaena* teeth; and the relative metastyle length, though close to that for *Hyaena brevirostris* AYMARD, also agrees with expectation for a *Percrocota* of this enormous size. If it were not for the large protocone of P^4 , the type of *H. salonicae* might well be referred to *C. gigantea*. Too little is known

of the possible variation in the protocone of P^4 in *C. gigantea* to warrant any definite conclusions, and the status of *H. salonicae* must remain an open question until more material is found.

EVOLUTIONARY RELATIONSHIPS

Three evolutionary lines may be distinguished among the Percrocutas. One comprises the species *C. carnifex*, *C. grandis*, *C. gigantea* and possibly *H. salonicae*. It is distinguished by the shortness of the carnassials and a great reduction of the talonid in M_1 (and presumably also by reduction of M^1). *C. carnifex* is close to the ancestral type, though seemingly somewhat specialized by the development of a unicuspid talonid. *C. grandis* and *C. gigantea* may represent successive stages in evolution toward larger size. Together with *H. brevirostris* and ?*H. salonicae*, *C. gigantea* is the largest hyaenid known.

This line appears to have taken its origin shortly before the first appearance of *C. carnifex*. Since this occurs at the beginning of the Lower Pliocene, the line probably originated in the upper Miocene.

The two other evolutionary lines are monotypic. *C. tungurensis* represents a highly precocious phylum; in spite of its early date, it is more specialized than the later *C. eximia*.

C. eximia is the representative of a more conservative, and highly successful line. Apparently, it is more closely allied to *C. carnifex* than to *C. tungurensis*.

The relationships of the *Percrocuta* group with other *Hyaenidae* may finally be briefly considered. It is clear that the group has very little to do with the genus *Hyaena*, the history of which apparently is fairly well known. *Hyaena* may be traced back through a series of increasingly primitive forms from Africa (*H. makapani* TOERIEN and *H. namaquensis* STROMER) to a stage practically identical with that seen in *Ictitherium* WAGNER, and there seems to be little room for doubt that *Hyaena* evolved fairly late in the Pliocene from *ictithere* ancestors.

The relationships between the *Percrocuta* group and the true *Crocotas* are more obscure. Certainly no known *Percrocuta*

is ancestral to *C. (Crocuta)*. The earliest known species of the nominate subgenus *C. sivalensis* from the lower Pleistocene of India, points back to a highly different kind of ancestor, with well-developed metaconid and long talonid in M_1 , large protocone in P^4 , and heterodont anterior premolars. Of all suggestions, that by KHOMENKO (1932) appears to me most probable: that *C. crocuta* has evolved from some form like *Lycyaena chaeretis* of the lower Pliocene — though *Hyaena borissiakii* KHOMENKO, indicated as a connecting link, is unlikely to figure in that history. Should this alternative prove to be true, a full generic separation of *Crocuta* and *Percrocuta* would be warranted. Pending further work throwing light on this question, it seems better at present to give *Percrocuta* subgeneric status.

The origin of the *Percrocutas* themselves is open to question. It would hardly seem to have taken place later than the middle Miocene, but no known forms bridge the gap between the highly specialized *Percrocutas* and the small viverrid or proto-hyaenid forms (*Semigenetta* HELBING, „*Progenetta*“ DEPÉRET) of that time. Future discoveries may point to a solution.

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Geological Institute of Helsingfors University

STRESZCZENIE

Autor omawia grupę hien późniejszego trzeciorzędu wyróżnioną przez PILGRIMA (1931) a nazwaną przez KRETZOIA (1938) *Percrocuta*. Autor uważa tę grupę za podrodzaj w obrębie rodzaju *Crocota* KAUP. Zalicza on tutaj następujące gatunki: *C. carnifex* (PILGRIM), *C. tungurensis* COLBERT, *C. eximia* (ROTH and WAGNER), *C. gigantea* (SCHLOSSER), *C. grandis* n. sp. i prawdopodobnie ?*Hyaena salonicae* ANDREWS. Wśród hien tej grupy z środkowych warstw Siwalik opisanych przez PILGRIMA (1932) wyróżnił autor dwie odrębne populacje. Ponieważ jednak typy dwu form opisanych przez PILGRIMA t.j. *C. gigantea latro* i *C. mordax* należą do jednej i tej samej populacji, przeto *C. mordax* PILGRIM okazuje się synonimem

C. eximia latro (PILGRIM), zaś druga grupa nazwana zostaje *C. grandis* n. sp. Autor omawia ogólne cechy podrodzaju *Percrocuta* KRETZOI, taksonomię form należących do tego podrodzaju, ich pokrewieństwa, rozmieszczenie czasowe i przestrzenne.

РЕЗЮМЕ

Автор описывает группы гиен позднего третичного периода, выделенную Пилгримом (1931) и названную Кретпоем (1938) — *Percrocuta*. Автор полагает, что группа эта является подродом в пределах рода *Crocuta* KAUP. К группе этой автор причисляет виды: *C. carnifex* (PILGRIM), *C. tungurensis* COLBERT, *C. eximia* (ROTH and WAGNER), *C. gigantea* (SCHLOSSER), *C. grandis* n. sp. и возможно так же? *Hyaena salonicae* ANDREWS. Из числа гиен этой группы, находящихся в средних слоях Сивалик и описанных Пилгримом (1932), автор выделяет две различные популяции. Так как типы двух форм, описанных Пилгримом — *C. gigantea latro* и *C. mordax*, принадлежат к одной и той же популяции, вследствие этого *C. mordax* PILGRIM оказывается синонимом *C. eximia latro* (PILGRIM); другая группа названа автором *C. grandis* n. sp. Автор оговаривает общие признаки подрода *Percrocuta* KRETZOI, таксономию форм, принадлежащих к этому подроду, их родство и расселение во времени и пространстве.

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