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Chronological and geographical variability of *Crocuta spelaea* (Carnivora, Hyaenidae) from the Pleistocene of Russia

Baryshnikov, G., 1999 - Chronological and geographical variability of *Crocuta spelaea* (Carnivora, Hyaenidae) from the Pleistocene of Russia - in: Haynes, G., Klimowicz, J. & Reumer, J.W.F. (eds.) – MAMMOTHS AND THE MAMMOTH FAUNA: STUDIES OF AN EXTINCT ECOSYSTEM – DEINSEA 6: 155-174 [ISSN 0923-9308]. Published 17 May 1999.

Geographic variation in *Crocuta spelaea* dentition, beginning from the Middle Pleistocene, can be seen as specialization in western and eastern Eurasia. The sizes of *C. spelaea* increase from the south to the northwest and northeast. The hyena of the Primorski Krai had the largest teeth.

Chronologische en geografische variatie in Crocuta spelaea (Carnivora, Hyaenidae) uit het Russische Pleistoceen – Geografische variatie in het gebied van de grottenhyena, vanaf het Midden Pleistoceen, wordt beschouwd als een specialisatie in westelijk en oostelijk Eurazië. De maten van de grottenhyena nemen toe van het zuiden naar het noordwesten en noordoosten. De hyena van Primorski Krai had de grootste gebits-elementen.

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Keywords: *Crocuta spelaea*, Russia, geographic variability, Pleistocene

INTRODUCTION

The cave hyena *Crocuta spelaea* (GOLDFUSS, 1823) from Pleistocene Eurasia is usually regarded as an extinct northern subspecies of the recent *C. crocuta* (ERXLEBEN, 1777) (Kurtén 1956, Werdelin & Solounias 1991). This assumption, based upon a formal similarity of skeletal features of both forms, is in fact debatable. The view that *C. spelaea* is a separate species is supported by the more carnivorous specialization of its dentition, as compared to *C. crocuta* (Baryshnikov 1995, Baryshnikov & Averianov 1995). One also may assume that the cave hyena had adaptations to life in a climate that had a long frosty period (adaptations predicted, for example, to be in features such as the development of a dense fur coat). The character

of bone assemblages of *C. spelaea* from European cave sites basically differs from that in Africa, permitting us to assume differences in behavior between *C. spelaea* and *C. crocuta* (Brugal *et al.* 1997). The cave hyena was probably an active predator of Pleistocene ungulates and may have lived in larger groups with a complex hierarchical structure.

An ancestor of *C. spelaea* was *C. sivalensis* (FALCONER ET CAUTLEY, 1868) from the Siwalik fauna of India, which during the Cromerian interglacial spread into the temperate latitudes of Eurasia (Kurtén 1956, 1957). I refer to *C. spelaea* all Pleistocene discoveries of the genus *Crocuta* from Europe, western

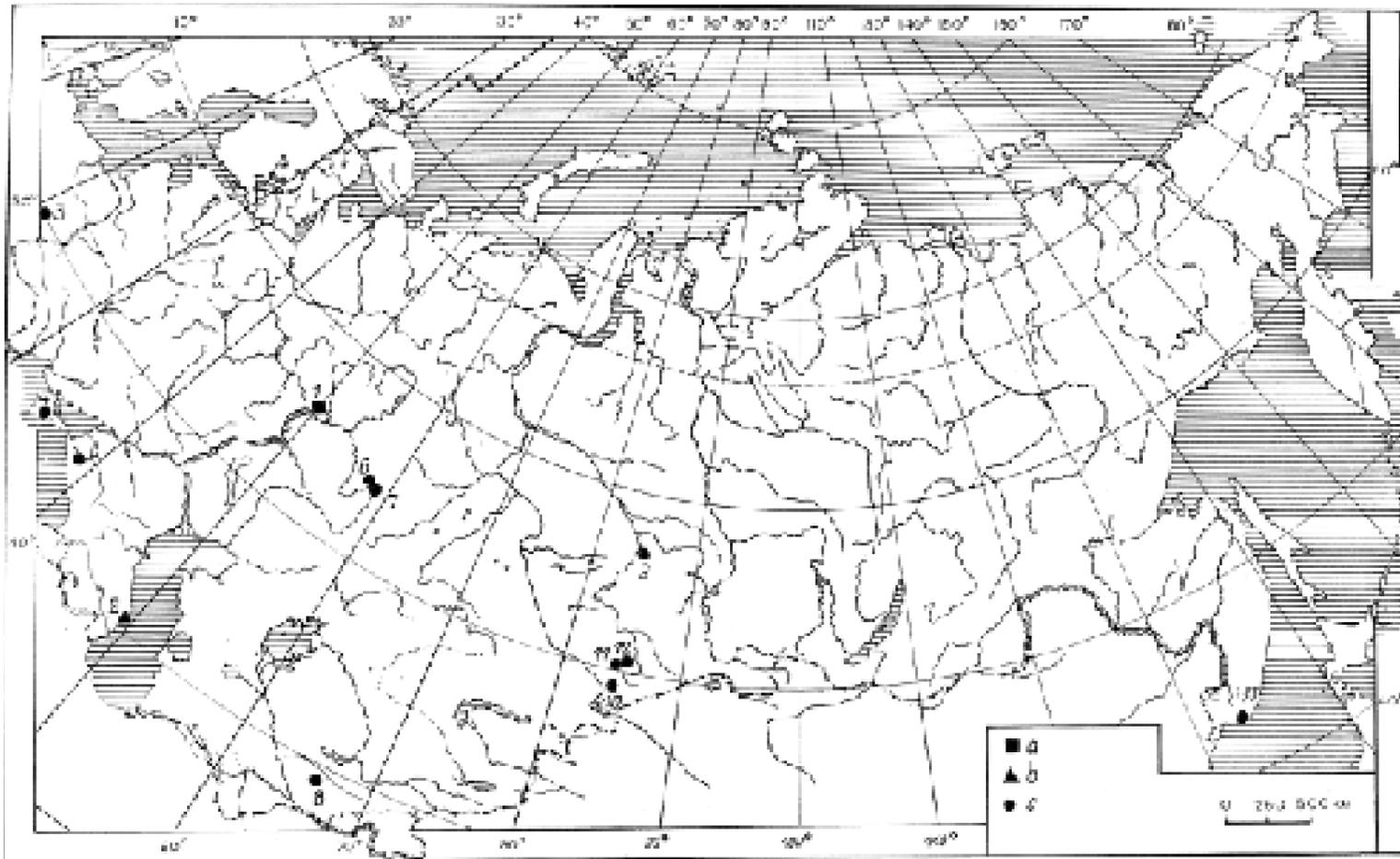


Figure 1 Localities with Pleistocene remains of *Crocuta spelaea* in Russia and adjacent territories: **a** - Cromerian-Mindel, **b** - Riss-Würm, **c** - Würm. **1** - Kazanka River, **2** - Binagady, **3** - Golabiec, **4** - Prolom 2, **5** - Ilskaya I, **6** - Nasorog Cave, **7** - Smelovskaya 2 Cave, **8** - Aman-Kutan, **9** - Krasnyi Yar, **10** - Bukhtarminskaya Cave, **11** - Ust-Kanskaya Cave, **12** - Denisova Cave, **13** - Geographical Society Cave.

Asia, middle Asia, Siberia and China; the genus evolved several subspecies replacing each other in time and space (Kurtén 1956, 1965, Bonifay 1971, Schutt 1971, Kurtén & Poulanos 1977).

In the former Soviet Union the earliest record of *C. spelaea* falls in the Cromerian/Mindel transitional period. During that time interval the remains of *Crocuta* are known from the Ukraine (Opolie, Sinyakovo), Russian Plain (Kazanka River), Northern Caucasus (Treugolnaya Cave), and Kazakhstan (Zhelesinskoe; Baryshnikov & Vereshchagin 1996). No significant discoveries are known for that area for the period from the Late Mindel up to the Riss, although remains of *Crocuta* from Kyrgystan (Sel-Ungur Cave, Mindel or Mindel-Riss) and Moldova (Starye Durutory, Riss ?) could belong to the same time interval. More information is available

on the localities of the last interglacial (Riss-Würm) in Moldova (Vykhvatintsy), Ukraine (Iliinka, Kiik-Koba) and Azerbaijan (Binagady). We have a better knowledge of the distribution of *C. spelaea* in the Early-Middle Würm (Fig. 1). In deposits of that period its abundant remains occur jointly with a complex of Mousterian stone implements. Cave hyena was found in Moldova, Crimea, the Northern Caucasus, the Southern Urals, middle Asia, Kazakhstan, and Southern Siberia eastwards up to the Angara River basin, while further in the east it appears again in the southern Primorski Krai where it penetrated from China (Baryshnikov & Vereshchagin 1996). In the Crimea and in Middle Asia *C. spelaea* disappears by the beginning of the early Paleolithic, but in the Urals and the Altai it could have survived until the main climatic minimum of the Late Pleistocene.

During the Pleistocene European *C. spelaea* demonstrated notable differences in the sizes of skull and teeth, observed when the discoveries from deposits of glacial and interglacial epochs are compared (Kurtén & Poulanos 1977, Klein & Scott 1989). However, the tendencies of geographic variation at different temporal levels of the Pleistocene are not sufficiently studied. In this paper the major tendencies of spatial and temporal variation of *C. spelaea* are discussed for the former Soviet Union and Western Europe. Most attention has been concentrated on molars, the sizes and proportions of which varied depending not only on the size of animals, but also on dietary specialization.

MATERIALS

The materials studied include sixteen samples of fossil hyena remains from the collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN); the Geological and Mineralogical Museum of Kazan University, Kazan, Russia (GMM); the Institute of Archaeology and Ethnography,

Russian Academy of Sciences, Novosibirsk (IAE); the Institute of Archaeology, Ukrainian Academy of Sciences, Kiev (IAU); the Institute of Systematics and Evolution of Animals, Krakow, Poland (ISE); l'Université Claude Bernard Lyon 1, Villeurbanne, France (UCB); l'Université Pantheon-Sorbonne, Paris, France (UPS); and the Laboratoire de Geologie du Quaternaire, Marseille-Luminy, France (LGQ) (Table 1).

Russia

KAZANKA RIVER. Complete skull with lower jaw from the Kazanka River in Tatarstan (GMM 191); Middle Pleistocene (Cromerian-Mindel).

ILSKAYA 1. Postcranial bones and lower cheek teeth (ZIN 19889). Mousterian open site at Il River (Kuban Basin), Northern Caucasus; Early Würm.

NOSOROG CAVE. Left mandible (ZIN 34477). A cave in the South Urals; apparently dated to the Early Würm.

SMELOVSKAYA 2 Cave. Approximately 45 *Crocota* remains (ZIN 34491). Upper Paleolithic site on Malyy Kizyl River, South Urals. *Crocota* remains come from layer 5, lying beneath the cultural layer. Radiocarbon dates are: layer 3-4: 31,000 +/- 1500 yBP (GIN-8401); 41,000 +/- 1800 yBP (GIN-8402).

KRASNYI YAR. Left mandible (ZIN 32752) from Ob River beach near village Krasnyi Yar in Tomsk Region (Fig. 2).

UST-KANSKAYA CAVE. Postcranial elements and isolated teeth of hyena (ZIN 34404) within highly fragmented ungulate bones, in a Mousterian cave site on Charysh River in Altai; Karginian interglacial Mousterian deposits.

DENISOVA CAVE. A few isolated bones and teeth (coll. IAE) from Mousterian (layers 12-20) and Upper Paleolithic (layers 9-11) site located on Anui River in Altai. Layer 21 has thermoluminescence dates 155,000 ± 31000 (RTL-546) and layer 14 as 69,000 ± 17000 (TL-9), and layer 11 radiocarbon date as >37,235 yBP (SOAN-2504).

GEOGRAPHICAL SOCIETY CAVE. More than 170 bones and teeth, including fragmented skull (Fig. 3) and few lower jaws (ZIN 34478-34490) mainly from a depth of 80-140 cm below the surface (layer 4); Upper Paleolithic site located at Partizanskaya River (= Suchan River) in southern Primorski Krai. Bones of horse and mammoth from a depth of 60-80 cm were dated by radiocarbon as 32,570 +/-1510 yBP (IGAN-341).

Table 1 The number of specimens studied.

Time Period & Locality	Maxilla	Mandible	Upper Isolate Cheek Teeth	Lower Isolate Cheek Teeth
Mindel				
Kazanka River	1	1	---	---
Mindel - Riss				
Lunel-Viel	10	11	4	3
Riss - Würm				
Binagady	5	7	3	3
Würm				
Jaurens	2	4	1	1
Arcy-sur-Cure	---	7	31	28
Golabiec	---	1	23	32
Prolom 2	3	4	46	40
Ilskaya 1	---	2	---	4
Nosorog Cave	---	1	---	---
Smelovskaya 2 Cave	---	---	2	4
Krasnyi Yar	---	1	---	---
Ust-Kanskaya Cave	---	---	3	4
Denisova Cave	---	---	2	1
Bukhtarninskaya Cave	---	---	---	3
Aman-Kutan	1	2	4	5
Geographical Society Cave	6	11	6	13
Total	28	52	125	141

Ukraine

PROLOM 2. 418 remains of hyena including fragments of lower jaws, limb bones and isolated teeth (coll. IAU). Mousterian cave site at the left bank of Biyuk Karasu River near Belogorsk City, Crimea; Early Würm.

Azerbaijan

BINAGADY. Numerous bone remains of hyena skulls without lower jaws (ZIN 24407) (Fig. 4) and 10 mandibles (ZIN 22382). Tar pit near Baku City; Riss-Würm (Eem).

Uzbekistan

AMAN-KUTAN. More than 55 fossil remains of hyena (ZIN 25217, 29058); Mousterian cave located on the western slopes of Zeravshan Ridge; Early Würm.

Kazakhstan

BUKHTARMINSKAYA CAVE. Small collection of fragments of bones and teeth (ZIN 34403); Upper Paleolithic cave site situated in Bukhtarma River mouth; Middle Würm.

France

LUNEL-VIEL. Numerous remains of cave hyena, including whole skulls and mandibles (LGQ 334, 368, 736, 2408, 2677, 2898, 5189, 12598); cave site is situated nearby Montpellier (Hérault) in the south of France; Mindel-Riss.

JAURENS. Hyena remains studied by the author are not abundant (UCB 300568, 300576, 300578, 300581, 300582, 300586); Cave located in the central part of France (Correze); Würm.

ARCY-SUR-CURE. Numerous remains include isolated teeth and bone fragments mainly from Mousterian deposits from Grotte Renne (levels XI-XIV) and Galerie Schoepfin (coll. UPS); several caves situated in the central part of France (Yonne) yielded Mousterian and Upper Paleolithic tools; Early and Middle Würm. Level XII in Grotte Renne has a radiocarbon date of 37,500 +/- 1600 yBP. Some teeth

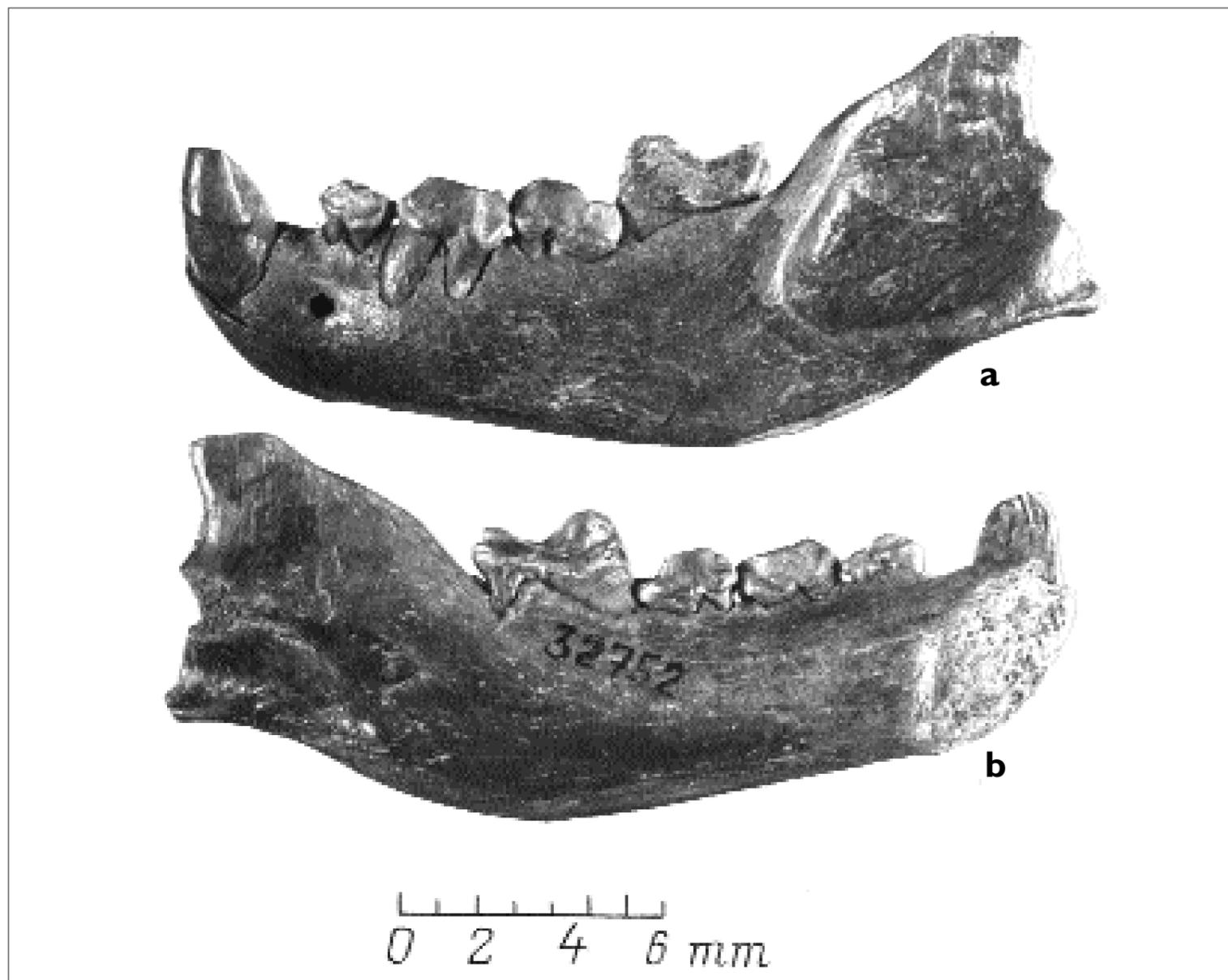


Figure 2. Left lower jaw of *Crocuta spelaea* from Krasnyi Yar in Western Siberia (coll. ZIN 32752). Labial (a) and lingual (b) views.

were unearthed from lower levels of Upper Paleolithic deposits in Grotte Renne (IX-X).

Poland

GOLABIEC. A series of molars and bones (ISE MF/37/60); cave site in the southern part of Poland; Würm.

Collections with small samples from some sites were placed into two groups: 'South Urals' with the teeth from Smelovskaya 2 Cave and Nosorog Cave, and 'Altai' - from Ust-Kanskaya Cave, Denisova Cave and Bukhtarminskaya Cave.

METHODS

The maximum length (L) and maximum width (W) of upper and lower cheek teeth were measured. In addition, the length of the metastyle (Lm) was measured on P4, and the length of the trigonid (Lt) on m1. Statistics include calculation of means (\bar{x}) and standard deviation (SD). I also used Component Analysis and Cluster Analysis of samples on euclidean distances with hierarchy dendrogram by the average linkage method in the statistical software SYSTAT.

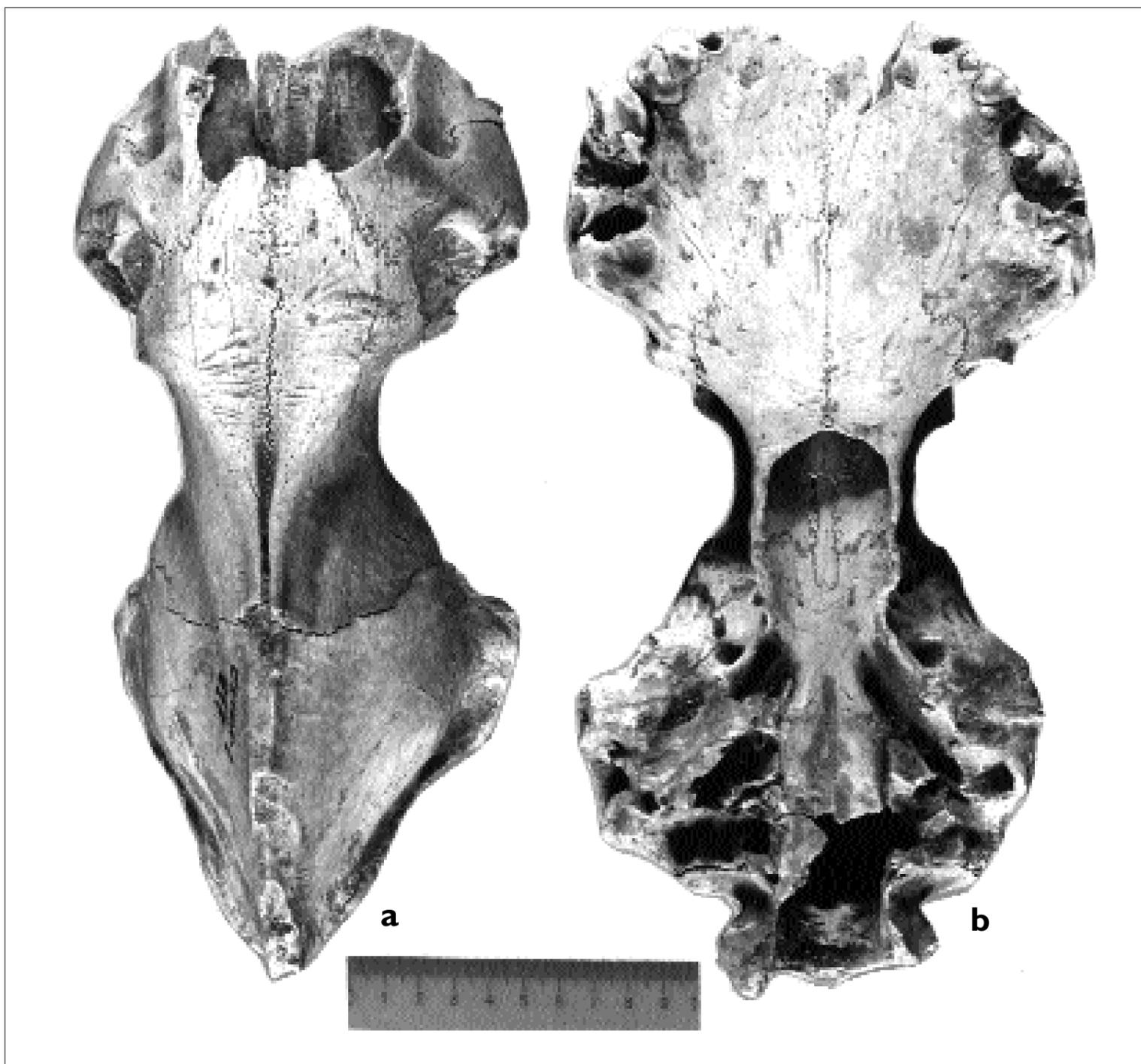


Figure 3 Cranium of *Crocuta spelaea ussuica* from Geographical Society Cave, Russian southern Far East (coll. ZIN 34478, holotype). Dorsal (a) and palatal (b) views.



Figure 4. Cranium of *Crocuta spelaea* from Binagady in eastern Transcaucasia (coll. ZIN 24407). Dorsal (a) and palatal (b) views.

RESULTS

Cranium

European populations of *C. spelaea* reveal fluctuations of average values of condyle basal length of the skull during the Pleistocene (Kurtén & Poulanos 1977). An increase of condyle basal length from a large (267 mm) in the Cromerian and Early Mindel (*C. spelaea praespelaea* SCHÜTT, 1971) to a very large size (279.5 mm) in the Mindel (*C. spelaea petralona* KURTÉN, 1977) is followed by an abrupt decline of its values (240-251 mm)

during the Mindel-Riss interglacial (*C. spelaea intermedia* BONIFAY, 1971). Next there was another insignificant increase (245-260 mm) in the Riss, another decline (236-262 mm) in the Riss-Würm interglacial and, eventually, the increase of the length up to its maximal values (240-288 mm) in the Würm glacial (*C. spelaea spelaea* GOLDFUSS, 1823). Therefore, the size of the individual animals was essentially different in the cold and warm climatic phases of the Pleistocene. Isolated data on condylar basal length in

Table 2 Geographical variability of length of P1-P4 (in mm) in *Crocota spelaea*. (Note: in Tables 2-6 and 8-12 *C. spelaea praspelaea* should read *C. spelaea praespelaea*.)

Time Period and Locality	n	range	x	SD
MIDDLE PLEISTOCENE				
Cromerian and Mindel				
<i>C. spelaea praspelaea</i>				
Mosbach, Germany (Schutt, 1971)	4	87.0 - 96.0	92.5	3.87
Kazanka River, Russian Plain (coll. MGM)	1	89.3	—	—
Mindel - Riss				
<i>C. spelaea intermedia</i>				
Lunel-Viel, France (coll. LGQ)	7	81.1 - 85.6	83.39	1.79
Riss				
<i>C. spelaea spelaea</i>				
Gargas, France (Clot, 1980)	3	86.4 - 89.6	87.7	—
LATE PLEISTOCENE				
Riss - Würm				
<i>C. spelaea spelaea</i>				
Binagady, Transcaucasia (coll. ZIN)	3	79.7 - 84.5	82.07	—
Würm				
<i>C. spelaea spelaea</i>				
Gerde, France (Clot, 1980)	1	91.4	—	—
Bouhadere, France (Clot, 1980)	4	85.8 - 91.0	87.45	2.40
Jaurens, France (coll. UCBL)	2	84.4 - 89.8	87.15	—
<i>C. spelaea ussuriica</i>				
Geographical Society Cave, Primorski Krai (coll. ZIN)	1	87.8	—	—

hyenas from other regions of Eurasia, such as from the Kazanka River in the Russian Plain, of Cromerian-Mindel age (268.5 mm), and from Binagady in the Transcaucasia, of Riss-Würm age (250.5 mm), are fully consistent with the European scheme. In *C. spelaea ultima* (MATSUMOTO, 1915) from Yenching-kou in China, from the Middle Pleistocene (Colbert & Hooijer 1953), the length of the skull (c. 260 mm) is only slightly less than in the Eurasian species of the same age, *C. spelaea praespelaea*.

Upper cheek teeth

The length of the upper dental row P1-P4 changed in time analogous to the change of condyle basal length of the skull (Table 2). No appreciable spatial differences are observed. At the same time, amongst average values of the length of the upper premolars (P2 + P3 + P4), a sample from the Geographical Society Cave (90.2, n = 4-7) is prominent; it exceeds all other series known for *Crocota* from the Middle and Late Pleistocene, including Mosbach and

Table 3 Measurements (mm) of first upper premolar P1 in *Crocota spelaea*.

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praspelaea</i>								
Kazanka River	1	8.4	—	—	1	7.8	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	3	6.1 - 7.1	6.73	—	3	5.8 - 6.3	6.07	—
<i>C. s. spelaea</i>								
Binagady	1	7.0	—	—	1	6.8	—	—
Jaurens	1	7.1	—	—	1	6.9	—	—
Arçay-sur-Cure	8	6.5 - 8.3	7.27	0.66	8	6.6 - 8.0	7.40	0.50
Prohm 2	8	6.9 - 8.5	7.61	0.57	8	6.7 - 8.8	7.66	0.64
Aman-Kutan	1	7.2	—	—	1	7.5	—	—
Alta	1	8.0	—	—	1	8.3	—	—
<i>C. s. ussuriica</i>								
Geographic Soc. Cave	4	6.9 - 8.2	7.55	0.64	4	6.2 - 8.5	7.57	0.97

Petralona Cave (Schütt 1971, Kurtén & Poulianos 1977).

P1 This relatively small tooth shows considerable variation in its proportions, which is typical of teeth not participating significantly in occlusion. It is relatively smaller in *C. spelaea* in comparison to the tooth in *C. crocuta* (Baryshnikov 1995). A decline in the relative size of P1 can be regarded as an index of carnivorous specialization of the dentition of the cave hyena. Such a reduction of the first premolar (up to its complete reduction in the Felidae) is observed in different lines of Aeluroidea at the stage of transition to myophagy. There are no appreciable differences in sizes of the tooth among the studied samples (Table 3).

P2 The large size of the tooth was typical of subspecies *C. s. praespelaea*, *C. s. ultima*, and particularly *C. s. petralona*, in which this tooth, along with other upper molars, was extremely wide (Kurtén & Poulianos 1977). In the samples studied, the largest sizes were noted for P2 from the Geographical Society Cave, and the smallest sizes were noted for P2 from Lunel-Viel and Aman-Kutan (Table 4). The teeth from Lunel-Viel are relatively wide, whereas in Late Pleistocene hyenas the crown is longer.

Table 4 Measurements (mm) of second upper premolar P2 in *Crocuta spelaea*

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praspelaea</i>								
Kazanka River	1	17.9	—	—	1	13.4	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	11	14.6 - 17.0	15.62	0.68	10	11.3 - 12.9	12.28	0.52
<i>C. s. spelaea</i>								
Binagndy	4	15.4 - 17.6	16.75	0.95	4	11.4 - 13.4	12.57	0.92
Jaurens	2	15.7 - 18.1	16.90	—	2	12.5 - 12.6	12.55	—
Arcy-sur-Cure	6	16.4 - 17.9	17.13	0.65	6	10.9 - 13.8	12.42	1.15
Prolom 2	13	15.8 - 19.8	17.40	1.17	13	12.0 - 14.8	13.24	0.93
Aman-Kutan	3	15.2 - 16.8	16.03	0.80	3	11.2 - 12.1	11.63	0.45
South Urals	1	17.8	—	—	1	12.8	—	—
Altai	2	18.3 - 18.7	18.50	—	2	12.0 - 13.2	12.60	—
<i>C. s. ussurica</i>								
Geographic Soc. Cave	5	16.0 - 20.9	18.72	1.76	5	11.5 - 15.0	13.42	1.31

It is elongated moderately lengthwise in samples from Binagady and Prolom 2 and is elongated more strongly in samples from Arcy-sur-Cure and Aman-Kutan. A relatively narrower P2 was noted in hyenas from the Late Pleistocene of southern Siberia.

P3 This tooth interacts with m1 during bone-crushing (Schütt 1971) and therefore its structure can be used to assess the adaptation of hyena dentition to feeding on carrion. In *C. spelaea* from Europe the main tendency of changing sizes and proportions of P3 is that in animals of interglacial epochs it was shorter and wider than in hyenas of glacial epochs (Kurtén & Poulianos 1977). A relative increase of the third premolar (as compared to the size of the carnassial tooth) is observed in *C. s. dorotheae* (Kurtén 1965) from the Levant. As regards *C. s. ultima* from the Middle Pleistocene of China, this subspecies is characterized by the extremely high crown of P3 (Kurtén 1956). This degree of increase in the height of the crown (hypsodontia) was not noted in other populations of *C. spelaea*, including the collection from the Geographical Society Cave. It indicates a specialization in *C. s. ultima* to splitting thick-walled tubular bones and tearing apart the remains of giant herbivores that were abundant in the Pleistocene lands-

caples of China. The ratio of length and width of the tooth in the samples that I have studied are shown in Fig. 5. It should note a relatively wide P3 from Lunel-Viel, and also an elongation of the crown in samples from the Geographical Society Cave. In the latter case the average value of P3 is maximal (Table 5). Whereas the former parameter indicates strengthening of P3 for the crushing of bones during the consumption of carrion, the latter is connected with the strengthening of carnivorous tendencies during myophagy of *C. spelaea*. Such variation could have occurred independently in different local populations. There were at least three manners of P3 modification in *C. spelaea*: an increase of absolute (*C. s. petralona*) and relative (*C. s. intermedia*) width of the tooth and increase of the height of its crown (*C. s. ultima*): a bone crushing adaptation, and also an increase of the absolute (*C. s. ussurica*) and relative (*C. s. spelaea*) length of the tooth: an adaptation to flesh cutting. The sizes of P3 in the *Crocuta* of the Late Pleistocene were weakly changing from Europe to the Altai, and only in the Russian Far East they were much larger and relatively narrower (in the subspecies *C. s. ussurica* Baryshnikov & Vereshchagin, 1996).

P4 In the evolution of *C. spelaea* one observes an increase of total sizes of P4 and the relative length of its metastyle towards the Late Pleistocene (Kurtén 1956, Kurtén & Poulianos 1977). My data also indicate that length of tooth varied in accordance with fluctuations of animal sizes, attaining larger values in glacial epochs (Table 6). The largest mean value of length of the upper carnassial tooth was found in the sample from Geographical Society Cave.

The relative length of the metastyle of P4 (Lm/L) characterizes a specialization of Carnivora to myophagy, and therefore it can be an index of carnivorous adaptation of *C. spelaea*. In the Mindel and Würm epochs the metastyle was elongating, whereas in the

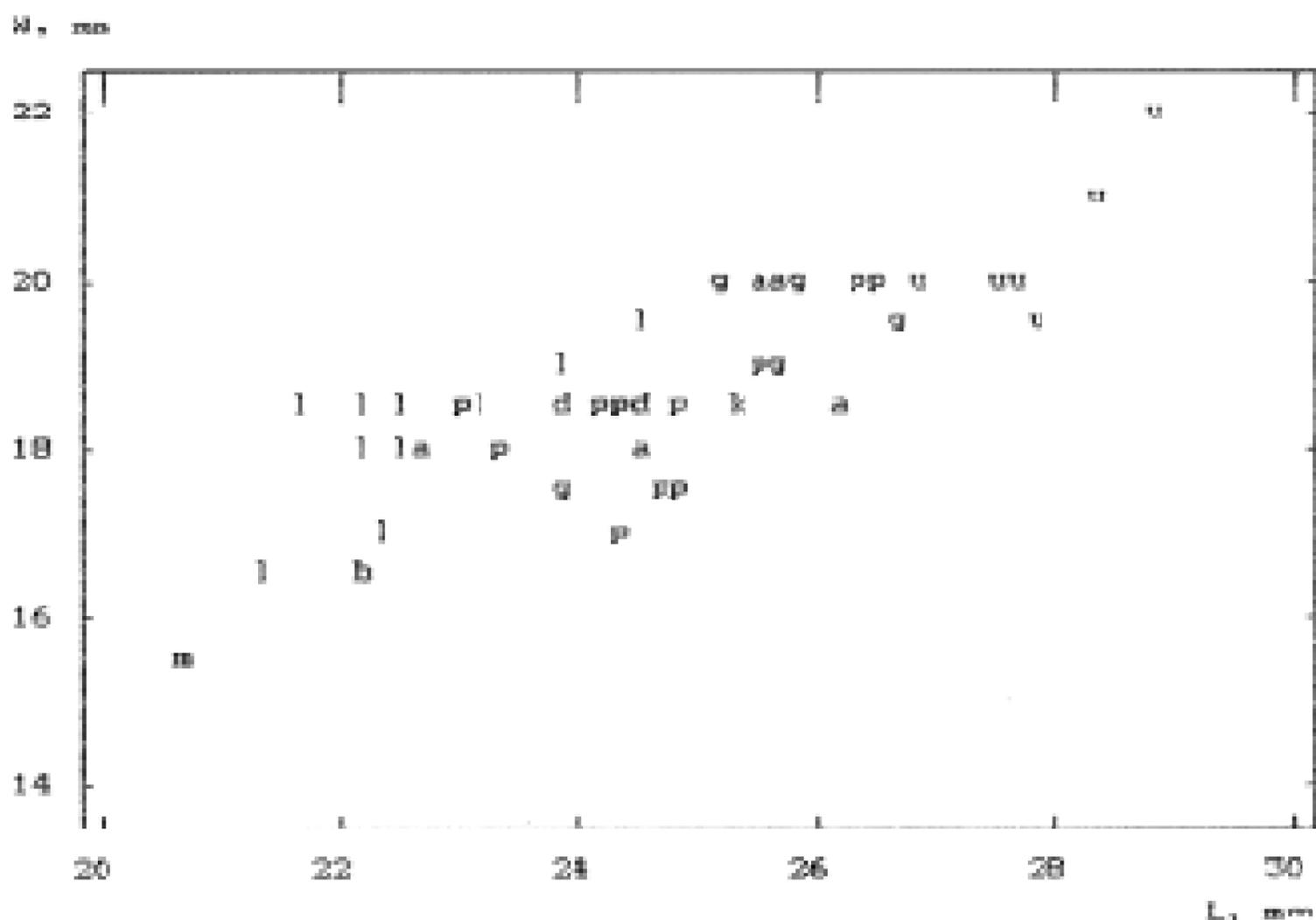


Figure 5 Scattergram of width (W) and length (L) of upper third premolar P3 in *Crocuta spelaea*. **a** - Arcy-sur-Cure, **b** - Binagady, **d** - Altai, **g** - Golabiec, **j** - Jaurens, **k** - Kazanka River, **l** - Lunel-Viel, **m** - Aman-Kutan, **p** - Prolom 2, **u** - Geographical Society Cave

Mindel-Riss and Riss-Würm it was relatively shortened (Fig. 6). The elongation of the metastyle in the glacial epochs of the Pleistocene indicates the growing role of active predation in the life of the cave hyena. More predatory habits were determined by the necessity to increase the consumption of flesh with its high caloric value, particularly in northern populations that lived in a cold climate with a long and harsh winter period. According to this character, the most advanced animals among the Würm *Crocuta* were from the northwestern part of the distribution range (Arcy-sur-Cure). In the *Crocuta* from the Geographical Society Cave, on the other hand, the general size of the carnassial tooth was larger and therefore the relative length of the metastyles was somewhat smaller.

General remarks Among the upper teeth, most important in the evolution of *Crocuta* are transformations of the P3 and P4. My analysis of the main components of length and width in both teeth in *C. spelaea* and *C. crocuta* (Table 7; Fig. 7) shows that the samples used were divided in factor space F1 x F2 into three groups. The greatest deviation was noted for *C. s. petralona*, known only from isolated specimens. This form was characterized by unusually wide upper premolars (Kurtén & Poulanos 1977). The second group consisted of recent *C. crocuta*, which is confirmed by its isolation from *C. spelaea*. As regards the pattern of samples of *C. spelaea*, four groups are distinguished within it: (b, d, l), (a, p, g), (m), (u). Each of the last three groups corresponds to subspecies *C. s. spelaea*, *C. s. praespelaea* and *C. s. ussurica*. The first group consists of

Table 5 Measurements (mm) of third upper premolar P3 in *Crocota spelaea*.

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praespelaea</i>								
Kazanka River	1	25.3	—	—	1	18.5	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	12	21.4 - 24.5	22.70	0.90	12	16.5 - 19.2	18.10	0.76
<i>C. s. spelaea</i>								
Binagady	1	22.2	—	—	1	16.4	—	—
Jaurens	1	24.6	—	—	1	18.1	—	—
Arcy-sur-Cure	5	22.7 - 26.1	24.90	1.36	5	17.7 - 19.7	18.62	1.00
Golabiec	9	23.0 - 26.7	24.99	1.09	9	17.3 - 19.6	18.58	0.79
Prolom 2	19	23.0 - 26.5	24.46	1.05	18	17.0 - 19.8	18.26	0.74
Aman-Kutan	1	20.7	—	—	1	15.4	—	—
South Urals	1	25.3	—	—	1	18.0	—	—
Altai	2	23.9 - 24.5	24.20	—	2	18.5 - 18.5	18.50	—
<i>C. s. ussurica</i>								
Geographic Soc. Cave	6	26.9 - 28.9	27.87	0.69	6	19.3 - 21.7	20.32	0.87

subspecies *C. s. dorotheae*, *C. s. intermedia*, and a sample from Binagady. It does not contradict the inclusion of *C. s. dorotheae* into the species *C. spelaea*, and also probably suggests that *C. spelaea* from Binagady deserves being placed in a separate subspecies (together with other hyenas of the last interglacial in Europe).

Lower cheek teeth

The distribution of average length values of the lower dental row p2-m1 in time shows that the largest sizes occurred in *Crocota* from Cromerian-Mindel and Würm, and the

Table 7 Correlations of characters with the first three principal components for upper cheek teeth.

Measurements	F1	F2	F3
Component loadings			
P3/ L	0.854	0.490	0.165
W	0.917	-0.320	0.227
P4/ L	0.943	0.208	-0.248
W	0.925	-0.348	-0.125
Percent of total			
variance explained	82.969	12.676	3.998

Table 6 Measurements (mm) of fourth upper premolar P4 in *Crocota spelaea*.

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praespelaea</i>								
Kazanka River	1	42.7	—	—	1	23.3	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	10	35.7 - 39.5	37.53	1.30	11	19.6 - 21.8	20.68	0.72
<i>C. s. spelaea</i>								
Binagady	8	36.6 - 42.2	39.64	1.95	8	18.7 - 23.9	21.76	1.87
Jaurens	2	40.0 - 41.6	40.80	—	2	21.6 - 23.3	22.45	—
Arcy-sur-Cure	12	38.8 - 43.3	40.86	1.44	12	20.0 - 24.9	21.64	1.40
Golabiec	5	38.8 - 42.1	40.80	1.24	6	20.6 - 23.7	22.33	1.04
Prolom 2	13	37.4 - 43.9	40.38	1.97	10	20.9 - 24.2	22.15	1.26
<i>C. s. ussurica</i>								
Geographic Soc. Cave	4	40.7 - 46.5	44.27	2.53	5	19.8 - 27.9	24.08	3.03

smallest occurred in cave hyenas from Mindel-Riss and Riss-Würm (Table 8). The sum of average indices of the length of four lower cheek teeth (p2+p3+p4+m1) attains its maximal value in materials from Mosbach and Petralona Cave (Schütt 1971, Kurtén & Poulanos 1977); in the Geographical Society Cave it was much lower (99.8 mm, n = 8-13). Among Würm *Crocota* individuals from Siberia the greatest lengths of P2-M/1 are found.

p2 The size and proportions of p2 in the studied material vary slightly and only in the sample from Lunel-Viel are its sizes notably smaller (Table 9). Relatively narrower were specimens from Binagady and Aman-Kutan (as compared to samples from Arcy-sur-Cure, Prolom 2, and the Geographical Society Cave). However, this variation is most likely not related to the sites' southern locations, since a subspecies which lived even farther south, *C. s. dorotheae*, had a relatively wide p2 (Kurtén 1965). Whereas in *C. s. praespelaea* the p2 was relatively narrow, in *C. s. petralona* it had a relatively wide crown (Schütt 1971, Kurtén & Poulanos 1977).

p3 Unlike in the P3, the sizes and proportions of p3 were changing slightly in the

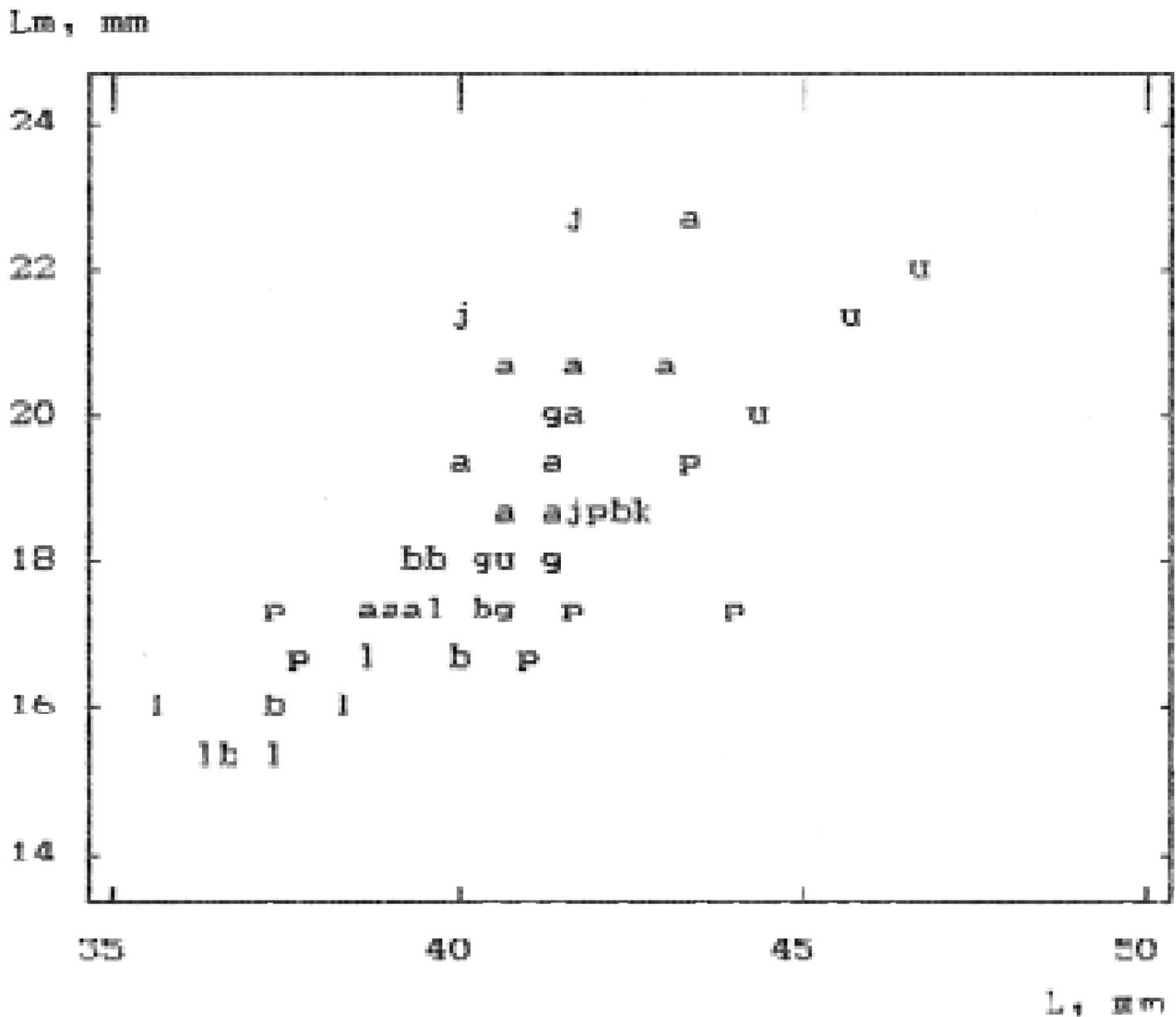


Figure 6 Scattergram of metastyle length (Lm) and maximal length (L) of fourth upper premolar P4 in *Crocota spelaea*. Symbols as in Fig 5.

evolution of *C. spelaea*. In bone-crushing the function of the lower premolar was evidently less significant than that of the upper one and it participated to a lesser degree in the process of dental specialization. The small sizes of p3 are typical of samples from Lunel-Viel, Binagady, Ilkaya 1, and Aman-Kutan, and large sizes are typical of Arcy-sur-Cure, sites of the Urals, and the Geographical Society Cave (Table 10). *C. s. praespelaea* and *C. s. petralona* also possessed a large p3. There is no chronostratigraphic pattern in the changes of proportions of the crown: it is relatively wide in Petralona

Cave, Aman-Kutan, Arcy-sur-Cure, and Golobiec, and relatively narrow in Binagady and the Geographical Society Cave.

p4 Variation in sizes of p4 had the same tendencies as in other lower premolars: its length increased in glacial times and declined in the interglacials (Table 11). The relative width of the tooth reveals insignificant variability, and only in animals from Mosbach, Petralona Cave, and Binagady was the tooth slightly narrower. The ratio of average values of the length of the p4 and the length of m1 was approximately the same,

Table 8 Geographical variability of length of p2-m1 (mm) in *Crocota spelaea*

Time Period and Locality	n	range	x	SD
MIDDLE PLEISTOCENE				
Cromerian and Mindel				
<i>C. spelaea praespelaea</i>				
Mosbach, Germany (Schütt, 1971)	2	94.0 - 99.0	96.5	—
Petralona Cave, Greece (Kurtén & Poulanos, 1977)	4	85.0 - 93.0	88.25	3.29
Kazanka River, Russian Plain (coll. MGB)	1	62.5	—	—
Mindel				
<i>C. spelaea petralona</i>				
Petralona Cave, Greece (Kurtén & Poulanos, 1977)	1	56.0	—	—
Mindel - Riss				
<i>C. spelaea intermedia</i>				
Lunel-Viel, France (coll. LGQ)	9	83.3 - 88.4	85.77	1.55
Riss				
<i>C. spelaea spohani</i>				
Gargas, France (Clot, 1980)	2	86.8 - 87.0	85.9	—
LATE PLEISTOCENE				
Riss - Würm				
<i>C. spelaea spohani</i>				
Lherat, France (Clot, 1980)	5	85.4 - 88.0	85.7	0.97
Binagady, Transcaucasia (coll. ZIN)	6	82.5 - 92.1	86.02	3.51
Würm				
<i>C. spelaea spohani</i>				
Arcy-sur-Cure, France (coll. UPSP)	4	85.7 - 94.1	90.05	3.18
Corda, France (Clot, 1980)	5	88.5 - 93.0	91.2	2.08
Pair-non-Pair, France (Clot, 1980)	6	82.5 - 94.4	88.4	4.17
Jaurens, France (Ballesio, 1979)	9	84.5 - 92.0	88.7	2.31
Oblazowa & Wierzchowski Gorna, Poland (coll. ISE)	2	92.9 - 95.2	94.05	—
Rips, Romania (Coleman, 1978)	1	86.5 - 98.9	92.5	—
Several Caves, Moldova (David, 1960)	5	89.0 - 92.0	90.5	—
Nosong Cave, South Ural (coll. ZIN)	1	89.8	—	—
Krasny Yar, Western Siberia (coll. ZIN)	1	95.5	—	—
<i>C. spelaea novator</i>				
Geographic Society Cave, Piatonki Krai (coll. ZIN)	3	91.2 - 98.3	93.83	—
Upper Cave of Choukoutien, China (Pei, 1960)	1	94.0	—	—
Wuji, China (Lu et al., 1985)	1	93.2	—	—

but in Mosbach and Petralona Cave the p4 was relatively more elongated (Schütt 1971, Kurtén & Poulanos 1977).

m1 The length of the lower carnassial tooth in *C. spelaea* also changed during the Pleistocene depending on the temperature factor (Table 12). Apart from that one can see distinctly that the length of m1 increased from south to north, from its minimal average values in Aman-Kutan to maximal ones in Jaurens and the Geographic Society Cave. In the evolution of *C. spelaea* the talonid of m1 became simpler and shorter (reflecting probably a specialization to myophagy).

Table 9 Measurements (mm) of second lower premolar p2 in *Crocota spelaea*

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praespelaea</i>								
Kazanka River	1	17.4	—	—	1	12.5	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	12	14.8 - 16.0	15.41	0.35	12	10.5 - 12.3	11.19	0.56
<i>C. s. spelaea</i>								
Binagady	7	15.0 - 18.5	16.44	1.36	7	10.4 - 13.0	11.63	1.06
Jaurens	3	16.1 - 17.4	16.67	—	3	11.4 - 13.2	12.37	—
Arcy-sur-Cure	12	14.7 - 18.0	16.40	0.99	12	11.2 - 14.4	12.29	0.97
Golabiec	3	16.7 - 16.7	16.70	—	3	11.8 - 12.1	12.00	—
Prolom 2	12	14.9 - 17.4	16.23	0.65	12	10.6 - 14.3	12.16	0.96
Ilkaya 1	3	15.8 - 17.6	16.67	—	3	11.1 - 11.7	11.47	—
Aman-Kutan	2	17.4 - 17.6	17.50	—	2	11.9 - 12.0	11.95	—
South Urals	1	6.8	—	—	1	13.0	—	—
Altai	3	17.3 - 18.3	17.97	—	3	12.8 - 13.3	13.10	—
Krasny Yar	1	6.9	—	—	1	13.4	—	—
<i>C. s. ussurica</i>								
Geographic Soc. Cave	10	15.5 - 18.3	17.12	0.98	10	10.1 - 14.0	12.77	1.13

Whereas in the *C. s. praespelaea* from Mosbach its length constituted on the average 12% of the total length of the tooth (Schütt 1971), in the Würm samples it did not exceed 10% (Baryshnikov 1995). The ratio of the length of the trigonid and the maximal length of m1 is shown in Fig. 8. The presence of a small metaconid on m1 varies considerably, and, as has been noted before (Kretzoi 1938, Kurtén 1956), is not a reliable systematic character. The frequency of occurrence of the metaconid varied from 23-29% in the Cromerian and Mindel (Mosbach, Petralona Cave) to 50% in the Mindel-Riss (Lunel-Viel), and then declined to 38% in the Riss (Chatillon-Saint-Jean), increased to 55% in the Riss-Würm (Binagady) and declined again to 41-43% in the Würm (Schütt 1971, Ballesio 1979, Baryshnikov & Vereshchagin 1996). According to the data of Kurtén & Poulanos (1977), the occurrence of the character on Riss-Würm sites of Europe is very low (11%). During the Würm the frequency of the presence of a metaconid declined from the Atlantic coast towards continental parts of Europe and Siberia: 46% in Britain (Kent's Cavern, n=37; Kurtén 1956), 30% in

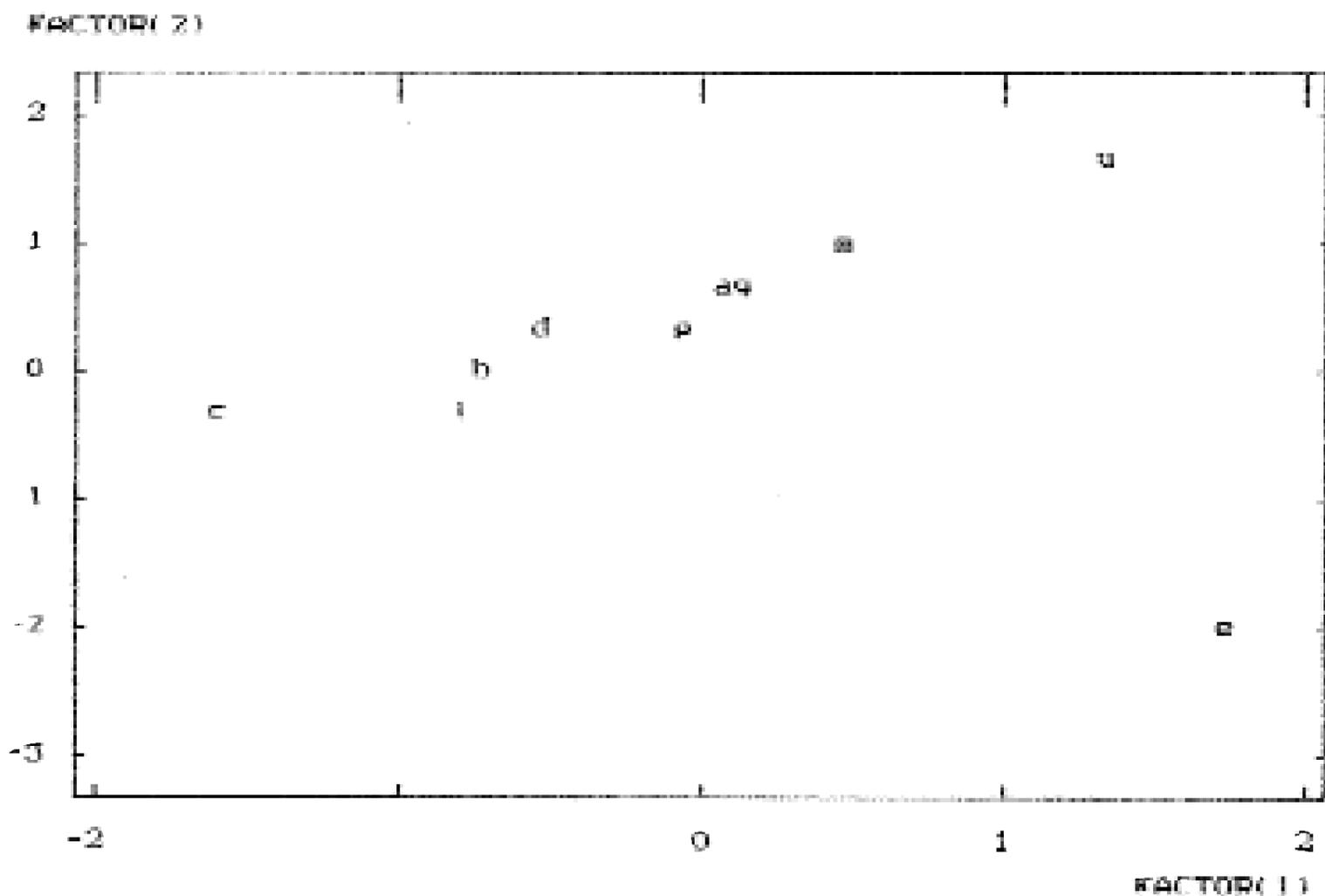


Figure 7 Principal component analysis based on length and width of P3 and length and width of P4 in *Crocuta spelaea*. **a** - Arcy-sur-Cure, **b** Binagady, **c** - *C. crocuta*, recent (coll. ZIN), **d** - *C. s. dorotheae* (Kurtén, 1965), **e** - *C. s. petralona* (Kurtén & Poulianos, 1977), **g** - Golabiec, **j** - Jaurens, **k** - Aman-Kutan, **l** - Lunel-Viel, **m** - *C. s. praespelaea*, Mosbach (Schütt, 1971), **p** - Prolom 2, **u** - Geographical Society Cave.

France (Arcy-sur-Cure, Jaurens, n=23), 27% in the Crimea (Prolom 2, Ayuvul-Koba, n=11), 25% in Western Siberia (Krasnyi Yar, Ust-Kanskaya Cave, Denisova Cave, n=4), 29% in the Russian Far East (Geographical Society Cave, n=7).

The above noted variation in the presence of a metaconid may be related to the temperature factor, the type of feeding of the animals, and peculiarities of local populations, in particular influenced by weakening of inter-population exchange of genes in the case of a more territorial or isolated way of life and restricted interclan contacts.

General remarks Characterizing the lower molars of *C. spelaea*, one should note that the decrease or increase of their sizes was related to the change of the sizes of the animals. Unlike the upper molars they do not demonstrate regular changes in crown proportions on different temporal levels of the Pleistocene. We only observe a strengthening of the cutting character of m1 (a shortening of the talonid) and reduction of its crushing structures (a decline of the occurrence frequency of a metaconid) in glacial epochs and in regions with a more rigorous climate. Analysis of the main components for length and width of p3 and m1 (Table 13; Fig. 9) did not indicate a distinct pattern in the distribution of samples. In the factor space F1xF2 they form seven groups (e), (c), (j), (m, u), (b), (a, g, p), (d, k, l). Of these the

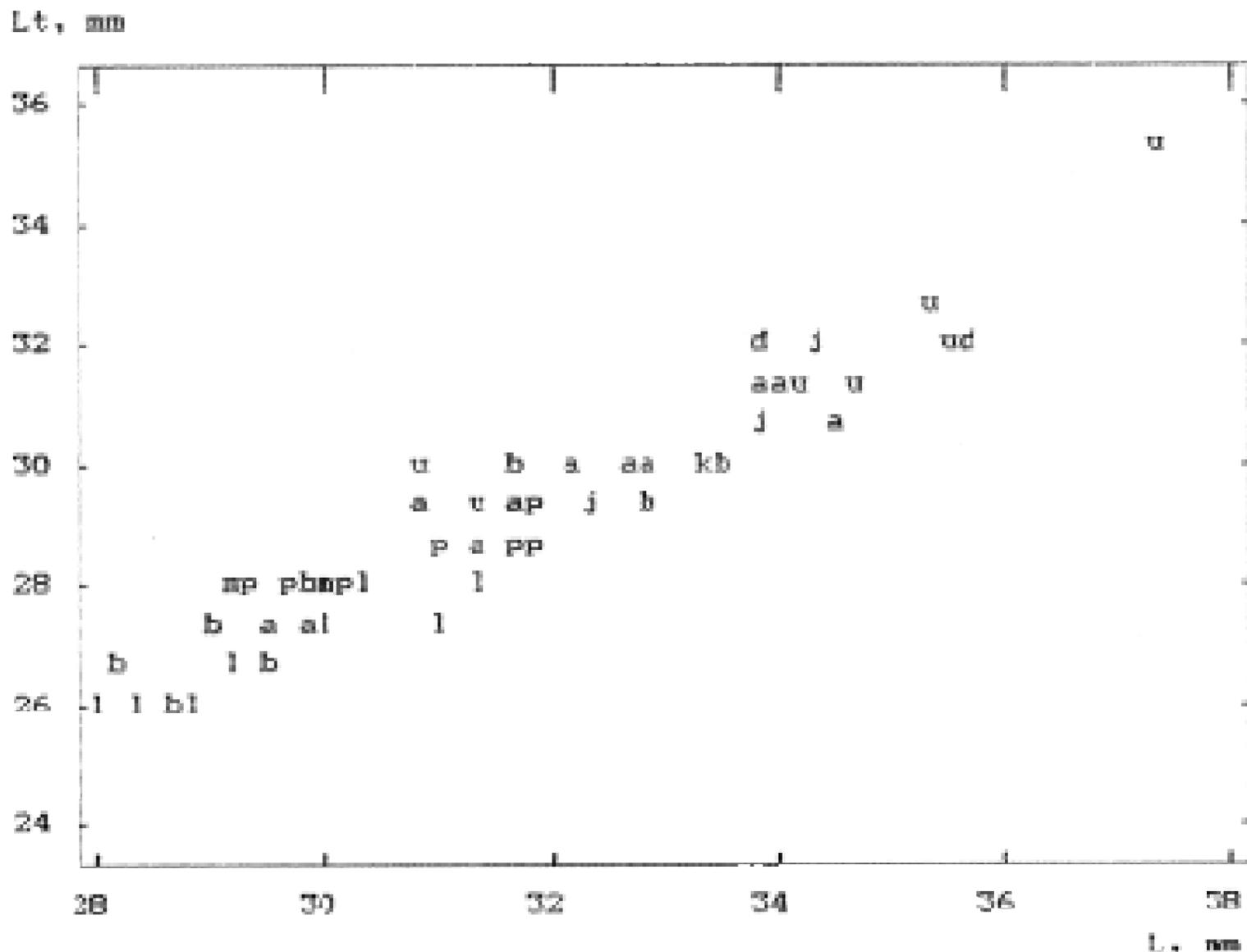


Figure 8 Scattergram of trigonid length (Lt) and maximum length (L) of first lower molar m1 in *Crocuta spelaea*. Symbols as in Fig. 5.

first two groups including *C. s. petralona* and recent *C. crocuta* are the most remote from the others. It noteworthy that the sample from Binagady is separated, and that the small *Crocuta* that inhabited a warmer climate are joined in one group: *C. s. dorotheae*, *C. s. intermedia*, and the hyena from Aman-Kutan.

DISCUSSION

Evolutionary trends

The paleontological record indicates that sizes of *C. spelaea* increased in the glacial epochs and decreased in the interglacial periods, and also increased from south towards the northeast within the same time interval. Therefore, change in the sizes of animals depended on the temperature factor and occurred according to the zoogeographic

regularity known as 'Bergman's rule'. That the change was determined by the climate is confirmed by an analogous variation of its sizes observed in other Carnivora from the Pleistocene of Eurasia (Kurtén 1968).

The dentition of *Crocuta* is most advanced in the Hyaenidae. Its transformation is of a dualistic nature: a parallel specialization to myophagy (elongation of P4 and particularly of its blade-shaped metastyle, and also a size increase of m1, accompanied by a reduction of the metaconid, and a shortening and simplification of the talonid) and a specialization to the crushing of large bones (an increase of the width and height of the crown of the P3 and p3). Analogous transformations have been noted also for the deciduous cheek teeth (Baryshnikov & Averianov 1995).

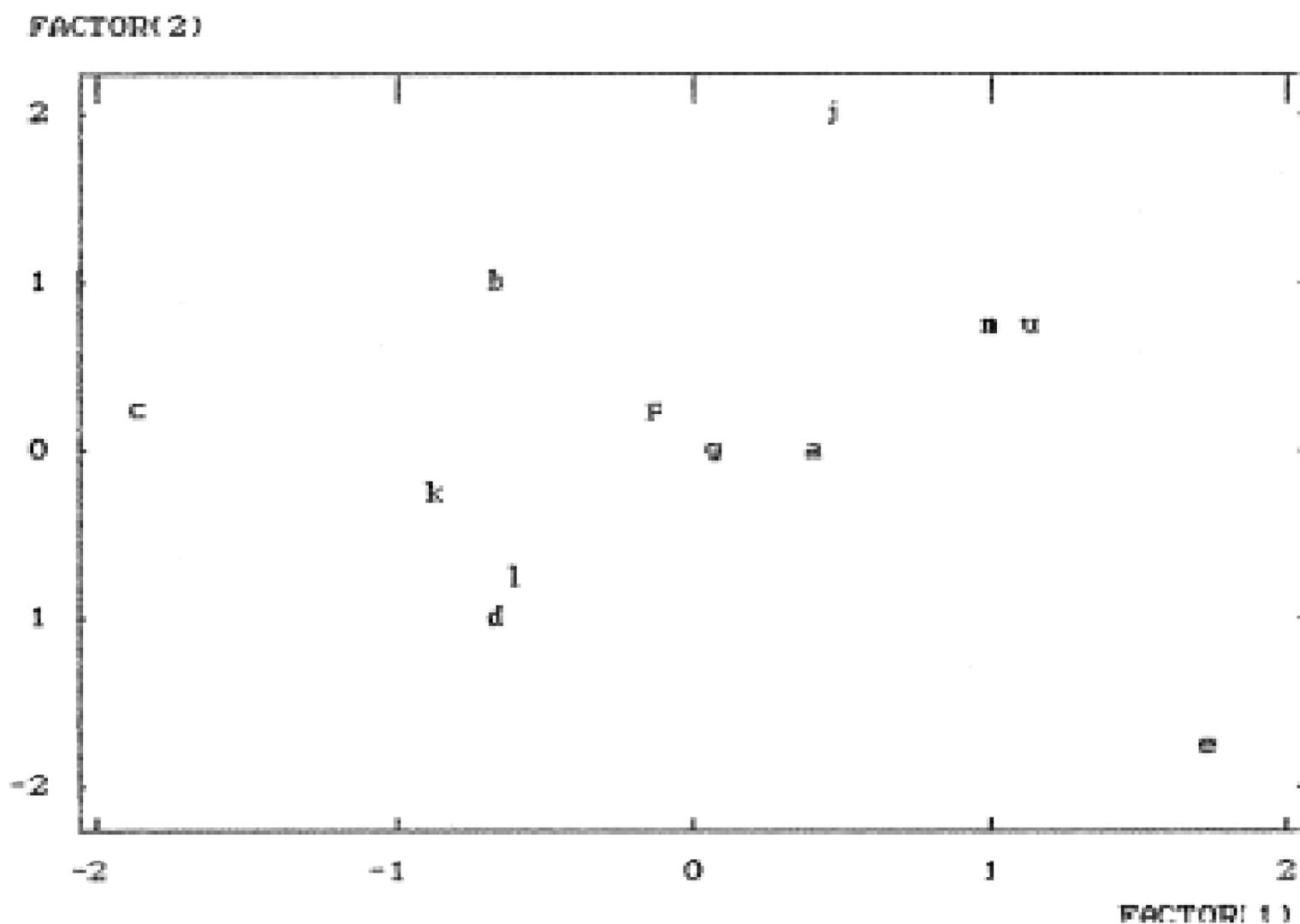


Figure 9 Principal component analysis based on width and length of p3 and width and length of m1 in *Crocuta spelaea*. Symbols as in Fig. 7.

The main evolutionary tendency of *C. spelaea* is connected with the strengthening of the carnivorous specialization of its dentition. It was the transition to myophagy, to active hunting in large groups, that permitted *C. spelaea* to inhabit geographic regions with long cold winters. However, the development of the cutting function of the teeth was neither unidirectional nor accumulative. Phases of carnivorous specialization associated with glacial periods were followed by despecialization phases in the interglacials. During the latter a return to the previous stage and development of bone-crushing rather than specialized cutting dentition occurred. Such variation in the dentition of *C. spelaea* can be accounted for by a shift in natural selection pressure on populations of the cave hyena in the interglacials (i.e., by favorable climatic

conditions, abundant food, and the consuming of carrion) and a reverse shift in glaciation epochs (unfavorable climatic conditions, the need for more higher-calory flesh, an increase in hunting activity, which was accompanied by competition for food with other large carnivores and primitive humans).

As in many other Pleistocene mammals, such as *Spelearctos*, for example (Baryshnikov 1997), the rates of evolutionary change of the upper molars in *C. spelaea* were somewhat higher than of lower ones. This is indicated by the fact that the difference between hyenas of the glacial and interglacial epochs were more distinct in the upper molars' morphometry.

Table 10 Measurements (mm) of third lower premolar p3 in *Crocota spelaea*.

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praspelaea</i>								
Kazanka River	1	22.8	—	—	1	16.8	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	12	21.0 - 23.1	22.10	0.69	12	15.2 - 17.6	16.06	0.70
<i>C. s. spelaea</i>								
Binagady	7	19.5 - 23.3	21.30	1.48	7	13.8 - 16.7	15.29	1.20
Jaurens	4	21.5 - 23.3	22.47	0.77	4	15.4 - 17.5	16.45	0.90
Arcy-sur-Cure	10	21.6 - 27.3	23.03	2.02	10	15.7 - 19.6	17.09	1.30
Golabiec	13	20.6 - 24.4	22.43	1.13	13	15.4 - 18.8	16.68	0.98
Prolom 2	14	21.0 - 23.4	22.03	0.79	14	14.8 - 18.2	16.34	0.80
Il'skaya 1	1	21.2	—	—	2	15.5 - 15.7	15.60	—
Aman-Kutan	3	20.0 - 21.8	21.00	—	3	15.7 - 16.4	16.03	—
South Urals	3	22.7 - 24.6	23.37	—	3	17.1 - 18.5	17.57	—
Krasnyi Yar	1	23.1	—	—	1	18.0	—	—
<i>C. s. ussurica</i>								
Geographic Soc. Cave	13	21.6 - 26.0	23.95	1.30	13	15.2 - 18.8	17.11	1.17

Table 11 Measurements (mm) of fourth lower premolar p4 in *Crocota spelaea*.

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praspelaea</i>								
Kazanka River	1	24.8	—	—	1	15.1	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	12	21.1 - 24.8	22.76	1.09	12	13.6 - 15.5	14.33	0.61
<i>C. s. spelaea</i>								
Binagady	5	21.4 - 25.9	23.68	1.71	5	12.6 - 15.4	14.28	1.33
Jaurens	3	23.5 - 24.3	23.97	—	3	14.7 - 15.7	15.17	—
Arcy-sur-Cure	19	22.8 - 25.7	23.92	0.77	18	13.1 - 15.9	14.82	0.73
Golabiec	8	23.4 - 25.5	24.37	0.67	8	14.3 - 16.7	15.41	0.78
Prolom 2	15	22.0 - 24.4	23.27	0.75	16	13.7 - 16.4	14.57	0.78
Aman-Kutan	3	21.2 - 22.8	22.23	—	3	12.6 - 14.5	13.83	1.07
South Urals	3	23.0 - 24.8	23.80	—	3	15.0 - 15.8	15.37	—
Krasnyi Yar	1	24.4	—	—	1	15.6	—	—
Altai	1	24.6	—	—	1	16.2	—	—
<i>C. s. ussurica</i>								
Geographic Soc. Cave	13	22.1 - 26.4	24.62	1.39	13	13.8 - 17.1	15.01	1.01

Geographical variability and taxonomy

Kurtén (1956) distinguished two extinct subspecies of *C. crocuta* in Eurasia: *C. crocuta spelaea* (GOLDFUSS) in Europa and *C. c. ultima* (MATSUMOTO) in China, thereby acknowledging the geographic difference between hyenas from western and eastern parts of the distribution range. Later, several more forms were described for the Pleistocene of

Eurasia. These forms may be regarded as both stratigraphic and geographic subspecies of *C. spelaea*. In the Middle Pleistocene the following forms are distinguished: *C. s. praspelaea* (Mosbach, Cromerian-Mindel), *C. s. petralona* (Petralona Cave, Mindel), *C. s. intermedia* (Lunel-Viel, Mindel-Riss) and *C. s. ultima* (from a certain marly district of Szechuan in China, Middle Pleistocene;

Table 12 Measurements (mm) of first lower molar m1 in *Crocota spelaea*.

Localities	Length				Width			
	n	range	x	SD	n	range	x	SD
<i>C. s. praspelaea</i>								
Kazanka River	1	33.7	—	—	1	14.0	—	—
<i>C. s. intermedia</i>								
Lunel-Viel	9	28.0 - 31.4	29.58	1.19	9	12.2 - 13.7	12.74	0.49
<i>C. s. spelaea</i>								
Binagady	10	28.1 - 33.5	30.19	1.85	10	12.4 - 15.3	13.41	0.97
Jaurens	4	32.4 - 34.4	33.55	0.84	3	14.0 - 14.5	14.20	—
Arcy-sur-Cure	12	29.5 - 34.5	32.11	1.59	12	13.2 - 14.6	13.83	0.42
Golabiec	6	29.7 - 33.7	31.20	1.64	6	13.0 - 14.4	13.78	0.46
Prolom 2	9	29.4 - 34.2	31.02	1.58	9	12.7 - 15.0	13.62	0.74
Il'skaya 1	4	30.5 - 32.8	31.47	0.97	4	12.9 - 14.0	13.57	0.53
Aman-Kutan	2	29.1 - 30.0	29.55	—	3	12.5 - 12.9	12.67	—
South Urals	1	29.6	—	—	1	11.8	—	—
Krasnyi Yar	1	33.8	—	—	1	13.6	—	—
Altai	3	29.9 - 35.6	33.10	—	3	12.8 - 15.4	14.13	—
<i>C. s. ussurica</i>								
Geographic Soc. Cave	8	30.8 - 37.4	34.11	2.17	8	13.6 - 15.1	14.31	0.52

Table 13 Correlations of characters with the first three principal components for lower cheek teeth.

Measurements	F1	F2	F3
Component loadings			
P/3 L	0.975	-0.096	-0.173
W	0.949	-0.298	0.018
M/1 L	0.931	0.353	-0.062
W	0.973	0.050	0.215
Percent of total			
variance explained	91.641	5.632	2.003

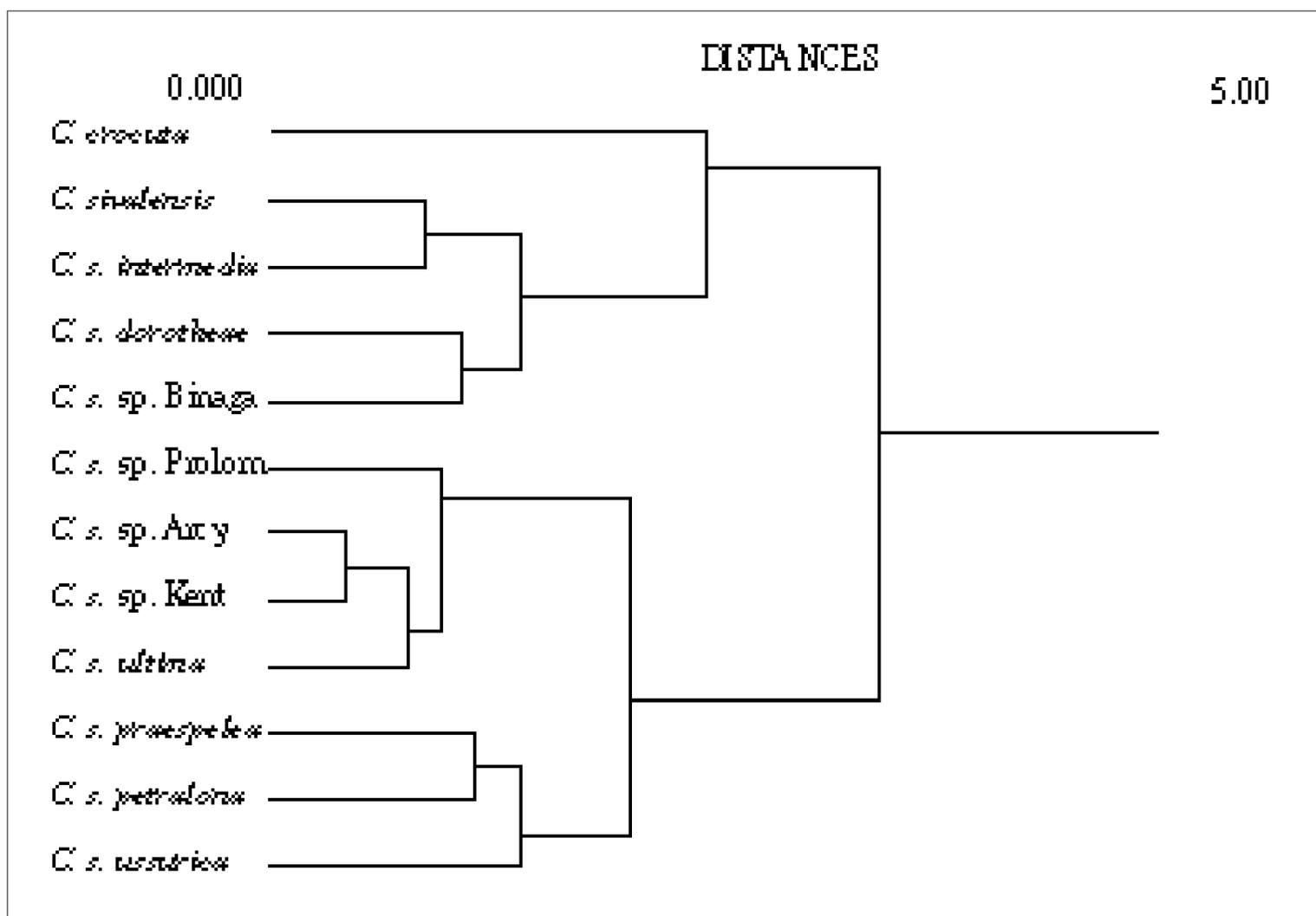


Fig. 10 Similarity dendrogram of samples of genus *Crocuta* based on length means of upper P2-P4 and lower p2-m1. Matrix and samples are in Table 14.

Matsumoto 1915, Bonifay 1971, Schütt 1971, Kurtén & Poulanos 1977). If we ignore *C. s. petralona*, which was a strongly deviating local form, the other subspecies supplant each other in a succession in time and space, demonstrating different trends of dental specialization.

From the Late Pleistocene onwards, the subspecies are based mainly on geographic variation in sizes: *C. s. spelaea* (Gailenreuther Cave, Würm), *C. s. dorotheae* (Zuttiyeh Cave, Würm), and *C. s. ussurica* (Geographical Society Cave, Würm; Goldfuss 1823, Kurtén 1965, Baryshnikov & Vereshchagin 1996). I refer cave hyena from the end of the Middle Pleistocene (Riss) and the Riss-Würm to *C. s. spelaea*, although it is possible that this form represents a separate subspecies. The distribution range of *C. s. spelaea* covered the whole of Europe eastwards up

to the Urals and possibly south of Western Siberia and Kazakhstan. A very small form *C. s. dorothea* is known only from the Levant. Similar to it in teeth sizes is the *Crocuta* from Aman-Kutan, but this form's taxonomic position is not clear yet. South of the Primorski Krai of Russia and northeastern China lived the large-toothed *C. s. ussurica*, the distribution range of which probably spread westwards up to the Altai.

Two groups can be distinguished in the similarity-dendrogram of *Crocuta*-samples by average values of the length of the upper (P2-P4) and lower (p2-m1) cheek teeth (Table 14; Fig. 10). One includes a small *Crocuta* from Africa (*C. crocuta*), two from the tropical and subtropical zones (*C. sivalensis*, *C. s. dorotheae*), and three from the interglacial epochs of the temperate zone of Eurasia (*C. s. intermedia*, *C. s. spelaea*, the

Table 14 Matrix of normalized euclidean distances within the 12 samples of *Crocota* based on mean measurements of length of upper (P2-P4) and lower (p2-m1) teeth; Key: **1** = *C. sivalensis* (Kurtén 1956); **2** = *C. crocuta* (Kurtén 1956); **3** = *C. s. praespelaea*, Mosbach (Schütt 1971); **4** = *C. s. petralona* (Kurtén & Poulianos 1977); **5** = *C. s. ultima* (Kurtén 1956); **6** = *C. s. intermedia*, Lunel-Viel; **7** = *C. s. spelaea*, Binagady; **8** = *C. s. spelaea*, Kent's Cavern (Kurtén 1956); **9** = *C. s. spelaea*, Arcy-sur-Cure; **10** = *C. s. spelaea*, Prolom 2; **11** = *C. s. ussurica*, Geographical Society Cave; **12** = *C. s. dorotheae* (Kurtén 1965).

	1	2	3	4	5	6	7	8	9	10	11
1	0.000										
2	1.884	0.000									
3	3.610	5.083	0.000								
4	4.025	5.522	1.005	0.000							
5	2.749	4.366	1.236	1.597	0.000						
6	0.809	1.581	3.610	4.078	2.824	0.000					
7	1.226	2.698	2.651	3.055	1.836	1.286	0.000				
8	2.454	4.052	1.219	1.740	0.599	2.526	1.519	0.000			
9	2.332	3.873	1.450	1.806	0.786	2.359	1.496	0.430	0.000		
10	1.747	3.356	1.952	2.345	1.186	1.879	1.036	0.814	0.669	0.000	
11	4.195	5.841	1.452	1.075	1.808	4.358	3.406	1.936	2.029	2.517	0.000
12	1.298	2.410	2.775	3.201	2.180	1.162	0.964	1.814	1.633	1.123	3.525

Binagady form). The other group includes two subgroups: a) large hyenas of cold epochs from the European Late Pleistocene (*C. s. spelaea*, different localities) and from the Middle Pleistocene of China (*C. s. ultima*); b) very large hyenas from the Middle Pleistocene of Europe (*C. s. praespelaea*, *C. s. petralona*) and from the Late Pleistocene of the Ussuri River region (*C. s. ussurica*). Note should be made of the isolated position of *C. s. ussurica* in the dendrogram, which confirms the hypothesis that this geographic form is a separate subspecies.

ACKNOWLEDGEMENTS

I would like to thank Prof. N. Vereshchagin (St. Petersburg, Russia), Dr. N. Fomicheva (Kazan, Russia), Prof. A. Derevianko (Novosibirsk, Russia), Prof. Yu. Kolossov (Kiev, Ukraine), Dr. A. Nadachowski (Krakow, Poland), Dr. C. Mourer-Chauviré (Lyon, France), Dr. F. David (Paris, France), Prof. M.-F. Bonifay and Dr. J.-Ph. Brugal (Marseille, France) for their help in studying collections. I thank Dr. A. Averianov (St. Petersburg) and reviewer Prof. R. Klein (Stanford University, USA) for his comments on the manuscript. The manuscript was translated into English by Tatyana Platonova and Olga Potapova, edited by Prof. Gary Haynes (Reno, USA).

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