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LATE PLEISTOCENE HYENA *CROCUTA ULTIMA USSURICA* (MAMMALIA: CARNIVORA: HYAENIDAE) FROM THE PALEOLITHIC SITE IN GEOGRAPHICAL SOCIETY CAVE IN THE RUSSIAN FAR EAST

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ABSTRACT

Fossil hyena remains recovered from Geographical Society Cave in the southern part of Primorskii Territory in Russia are referred, as a result of this study, to *Crocuta ultima ussurica*. The available radiocarbon dates define a time of the fossiliferous layer as the warm stage of the Late Pleistocene (MIS 3). Morphological difference between *C. ultima ussurica* and *C. crocuta spelaea* appeared to be as follows: the former species has more robust (with regards to the skull size) cheek teeth implying bone-crushing adaptation; the latter species exhibits more carnivorous specialization. Taphonomical analysis of the bone assemblage suggests the cave was used as a hyena den; no essential dissimilarity is observed between hyena dens in Europe/Western Siberia and in the Russian Far East. The existence of two chronosubspecies is proposed: *C. ultima ultima* from the Middle Pleistocene of China and *C. u. ussurica* from the Late Pleistocene of the Russian Far East and China.

Key-words: Hyaenidae, Late Pleistocene, Paleolithic cave sites, Russian Far East, taphonomy, taxonomy

ПОЗДНЕПЛЕЙСТОЦЕНОВАЯ ГИЕНА *CROCUTA ULTIMA USSURICA* (MAMMALIA: CARNIVORA: HYAENIDAE) ИЗ ПАЛЕОЛИТИЧЕСКОЙ СТОЯНКИ В ПЕЩЕРЕ ГЕОГРАФИЧЕСКОГО ОБЩЕСТВА НА ДАЛЬНЕМ ВОСТОКЕ РОССИИ

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РЕЗЮМЕ

Исследованы ископаемые остатки гиены из пещеры Географического общества (Geographical Society Cave) на юге Приморского края, Россия, которые отнесены к *Crocuta ultima ussurica*. Радиоуглеродные даты помещают время формирования костеносного слоя к теплой стадии позднего плейстоцена (MIS 3). Показаны морфологические отличия *C. ultima ussurica* от *C. crocuta spelaea*; первый вид обладал более крупными (относительно размеров черепа) щечными зубами с костедробящей адаптацией, в то время как озубление второго вида имело более хищническую специализацию. Тафономический анализ костного скопления в пещере указывает на то, что она использовалась гиенами как логово; не обнаружено существенных различий между гиеновыми логовами в Европе/Западной Сибири и Дальнем Востоке России. Предполагается два сменяющих друг друга хроноподвида: *C. ultima ultima* из среднего плейстоцена Китая и *C. u. ussurica* из позднего плейстоцена Дальнего Востока и Китая.

Ключевые слова: Hyaenidae, поздний плейстоцен, палеолитические пещерные стоянки, Дальний восток России, тафономия, таксономия

INTRODUCTION

Fossil remains of hyenas are found in numerous cave localities of the Late Pleistocene of Eurasia, excepting northern regions. In Europe, fossil hyenas are known to belong to *Crocuta spelaea* (Goldfuss, 1823) described on the basis of the skull from the Zoolithen Cave at Burggeilenreuth in southern Germany and recently reexamined by Diedrich (2008).

The cave hyena (*C. spelaea*) was regarded for a long time as a separate species (Baryshnikov 1995, 1999a; Brugal et al. 1997). It involved not only the specimens from Europe, but also the specimens of fossil hyenas from Ural and south Siberia (Baryshnikov 1999a). Now it is considered to be an extinct subspecies of the recent spotted hyena *C. crocuta* (Erxleben, 1777) occurring in Africa southward of Sahara (Kurtén 1956, 1968; Werdelin and Solounias 1991 etc.). This opinion is confirmed by molecular data (Rohland et al. 2005).

The origin of the crocut hyenas is associated with Africa (Ficarelli and Torre 1970; Turner 1990; Lewis and Werdelin 2010; Martínez-Navarro 2010; Sardella and Petrucci 2012). The earliest findings document their presence from the Upper Laetoli Beds (3.85–3.63 Ma, as *Crocuta dietrichi* Petter et Howell, 1989) and from Kataboi Member of the Nachukui Formation (>3.4 Ma, as *C. eturono* Werdelin et Lewis, 2008) (Petter and Howell 1989; Werdelin and Lewis 2005, 2008; Lewis and Werdelin 2010; Morales et al. 2011). The age of these findings coincides with the presumable time of division of the clade *Crocuta* from the clade *Hyaena* + *Parahyaena*, occurring, according to molecular clock, nearly 4.2 Ma (Koepfli et al. 2006).

Paleontological record fixes the first appearance of spotted hyena in Europe in the latest Early Pleistocene. The fossils were recovered in the lower unit TD 4/5 of Atapuerca in Spain, near 0.78 Ma (García and Arsuaga 2001), as well as in several localities of Italy (karst fissures at Domegliara Selva Vecchia and Casal Selce, 0.7–0.8 Ma; Azzaroli 1983; Sardella and Petrucci 2012). In the Middle Pleistocene, spotted hyena was widely distributed throughout Europe, being represented by subspecies: *Crocuta crocuta praespelaea* Schütt, 1971, *C. c. intermedia* Bonifay, 1971, and *C. c. petralonae* Kurtén et Poulianos, 1977 (Schütt 1971; Bonifay 1971; Kurtén and Poulianos 1977).

In Asia, first fossil registration of *Crocuta* is dated by the Early Pleistocene of China (*C. honanensis* (Zdansky, 1924)) from Shanxi; Qiu 1987; Tseng and Chang 2007) and India (“C”. *sivalensis* (Falconer, 1867) from Upper Sivalik; Khan 1972; Verma et al. 2002). The lower level in Upper Siwalik is comparable with the zone MN16 in Europe (near 3.0 Ma) (Wang et al. 2013). The examination of the type specimen of *C. sivalensis* assigned it to *Pliocrocuta perrieri* (Croizet et Jobert, 1828); therefore, the name *Hyaena sivalensis* (later *Crocuta sivalensis*) should be regarded as a junior subjective synonym of *P. perrieri* (Werdelin and Lewis 2012). Hyenas, which are morphologicaly similar to *C. crocuta*, are known from the Longdan Basin of China (ca. 2.2 Ma), and possibly from the Pinjor Formation of Indo-Pakistan (Qiu et al. 2004; Turner 2004; Lewis and Werdelin 2010; Patnaik and Nanda 2010).

A single premolar P4 from Szechuan in China provided a basis for description of the species *Hyaena ultima* (Matsumoto, 1915), associated with fauna, correlative with that of the famous Peking Man site at Zhoukoudian 1, northeastern China, dated as 0.69–0.42 Ma (Qiu 2006). The specimens of this taxon found in Taiwan have been assigned to the late Middle Pleistocene (Tseng and Chang 2007). Kurtén (1956), studying Pleistocene collections from Europe and southeastern Asia, came to the conclusion that *Hyena ultima* represents the spotted hyena and should be regarded as the fossil subspecies *Crocuta crocuta ultima*. This subspecies is characterized by the dentition as heavy as that of *C. c. spelaea*, and its P3 “more hypsodont than in other subspecies” (Kurtén 1956: 34). Pei (1940) referred to this taxon also the Late Pleistocene hyena specimens from Upper Cave at Zhoukoudian. He noted that the skeleton measurements of *C. crocuta ultima* are similar to those of *C. c. crocuta*, whereas the teeth are as large as those of the cave hyena. Kurtén (1956) approved the assignment of the material from the Late Pleistocene localities of China to *C. c. ultima*.

Analysis of ancient mtDNA revealed that spotted hyenas (*Crocuta crocuta*) are divided into three haplotypes, which are associated with three waves of their migration from Africa to Eurasia (Rohland et al. 2005). The earliest event of migration is assigned to the Early Pleistocene (3.48 Ma), when migrants reached Eastern Asia, surviving there till the Late Pleistocene. The presence of two haplotypes diverged nearly 1.46 Ma has been found in the European cave hyena (Rohland et al. 2005). One group incorporates animals from Europe and Southern

Africa; another comprises individuals from Europe and Northern Africa. Therefore, spotted hyenas twice dispersed to Europe, the latest migration wave occurring in the second half of Middle Pleistocene (0.36 Ma) (Rohland et al. 2005). In my opinion, the time of splitting of aforementioned haplotypes seems to be too early and it contradicts with the available paleontological record.

The new study of ancient mtDNA of spotted hyenas has been recently obtained, involving the Chinese material (Sheng et al. 2014). It reveals a similar model of genetic diversity of *C. crocuta* and testifies an isolated position of East Asian specimens. It is hypothesized that *C. crocuta* originated from *C. praespelaea*; the evolutionary changes predominantly took place in the steppe zone of Eurasia, and the recent African distribution range of this species is relict. Calculations of the authors of aforementioned study reveal the later time of the divergence of haplotypes: East Asian clade diverged 225 ka BP, European/South African clades diverged 186 ka BP, whereas the European/North African clades divided 64 ka BP (Sheng et al. 2014). With regard of the available paleontological data, the time of isolation of the East Asian hyenas was estimated as nearly 420 ka BP.

The results of both analyses revealed the presence of two haplotypes in the cave hyenas from the Late Pleistocene of Europe. The morphological difference between animals belonging to these haplotypes was not defined; therefore, I conditionally refer all European cave hyenas to *C. c. spelaea*.

Study of geographical variability of spotted hyena from the Late Pleistocene of Northern Eurasia did not reveal marked changes of morphological characters on the area extending from British Isles on the West to Baikal Lake on the East, which provides the possibility to consider the animals from this territory belonging to the *C. c. spelaea*. Hyenas from the Russian Far East revealed cheek teeth larger in average, so the Far Eastern specimens have been described as the subspecies *C. spelaea ussurica* Baryshnikov et Vereshchagin, 1996, on the basis of the sample from Geographical Society Cave in Primorskii Territory (Baryshnikov and Vereshchagin 1996; Baryshnikov 1999a). The taxonomic distinctness of the Russian Far-Eastern hyena has been confirmed by analyses of the ancient mtDNA, placing examined specimens from Geographical Society Cave into a separate clade of East Asian spotted hyenas (Rohland et al. 2005).

Baryshnikov and Vereshchagin (1996), characterizing the subspecies *ussurica*, noted that the dental system of the cave hyena *C. c. spelaea* from Europe and South Siberia demonstrates, in comparison with that of the recent *C. crocuta*, a progress of predatory specialization whereas *C. ultima* from Eastern Asia reveals in the Late Pleistocene a transformation of bone-crushing adaptations. *Crocuta spelaea ussurica* shows morphometrical similarity to *C. ultima* (the data used for the comparison were taken from the publication by Kurtén (1956)), differing from the latter taxon by longer, on average, P3 and P4 as well as by less developed hypsodonty of P3, comparatively more elongated metastyle of P4, and shortened talonid of m1 (Baryshnikov and Vereshchagin 1996: 56).

Therefore, the available data testify morphological-ecological distinctness of the spotted hyena from Eastern Asia. With regards of its genetic isolation from animals in Africa and Europe, *C. ultima* may be considered as a taxon of a species level, as has been already suggested by other researchers (Qui 2006; Tong et al. 2011). In the present study, I accept two subspecies of *C. ultima*: *C. u. ultima* from the Middle Pleistocene and *C. u. ussurica* from the Late Pleistocene, which has been recently declared (Baryshnikov and Baryshnikova 2013).

Spotted hyenas were an essential component of the Pleistocene mammal associations in Eurasia as scavengers and active hunters. They preferred open plain biotopes since their remains are absent in the Great Caucasus within the sites located in the forest zone and in high-mountains (> 1200 m above sea level) (Baryshnikov and Vereshchagin 1996).

Hyena mode of life is very important for the paleontological record since these animals accumulate bones of larger mammals, which were directly hunted by them or obtained as carrion. Hyenas quite often brought the pray to their dens, especially to cave ones, to consume it or to feed cubs; therefore, bones or bone fragments were buried in caves.

Geographical Society Cave represents a depository of large bone assemblage in the southern part of the Russian Far East. The remarkable character of the fauna of this region is the co-existence of the northern and southern species there. Views on the development of such biological peculiarity were substantiated for a long time by the data on the recent distribution of animals (for example, Matiushkin 1972). Therefore it was important to obtain paleontological record allowing documentation of principal stages of the Pleistocene history of the fauna. In 1963, students of local lore, E. Leshok and V. Shabunin, discovered bone-containing caves in the southern part of Primorskii Territory. In 1966 and 1967, N. Ovodov, under the supervision of Professors N. Vereshchagin and A. Okladnikov, has carried out excavations in 8 caves, including Geographical Society Cave, and collected paleontological and archeological material. He determined the osteological collection and published the results of his study (Ovodov 1977). His results have been supplemented by the data on the panther-like cat referred to *Panthera tigris* (Vereshchagin 1971) and on the cave hyena (Baryshnikov and Vereshchagin 1996; Baryshnikov 1999a).

The purpose of the present communication is a comparative morphological analysis of all fossil hyena bone material from Geographical Society Cave, as well as definition of the taphonomical type of this bone accumulation. The examined collection is kept in Zoological Institute of Russian Academy of Sciences in Saint Petersburg.

LOCALITY AND MATERIAL

Geographical Society Cave (peshchera imeni Geographicheskogo Obshchestva in Russian) (42°52´N; 133°00´E) is situated in the Lozovyi Range (Khandolaz) near Ekaterinovka Village, approximately 20 km from Nakhodka City (Partizanskii District of Primorskii Territory). It is placed on the right bank of Partizanskaya River (former Suchan River) at height 12 m above river level. The length of the major cave corridor constitutes 36 m. The height at the entrance is 1.6 m and width 0.7 m. The cave floor goes down from the entrance, leading to the small chamber being 1.5 m in breadth and with the flat floor (Abramova 1989).

The thickness of crumbly cave strata reaches 3.5 m to 5 m. Six lithological layers (1–6) have been recognized there. Pleistocene mammal remains were recovered predominantly from the layer 4 (1 m of thickness), which is formed by a heavy clay colored from light-brown to fuscous and dark brown tints and containing numerous limestone debris (Ovodov 1977). Faunal findings were supplemented with the stone industries of Paleolithic type (Okladnikov et al. 1968). Faunal and archeological findings were also taken from the upper part of the layer 5 (0.6 m of thickness) formed by ochreous-brown clay with inclusions of calcite-crusts. Many collected bones have been provided with numerals, not designating a layer but the depth of specimen deposition.

Scant upper-Paleolithic industry is represented by large pebbles having used as cores, flakes, and split pebbles. Presumably, the cave was exploited for the initial processing of stone; this hypothesis is confirmed by the absence of implements (Derevianko 1983). An item produced from the basis of elk antler, which was found there before the beginning of excavations, is not probably associated with the stone tools (Abramova 1989).

Palinological analysis of brown clay deposits at depth of 1.3 – 1.7 m, which contain limestone detritus and fragments of bones, revealed a presence of pollen of coniferous and broad-leafed plants as well as the birch and various herbs. It confirms these deposits to have formed during a warm period (Alekseev 1978).

The hyena bone-fragments served a basis for obtaining four AMS ^{14}C dates: >37000 (AA-37072), >36000 (AA-37073), >39000 (AA-37074), 34510±1800 (AA-38230) (Kuzmin et al. 2001). Subsequently additional two, earlier, dates have been obtained: 46000±700 (OxA-17046) and 48650±2380/1840 (KIA-25285) (Rohland et al. 2005; Stuart and Lister 2014). These dates, together with the results of palinological analysis, provide a possibility to refer the bone-bearing horizon incorporating hyena fossils to the latest interglacial (or interstadial), which is denoted as Karginian or Molotkov termochron in Siberia (24–57 ka for Western Siberia; Volkova 2009). In that time, many species, including *C. ultima*, presumably, spread their ranges northwards.

Ovodov (1977) calculated that hyena is represented in Geographical Society Cave by 169 bones at least from 10 individuals. Collection examined by me includes 1 damaged skull, 15 cranial fragments, 19 isolated upper teeth, 23 mandible fragments, 23 isolated lower teeth, 70 tooth fragments, 2 immature mandible fragments, 2 milk teeth, 2 vertebral fragments, 22 bone fragments; altogether 179 specimens. One coprolite is also present.

In addition to the material from Geographical Society Cave, several samples found in neighboring caves have been examined: 2 teeth from Tigrovaya Cave and 1 tooth from Spiashchaya Krasavitsa Cave. For comparison, collections of other museums whose abbreviated titles are provided below were used. Teeth and bones were measured with calipers with accuracy up to 0.5 mm.

Institutional abbreviations. CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; GMMKU, Geology-Mineralogy Museum of Kazan University; ISAK, Institute of Systematics and Evolution of Animals, Krakow, Poland; MENHK, Museum of Ethnography and Natural History, Kishinev, Moldova Republic; MEU, Museum of Evolution, Uppsala, Sweden; MMB, Moravsky Museum (Anthropos), Brno, Czech Republic; NHM, Natural History Museum, London, Great Britain; NHMP, Natural History Museum, Prague, Czech Respublik; NMM, Naturhistorisches Museum, Mainz, Germany; SNMB, Slovak National Museum, Bratislava, Slovakia; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Measurements. *Dental measurements*: *H* – greatest height, *L* – greatest length, *Lmts* – length of metastyle blade of P4, *Ltrd* – length of trigonid, *W* – greatest width. *Bone measurements* (see von den Driesch 1976): *Bd* – breadth of the distal end, *Bp* – breadth of the proximal end, *Dd* –breadth of the distal end, *Dp* – breadth of the proximal end, *GB* – greatest breath, *GL* – greatest length, *SD* – breadth of the diaphysis in medium part.

SYSTEMATICS

Family Hyaenidae Gray, 1821

Genus *Crocuta* Kaup, 1828

†*Crocuta ultima* (Matsumoto, 1915)

†*Crocuta ultima ussurica* Baryshnikov et Vereshchagin, 1996

†*Crocuta spelaea ussurica* Baryshnikov, Vereshchagin 1996: 55, Fig. 5 (Geographical Society Cave, Primorskii Territory, Russia; holotype – skull ZIN 34478, ad.).

Description. *Skull.* The skull is almost complete (ZIN 34478, holotype), rostral part, nasal bones, and zygomatic arcs are broken off (Fig. 1). The occipital condyles, sagittal crest, postorbital processes, and maxillas are also partly lost. Dimensions of ZIN 34478 are similar to those of *C. ultima* from Dabusu in China (Tang et al. 2003), resembling cranial dimensions of *C. crocuta spelaea* from European locality (Table 1).

The foramen infraorbitale is located above the middle part of P3, as in *C. ultima* from the Locality 100 in Northern China (see Zdansky 1925). The hard palate of ZIN 34478 is very broad, exceeding in the greatest palatal breadth most examined specimens of *C. crocuta spelaea* and approximating to the robust skull of *C. praespelaea* from Kazanka River in European Russia (Table 1). A broad hard palate is also observed in the skull of *C. ultima* from Upper Cave at Zhoukoudian in China (Pei 1940). Teeth in the specimen from Geographical Society Cave are represented only by the right P2 and by the fragment of right P3. No trace of the molar M1 is seen, while this tooth is present in *C. ultima* from the Locality 100. The tooth P2 is remarkable by the large size, being noticeably more robust than this tooth in skulls of similar size of *C. crocuta spelaea*. This peculiarity is also characteristic of other specimens of *C. ultima*. For example P4 in the skull from Upper Cave at Zhoukoudian (total cranial length 313 mm) is as long as 42.9 mm (Pei 1940) whereas the skull of *C. c. spelaea* from Sloup Cave in Czech Republic with the similar total cranial length (318.4 mm) has pronouncedly shorter P4 (38.8 mm) (Table 1).

Other cranial fragments are represented in the collection from Geographical Society Cave by the skull rostral part with the incisor row, right canine and right P1 (ZIN 34490-1; Fig. 2), by the skull occipital portion (ZIN 34490-5), and by several maxilla fragments (ZIN 34479, 34480, etc.) The length of premolar row P1–P4 constitutes 87.8 mm (ZIN 34480), the length of premolar row P3–P4 varies from 64.3 mm to 72.1 mm (n=4).

Several mandibles have been found (Fig. 3, 4). Generally, hyena mandibles are found in cave deposits to be broken out into the left and right bones; however, several mandible bones in the material from Geographical Society Cave kept coalescence. These specimens belong to the old individuals, which are confirmed by the pronounced wear of the tooth crowns.

Mandible morphology resembles that of *C. c. spelaea*, the bones being however more massive and with larger mental foramen. The length of lower tooth row p2-m1 varies from 91.2 mm to 98.3 mm (n=3), similarly with that known for Upper Cave at Zhoukoudian (Pei 1940). Comparison with the specimens of *C. c. spelaea* with the tooth row of equal length reveals in hyenas from Geographical Society Cave the higher mandibular body (Table 2). This peculiarity may be treated as a character of the reinforcement of mandibles for crushing robust long bones.

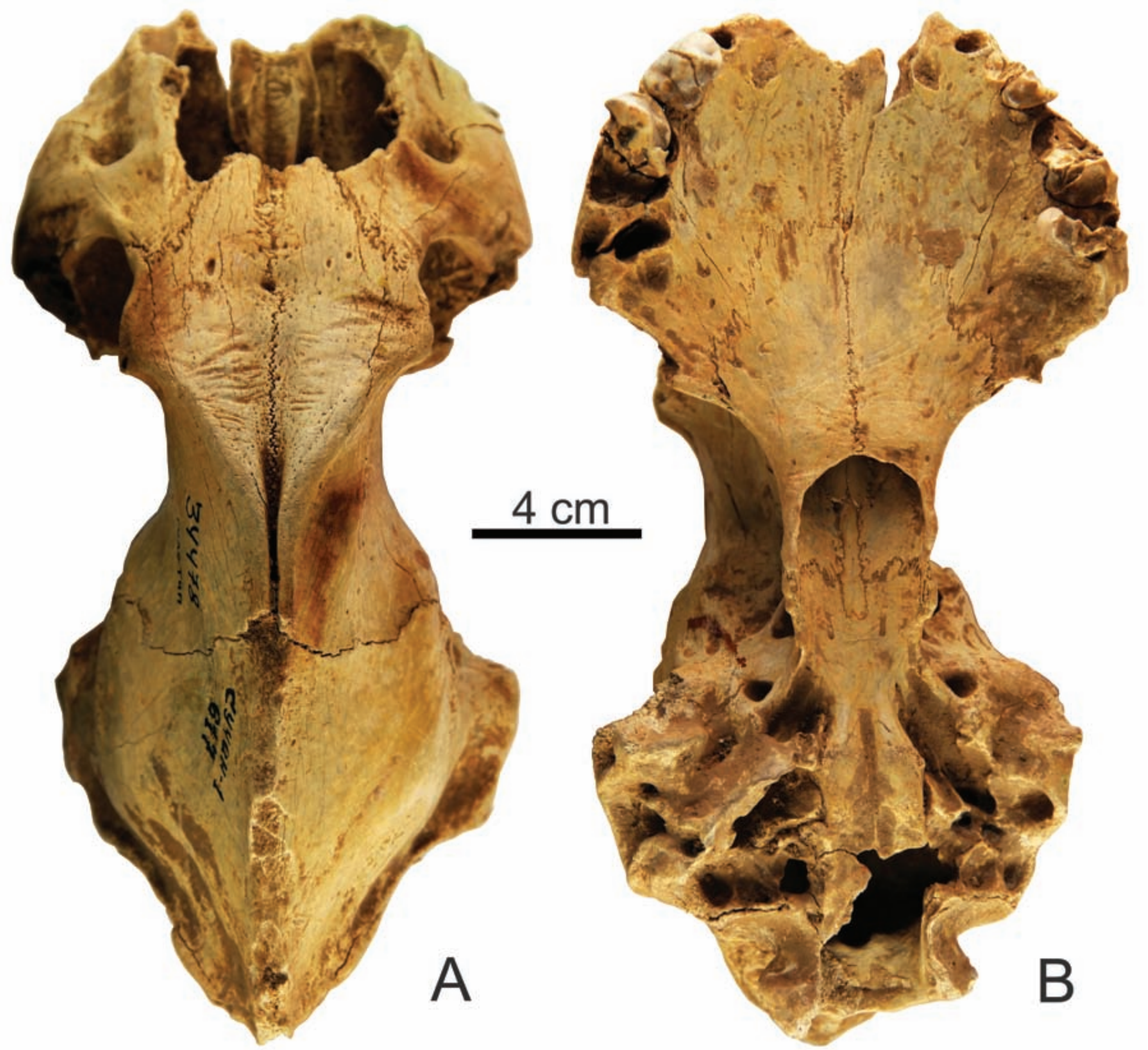

Fig. 1. Skull of *Crocuta ultima ussurica* (ZIN 34478, holotype) from Geographical Society Cave; dorsal (A) and ventral (B) views.

Fig. 2. Incisor row, upper canine and P1 of *Crocuta ultima ussurica* (ZIN 34490-1); occlusal view.

Table 1. Measurements (mm) of skull of Pleistocene hyenas of the genus *Crocuta*. Measurements are given according to von den Driesch (1976: Fig. 17). Abbreviations: 2 – condylobasal length, 7 – upper neurocranium length, 13a – length of P1-P4, 18 – greatest mastoid breadth, 22 – greatest neucranium breadth, 24 – frontal breadth, 25 – least breadth between the orbits, 26 – greatest palatal breadth, 26a – breadth of palatal near choan, 29 – facial breadth between the infraorbital foramina, 32 – height of the occipital triangle.

Measurements	*C. ultima*		*C. crocuta spelaea*			*C. praespelaea*	
	C. u. ussurica	*C. u. ultima*					
	Geographical Society Cave, Russia	Locality 100, China	Binagady, Azerbaijan	Javorka Cave, Czech Republic	Sloup Cave, Czech Republic	Kazanka River, Russia	Mosbach, Germany
	ZIN 34478, holotype, ad.	MEU 2499, sad.	ZIN 24407-286	MMB 114891	MMB n/n	GMMKU 191	NMM 1962/1452, holotype, ad.
2		233.2	251.0	268.3	272.4	268.5	268.0
7	ca157.2	143.3	166.5		182.2	176.0	164.2
13a		90.3	79.8	93.6	90.6	89.3	87.1
18	112.0	ca105.3	104.5	113.5	113.0	110.0	106.3
22	87.5		86.3	77.5	72.2	85.0	83.5
24	ca77		103.6			95.0	
25	64.3		64.9	72.0	69.9	70.5	ca66.0
26	127.0	117.0	111.5	123.5	117.8	129.8	121.3
26a	35.4		36.5		39.2		38.0
29	69.4	59.2	67.0	71.0	70.8	69.7	65.5
32	ca102.7		110.0	110.0	119.1	91.0	108.5
Teeth							
LC1				17.7	16.7	19.2	18.7
LC1				15.0	12.1	13.6	13.3
LP1		8.0	7.1	7.0	8.7	8.4	7.2
WP1		7.6	7.1	7.9	7.7	7.8	7.9
LP2	18.7	19.3	15.7	18.2	18.3	17.9	17.4
WP2	12.9	14.2	11.5	14.4	14.6	13.4	12.9
LP3		26.5	22.1	24.9	24.7	25.3	25.5
WP3		20.1	16.4	18.8	18.6	18.5	18.5
LP4		43.0	36.1	42.1	38.8	42.7	39.2
LmstP4		18.2	14.4	19.3	16.2	18.3	14.8
WP4		25.0	18.1	23.1	21.4	23.3	22.2

Deciduous teeth. The collection from Geographical Society Cave comprises cub remains: the left mandible (ZIN 34490-31) with fragments of d2 and d3, alveolus of d4, and erupting m1 (Fig. 5A). There are also two isolated d4 (ZIN 34490-32, 33), one of which (ZIN 34490-33), most probably, dropped out from the mandible. The size of mandible ZIN 34490-31 are markedly larger as compared to those of the recent *C. crocuta* of similar age (alveolar length d2–d4 constitutes 43 mm; height (in front of d3) is 38.5 mm).

Dimensions of lower deciduous teeth do not differ from those of *C. c. spelaea* (Table 3). The crown of d3 is nearly equally wide in its anterior and posterior portions (narrowed anteriorly in felids). The tooth has additional cuspids before and behind the main cusp (Fig. 5A). A large postcingulid is developed at the base of posterior additional cuspid. The recent *C. crocuta* (ZIN 1461) reveals that the posterior additional cuspid does not border with the main cusp, being shifted posteriorly, on “talonid”. The lower d4 is shaped characteristically of the spotted hyenas, with the large trenchant talonid whose edges are elevated over the inner portion. Both available specimens exhibit slender metastyle (Fig. 5B–E).

Fig. 3. Mandibles of *Crocuta ultima ussurica*; occlusal views: A – ZIN 34484; B – ZIN 34486; C – ZIN 34485.

Table 2. Measurements (mm) of mandibles of Pleistocene *Crocuta*.

Measurements	*C. ultima ussurica*			*C. crocuta spelaea*							*C. praespelaea*
	Geographical Society Cave, Russia			Binagady, Azerbaijan			Tornewton, England			Oblasova, Poland	Kazanka River, Russia
	ZIN 34484	ZIN 34487	ZIN 34486	ZIN 22382-13	ZIN 22382-40	ZIN 22382-42	NHM 597	NHM 697	NHM 856	ISAK 340/90	GMMKU 191
Lc1-m1	120.0	117.4		105.3	115.8	111.9	109.8	113.5	112.4	130.2	116.3
Lp2-m1	92.0	91.2	98.3	82.5	92.4	86.0	87.2	90.5	89.3	92.9	92.5
Lp2-p4	59.7	61.6		55.9	64.2	59.1	58.2	59.9	60.3		63.0
Height before p2	42.5	ca45.7	47.4	37.1	40.9	41.2	38.3	39.4	40.3	42.3	43.0
Teeth											
Lc1	18.2	18.4			16.4	15.8	16.0	16.6	18.4	18.0	
Lc1	15.2	15.1			14.1	13.4	12.8	13.9	14.4	15.8	
Lp2	15.5	16.6	16.2	15.5	17.7	15.6	15.4	15.7	16.4	14.9	17.4
Wp2	10.1	13.4	13.1	10.9	12.3	11.8	12.0	11.5	12.8	11.6	12.5
Lp3	22.8	24.0	25.2	19.9	23.0	22.2	21.0	22.6	22.5	20.1	22.8
Wp3	17.0	17.0	18.0	13.9	16.5	15.6	14.7	16.1	17.0	16.0	16.8
Lp4	24.9	24.3		21.5	25.8	24.3	23.2	24.4	22.8	23.2	24.8
Wp4	15.0	15.0		12.6	14.7	15.5	13.8	14.9	15.2	14.8	15.1
Lm1	34.1	ca33.7	37.4	28.4	34.1	30.1	32.7	32.6	32.4	32.1	33.7
Lm1trd	30.9	-	34.7	25.8	29.6	27.3	30.2	29.7	30.2	28.0	
Wm1	13.6	14.7	13.0	13.1	14.5	13.3	13.0	13.2	14.5	12.2	14.0

Table 3. Measurements (mm) of lower deciduous teeth of *Crocuta ultima* and *C. crocuta*.

Localities	Museum number	Wd2	Ld3	Wd3	Ld4	Ltrdd4	Wd4	Hd4
			C. ultima ussurica					
Geographical Society Cave, Russia	ZIN 34490-31	5.0	13.0	6.3				
	ZIN 34490-33				18.8	15.1	7.8	8.7
	ZIN 34490-32				21.8	17.8	8.5	9.8
			C. crocuta spelaea					
Tornewton, England	NHM 26851	5.0						
	NHM 38356	5.0						
	NHM 38447	5.1						
	NHM 1943		13.7	6.8				
	NHM 38591		13.9	6.7				
	NHM 38592		14.0	6.8				
	NHM 38593		14.4	6.4				
	NHM 38594		12.3	6.1				
	NHM 38596		13.2	6.7				
	NHM 38597		13.3	6.8				
	NHN 38598		13.7	6.5				
	NHM 1945				19.2	15.0	7.6	10.2
	NHM 26850				19.7	15.7	7.7	8.7
	NHM 38526				19.4	15.3	7.3	9.8
	NHM 38527				21.3	16.8	8.2	10.9
	NHM 38528				20.8	16.0	7.9	9.8
	NHM 38529				21.2	16.6	8.2	11.7
	NHM 38530				20.0	15.3	7.6	10.3
	NHM 38531				21.5	16.5	8.0	11.0
	NHM 38533				21.9	17.0	8.8	9.9
	NHM 38534				19.3	15.0	7.7	10.5
	NHM 38535				19.1	14.7	7.2	10.1
	NHM 38537				20.0	15.7	7.8	10.5
	NHM 38538				20.0	16.1	7.3	10.3
	NHM 38672				21.8	17.9	8.4	11.4
Švédův stůl, Czech Republik	MMB n/n	5.4	13.6	6.3	19.4	15.4	7.5	9.5
Vykhvatintsy, Moldova	MENHK 5-308	5.3	14.2	6.9	18.9	14.7	7.4	
	MENHK 5-317		12.7	7.4				
Buteshty, Moldova	MENHK n/n				19.6	15.1	8.0	
Binagady, Azerbaijan	ZIN 22382-50	5.6						
	ZIN 22382-51		12.9	6.9				

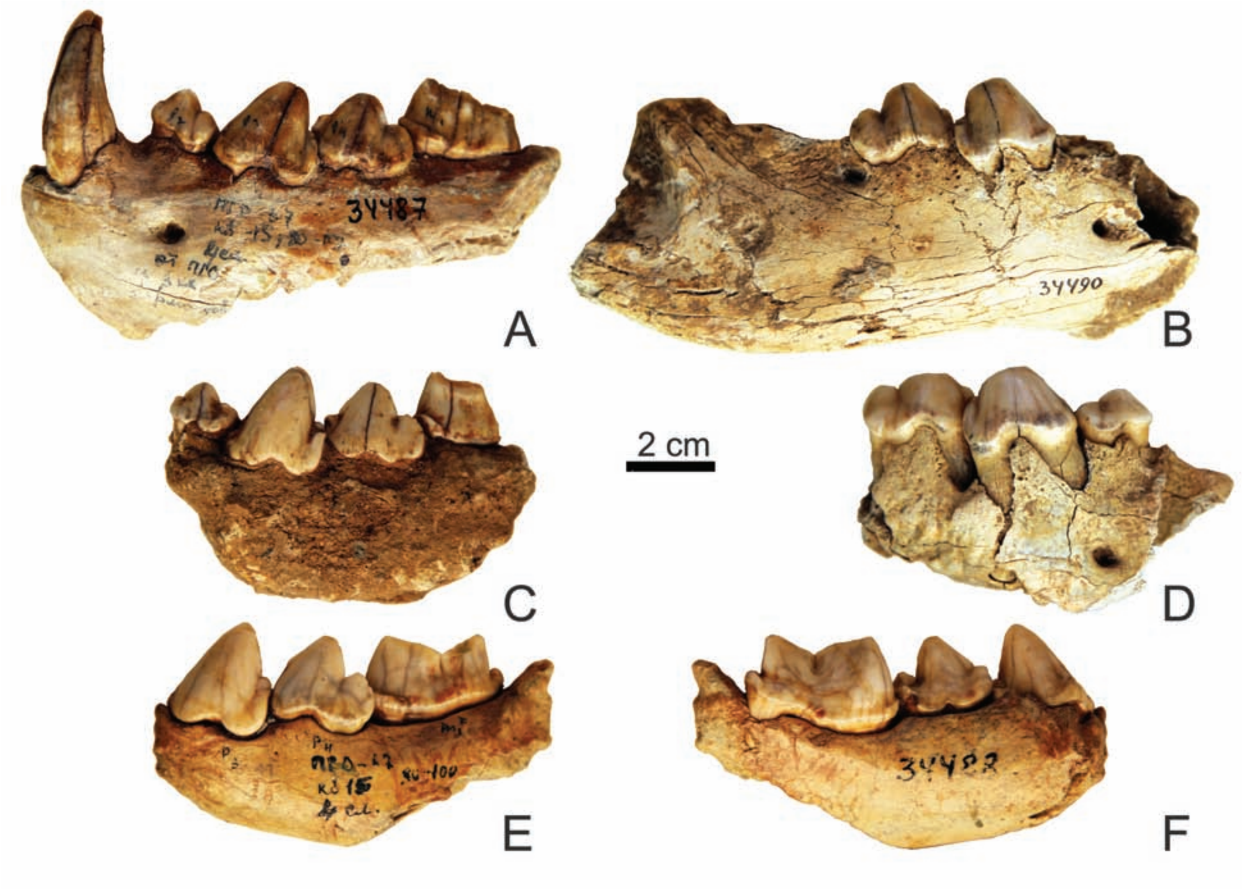

Fig. 4. Mandible fragments of *Crocuta ultima ussurica*; labial (A – E) and medial (F) views: A – ZIN 34487; B – ZIN 34490-7; C – ZIN 34490-10; D – ZIN 34490-9; E, F – ZIN 34488.

Permanent teeth. Upper incisors and canines of the hyena from Geographical Society Cave (Fig. 6) do not differ by their shape from those of *C. crocuta spelaea* (Table 4). The width of the upper canine varies from 14.0 mm to 15.2 mm (on average, 14.48 mm, n=6). Two samples of *C. c. spelaea* (Arcy-sur-Cure in France and Prolom 2 in Ukraine) examined by my revealed mean values for this measurement to be markedly smaller (13.30 mm, n=17). Frequency distribution of upper canine width is unimodal, which provides no grounds for sexual segregation of specimens.

The morphology of upper premolars is similar to that of *C. c. spelaea*, but the teeth are larger in size (Table 5). P1 is one-cuspid. The crown of P2 is widened in posterior part; the low massive additional cusp is developed behind the main cusp (Fig. 7).

P3 looks like a high cone with the cingulum running at its base, along the inner margin. Mean values of the greatest length (26.87 mm, n=9) and the greatest width (19.72 mm, n=9) noticeably exceed those of *C. c. spelaea* (24.22 mm and 18.04 mm correspondingly, n=21). In occlusion, this tooth contacts with the lower premolar p3, taking a part in crushing of large bones of hyena prey. Most specimens of P3 from Geographical Society Cave are worn to a variable degree, which makes it impossible to determine the index of hypsodonty (ratio between the crown height and its length). Only in the specimen ZIN 34481 the crown of erupting P3 shows a complete height (30 mm); by the index of hypsononty (106%) this tooth does not exceed the limits of variation determined for *C. c. spelaea* (Kurtén 1956).

P4 is very large, with a trenchant metastylar blade and well-developed protocone (Fig. 8). Its greatest length (mean value is 44.06 mm, n=5) markedly exceeds that of *C. c. spelaea* (mean value is 40.32 mm, n=22). In case of equal-in-length tooth crowns,

Table 4. Measurements (mm) of upper incisors and canines of Pleistocene *Crocuta*.

Localities	Museum number	LI1	WI1	LI2	WI2	LI3	WI3	LC1	WC1
C. ultima ussurica									
Geographical Society Cave, Russia	ZIN 34490-1	9.3	5.9	10.5	7.3	15.0	12.3	20.5	14.6
	ZIN 34490-42	8.6	6.5	10.9	7.7	13.7	11.4		
	ZIN 34490-75			9.3	8.6				
	ZIN 34490-35					14.3	11.9		
	ZIN 34490-37							20.0	14.6
	ZIN 34490-39							16.0	14.0
	ZIN 34490-38							17.5	14.0
	ZIN 34490-41							19.3	15.2
	ZIN 34490-40							19.3	14.5
Tigrovaya, Russia	ZIN 36797-1					12.8	10.8		
	ZIN 36797-2					13.0	10.7		
C. crocuta spelaea									
Tornewton, England	NHM 14274							17.5	13.5
	NHM 18982							16.5	11.7
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4247					13.4	10.0		
Javorka Cave, Czech Republic	MMB 114891	8.4	6.1	10.8	7.6	14.7	11.2	17.7	15.0
Moravian Karst, Czech Republic	MMB n/n							18.9	14.2
Raj, Poland	ISAK 1253/74			9.0	6.2	14.4	10.1		
						13.7	10.2		
								22.5	15.4
Kosh-Koba, Ukraine	ZIN 15977-43	7.2	5.0						
	ZIN 15977-44	8.4	5.2						
	ZIN 15977-21			9.3	6.3				
	ZIN 15977-42			8.2	6.5				
	ZIN 15977-9					11.7	9.0		
	ZIN 15977-10					12.3	9.7		
	ZIN 15977-27					11.4	9.9		
	ZIN 15977-18							17.5	13.2
	ZIN 15977-19							15.1	12.4
	ZIN 15977-32							15.7	13.4
	ZIN 15977-23							17.9	–
	ZIN 15977-24							17.2	13.2
	ZIN 15977-49							15.7	12.9
	ZIN 15977-68							16.2	13.7
Ayuvul-Koba, Ukraine	ZIN 15978-17					12.7	10.1		
	ZIN 15978-16							15.9	13.8
Binagady, Azerbaijan	ZIN 22382-35							17.2	13.1
Aman-Kutan, Uzbekistan	ZIN 29058					11.0	10.3		
						10.8	10.3		
						12.7	9.4		
						10.0	9.6		
C. praespelaea									
Kazanka River, Russia	GMMKU 191	8.9	6.4	11.0	7.8	12.8	11.0	19.2	13.6

Table 5. Measurements (mm) of upper cheek teeth of *Crocuta ultima* and *C. crocuta*.

Localities	Museum number	LP1	WP1	LP2	WP2	LP3	WP3	LP4	LmtsP4	WP4
C. ultima ussurica										
Geographical Society Cave, Russia	ZIN 34479	8.2	8.5	20.9	15.0	27.9	19.3	–	–	22.7
	ZIN 34490-1	8.3	8.2							
	ZIN 34490-36	8.7	7.9							
	ZIN 34490-2			19.2	13.7	27.7	20.0			
	ZIN 34490-3			18.8	14.0	26.9	19.9			
	ZIN 34481					ca28.9	21.7	46.5	21.8	27.9
	ZIN 34482					28.3	21.0	45.5	20.8	25.3
	ZIN 34483					27.5	20.0	44.4	19.8	24.7
	ZIN 34490-43			20.0	14.0					
	ZIN 34490-44					26.8	19.9			
	ZIN 34490-45					24.8	19.4			
	ZIN 34490-4							43.2	18.7	22.7
	ZIN 34480	6.9	6.2	16.0	11.5	ca23.0	16.3	ca40.7	ca17.4	19.8
C. crocuta spelaea										
Tornewton, England	NHM 599			17.3	12.8	23.9	17.0	39.8	17.1	21.0
	NHM 600	9.2	8.0	18.1	14.4	25.1	19.1			
	NHM 854			19.3	15.3	26.4	20.4	44.4	19.3	23.9
	NHM 959			15.4	11.7	23.4	17.2	38.6	16.2	20.3
	NHM 14274	8.0	7.5	16.6	12.5	24.8	18.0	39.8	19.0	22.3
	NHM 16693			17.3	14.0	24.4	18.0	40.7	17.1	22.2
	NHM 16695	6.6	6.3	18.5	13.3	24.8	17.8	38.8	16.7	21.7
	NHM 16703			17.0	13.2	23.4	18.6	38.5	16.0	21.3
	NHM 18982			17.8	14.4	25.5	19.0	42.6	19.1	22.9
Srbsko Chlum Komin Cave, Czech Republic	NHMP R4197							42.9	19.3	22.4
Moravian Karst, Czech Republic	MMB n/n	8.1	7.7	18.5	13.4	26.6	18.4	43.6	18.7	23.0
Raj, Poland	ISAK 1253/74					24.2	18.9	41.0	18.1	22.5
								40.0	19.0	22.2
Wierzchowska Górna, Poland	ISAK 286/60					24.7	18.0	–	–	24.8
Buteshty, Moldova	MENHK n/n			20.6	10.9	24.6	17.4			
Kosh-Koba, Ukraine	ZIN 15977-15	8.4	7.6			23.5	18.0			
	ZIN 15977-4							38.8	16.0	22.1
	ZIN 15977-5							38.5	15.6	–
	ZIN 15977-6					24.6	17.5			
	ZIN 15977-8					24.1	18.4			
	ZIN 15977-11	8.7	7.8							
	ZIN 15977-13					23.2	18.0			
	ZIN 15977-14							39.0	15.9	21.8
	ZIN 15977-29			17.7	13.1					
	ZIN 15977-30			17.2	12.9					
Ayuvul-Koba, Ukraine	ZIN 15978-15							40.7	16.8	–
	ZIN 15978-20							39.2	17.6	23.2
Staroselie, Ukraine	ZIN 25644-3					21.5	17.4			
Chokurcha, Ukraine	ZIN 34387			16.1	12.2	25.4	19.0	39.8	16.7	22.3
	ZIN n/n							37.8	16.8	20.4
Binagady, Azerbajan	ZIN 22382-33							40.5	16.0	23.1
	ZIN 22382-35			17.5	13.2	23.9	17.4	40.3	16.1	20.9
	ZIN 22382-36							41.8	16.0	22.5
Aman-Kutan, Uzbekistan	ZIN 29058	7.2	7.5			20.7	15.4	33.3	13.9	18.8

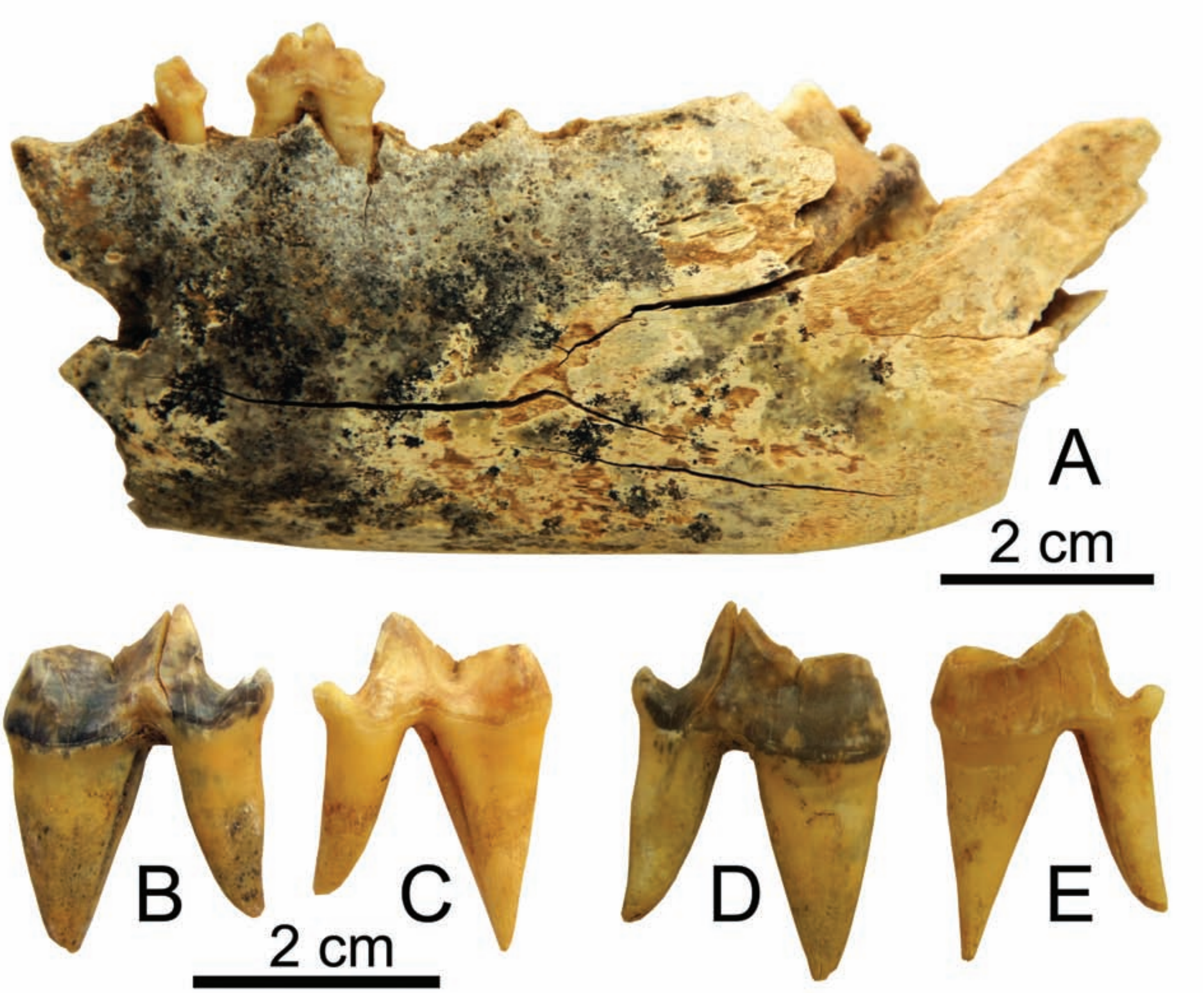

Fig. 5. Left mandibule with deciduous teeth (fragment of d2 and d3) (A) and isolate deciduous teeth d4, left (B, D) and right (C, E), of *Crocuta ultima ussurica*; labial (A, D, E) and medial (B, C) views: A – ZIN 34490-31; B, D – ZIN 34490-32; C, E – ZIN 34490-33.

hyenas from Geographical Society Cave have the blades shorter than those in *C. c. spelaea*. This feature approximates it to the Middle Pleistocene taxa *C. ultima ultima* and *C. praespelaea*, which also have a shortened blade of P4 (Table 1). Therefore the cutting capacity of the upper carnassial tooth was weakened in *C. u. ussurica* and the tooth morphology exhibits less developed carnivorous specialization in comparison with *C. c. spelaea*.

The lower incisors are few in number in the collection (Table 6). Lower canines, in the crown shape, are similar to those of *C. c. spelaea* (Fig. 6). Their width varies from 13.2 to 15.7 mm (on average 14.53 mm, n=12). Two examined samples of *C. c. spelaea* (Arcy-sur-Cure in France and Prolom 2 in Ukraine) revealed smaller mean value of the width of lower canine (13.81 mm, n=25). Presumably, this difference may be explained not only by smaller size of canines in the European hyena, but also by different ratio between males and females in the samples compared.

The lower premolars are shaped similarly with other spotted hyenas. The crown of p2 is widened in the posterior part; additional cusps are developed in front of and behind the main cusp. By the length and width, the specimens from Geographical Society Cave do not differ from the teeth of *C. c. spelaea* (Table 7).

The premolar p3 is conical, with strong ridges on the anterior and posterior sides of the cone. By their length (on average 23.87 mm, n=11), teeth from Geographical Society Cave markedly exceed those of *C. c. spelaea* (on average 22.36 mm, n=20); meantime, the examined samples coincide by the mean values of the p3 width.

The crown of premolar p4 is narrow; the structure resembling a talonid with two cuspids is developed behind the main cusp. The divergence in the tooth dimensions from *C. c. spelaea* is less pronounced than that observed for p3.

The lower carnassial tooth m1 is trenchant, with well-marked talonid (Fig. 9). By the greatest length (on average 33.29 mm, n=10) the sample from Geographical Society Cave noticeably exceeds the examined collection of *C. c. spelaea* (on average 31.99 mm, n=17). Mean values of the greatest width differ less pronouncedly (14.34 mm, n=10 and 13.82 mm, n=17 correspondingly). The talonid is very short (the trigonid constituting 90–96% of the tooth length), which distinguishes the hyena of Geographical Society Cave from *C. praespelaea* whose trigonid being less than 90% of the m1 length (Kurtén and Poulianos 1977). Seven specimens revealed to have the metaconid (29% of the total sample); in *C. c. spelaea* its occurrence varies from 22% (Prolom 2, Ukraine, n=9) and 25% (Arcy-sur-Cure, France, n=12) to 39% (Tornewton, England, n=38) and 55% (Binagady, Azerbaijan, n=11).

Postcranial bones. The hyena postcranial skeleton is represented by several bones. These are fragment of the sixth cervical vertebra (ZIN 34490-60), fragments of radius (ZIN 34490-63) and tibia (ZIN 34490-62) as well as several short bones of the fore and hind limbs (Fig. 10).

Cervical vertebra ZIN 34490-60 are markedly larger than in the recent African spotted hyena *C. crocuta*. Breadth across the caudal articular process constitutes 71.3 mm. *C. ultima ussurica* had, therefore, strong neck allowing animals to bear large prey in their teeth.

The dimensions of limb bones resemble those of *C. crocuta spelaea* and the recent spotted hyena *C. crocuta* (Table 8). These data testify the shorter-limbed skeleton in *C. ultima*, which was hypothesized by Kurtén (1956).

Comparison. Hyena from Geographical Society Cave exhibits a morphological similarity with the fossil hyena from Upper Cave at Zhoukoudian in China, also characterizing by the combination of very large teeth with rather small size of the limb bones

Fig. 6. Upper (A, B) and lower (C – G) canines of *Crocuta ultima ussurica*; labial view: A – ZIN 34490-38; B – ZIN 34490-37; C – ZIN 34490-49; D – ZIN 34490-52; E – ZIN 34490-48; F – ZIN 34490-47; G – ZIN 34490-46.

Table 6. Measurements (mm) of lower incisors and canines of *Crocuta ultima* and *C. crocuta*.

Localities	Museum number	Li2	Wi2	Li3	Wi3	Lc1	Wc1
	C. ultima ussurica						
Geographical Society Cave, Russia	ZIN 34484	9.5	6.6	10.8	10.3	17.9	14.8
	ZIN 34490-70	8.5	6.1				
	ZIN 34490-72			8.8	8.7		
	ZIN 34490-71			9.1	9.2		
	ZIN 34490-67			9.5	9.1		
	ZIN 34490-68			10.7	10.5		
	ZIN 34490-74			9.3	9.4		
	ZIN 34487					18.8	14.2
	ZIN 34485					18.0	14.2
	ZIN 34490-46					22.0	15.7
	ZIN 34490-47					18.7	14.1
	ZIN 34490-48					18.4	14.5
	ZIN 34490-49					19.2	14.1
	ZIN 34490-50					18.8	14.9
	ZIN 34490-51					16.1	14.3
	ZIN 34490-52					16.3	13.2
	ZIN 34490-53					18.6	15.1
	ZIN 34490-54					21.8	15.3
	C. crocuta spelaea						
Tornewton, England	NHM 597					16.0	12.8
	NHM 697					16.6	13.9
	NHM 750					17.0	13.8
	NHM 856					18.4	14.4
	NHM 15434					17.0	12.5
	NHM 16700					16.4	13.5
	NHM 16701					16.6	13.4
	NHM 18982					16.1	12.5
	NHM 44716					16.3	13.1
Srbsko Chlum Komin Cave, Czech Republic	NHMP n/n					15.9	13.0
Barova, Czech Republik	MMB n/n	9.1	4.9	11.1	9.5	18.6	15.2
Čertova pec, Slovakia	SNMB n/n					17.4	13.4
Raj, Poland	ISAK 1253/74					19.7	14.0
Buteshty, Moldova	MENHK 11466-1					16.6	13.4
Kosh-Koba, Ukraine	ZIN 15977-45	9.0	5.1				
	ZIN 15977-1			10.2	8.7		
	ZIN 15977-2			11.1	10.0		
	ZIN 15977-46			9.8	8.6		
	ZIN 15977-48			10.3	9.7		
	ZIN 15977-31					16.9	13.2
	ZIN 15977-70					17.1	13.4
	ZIN 15977-69					17.0	14.0
Adzhi-Koba, Ukraine	ZIN n/n					16.0	13.5
	ZIN n/n					16.4	13.7

Table 7. Measurements (mm) of lower cheek teeth of *Crocuta ultima* and *C. crocuta*.

Localities	Museum number	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Ltrdm1	Wm1
				C. ultima ussurica						
Geographical Society Cave, Russia										
	ZIN 34485	17.3	12.4	23.9	18.0					
	ZIN 34488			24.8	-	26.3	16.1	35.4	32.5	15.1
	ZIN 34489					22.5	14.0	31.4	28.9	13.8
	ZIN 34490-7			23.5	16.2	25.1	14.3			
	ZIN 34490-8	17.5	12.8	24.7	18.8					
	ZIN 34490-9	17.9	14.0	26.0	18.5	26.2	16.0			
	ZIN 34490-10	16.0	11.8	23.7	16.4	24.2	13.8			
	ZIN 34490-12			25.5	18.7	26.4	15.6			
	ZIN 34490-17	17.7	13.1	23.7	16.7					
	ZIN 34490-18			21.6	15.2	22.1	13.8			
	ZIN 34490-16	18.3	13.6							
	ZIN 34490-55			22.0	16.0					
	ZIN 34490-56			23.2	17.6					
	ZIN 34490-14					25.8	15.6			
	ZIN 34490-19					24.9	17.1			
	ZIN 34490-58					23.8	14.4			
	ZIN 34490-59					23.6	14.5			
	ZIN 34490-20							35.4	32.5	15.1
	ZIN 34490-21							31.4	28.9	13.8
	ZIN 34490-22							34.6	31.1	14.3
	ZIN 34490-23							30.8	29.5	13.9
	ZIN 34490-25							35.5	32.0	14.4
	ZIN 34490-26							29.9	28.4	12.9
	ZIN 34490-27							35.1	31.5	15.0
	ZIN 34490-28							33.4	-	15.1
				C. crocuta spelaea						
Tornewton, England	NHM 595	15.9	12.2	22.0	16.6	23.8	15.0	31.8	28.7	-
	NHM 856	16.4	12.8	22.5	17.0	22.8	15.2	32.4	30.2	14.5
	NHM 14173	16.2	13.2			25.8	16.3	33.5	30.4	14.9
	NHM 16696	17.2	12.8	24.5	17.5	24.8	15.1	33.8	30.6	14.3
	NHM 16701	17.7	13.8			25.3	14.4	34.1	30.0	13.6
	NHM 16702	16.8	13.0	23.8	18.2	25.3	15.7	32.4	29.4	14.7
	NHM 16762	15.8	11.3	23.5	16.1	23.3	15.1			
	NHM 17932	15.2	12.0	22.1	16.6	23.4	14.6	30.5	28.0	13.4
	NHM 17988	15.7	11.7	23.0	16.4	24.3	15.0	32.3	29.1	13.5
	NHM 44716	16.0	11.7	22.0	16.7	23.9	15.4	33.0	29.2	14.4
Barova, Czech Republik	MMB n/n	17.6	12.9	25.1	17.6	25.0	15.5			
Raj, Poland	ISAK 1253/74	16.2	11.4	23.5	14.1	22.2	16.6	29.7	28.3	13.5
Čertova pec, Slovakia	SNMB n/n	17.1	14.0	22.9	17.3	26.8	15.6	34.8	31.0	15.1
Buteshty, Moldova	MENHK 11466-1	16.7	11.5	21.7	17.2	23.9	15.8			
	MENHK 11466-2			22.0	16.6	24.3	14.7	32.3	29.1	13.7
Kosh-Koba, Ukraine	ZIN 15977-36	17.5	11.8							
	ZIN 15977-40	17.9	14.2							
	ZIN 15977-56	17.5	13.5							
	ZIN 15977-59	16.8	12.3							
	ZIN 15977-54			21.6	16.2					
	ZIN 15977-55			21.4	15.8					

Table 7. *Continued*

Localities	Museum number	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Ltrdm1	Wm1
	ZIN 15977-34					26.2	17.3			
	ZIN 15977-35					24.5	14.9			
	ZIN 15977-51					23.5	14.9			
	ZIN 15977-66					22.8	14.3			
Ayuvul-Koba, Ukraine	ZIN 15978-19							32.7	29.8	14.3
	ZIN 15978-31	17.3	13.3	23.4	17.1	23.7	16.3	33.3	30.6	14.6
Binagady, Azerbajan	ZIN 22382-37	15.6	10.4	20.0	13.7			29.0	26.7	13.0
	ZIN 22382-39	15.0	10.7	20.8	15.0	21.8	13.2	28.8	26.0	12.0
	ZIN 22382-41	16.9	12.4	21.5	15.4			29.4	26.6	12.7
Aman-Kutan, Uzbekistan	ZIN 29058-1	17.6	12.0	20.0	16.0	22.8	14.5	30.0	27.4	12.9

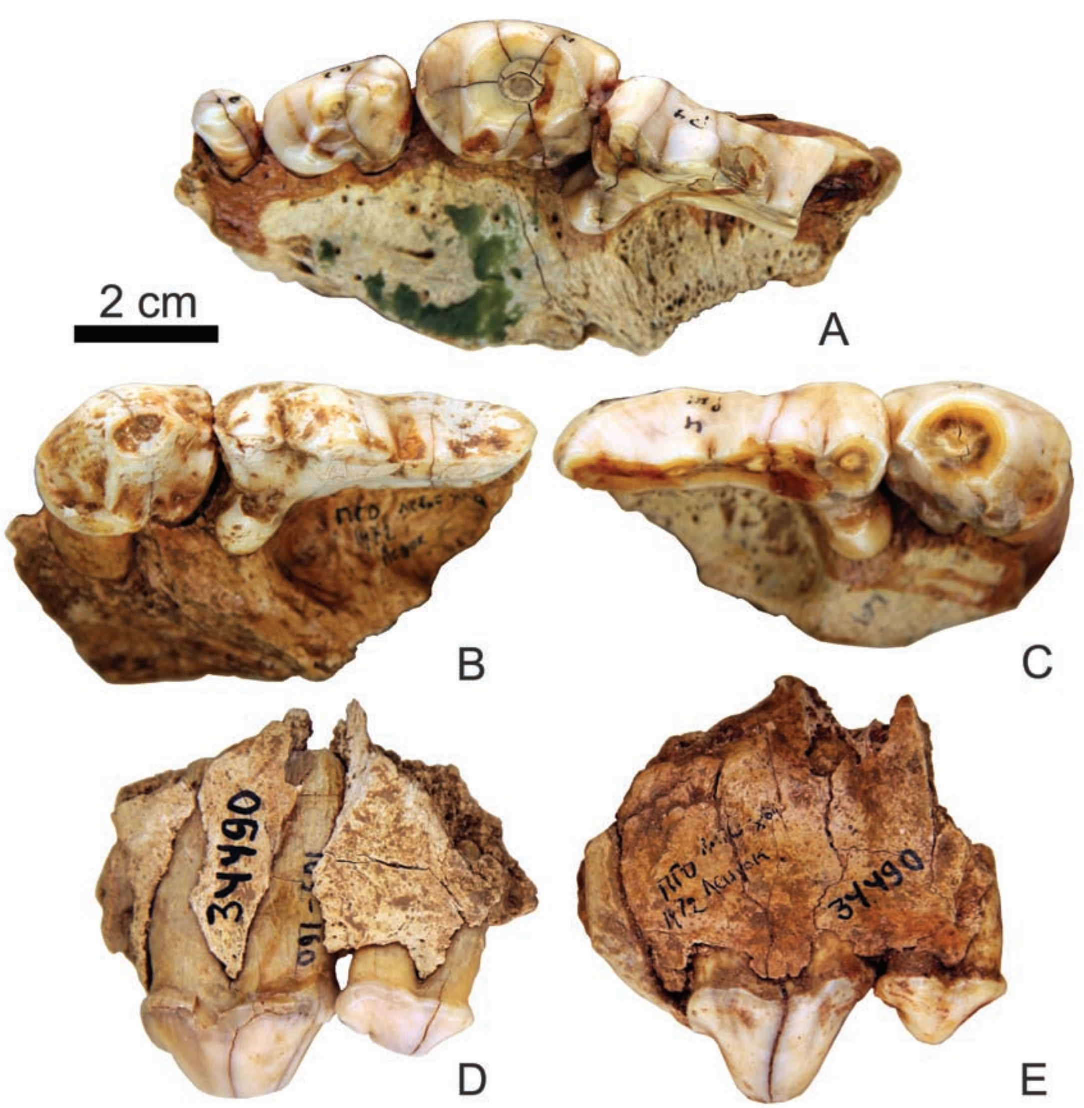

Fig. 7. Maxillary teeth of *Crocuta ultima ussurica*; occlusal (A–C) and lateral (D, E) views: A – ZIN 34479; B – ZIN 34483; C – ZIN 34482; D – ZIN 34490-2; E – ZIN 34490-3.

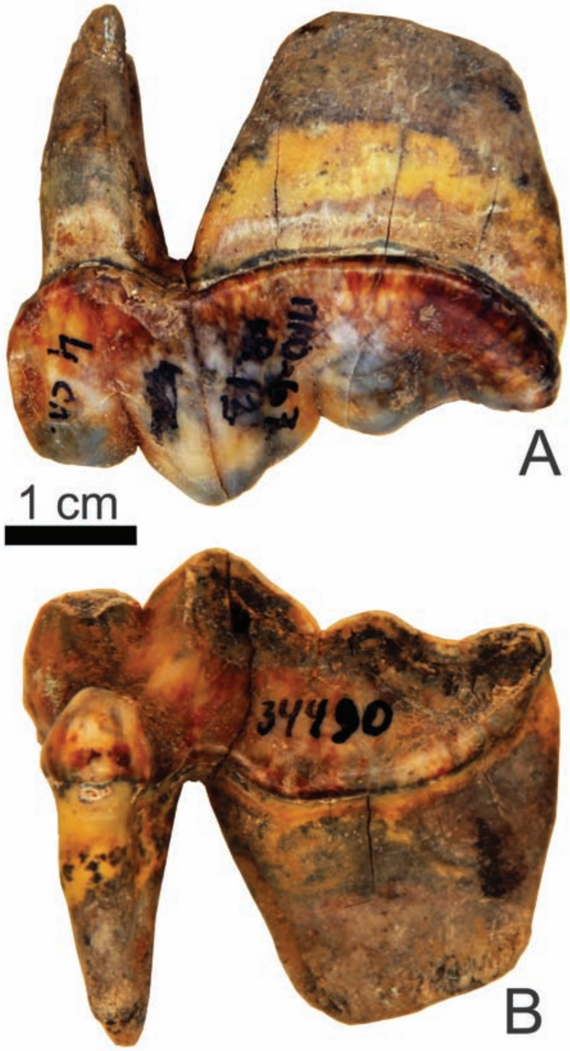

Fig. 8. Left upper carnassial tooth P4 (ZIN 34490-4) of *Crocuta ultima ussurica*; labial (A) and medial (B) views.

Fig. 10. Right metacarpal 3 (A), left metacarpal 4 (B) and right calcaneus (C) of *Crocuta ultima ussurica*; labial (B), medial (A) and dorsal (C) views: A – ZIN 34490-81; B – ZIN 34490-82; C – ZIN 34490-66.

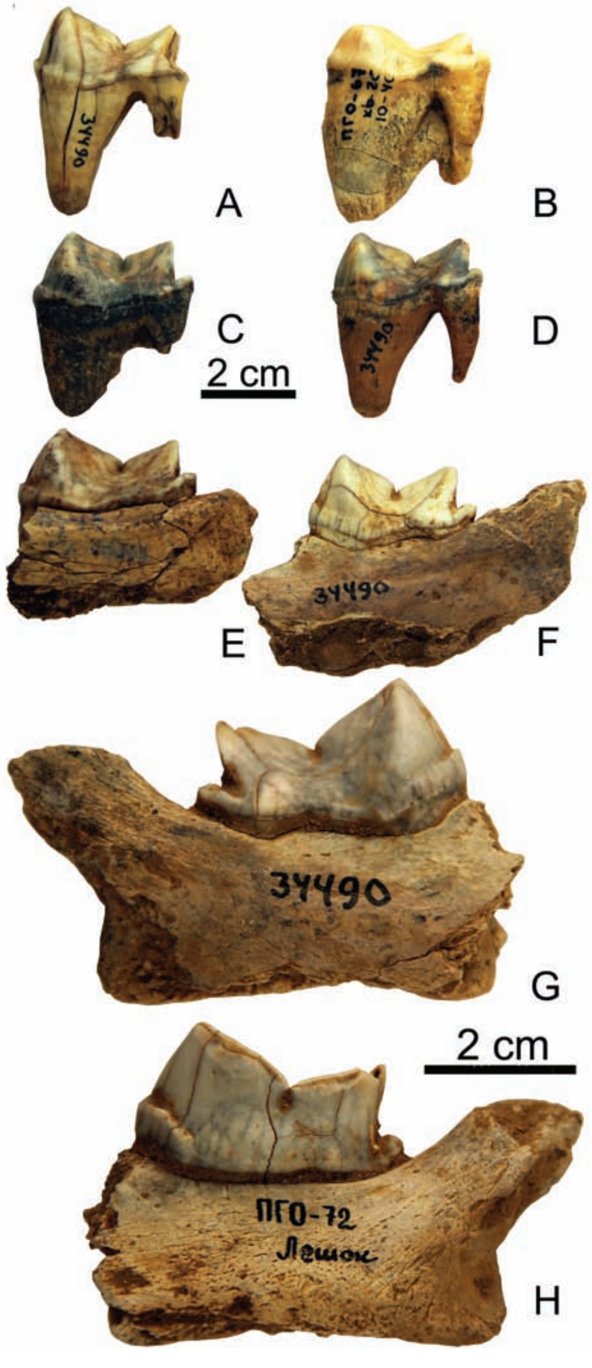

Fig. 9. Right (A–F) and left (G, H) lower carnassial tooth m1 of *Crocuta ultima ussurica*; labial (H) and medial (A–G) views: A – ZIN 34490-26; B – ZIN 34490-25; C – ZIN 34490-28; D – ZIN 34490-27; E – ZIN 34490-2; F – ZIN 34490-22; G, H – ZIN 34490-20.

Table 8. Measurements (mm) of limb bones of *Crocuta ultima* and *C. crocuta*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd	GB
Radius								
C. ultima ussurica								
Geographical Society Cave, Russia	ZIN 34490-63				24.2			
C. crocuta spelaea								
Srbsko Chlum Komin Cave, Czech Republic	NHMP n/n				23.0			
	NHMP n/n				22.6			
Binagady, Azerbaijan					23.4			
C. crocuta, recent	ZIN 11471				22.1			
Mc3								
C. ultima ussurica								
Geographical Society Cave, Russia	ZIN 34490-81		16.5	23.3	13.1			
C. crocuta spelaea								
Binagady, Azerbaijan	ZIN 22382-28	97.0	15.6	20.5	11.8	16.0	16.0	
C. crocuta, recent	ZIN 11471	92.4	15.5	19.6	11.4	15.8	14.9	
Mc 4								
C. ultima ussurica								
Geographical Society Cave, Russia	ZIN 34490-82	88.7	12.7	19.7	11.7	14.3	14.0	
C. crocuta spelaea								
Srbsko Chlum Komin Cave, Czech Republic	NHMP n/n	91.2	17.8	21.3	12.0	16.3	16.1	
	NHMP n/n	89.4	17.7	20.8	12.0	16.4	16.0	
Binagady, Azerbaijan	ZIN 22382-25	92.2	14.4	18.5	11.0	15.0	14.7	
C. crocuta, recent	ZIN 11471	88.8	11.9	16.4	12.4	14.0	14.0	
Patella								
C. ultima ussurica								
Geographical Society Cave, Russia	ZIN 34490-64							24.2
C. crocuta spelaea								
Srbsko Chlum Komin Cave, Czech Republic	NHMP n/n							25.0
C. crocuta, recent	ZIN 11471							21.3
Tibia								
C. ultima ussurica								
Geographical Society Cave, Russia	ZIN 34490-62				21.8			
C. crocuta spelaea								
Srbsko Chlum Komin Cave, Czech Republic	NHMP n/n				20.1			
	NHMP n/n				19.2			
C. crocuta, recent	ZIN 11471				18.2			
Calcaneus								
C. ultima ussurica								
Geographical Society Cave, Russia	ZIN 34490-66	67.1						32.6
C. crocuta spelaea								
Srbsko Chlum Komin Cave, Czech Republic	NHMP n/n	67.6						32.2
	NHMP R969	65.4						32.1
	NHMP 4455	62.2						28.2
Binagady, Azerbaijan	ZIN 22382-17	63.4						28.4
C. crocuta, recent	ZIN 11471	62.8						29.5

(Pei 1940). Taxonomic similarity of hyenas from the Late Pleistocene of Russian Far East with those from North-East China is also ascertained by the results of molecular analysis placing them into a single haplogroup (Sheng et al. 2013). This group should be designated as "*ussurica*", since it has been established on the basis of material from Geographical Society Cave.

I possess only fragmentary information on *C. ultima* from the Middle Pleistocene of China. The length of the upper carnassial tooth P4 of the type specimen (42.0 mm; Zdansky 1925) and that of the specimen from Locality 100 (43.0 mm) is less significant than minimum parameters of this length in the collection from Geographical Society Cave. The skull from Locality 100 exhibits shortened metastylar blade and the presence of M1 (archaic character, similar to *C. praespelaea*; see Schütt 1971). Meanwhile the greatest length of m1, judging from the published information on the localities Zhoukoudian 1 and Locality 100 (30.6–35.5 mm, n=3; Zdansky 1927; Pei 1934), corresponds to such parameters in the sample from Geographical Society Cave.

The comparison of approximately equal-in-size skulls of skulls of *C. ultima* from China and *C. c. spelaea* from Europe revealed the specimens from China has more robust cheek teeth. This character is observed in the hyena from Geographical Society Cave (see above), i.e. it is characteristic of the hyena *C. ultima* of the Late Pleistocene as well as of the Middle Pleistocene.

Thus, the morphological similarity provides a possibility to refer Pleistocene spotted hyenas from Eastern Asia to a single species *C. ultima*. It is characterized by the large greatest palatal breadth of skull (similar to *C. praespelaea*), the large size of cheek teeth (absolute and comparative) and by the short metastylar blade of P4. Two subspecies may be recognized: *C. ultima ultima* from the Middle Pleistocene of China and *C. u. ussurica* from the Late Pleistocene of Russian Far East and China. The first subspecies seems to be more archaic (smaller dimensions of cheek teeth, presence of M1 etc.).

Most probably, both subspecies belong to the group of East-Asian spotted hyenas, which was established as a result of study of the ancient mtDNA (Rohland et al. 2005, Sheng et al. 2013); however, it is not steel proved for the older subspecies.

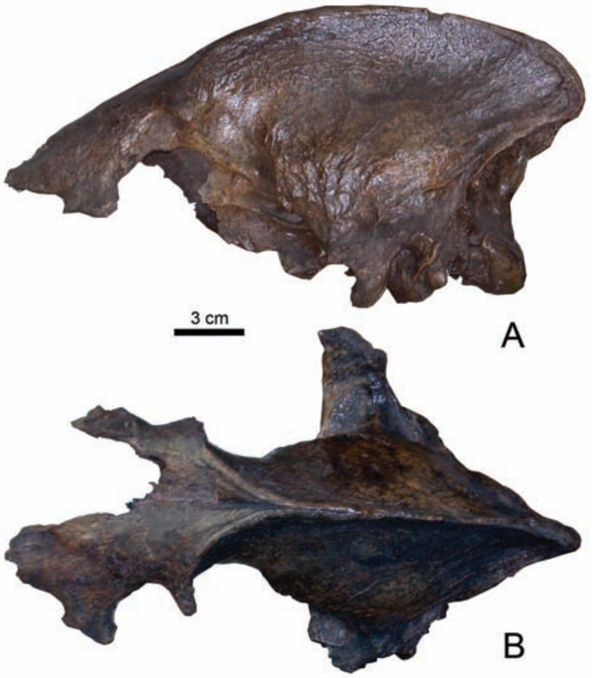

Fig. 11. Skull fragment of *Crocuta* cf. *ultima* (CCMGE 2-3922) from Zaigraevo, Kurba River in Buryat Republic, Russia; lateral (A) and dorsal (B) views.

Morphological differences between the Late Pleistocene hyenas of Europe (*C. crocuta spelaea*) and animals from the Russian Far East (*C. ultima ussurica*) were defined during the examination of the collection from Geographical Society Cave. These are pronouncedly smaller size of the cheek teeth (including premolars P3/p3), and longer metastylar blade of P4 in the European hyena. It may be hypothesized a bone-crushing tooth adaptation for the East-Asian hyenas belonging to the species *C. ultima* and a cutting (carnivorous) adaptation for the European hyena *C. crocuta spelaea*, which has been already supposed by Kurtén (1956).

C. ultima ussurica resembles *C. praespelaea* by shorten metastylar blade of P4 (with regards to its greatest length) (see Schütt 1971). At the same time, proportions of m1 (ratio between the trigonid length and the tooth greatest length) as well as the ratio between the p4 length and m1 length place the hyena from Geographic Society Cave more close to *C. crocuta spelaea* instead of *C. praespelaea*.

In Russia, *C. ultima* was found in the southern part of Primorskii Territory (Geographical Society Cave and scarce finds from neighboring localities: Tigrovaya Cave and Spiashchaya Krasavitsa Cave). Presumably, a large fragment of the spotted-hyena occipital bone (CCMGE 2-3926) from the locality

Zaigraevo, Kurba River in Transbaikalia, that was earlier attributed to *Crocuta* cf. *spelaea praespelaea* (Baryshnikov and Vereshchagin 1996)), is also referred to this species (Fig. 11). Its dimensions (mm): upper neurocranium length 173.4, greatest neurocranium breadth 75.5, breadth of the postorbital constriction 46.0, least breadth between the orbits 68.4, greatest breadth of the occipital condyles 61.1, greatest mastoid breadth 108.3, height of the occipital triangle 111.5. The absence of cheek teeth provides no grounds for precise specific attribution of this find; therefore, I designate it as *Crocuta* cf. *ultima*.

TAPHONOMY

The morphological differences between *C. ultima* and *C. crocuta spelaea* with respect to the dentition suggest some difference between these species with respect to diet, foraging, and other behavior. It is therefore important to undertake comparative taphonomic analyses of the cave localities yielding remains of *C. ultima* and those of *C. crocuta spelaea*.

Number of fossil remains and minimal number of individuals. According to Ovodov (1977), nearly half of collection from Geographical Society Cave, which contains 4850 large mammal remains, consists of deer *Cervus elaphus/nippon* (46%). The proportion of carnivores is high (22.9%) and comparable to other carnivore bone accumulations. Hyena bone fragments are rare (3.5%).

In West European and Northern Caucasus sites with mixed bone assemblages, hyena remains constitute less than 5% of the collection (for example in Il'skaya open site in Kuban River basin 0.8%; Hoffecker et al. 1991); however, in hyena dens, the proportion of hyena remains reaches 10% of the total, and several sites (Tornewton, Uphill, Teufelslucken) were found to contain more than 30% (Fosse 1999). Similar indices were calculated for the hyena dens in the rockshelter Prolom 2 (6.4%) in Crimea, Eastern Europe, and in Denisova Cave (9.4%) in the Altai, Western Siberia (Enloe et al. 2000; Derevianko et al. 2003); it should be mentioned, however, this index is only 1.3% in small Barakaevskaya Cave, Northern Caucasus (Hoffecker and Baryshnikov 1998). Therefore, the hyena assemblage in Geographical Society Cave seems to be atypical in relative abundance to that of the cave dens of *C. crocuta spelaea*.

The minimal number of adult individuals in the examined collection, calculated on the basis of presence of m1 (without taking into consideration the degree of wear) constitutes nine animals. Similar calculations, based on the presence of p3 in the collection from Geographical Society Cave (accounting for the degree of wear), indicates the presence of 14 adults and 2 immature individuals (p3 erupting or unworn). There are also 2 cubs detected by lower milk teeth. In sum, the remains at least of 16 hyenas were recovered in the cave.

Pattern of fragmentation. Geographical Society Cave contains a complete hyena skull, large cranial fragment, and three nearly intact mandibles; at the same time, most cranial and mandibular fragments are fragmented, some represented only by teeth. Intact long bones are absent, short bones are scarce.

All hyena mandibles (excepting ZIN 34490-7) exhibit broken lower margins (in front of the symphysis) (Fig. 3). These mandibles may have been damaged by large carnivores cracking them along the mandibular canal; as a result, tooth roots are frequently exposed in a break (see also Brain 1981; Stiner 1994). Most probably, mandibles were gnawed by other hyenas, and examples of cannibalism or consumption of congener corpses have been recorded in the cave sites of Southern Siberia (Baryshnikov 1999b; Derevianko et al. 2003).

Age composition. Kruuk (1972) defined five age-classes for *C. crocuta*, based on the level of wear of the third lower premolar p3. The collection of p3 from Geographical Society Cave was classified into these categories as follows: I – 2 specimens, II – 6, III – 3, IV – 5, V – 4; total of 20 specimens. Adult animals (age-classes III and IV) constitute less than half of examined sample, and recent populations of hyenas from Serengeti and Ngorongoro in Africa reveal predominance of this age-class (Kruuk 1972). By contrast, the mortality profile in the Serengeti and Ngorongoro is dominated by young and old animals, which is comparable to that of *C. ultima ussurica* in Geographical Society Cave. This suggests the presence of cubs in the cave.

Season of death. The examined collection includes a cub mandible with deciduous cheek teeth and erupting m1 (Fig. 5A). It seems that the latter tooth did not protrude from the gum and the animal had in life only milk teeth. Cubs of the recent *C. crocuta* are known to replace milk teeth with permanent ones at 15 months from birth (Jaarsveld et al. 1987); therefore, the age of the fossil hyena cub may be estimated at about 10–12 months.

In East Africa, cubs of modern *C. crocuta* are born at any time of the year; however, there may be a birth peak in the wet season (Kruuk 1972). In southern Africa, a slight peak of birth is observed at the end of summer, which is a result of slight peak of mating in the beginning of summer, when prey are abundant for spotted hyenas (calving of ungulates) (Lindeque and Skinner 1982).

In the southern part of the Russian Far East, hyenas probably produced offspring at the same time as other large carnivores. The timing varies significantly in various recent species: March to April (glutton); April to May (wolf); April to November (tiger), all the year round, but primarily from March to June (leopard) (Pikunov and Korkishko 1992; Yudin and Yudina 2009; Tumanov and Kozhechkin 2012; Yudin 2013). Most often, carnivore young are born in the spring (especially in glutton and wolf regularly consuming carrion). It appears likely that cubs of *C. ultima ussurica* often were born early in the spring, when hunted prey was supplemented by the carrion obtained from melting snow, which provided females with improved feeding of their young. Mating of fossil hyenas presumably occurred in the late spring or in the beginning of summer (when ungulates are calving). Therefore, the death of the cub whose remains were found in Geographical Society Cave, occurred, most probably, at the end of winter or in early spring.

Representation of skeletal elements. The available collection of fossil remains of hyena from Geographical Society Cave exhibits mostly cranial and mandibular pieces, as well as isolated teeth and their fragments. Postcranial bones are scarce (less 15% of total hyena remains). Similar situation is known for the European cave localities with hyena dens. According to Fosse (1999), this may be explained by that hyenas and their cubs chew bones of perished hyenas in their dens, with only hardest, not attractable as a food, parts of skeleton remaining unutilized.

Surficial damage. Many hyena bones found in the Geographical Society Cave reveal traces of gnawing by large carnivores (most probably by other hyenas). The skull (ZIN 34478) is found to have such traces looking like numerous elongated narrow furrows on its frontal part (Fig. 12A); the sagittal crest is also gnawed. Other signs of gnawing are observed on the radius and tibia fragments (Fig. 12B). These bones might be damaged by hyena cubs. Noteworthy, tooth marks from large carnivores are recorded in many cave sites with presence of *C. crocuta spelaea* there (for example, in Denisova Cave, Dvuglazka Cave, Razboinich'ya Cave; see Turner et al. 2013).

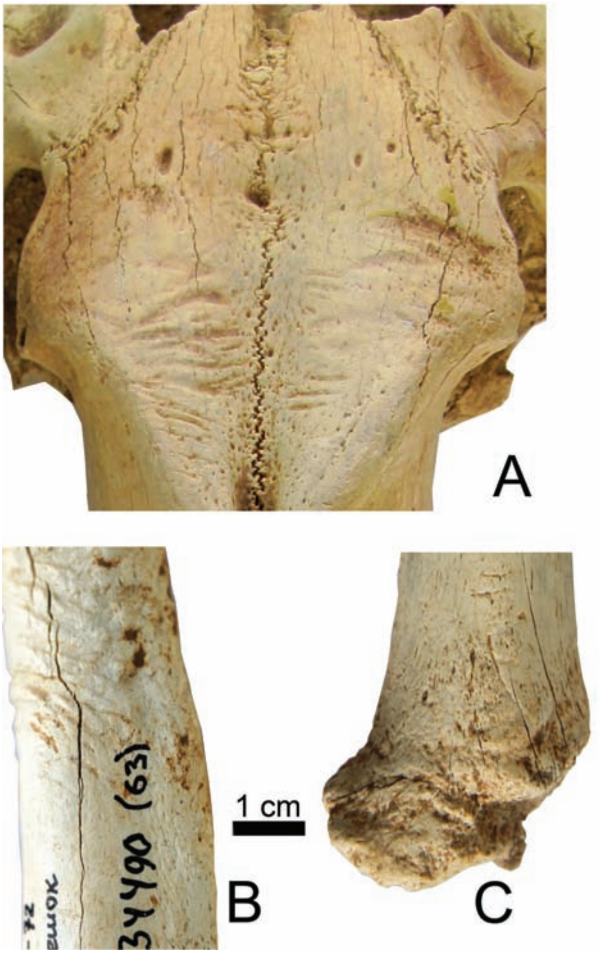

Fig. 12. Tooth marks of carnivores on bones of *Crocuta ultima ussurica* from Geographical Society Cave: A – frontal part of skull (ZIN 34478); B – proximal part of radius (ZIN 34490-63); C – distal part of tibia (ZIN 34490-62).

No cut-marks from the stone tools as well as burnt hyena bones were found in Geographical Society Cave.

Coprolite. There is the coprolite (ZIN 34490-66, collector Leshok, 1972; Fig. 13) in the collection from Geographical Society Cave with the well-defined narrow groove dividing it into two parts resembling a mushroom with a spherical cap and wide and short stem. Presumably this specimen was formed by two fused coprolites. The maximum diameter of the "cap" is 4 cm. The coprolite is formed by dense cemented dejection saturated with bone crumb. Most probably, it may be associated with the hyena, since coprolites

Fig. 13. Coprolite (ZIN 34490-66) of *Crocuta ultima ussurica*.

frequently occur within cave hyena-dens, e.g. in Petralona Cave in Greece, in Razboinich'ya and Denisova Cave in Altai (Baryshnikov and Tsukala 2010, Derevianko et al. 2003, Turner et al. 2013).

Modification of bones of prey. The recent spotted hyenas mostly inhabit open biotopes of Eastern Africa (savanna, steppe), hunting there zebras as well as gnu and other antelopes (Kruuk 1972). Presumably, the Pleistocene hyenas of the Russian Far East also occurred and hunted in steppe and forest-steppe landscapes. Their main prey involved, apparently, large ungulates: horse (*Equus dalianensis* Zhow, Sun, Xu et Li, 1985), bison (*Bison priscus* (Bojanus, 1827)) and deer (*Cervus elaphus/nippon*). Bone remains of these species are common in Geographical Society Cave; according to data by Ovodov (1977), horse constitutes 4.7% of total large mammal remains, bison 4.0% and deer 46%. Long limb bones of horses and bison are broken and longitudinally cleft (Fig. 14). Several fragments reveal the bone substance to be crushed and chewed up by large carnivores, probably by hyenas. Wolf (*Canis lupus* L., 1758), whose fossil remains have been also found in Geographical Society Cave, is characterized by scooping out of cancellous bone tissue and by puncture tooth marks (Fosse et al. 2012); however, it is hard to distinguish hyena tooth marks from wolf tooth marks (tooth pit length produced by hyenas on dense shafts is larger, see Sala et al. 2014). Horse bones with signs of hyena damage are found within the European cave locations of *C. crocuta spelaea*, for example, in Westeregeln and Srbsko Chlum Komin Cave in Czech Republic (Diedrich 2012a, b).

Fig. 14. Horse (A) and bison (B) bones from Geographical Society Cave, crushed and gnawed by large carnivores (presumably, by hyenas).

Interestingly, the bone collection from Geographical Society Cave contains remains of woolly mammoth (*Mammuthus primigenius* (Blumenbach, 1799)) and woolly rhino (*Coelodonta antiquitatis* (Blumenbach, 1799)). These fossils are referred to adult animals (with exception of two teeth of juvenile mammoth) and exhibit tooth marks produced by large carnivores. Traces of gnawing are especially characteristic of the bones of rhino (Fig. 15). The recent African spotted hyenas are able to attack rhino

Fig. 15. Woolly rhino bones from Geographical Society Cave with signs of gnawing by large carnivores (presumably, by hyenas).

females with calves (Kruuk 1972), and the European hyena localities are found to comprise remains of the rhino calves, which might be hunted by *C. crocuta spelaea* (Diedrich 2012a). However, rhino and mammoth bones in Geographical Society Cave were, most probably, accumulated by hyenas as a result of scavenging. Gnawed bones of the woolly rhino have been found in many hyena dens of Western and Eastern Europe as well as in Southern Siberia (Diedrich 2012a, b; Derevianko et al. 2003).

Dens of recent *C. crocuta* are characterized by a presence of bone fragments of the hyena prey, which had initially got to hyena stomachs and then were eructed with other hardly digestible matters (bones, teeth, hair) (Bearder 1977; Brain 1981; Sillero-Zubiri and Gottelli 1992). These bone fragments bear traces of action by digestive juices (bone surface is damaged; teeth are deprived of enamel, etc.). Many signs of the acidic corrosion were found to present in dens of *C. c. spelaea* in grotto Prolom 2 in Crimea and numerous caves in Southern Siberia (Enloe et al. 2000; Derevianko et al. 2003; Turner et al. 2013).

Meantime, similar findings have not been recorded in Geographical Society Cave (with the probable exception for one foal phalanx and one wolf metapodial). Probably, this is not associated with the difference in the feeding behavior between *C. ultima ussurica* and *C. crocuta spelaea*, but can be a result of configuration of the cave cavity. In Geographical Society Cave, the chamber with the hyena den is distanced from the entrance by a long and narrow corridor complicating animals to penetrate deep into the cave; whereas grotto Prolom 2 and Denisova Cave, on the contrary, have wide entrances. These rock shelters have been easily accessible for hyenas.

Summary and discussion. The produced taphonomical analysis revealed a great similarity between the osteological collection from Geographical Society Cave and bone material from the cave sites with dens of *C. crocuta spelaea* in Europe and Southern Siberia. This makes it possible to suggest that Geographical Society Cave has been also a hyena den in the Late Pleistocene.

Signs ascertained this hypothesis seem to be as follows: presence of numerous carnivore remains (including hyena bone fragments), predominance of hyena cranial elements over postcranial parts, presence of juvenile hyena remains, pronounced bone fragmentation (including hyena bones), high frequency of marks left by hyenas (crushed bones, bones with traces of acid corrosion and other hyena food remains), presence of hyena coprolites and gnaw rhino bones (see also Brugal et al. 1997, Fosse 1999).

A peculiarity of bone assemblage in Geographical Society Cave (which differs from those in the European hyena cave-localities) appears to be nearly the absence of bones having been in the hyena stomachs. Another feature of this bone assemblage seems to be an insignificant proportion of the hyena remains there (with regards to the total number of large-animal bones) as well as their more pronounced modification (even the destruction of hard hyena mandibles, which often remain intact in the European caves: see Diedrich 2012a, b).

These taphonomical characteristics of the bone material from Geographical Society Cave provide a possibility to suspect that a group of hyenas inhabiting the cave was rather small, and the cave was active used by hyenas for rearing cubs and for the rest. The recent African spotted hyenas may change their foraging habits depending on the size of clan: large groups of animals actively hunt, whereas small groups prefer scavenging (Beader 1977). Fossil hyenas from Geographical Society Cave might be mainly collectors of carrion.

CONCLUSION

The analysis refers the hyena bones from Geographical Society Cave in the Russian Far East to *Crocuta ultima* originally described from China. Available radiocarbon dates define the time of accumulation of the bone material to the warm interval of Late Pleistocene (MIS 3), when the distribution range of this taxon might be expanded northwards.

The fossil Chinese hyena is generally regarded as a subspecies *C. crocuta ultima*; however, its taxonomic rank should be raised to the species level. The grounds for this seem to be the results of analysis of mtDNA (the taxon belongs to a separate clade whose representatives were not recorded in Europe and Africa) as well as morphological characters (in *C. ultima* the robust mandibles are accompanied with shortened limbs; its check teeth are large with regards to the skull size and accommodated for bone-crushing, whereas the dentition of *C. crocuta spelaea* reveals more carnivorous adaptation). This suggests the evolutionary distinctness of the Chinese hyena and its ecological specialty. *Crocuta ultima* was not so active hunter as *C. crocuta*, but predominantly gathered and consumed carrion.

The common ancestor of *C. crocuta* and *C. ultima* appears to be *C. praespelaea* described from the locality Mosbach in Germany, whose geological age is ascertained as 0.302 Ma (Lister, Brandon 1991). The earliest finding of this species was recorded in Europe in Atapuerca, Spain (0.78 Ma) (Garsia and Arsuaga 2001); an archaic morph of the spotted hyena of similar age (near 0.99 Ma) has been found in Africa in Olorgesailie, Kenya (Werdelin and Lewis 2005). Most probably, *C. praespelaea*, dispersing throughout the steppe zone of Eurasia, has diverged around 0.5 Ma to form *C. ultima* in Eastern Asia and *C. crocuta* in Europe, Western Asia, and Africa.

Similar evolutionary scenario was realized by lions. *Panthera fossilis* (von Reichenau, 1906), spread in Eurasia from Africa near 0.6 Ma, gave rise to two phylogenetic lineages: recent Afro-Asian *P. leo* (L., 1758), and fossil lions, that late divided to Pleistocene Eurasian cave lion *P. spelaea* (Goldfuss, 1810), and Pleistocene North American lion *P. atrox* (Leidy, 1853) (Burger et al. 2004; Barnett et al. 2009).

Crocuta ultima has two chronosubpecies: *C. u. ultima* from the Middle Pleistocene and *C. u. ussurica* from the Late Pleistocene. According to the molecular data, the latter subspecies, which was described on the basis of material from Geographical Society Cave, inhabited the southern part of Russian Far East and northeastern regions of China.

Morphological difference between *C. ultima* and *C. crocuta spelaea* suggests dissimilarities in their feeding and foraging; at the same time, the results of taphonomical analysis reveal no reliable difference between bone assemblages in the hyena caves of Europe and Russian Far East.

Accumulation of the hyena remains in Geographical Society Cave might be substantiated by the death of animals by starvation in winter time as well as was a result of severe battles with large felids, wolves, and hyenas from other clans. Antagonistic actions between the recent *C. crocuta* and lions (*Panthera leo*) are known in Africa (Kruuk 1972); similar actions are also hypothesized for *C. c. spelaea* in Europe (Diedrich 2011).

The distribution range *C. ultima ussurica* apparently did not extend northwards to 43°N (to 52°N for *C.* cf. *ultima* in Transbaikalia); whereas *C. crocuta spelaea* is recorded in Ural Mountains and in Western Siberia up to 56°N (Baryshnikov, Vereshchagin 1996). No hyenas were found in the Late Pleistocene in the northern regions of Eurasia. The probable explanation for this seems to be not the absence of the appropriate prey as think Turner et al. (2013), since horses, red deer, reindeer, and antelope-saiga occurred up to the Arctic coast, but the existence of permafrost. It prevented animals from digging deep holes for saving their cubs, which might become (in the absence or scarcity of rocky shelters) a light prey for lions, wolves, and bears. This hypothesis is confirmed by the fact that the northern border of the hyena distribution range coincides with the southern limit of the Late Pleistocene permafrost in Siberia (see Velichko 2002).

Despite Geographical Society Cave is found to contain some stone artifacts, there is no evidence (such as cut-marks on bones or signs of burning) of utilization of hyenas by ancient hominins. Humans, probably, used the cave only as a short-termed shelter.

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