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Mammuthus primigenius from the Crimea and the Caucasus

Baryshnikov, G., 2003 - *Mammuthus primigenius* from the Crimea and the Caucasus - in: Reumer, J.W.F, De Vos, J. & Mol, D. (eds.) - ADVANCES IN MAMMOTH RESEARCH (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999) - DEINSEA 9: 41-56 [ISSN 0923-9308] Published 24 May 2003

Morphometric characteristics are given for mammoth remains from seven Mousterian sites in the Crimea and Caucasus. Molars possess thick enamel and a low lamellar frequency corresponding to the early *Mammuthus primigenius* in Eastern Europe. This woolly mammoth, together with other thermophilous and mesophilous large mammal species, became extinct in the Crimea and Caucasus at the end of the Mousterian.

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Key words: *Mammuthus primigenius*, teeth, evolution, Caucasus, Crimea, Paleolithic

INTRODUCTION

A major focus of research on *Mammuthus primigenius* (BLUMENBACH, 1799) is the elucidation of its geographical and temporal variation and intraspecific taxonomy. The resolution of these problems lies in the morphometrical analysis of regional samples, such as those from the Crimea and the Caucasus in Eastern Europe. The subject of this paper is the collection of mammoth teeth and bones from Paleolithic sites of the Caucasus and the Crimea (Fig. 1). Although this material is limited in quantity as well as fragmentary, it possesses a geological context. This permits us to identify the morphometric characteristics of *M. primigenius* in this region at the beginning of the Late Pleistocene.

MATERIALS AND METHODS

The collections studied are stored at the Zoological Institute, Russian Academy of Sciences in Saint-Petersburg (ZIN) and in the Archeological Institute, Ukrainian Academy of Sciences in Kiev (AI). They include material from three localities in the Caucasus (ZIN) and four localities in the Crimea (three at ZIN, one at AI). Mammoth molars (n=70), several fragments of tusk, mandibles, vertebrae, and limb bones were examined. Standard techniques for measuring the teeth were used (Garutt & Foronova 1976). Lamellar frequency per 10 cm and average length of one lamella was calculated from the occlusal surface. For tooth fragments, the lamellar frequency per 5 cm was determined and then its value was doubled. Enamel thickness was calculated as a mean of 4-8 measurements for different parts of the crown.

The following abbreviations are used for the limb bones: Bd - breadth of the distal end, Bp - breadth of the proximal end, Dd - depth of the distal end, Dp - depth of the proximal end, GB - greatest breadth, GD - greatest depth, GL - greatest length, and SD - smallest breadth of the diaphysis.

THE CAUCASUS

In the Caucasus region, fossil bones and teeth of *M. primigenius* have been found primarily in areas north of the Greater Caucasus Range (Vereshchagin 1959). These are associated with low river terraces of the Kuban River, Kuma River, and Terek River (Fig. 1). In the Paleolithic of the Northern Caucasus, large assemblages of mammoth remains were recovered from the early Mousterian open-air sites of Ilskaya 1 and Ilskaya 2, situated on the margin of the northern foothills of the Greater Caucasus Range. Several bones were found also from Dakhovskaya Cave, located in the zone of the low mountains.

Ilskaya 1 & 2

These sites are located on the third terrace level of the Il River, roughly 40 km southwest of the Krasnodar. Ilskaya 1 was excavated during 1926-1928 and 1936-1937 and by S. Zamyatnin and V. Gorodzov and during 1963-1969 by N. Praslov. Ilskaya 2 is situated approximately 150 m from the first site, and was excavated by V. Shchelinski during 1981-1991. I participated in the field research in 1982-1988. A total of 55 mammoth bones and teeth were reported to be recovered during the 1926-1937 excavations, but only a few specimens are now present in the collection (Hoffecker *et al.* 1991). A total of 87 mammoth remains were recorded in the upper cultural layers from the 1967-1969 excavations (no mammoth remains were reported in 1963). I have studied nine mammoth teeth from Ilskaya 1: two D4 (ZIN 34848, 34850), two d4 (ZIN 34847, 34849) and m1 (ZIN 19882-12) from the 1926-1937 excavations, and a D3 (ZIN 34851), D4 (ZIN 34854), M1 (ZIN 34852) and M2 (ZIN 34853) from upper layers (horizons 4-7) searched during the 1967-1969 excavations.

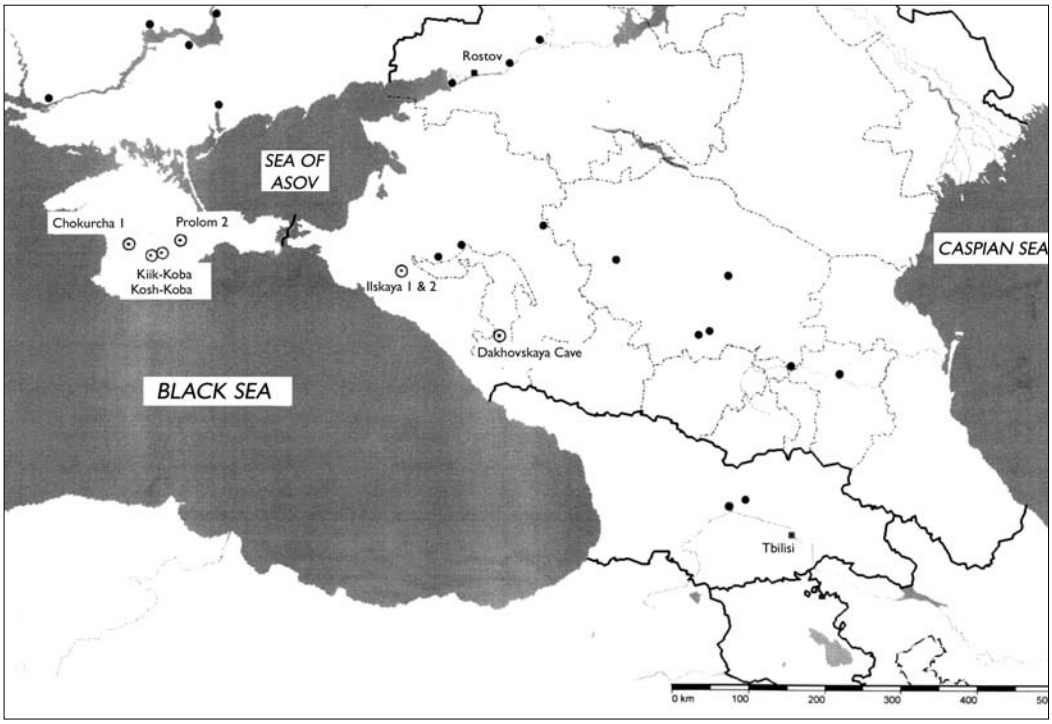

Figure 1 Distribution of woolly mammoth (*Mammuthus primigenius*) (black circles) and studied sites in the Crimea and Caucasus (light circles with black dots).

There is also a radius fragment from horizon 4 recovered during the 1969 excavation.

At Ilskaya 2, mammoth remains were excavated from the third river terrace alluvium, which is dated to the Mikulino (=Eemian) Interglacial (Shchelinski 1985), and also from the overlying colluvial loams. The lower part of the sediments (layers 6-7) is saturated with oil, and thus mammoth remains are well preserved here. In the upper part of deposits (layers 4-5), bones are heavily weathered. At Ilskaya 2, 329 mammoth remains belonging to a minimum of 11 individuals were recorded (Baryshnikov & Hoffecker 1994). In layers 6-7 most bones are intact, but some are broken into smaller fragments. The tusk (ZIN 34860) of an adult female (alveolar diameter of 65 x 73 cm), a complete upper M3, an adult female mandible with left second and third molars (ZIN 34858), vertebrae, and longbone fragments were identified. Most elements of the skeleton are present in layer 5. Bones of the metacarpus and metatarsus occur more frequently than in layer 4. A deciduous tusk (ZIN 34861) exhibits a length of 130 mm and a diameter of 23 x 18 mm, and its apex is sharpened and protrudes 20 mm from the alveolus.

In layer 4 a large concentration of bones was found, including elements of the axial skeleton such as the mandible, tusks, vertebrae, and ribs (often complete), and of the appendicular skeleton such as the scapula, humerus, tibia, calcaneus, and phalanges. Many of the long bones lack epiphyses, the dorsal and ventral ends of ribs and spinous processes of vertebrae are frequently broken. A complete adult mandible (ZIN 34859) with third molars (male), and a small mandible with the second molar (female?) were recovered. One of the tusks (290 mm in length) and a large tibia apparently belonged to a male (Baryshnikov & Hoffecker 1994). Bones from layers 4-5 are heavily mineralized. A majority of them are too heavily weathered for morphometric analysis. Therefore, measurements were taken on the mandible from layer 6 (ZIN 34858), mandible from layer 4 (ZIN 34859), M3 from layer 7 (ZIN 34857), and two d4 (ZIN 34856, 34863), m1 (ZIN 34862), and m2 (ZIN 34855) from layer 4, and on six autopodium bones from layers 4-5.

The composition of the large mammal faunas from both sites is similar and includes the following (Hoffecker *et al*. 1991, Baryshnikov & Hoffecker 1994): *Vulpes vulpes*, *Vulpes corsac*, *Canis lupus*, *Cuon alpinus*, *Ursus spelaeus*, *Crocuta spelaea*, *Equus hydruntinus*, *Equus ferus*, *Megaloceros giganteus*, *Cervus elaphus*, *Bison priscus*, *Saiga tatarica*, and *Capra* sp. Several teeth of *Arvicola terrestris* (L., 1758) were found in layers 5-6 at Ilskaya 2. They are small (M1 L=3.6 mm, M2 L=2.5 mm, m1 W=1.5 mm) and exhibit equal thickness of enamel on the anterior and posterior sides of conid (K=1.0), which is characteristic of *A. terrestris* of Mikulino (= Eemian) age on the Russian Plain (Markova 1986). The left mandible of a horse (ZIN 34864) from layer 5 may be assigned to *Equus ferus taubachensis* REICHENAU, 1915 on the basis of the postflexid index of the p2 (48.8%) and correlation of p2/p3 lengths (109.8%; see Eisenmann 1981). The presence of both these species dates the basal sediment at Ilskaya 2 to the beginning of the Late Pleistocene.

The size of both mammoth mandibles (Table 1) is typical for *M. primigenius* (Averianov *et al*. 1992), and the difference in their dimensions may be attributed to sexual and ontogenetic variation. Measurable limb bones (Table 2) are not common, but are sufficient to indicate that the Ilskaya 1 & 2 mammoths were comparable to a male late *M. primigenius* from the Mokhovaya River on the Taimyr Peninsula (Averianov 1994), but smaller than a male *M. trogontherii* POHLIG, 1885 from Azov on the Lower Don River (Garutt & Baigusheva 1987). The upper and lower molars primarily belong to first generation teeth (Tables 3, 4). Measurements on M3/m3 from Ilskaya 1 & 2

Table 1 Sizes of mandibles of *Mammuthus primigenius* from Iskaya 2.

Measurements, mm	Layer 4 m3, male	Layer 6 m2-3, female
Length from anterior basal symphysis to anterior alveolar border	241	218
Length from anterior basal symphysis to point of anterior insertion of the vertical ramus	346	280
Length of the symphysis	136	115
Depth of horizontal ramus beneath anterior alveolar border	188	190
Depth of horizontal ramus beneath anterior insertion of the vertical ramus	156	132

are similar to those of mammoth in the cold-loving assemblage from the late Mousterian site of Molodova 5 (culture layer 11) on the Dnestr River, which were assigned by Alexeeva (1987: 156) to early *M. primigenius*. However the M3/m3 teeth from Molodova 5 have thinner enamel (1.2-1.6 mm).

Comparison with the mammoth from the Upper Paleolithic sites of Kostenki 1 (layer 1) and Eliseevichi on the Russian Plain (Urbanas 1980) demonstrated that the D3/d3, D4/d4, and M1/m1 from Ilskaya 1 & 2 have slightly thicker enamel, and the M2/m2 and M3/m3 are characterized by fewer lamellae.

Dakhovskaya Cave

This site is located on the left bank of Belaya River near the village of Dakhovskaya, roughly 150 km southeast of the Ilskaya sites. It is situated at an elevation of about 900 m above sea level. A. Formozov excavated it in 1958. At a depth of 5 m from the surface, up to 80 poorly preserved bone fragments were collected together with isolated Mousterian artifacts (Formozov 1965).

Vereshchagin (1959) identified the following taxa from Dakhovskaya Cave: *Lepus europaeus*, *Cricetus cricetus*, *Canis* sp., *Vulpes* sp., *Ursus spelaeus*, *Meles meles*, *Crocuta spelaea*, *Panthera spelaea*, *Felis* cf. *silvestris*, *Elephas* cf. *primigenius*, *Cervus elaphus*, *Megaceros euryceros*, *Bison priscus* and *Capra* cf. *caucasica*. According to Vereshchagin (1959) fourteen mammoth bone fragments were recovered from Dakhovskaya Cave, but the current collection includes only six fragments from one adult individual. Only one very large metatarsal IV is preserved completely. Its dimensions (Table 2: Mtt 4) are considerably larger than those of the male late *M. primigenius* from Mokhovaya River (Averianov 1994).

Transcaucasia

Mammoth remains have not been found in Paleolithic sites of the Transcaucasus, although isolated teeth were recovered from river terraces near Dusheti and Gori in Georgia (Burchak-Abramovich 1946; Gabunia 1952). The Greater Caucasus Range was the southern limit of the distribution of *M. primigenius*, and only rarely did animals overcome this barrier and enter central Transcaucasia. Gabunia (1952) identified an unworn M1 from Gori as the tooth of a dwarf mammoth. According to his description, this molar has 12 lamellae, crown length of 120 mm, crown width of 62 mm, crown height of 140 mm, lamellar frequency of 10, length of one lamella of 6 -7.5 mm, and enamel thickness of 1.5 mm. These measurements are well within the range of molars D4/M1 from Ilskaya 1 & 2, and there is no reason to attribute the tooth from Transcaucasia to a dwarf mammoth.

Table 2 Sizes of limb bones of *Mammuthus primigenius* from Ilskaya 1, Ilskaya 2 and Dakhovskaya Cave in the Caucasus.

Bone	Measurements, mm	Ilskaya 1	Ilskaya 2	Dakhovskaya Cave
Radius	Bp	111		
	Dp	85		
Os intermedium	GL		55, 107	
	GB		94, 157	
	GD		97, 142	
Calcaneus	GL		-, 194	
	GB		146, 156	
Mtt 3	GL		125	
	Bp		63	
	Dp		77	
	SD		54	
	Bd		67	
	Dd		62	
Mtt 4	GL			133
	Bp			75
	Dp			81
	SD			62
	Bd			74
	Dd			78

Caucasus mammoths

On the basis of lamellar frequency and thickness of enamel, the upper and lower molars from layers 6 - 7 at Ilskaya 2 are more derived than the teeth of *M. trogontherii chosaricus* (Dubrovo 1966), and may be assigned to *M. primigenius*. Gromova (1932) identified elephant molars from Ilskaya 1 as belonging to *M. primigenius*, and Vereshchagin (1959: 97) interpreted them as the late mammoth. In a later paleontological analysis (Hoffecker *et al.* 1991), they were assigned to the earlier mammoth and classified as *Mammuthus* cf. *chosaricus*.

The present investigation confirms attribution of the mammoth from Ilskaya 1 & 2 to early *M. primigenius*. The M3 from Girei quarry near Kuban River (Eemian ?), which has a lamellar frequency of 7.5 (calculated from the drawing by Vereshchagin 1959: fig.175, 5a), and the mammoth teeth from the Transcaucasia, may also be assigned to this taxon. The ZIN collections contain two M3s (13897, 34861) from the Northern Caucasus (locality unknown). Their parameters are as follows: length of crown 254, >246 mm; width of crown 110, 109 mm; height of crown 194, 218 mm; number of lamellae >17, >15; lamellar frequency 8, 7; length of one lamella 13.5, 14.5 mm; and thickness of enamel 2.2, 2.1 mm. Both specimens are larger than the molars from Ilskaya 2; the length of one lamella is larger and the enamel thicker than the latter. With respect to the width of crown these teeth are similar to those of *M. trogontherii chosaricus*, but in terms of the

frequency of lamellae, they are more derivative. The teeth resemble those of early *M. primigenius* from Kamensk on the Seversky Donets River on the south Russian Plain, dated to pre-Mousterian time (Baigusheva 1980). Although only several complete M3/m3s were available for my analysis, I classify the Caucasus mammoth as early *M. primigenius* with thick enamel. Two forms appear to be present: an earlier larger form, and a later smaller variant, both of which are included in the Mousterian fauna.

THE CRIMEA

In the Crimea, bone and teeth fragments of *M. primigenius* were found in many Mousterian sites located in the foothills and low mountains: Prolom 2, Zaskalnaya 5 & 6, Krasnaya Balka, Kiik-Koba, Chokurcha 1, Staroselie, Shaitan-Koba and others (Gromova & Gromov 1937, Gromov 1948, Vereshchagin & Baryshnikov 1980, Kolossov et al. 1993, Baryshnikov 1995). Mammoth remains are not abundant in these sites and only at Chokurcha 1 there is a large sample. Mammoth remains were not present in Adzhi-Koba Cave, situated at 900 m above sea level.

Chokurcha 1 Cave

This cave is situated at the east edge of the city of Simferopol on the left bank of the Malyi Salgir River, at an elevation of 8 m above the river level. N. Ernst excavated it during 1928-1931. A Pleistocene yellow loam varies in thickness from 1 m in the cave to 4 m on the adjoining slope. It has been divided into three Mousterian cultural layers (strata 2-4), but strata did not subdivide the faunal remains. Mammoth bones concentrated over an area of 18 m^2 were found on the contact of layers 3 and 4, near the original entrance to the cave (Ernst 1934); they belong to a minimum of 20 individuals. It has been suggested that they represent the remains of an ancient human structure (Liubine 1970).

Accompanying fauna include the following (Vereshchagin & Baryshnikov 1980): *Lepus europaeus*, *Citellus* cf. *pygmaeus*, *Citellus* sp., *Marmota* cf. *bobac*, *Allactaga jaculus*, *Allactagulus* cf. *acontion*, *Lagurus luteus*, *Microtus arvalis*, *Canis lupus*, *Vulpes corsac*, *Ursus arctos*, *Ursus spelaeus*, *Putorius eversmannii*, *Meles meles*, *Crocuta spelaea*, *Equus caballus*, *Equus hydruntinus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *Saiga tatarica*, and *Bison priscus*.

According to N. Vereshchagin, the 1954 collection from Chokurcha 1 contained 3040 mammoth bone and teeth fragments (Vereshchagin & Baryshnikov 1980). I stu-

Table 3 Dimensions of upper cheek teeth of *Mammuthus primigenius* from Ilskaya 1 and 2

Measurements	D3	D4			M1	M2	M3
	n=1	n	range	x	n=1	n=1	n=1
Length of crown (mm)						211	272
Width of crown (mm)	33.5				69	78	82
Height of crown (mm)	34				109	152	181
Number of lamellae							21
Lamellar frequency per 10 cm		2	10,10	-	10	10	8
Average length of one lamella (mm)	7	3	7-11.5	10.0	9.7	10	12.4
Thickness of enamel (mm)	1.2	3	1.0-1.6	1.23	2.0	1.5	1.7

Table 4 Dimensions of lower cheek teeth of *Mammuthus primigenius* from Ilskaya 1 and 2.

Measurements	d4			m1	m2	m3
	n	range	x	n=2	n=2	n=2
Length of crown (mm)	2	114,118	-			>205
Width of crown (mm)	4	50-53	52.0	-,56	73,75.5	88,81.5
Height of crown (mm)	1	74	-	105,81		
Number of lamellae	2	12,12	-	>10		>18
Lamellar frequency per 10 cm	4	10-11	10.5	10,10	10,8	7,8
Average length of one lamella (mm)	4	9-10.5	9.6	10.5,10.3	17,12	12.5,12.4
Thickness of enamel (mm)	4	0.9-1.7	1.20	1.1,1.9	2.1,2.2	2.4,1.8

died 17 upper teeth: 2 D4 (ZIN 29978, 29981), 9 M1 (ZIN 29985, 29989, 29995-29997, 29999, 30001, 30002, 30023), and 4 M2 (ZIN 29982, 29984, 29986, 30000), 2 M3 (ZIN 30024, 30025), and 26 lower teeth: 2 d3 (ZIN 29895, 29896), 8 d4 (ZIN 29894, 29897, 29898, 29974- 29976, 29979, 29980), 3 m1 (ZIN 29988, 29992, 30031), 7 m2 (ZIN 29983, 29987, 30008-30011, 30022), and 6 m3 (ZIN 29998, 30003, 30026, 30027, 30029, 30030). There are also mandible fragments, a second cervical vertebra, and several fragments of limb bones. The molars from Chokurcha 1 (Tables 5, 6), with respect to the length of one lamella and the thickness of enamel, are similar to the samples from Ilskaya 1 & 2. They differ from the M3/m3 from Mousterian layer 11 at Molodova 5 (see Alexeeva 1987) in terms of a wider crown and thicker enamel. Thus, the mammoth from Chokurcha 1 belongs to the early *M. primigenius* with thick enamel on the occlusal surface of the teeth that has been previously mentioned (Foronova & Zudin 1986).

Kiik-Koba Cave

The small cave of Kiik-Koba is situated on the right bank of Zuya River, 25 km east of Simferopol. Its elevation above the modern river is 120 m. It was excavated by G. Bonch-Osmolovski in 1924-1926. The depth of the cave deposits ranges from 0.2 m to 1.5 m. They have been divided into 7 lithological strata and two Mousterian cultural layers. In the lower cultural layer the bones of two Neanderthal individuals were found (Bonch-Osmolovski 1940). Kiik-Koba represents one of the most ancient sites in the Crimea. Its lower layer dates to the last Interglacial (Mikulino = Eemian; Kolossov *et al*. 1993). The upper layer is older than layer 3 of Kabazi 2, which yielded a mean electron spin resonance (ESR) date of 69 thousand years (see Chabai 1998, Rink *et al*. 1998).

Mammoth remains were recovered only from the upper cultural layer. Accompanying fauna from this layer included the following taxa (Gromova & Gromov 1937): *Bos* sp.? (cf. *Bison priscus*), *Ovis* sp.? (cf. *argaloides*), *Saiga tatarica*, *Cervus euryceros*, *Cervus elaphus*, *Rangifer tarandus*, *Sus scrofa*, *Rhinoceros antiquitatis*, *Equus* (*Equus*) *caballus*, *Equus* (*Asinus*) sp.?, *Canis lupus*, *Vulpes vulpes*, *Vulpes lagopus*, *Vulpes corsac*, *Ursus arctos*, *Hyaena spelaea*, *Lepus* sp., *Citellus rufescens*, *Cricetus cricetus*, *Lagurus luteus*, and *Allactaga jaculus*.

A total of 43 mammoth remains belonging to a minimum of three individuals were found at Kiik-Koba (Gromova & Gromov 1937). The distal limb bones in the current collection (ZIN 15952) are relatively small (Table 7), which appears to be a function of sexual dimorphism.

Table 5 Dimensions of upper cheek teeth of *Mammuthus primigenius* from Chokurcha 1.

Measurements	D4	M1			M2			M3
	n=2	n	range	x	n	range	x	n=1
Length of crown (mm)		2	110.5,117.5	-	1	150	-	
Width of crown (mm)	47.5,-	6	59-71	65.0	4	70-85	77.6	114
Height of crown (mm)		5	102-140	128.2	1	150	-	162
Number of lamellae			>10		1	15	-	
Lamellar frequency per 10 cm		7	10-12	10.4	4	9-11	9.9	7
Average length of one lamella (mm)	9.2,9.2	6	8.5-11	9.9	4	9.5-10.5	9.9	14.5
Thickness of enamel (mm)	1.7,2.2	5	1.6-2.2	1.81	4	1.5-2.2	1.97	2.3

Kosh-Koba Cave

This dual-chamber cave is situated 400 m from Kiik-Koba Cave. G. Bonch-Osmolovski excavated it in 1923. In the second chamber there are 4 lithological layers. Layer 3 contained isolated Mousterian stone artifacts and fragmented bones (Kolossov *et al*. 1993). Five mammoth bones from one individual were recovered (Gromova & Gromov 1937). The ZIN collection (15953) contains a d3 and several bone fragments from one adult individual.

Accompanying fauna include (Gromova & Gromov 1937): *Bos* sp.? (cf. *Bison priscus*), *Saiga tatarica*, *Cervus euryceros*, *Cervus elaphus*, *Rangifer tarandus*, *Sus scrofa*, *Rhinoceros antiquitatis*, *Equus* (*Equus*) *caballus*, *Equus* (*Asinus*) sp.?, *Canis lupus*, *Vulpes vulpes*, *Vulpes lagopus*, *Ursus spelaeus*, and *Hyaena spelaea*.

The fragment of the left d3 yielded the following measurements: width of crown 34.5 mm, height of crown 34 mm, length of one lamella 7 mm, and thickness of enamel 1.4 mm. These are similar to measurements on the specimens from Chokurcha 1.

Prolom 2 Cave

This small cave is situated on the left bank of Kuchuk-Karasu River and north of the city of Belogorsk. The elevation above the river is 22 m. It was excavated by Y. Kolossov in 1981-1982 and 1985. I participated in the field research during 1985. Four early Mousterian cultural layers were identified, containing numerous stone tools and large mammal remains (Kolossov *et al*. 1993). The majority of bones were heavily fragmented, but near the rear wall of the cave a concentration of large bone fragments ('kostishche') was encountered in layer 2.

Accompanying fauna include (Eisenmann & Baryshnikov 1994; Baryshnikov 1995): *Lepus europaeus*, *Marmota bobac*, *Allactaga jaculus*, *Ellobius talpinus*, *Lagurus lagurus*, *Eolagurus luteus*, *Cricetus cricetus*, *Microtus* cf. *M. gregalis*, *Microtus* cf. *M. agrestis*, *Microtus arvalis*, *Vulpes corsac*, V*ulpes vulpes*, *Alopex lagopus*, *Canis lupus*, *Spelearctos spelaeus*, *Putorius eversmanni*, *Crocuta spelaea*, *Panthera spelaea*, *Coelodonta antiquitatis*, *Equus* cf. *E. taubachensis*, *E. hydruntinus*, *Rangifer tarandus*, *Megaloceros giganteus*, *Cervus elaphus*, *Procapra* sp., *Bison priscus*, *Bos primigenius*, and *Saiga tatarica*. The composition of the fauna suggests that the sediments are of early Valdai (= early Weichselian) age. Layers 3-4 in Prolom 2 are thought to be contemporaneous to layer 3 at Kabazi 2 (Chabai 1998).

A total of 120 mammoth remains belonging to a minimum of 10 individuals of different

Table 6 Dimensions of lower cheek teeth of *Mammuthus primigenius* from Chokurcha1.

Measure-ments	d3	d4			m1			m2			m3		
	n=2	n	range	x	n	range	x	n	range	x	n	range	x
Length of crown (mm)		2	92,120	-				2	156,180	-	1	240	-
Width of crown (mm)	31,33	8	42-56	50.2	3	56-70	61.2	6	61-76	68.1	3	73-93.5	83.5
Height of crown (mm)	-,23	4	76-88	82	1	100	-	4	100-139	115	3	135-150	140
Number of lamellae		1	10	-					>14			>15	
Lamellar frequency per 10 cm		6	10-12	11.3	3	8-11	9.7	6	9-9	9.0	4	7.5-10	8.9
Average length of one lamella (mm)	7.5,6.5	8	6.5-10	8.8	3	9.5-12	10.4	6	10-12	10.9	4	11-14	11.7
Thickness of enamel (mm)	1.4,1.5	7	1.5-1.8	1.73	3	1.7-2.1	1.86	6	1.7-2.5	1.99	3	2.3-2.5	2.41

ontogenetic stages from prenatal to adult are present. They include the fragment of a mandible, longbones and smaller limb bones: ulnae, capitatum, cuboid, intermedium, and astragalus. All of them, except the mandible, represent adult animals. Measurements (see Table 7) indicate that the bones from Prolom 2 are comparable to those of earlier *M. primigenius*, found near the Kama River in northern Russia (Averianov *et al*. 1992). Most of the remains are of isolated teeth. They are represented primarily by teeth of early ontogenetic substitutions. Fifteen of them have been measured: upper molars: three D3, two D4, two M1, and one M2; lower molars: two d2, one d3, two d4, and two m1.

In layer 3 a deciduous tusk (dI2) was recovered; its length is 62 mm and maximum diameter is 11 mm. In *M. primigenius*, this tusk erupted at the end of the first month of life, and was shed at 11-13 months (Mashchenko 1998). In layer 2 and layer 3, unworn lower d2s with 4 lamellae were found. They possess two roots, which are not yet developed in one specimen. The teeth are smaller than those of a baby mammoth found in permafrost on Yamal Peninsula (ZIN 34201). The latter d2 exhibits a length of 13.9 mm and width of 11.2 mm; the tooth plates are slightly worn. The Yamal baby mammoth perished at an age of about 3 months. I conclude therefore that the young teeth from Prolom 2 belonged to fetal animals; the pregnant female may have died during late winter or early spring. Tooth measurements from Prolom (Table 8, 9) are similar to those from Chokurcha 1, but the enamel in the Prolom 2 specimens is somewhat thinner. In terms of the maximum crown width and enamel thickness, the D3-4/d3-4 from Prolom 2 resemble the teeth from Mousterian layer 11 at Molodova 5 on the Dnestr River (see Alexeeva 1987), but the absence of M3/m3 at Prolom 2 precludes firm conclusions regarding their similarities.

Crimean mammoths

On the basis of the thick enamel, the mammoth teeth from the Crimean sites in the collection (e.g. Kiik-Koba, layer 4, Chokurcha 1) have been provisionally assigned to

Table 7 Sizes of limb bones of *Mammuthus primigenius* from Kiik-Koba and Prolom 2.

Bone	Measurements, mm	Kiik-Koba	Prolom 2
Os carpi ulnare	GL	71	61
	GB	70	-
	GD	112	101
Os capitatum	GL		103
	GB		122
Os intermedium	GL	86	72
	GB	136	119
	GD	126	107
Os pisiforme	Bp	27.5	
	Dp	44	
Mtc 1	Bp	42.6	
	Dp	70	
Astragalus	GL		115
	GB		128
Os cuboideum	GL		44
	GB		101
Mtt 3	Bp	51	
	Dp	63.5	

Elephas (cf.) *trogontherii* (Gromov 1948: 235, Table 11). There is no doubt now that all mammoth remains from the Paleolithic sites of the Crimea belong to the early *M. primigenius*. The Crimean mammoths are very similar to the mammoths from Ilskaya 1 & 2 in the Northern Caucasus, and represent the same stage of evolution of the species during the early Late Pleistocene in the southern part of Eastern Europe.

DISCUSSION

For the woolly mammoth of Eastern Europe and Siberia, two stratigraphically successive forms have been identified: early *M. primigenius* (Saalian and Eemian) and later *M. primigenius* (Weichselian). The two forms are differentiated by the transformation of the dentition (Gromov 1948; Vangengeim 1961; Alexeeva 1980, 1990), and their classification is based on M3/m3 (see Gromov & Garutt 1975: 459). In Eastern Europe, the early mammoth was present from the Odintsovo Interglacial (= Treene) to the early Valdai (= early Weichselian). The temporal boundary between earlier and later *M. primigenius* coincides with the end of the Mousterian (Alexeeva 1980). These stages have not been formalised, because the proposed name for the early mammoth subspecies *M. primigenius pavlowae* (Gromov 1961) is a nomen nudum. This name has not been assigned to a particular specimen, but only to a stage of dental transformation, which is contrary to the rules of zoological nomenclature (see Averianov *et al*. 1992: 73).

On the basis of lamellar frequency and enamel thickness in M3/m3, mammoths from the Mousterian sites in the Northern Caucasus (Ilskaya 2) and Crimea (Chokurcha 1) can clearly be distinguished from mammoths of Upper Paleolithic sites in Eastern Europe

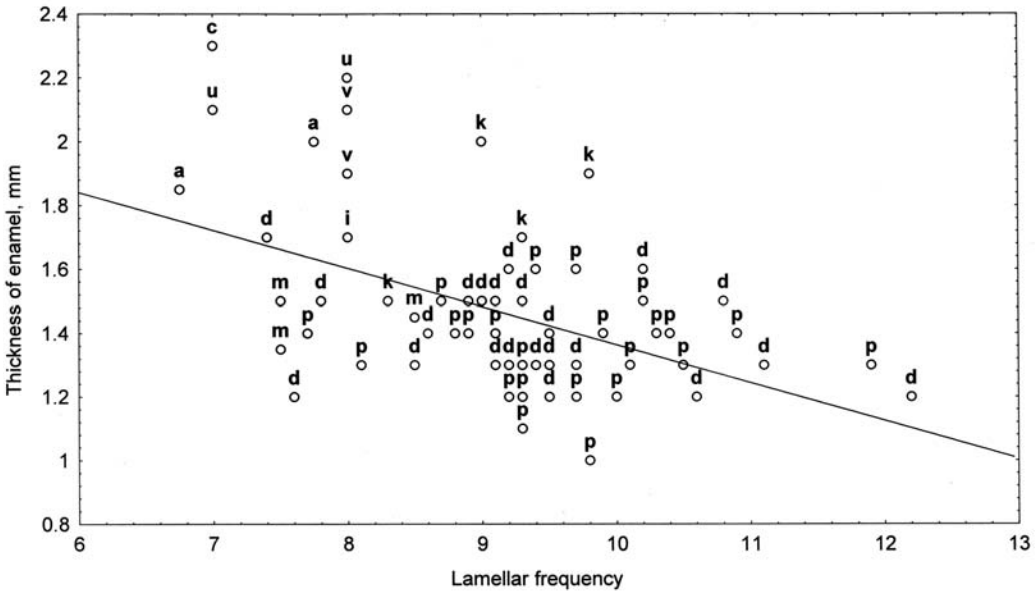

Figure 2 Diagram plotting relationships between enamel thickness and lamellar frequency of the third upper molar M3 in *Mammuthus primigenius* of Eastern Europe. **a** - Kamensk (after Baigusheva 1980) **c** - Chokurcha 1 **d** - Dolne Vestonice **i** - Ilskaya 2 **k** - Kostenki **m** - Molodova 5 (after Alexeeva 1987) **n** - neotype of *M. primigenius* **p** - Przhedmosti **s** - Mysy (after Averianov *et al.* 1992) **u** - Northern Caucasus, localities unknown **v** - Kamskoe Ustie (after Averianov *et al.* 1992).

(e.g., Kostenki, Dolni Vestonice, and Przhedmosti) and also from the neotype of *M. primigenius* (Fig. 2, 3). It is interesting to note that there is a wide range of morphometric values in the larger samples from these sites. The studied samples in Figures 2 and 3 comprise two groups. The first (earlier *M. primigenius*) includes the molars from Ilskaya 2, Chokurcha 1, Northern Caucasus (localities unknown), Kamensk on the Seversky Donets, and Kamskoe Ustie on the Kama River. The second group (late *M. primigenius*) includes the specimens from Dolni Vestonice and Przhedmosti in the Czech Republic, and from the neotype of *M. primigenius*. The samples from the late Mousterian site of Molodova 5 on the Dnestr River and the early Upper Paleolithic sites at Kostenki on the Middle Don River occupy a transitional position. Molars from Molodova 5 display thin enamel and lower lamellar frequency, while molars from Kostenki possess thicker enamel and higher lamellar frequency.

Foronova & Zudin (1986) proposed the original approach for studying molar evolution in the *Archidiskodon-Mammuthus* lineage from Northern Eurasia. They distinguished several successive stages of phenotype stabilisation associated with mammoth dental specialisations. For *M. primigenius* from Europe, together with the main succession (clusters E11, E5), stages of stabilisation that are characteristic of mammoths with thick enamel (E9, E6) and with thin enamel (E8, E7) were identified (see Foronova & Zudin 1986: fig.1). Cluster E11 follows cluster E12, including the holotype of *M. trogontherii chosaricus* DUBROVO, 1966. Using the Foronova & Zudin approach, I observed the following distribution for the samples from Eastern Europe: E11 (Kamensk and Northern Caucasus, unknown localities), E9 (Ilskaya 1 & 2, Chokurcha 1 and Kamskoe Ustie), E8 (Molodova 5 and Mysy), and E5 (Dolni Vestonice, Przhedmosti and the neotype of *M. primigenius*). Molars from Kostenki fell near clusters E9 and E8. Lower m3 from Weimar-Ehringsdorf in Germany (Gromov & Garutt

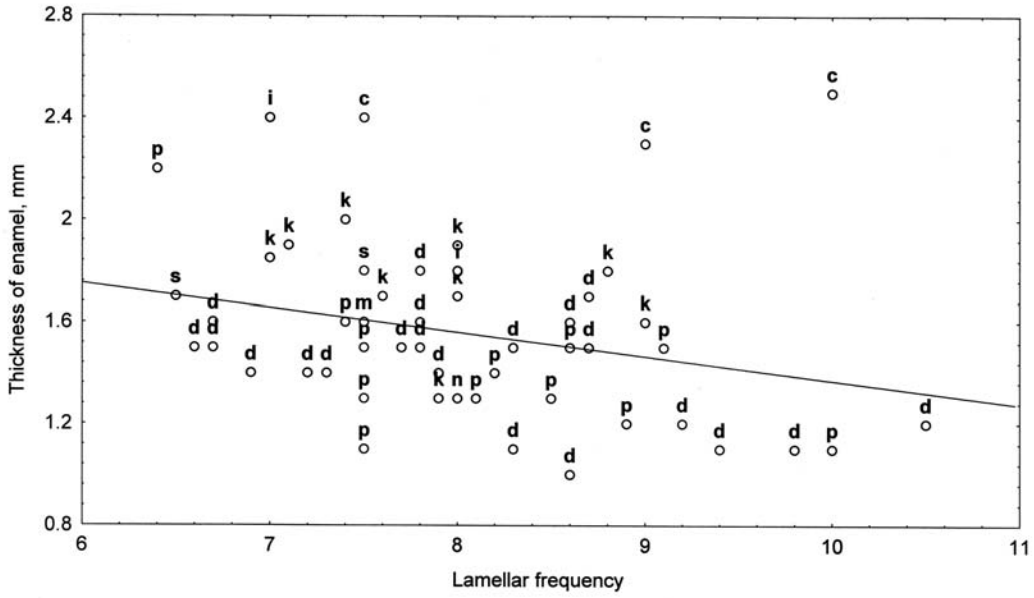

Figure 3 Diagram plotting relationships between enamel thickness and lamellar frequency of the third lower molar m3 in *Mammuthus primigenius* of Eastern Europe. Lettering as in Figure 2.

1975) were placed in cluster E11. Specimens from Berelekh River in Northeastern Siberia (ZIN 30957) may be assigned to cluster E2, other examples of which I have not found in the specimens studied from Eastern Europe. The teeth from Berelekh possess very high lamellar frequencies, which can be entirely accounted for in terms of their small size (Lister & Joysey 1992).

Thus, variation in *M. primigenius* enamel thickness is observed during its evolution. Thicker enamel may have been related to a diet of softer food, which was characteristic for mammoths living in the warm intervals of the Pleistocene and in the southern regions (e.g., Ilskaya 1 & 2, Chokurcha 1). Thinner enamel is associated with a 'periglacial specialisation' entailing increased chewing function for mastication of rough grass (Foronova & Zudin 1986: 25, 27).

CONCLUSION

Palaeozoologists have often discussed the problem of the broad geographic and stratigraphic variability of *M. primigenius* and its complex intraspecific taxonomy (Baigusheva 1980; Lister 1996). Woolly mammoth was apparently distinguished by wide mobility of family groups and extended seasonal migrations (Mashchenko 1998). Therefore, the distributional ranges of intraspecific taxa were very large, although morphological isolation of local populations also occurred, for example on Wrangel Island (Garutt *et al*. 1993).

Recognition of the intraspecific structure of *M. primigenius* was possible after the designation of its neotype (Garutt *et al*. 1990) and analysis of the stages of transformation of its dentition (Foronova & Zudin 1986). During the past 200 years, several dozen names have been proposed for fossil elephants that have now become synonymies of *M. primigenius*. Thus, it is necessary to carry out a taxonomic revision for woolly mammoth. For Eastern Europe, at least two chronosubspecies (early mammoth and late mammoth) may be identified. The distributional range of late mammoth (*M. primigenius primigenius*) included Europe and Western and Eastern Siberia during the late Weichselian (=

Table 8 Dimensions of upper cheek teeth of *Mammuthus primigenius* from the Prolom 2

Measurements	D3			D4	M1	M2
	n	range	x	n=2	n=2	n=1
Length of crown (mm)	1	57.5	-		111, -	
Width of crown (mm)	3	24-38	29.3	44.5,48	53,68	
Height of crown (mm)	1	46	-	-, 70	72, -	148
Number of lamellae	1	6	-		11, -	
Lamellar frequency per 10 cm	1	12	-	10,11	11, -	
Average length of one lamella (mm)	3	6.5-7.5	7.0	8,7	9,8	12
Thickness of enamel (mm)	3	1.1-1.2	1.15	1.4,1.5	1.4,2.0	1.3

Table 9 Dimensions of lower cheek teeth of *Mammuthus primigenius* from the Prolom 2

Measurements	d2	d3	d4	m1
	n=2	n=1	n=2	n=2
Length of crown (mm)	12.2,12.5		108, -	
Width of crown (mm)	10.3,10.0	32	45.5,45	45, -
Height of crown (mm)	15.0,13.o		63,72	63, -
Number of lamellae	4,4		14, -	
Lamellar frequency per 10 cm			11,12	12, -
Average length of one lamella (mm)	3.0,3.1	8	7.5,7	8,7
Thickness of enamel (mm)	0.5,0.6	1.2	1.1,1.1	1.6,1.5

late Valdai, Sartan; see Averianov *et al*. 1995).

The other chronosubspecies (early mammoth) included the populations of *M. primigenius* from the Saalian and the Eemian. Several names were proposed for these, such as '*Elephas*' *intermedius* JOURDAN, 1861 for remains from loess deposits near Lyon in France, and *M. primigenius fraasi* DIETRICH, 1912 for the Saalian skeleton from Steinheim in Germany (Lister 1996: 210, 211). Molars of both type specimens exhibit thin enamel and belong to clusters E8 and E7, respectively (Foronova & Zudin 1986: fig.1). As mentioned above, enamel thickness probably changed in response to environmental and dietary shifts. Therefore, the mammoths with thick enamel from Kamensk (cluster E11) and the Mousterian sites of the Crimea and Caucasus (cluster E9) also may be included in the 'intermedius/fraasi' group. *M. primigenius* is absent from Upper Paleolithic sites of the Caucasus and Crimea. At that time it probably had become locally extinct, and the southern boundary of its distributional range shifted to the north. Along with mammoth, other large mammals of the Mousterian fauna disappeared, including *Crocuta spelaea*, *Coelodonta antiquitatis*, *Equus ferus taubachensis*, and *Megaloceros giganteus*.

The regional extinction of the woolly mammoth may be related to the Mousterian population that inhabited the Caucasus and Crimea. The local Mousterian population continued to occupy these areas through the middle of the Last Glacial, probably because of milder climates and a relative abundance of plant foods. The deterioration of climates in the second half of the Late Pleistocene (late Weichselian) led to the disappearance of thermophilous and mesophilous large mammal species in the Crimea and Northern

Caucasus. At the same time, the increased aridity of the steppe zone in the south Russian Plain most likely prevented northern mammoths from extending their range into the Caucasus and Crimea.

ACKNOWLEDGEMENTS

I am grateful to the archaeologists prof. V. Shchelinski and prof. N. Praslov (Institute for the History of Material Culture, Russian Academy of Sciences, St. Petersburg) and prof. Y. Kolossov (Archaeological Institute, Ukrainian Academy of Sciences, Kiev) for their invitation to study mammoth collections. The molar measurements from Kostenki, Dolni Vestonice, and Przhedmosti, and on the neotype of *M. primigenius*, were kindly provided by dr A. Averianov and the late dr V. Garutt (ZIN). During my study, I was assisted by prof. N. Vereshchagin, dr A. Averianov, O. Potapova, dr A. Kasparov, dr Svetlana Baryshnikova (ZIN), and dr V. Stepanchuk (AI). I am grateful to dr J. Hoffecker (University of Colorado, USA) for editing the English text. My special thanks to dr J.W.F. Reumer and mr Dick Mol for the opportunity to participate in the 2nd International Mammoth Conference in Rotterdam, the Netherlands.

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received 18 May 1999

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM
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