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The Sevsk woolly mammoth (*Mammuthus primigenius*) site in Russia: Taphonomic, biological and behavioral interpretations

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Abstract

Excavations at Sevsk, Bryansk Region, Russia, by the Paleontological Institute of the Russian Academy of Sciences in 1988–1991 recovered 3800 bones of woolly mammoth (*Mammuthus primigenius* Blum.) representing a minimum of 33 individuals. The locality is one of the largest naturally occurring deposits of mammoth remains in Europe and is inferred to be a catastrophic death assemblage. The material includes five skeletons of juvenile mammoths, from 1 month to 6 or 7 years of age, as well as partial skeletons and isolated bones of adult individuals. A femur and humerus of an approximately 10–12-month-old fetus are also among the finds. Morphological features suggest that the Sevsk mammoths belonged to one family group; the age structure and sexual composition of the assemblage do not differ significantly from that of a family group of Modern African elephants. In contrast to other localities in Siberia and central Russia, relatively more (about 45% of individuals) prepubertal animals are preserved at Sevsk. Radiocarbon dates indicate that the mammoths died about 14,000 years ago. Data from diatoms, pollen and rodents, as well as archeological evidence, corroborate this age, and provide the basis for a paleoenvironmental reconstruction at the end of the Valdaian Glaciation in western Russia.

1. Introduction

Remains of the woolly mammoth, *Mammuthus primigenius*, are common in late Pleistocene sediments of the Russian Plain. The locality reported here, near Sevsk (Bryansk Region, Russia) (Fig. 1A), differs from other large localities in Russia and elsewhere in Europe in representing a natural, catastrophic accumulation of mammoth remains, permitting us to reconstruct the environment, mode of life, and cause of death of a mammoth herd that inhabited this region at the end of the Pleistocene. Detailed studies of pollen, diatoms and small mammals were significant in this analysis. The results indicate a specific taphonomic setting that allows us to document for the first time a family group within a population of *M. primigenius*.

The bone bed was discovered in the summer of 1988 during excavations in a sand quarry near the town of Sevsk. The remains were concentrated in a small area, where a local company was mining sand for municipal road construction. The fossil discovery was reported to the Paleontological Institute by engineer S.N. Seregin. Before the team from the Paleontological Institute began work at the locality, about 500 m^2 of the bone-bearing sand had been removed by the quarrying operation. Commercial operations at the quarry halted in 1991 but have since been resumed.

The quarry is exposed in the terrace on the east side of a 1.5 km long ravine running parallel to the Sev River valley. The ravine is obviously part of the late Pleistocene Sev River channel. The terrace, including the fossil locality, forms a sort of peninsula, previously

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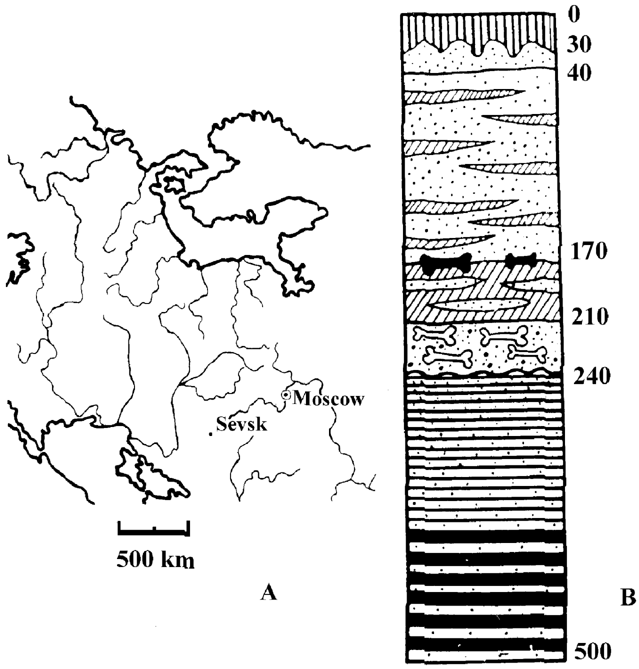

Fig. 1. (A) Location of Sevsk (Bryansk region), Russia. Scale bar equals 500 km. (B) Stratigraphic section of the Sevsk quarry (cm). Apparent thickness of the alluvial deposits is about 5 m; buried soils are absent (Lavrov, 1992; Maschenko, 1992). 0–30 cm—modern soil. 30–40 cm—yellow-gray, fine-grained sand. 40–170 cm—alternation of the yellow-brown sands and dark-brown clay (thickness of interbeds is 3–7 cm). 170–210 cm—dark-brown clay with yellow sand interbeds (thickness up to 0.2–0.5 cm). Upper bone-bearing layer. 210–240 cm—light-gray, medium-grained sands. Main bone-bearing layer. Granite-gneiss cobbles and boulders up to 30 cm in diameter occur on boundary with the underlying layer. These are probably moraine traces. 240–500 cm—gray, fine-grained sand of alluvial deposits, the top of the layer bears traces of erosion and has cryogenic interruptions of bedding.

eroded by the river on the west side, when it formed the ravine, and now eroded on the east side by the present-day river. The present-day Sev River channel is several hundred meters from the quarry, and the locality occurs about 6 m above the present water level. During the past 50 years, the base level of the Sev River has dropped 1.0–1.5 m, and the river is eroding sediments deposited in recent time. Before the commercial operations at the quarry began, the terrace deposits were not exposed.

2. Stratigraphy and age of the site

The bone-bearing deposits consist of alluvial sands and clay (Fig. 1B). The thickness of the section exposed during commercial quarrying is about 5 m (Lavrov, 1992; Maschenko, 1992, 2002). The base of the section lacks vertebrate remains. Higher in the section, alluvial sands, occurring up to a depth of 240 cm beneath the present-day surface, are replaced by alluvial sands of cut-off origin that contain most of the bone material (up to a depth of 210 cm). This 240–210 cm depth interval thus represents the main, lower bone-bearing layer. Clay with interbedded sand occur above this, from 210 to 170 cm depth. This clay and sand stratum represents the upper bone-bearing layer. Alternating beds of sand and clay occur from 170 to 40 cm. Fine-grained sands comprise the 40–30 cm bed, which is overlaid by modern soil. All lithologic units of the section, except the modern soil, were formed as separate alluviations.

At the base of the main bone-bearing layer, there is a concentration of granite-gneiss rocks ranging in diameter from >0.5 to 30 cm and interpreted as moraine deposits. The lower boundary of the bone-bearing layer is irregular, with dips and local depressions on the erosional surface of the underlying bed. The top of the lowermost alluvial deposits in one area of the outcrop exhibits cryogenic disturbances connected with ancient frost processes.

The two strata containing mammoth remains dip toward the central axis of the bone-bearing lens (Fig. 2A, B). The bone-bearing layers reach their maximum thickness in the central part of the lens and then thin peripherally to no more than 5 cm (Fig. 2A). The radiocarbon age (GIN [Geochronological Laboratory, Geological Institute of the Russian Academy of Sciences] 5778) of the mammoth bones from the main bone-bearing layer (240–210 cm depth) is $13{,}950 \pm 70$ years BP. A tusk from the top of the bone-bearing layer (210–170 cm below surface) has been radiocarbon dated at $13{,}680 \pm 60$ years BP (GIN 6209).

3. Analysis of the diatom flora

Diatom species change appreciably through the section. Fifty-eight species belonging to 18 genera of the classes Centrophyceae and Pennatophyceae were identified. *Eunotia*, *Pinnularia*, *Cymbella*, and *Gomphonema* are the most diverse genera. All forms are relatively rare (the occurrence is 1–10 frustules per slide) (Fig. 3).

The diatoms are subdivided into two main ecological groups: planktonic and benthic. There are three planktonic species (5.3% of total species richness); *Aulacosira italica* (Ehr.) Kütz., *Stephanodiscus minutulus* (Kütz.) Cleve and Möller, and *Tabellaria fenestrata* (Lyngb.) Kütz. These occur throughout the section, but are predominant below the bone-bearing layer. Bottom forms, 25 taxa in nine genera, represent 43.9% of the total species. The genus *Pinnularia* is most diverse. *Navicula*, *Caloneis*, and *Nitzschia* occur only in the lowermost part of the section, below 450 cm.

Epiphytes are represented by six genera (29 species; 50.9% of the total number of species). *Eunotia* occurs throughout the section, but is most numerous in the

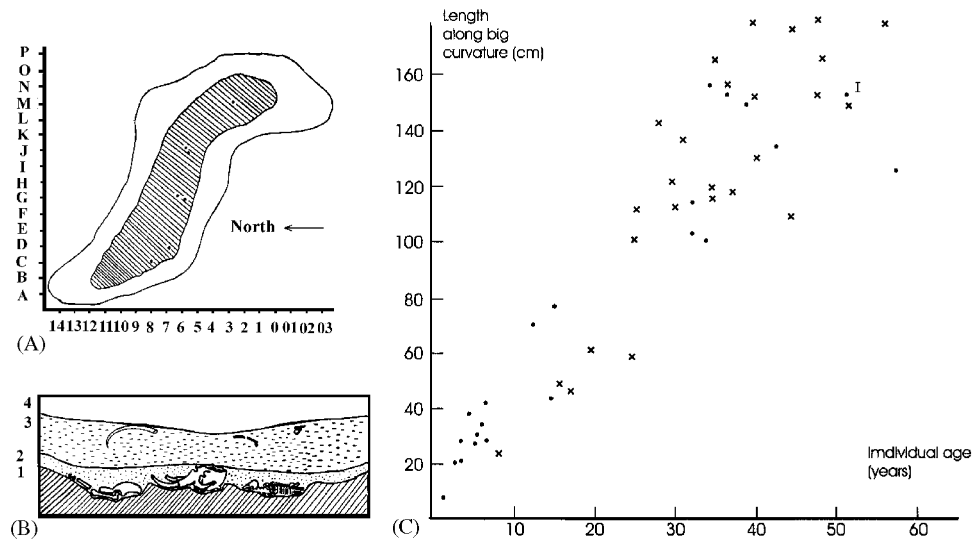

Fig. 2. Distribution of bones in the Sevsk locality and size composition of the female mammoth tusks from Sevsk and Berelekh, Siberia (Vereshchagin and Tikhonov, 1986). (A) Vertical axis: letter symbols of the quadrants in the excavation; horizontal axis: numerical symbols of the quadrants. Size of each quadrant is 2 × 2 m. A straight line demonstrates the total area of the bone-bearing lens. The outer solid line represents the total area of the bone-bearing lens. The hatched central area is the maximum concentration of bones in the lens. Dots indicate the location of the complete skeletons of young animals and partial skeletons of adults. (B) vertical profile of excavation (boundary of the quadrants Ж 7, Ж 6): 1—alluvial sand deposits underlying the bone-bearing lens; 2—lower bone-bearing layer (240–210 cm in the section; Fig. 1) includes well-preserved bones, skeletons and skeletal fragments. The bones of this layer are shown: a female skull with disarticulated parietal bones (probably the skull vertex may have protruded up into layer number 3 above, and broken off), the skeleton of the 1-year-old baby mammoth in the microrelief depression behind the skull, and a female hind limb with half-pelvis; 3—the upper part of the bone-bearing layer with isolated bones does not contain any complete skeletons or skeletal fragments (210–170 cm in the section; Fig. 2); 4—deposits overlaying the bone-bearing layer. (C) Size comparison of female mammoth tusks from Sevsk and Berelekh, Siberia. Vertical axis—the length on the outside curvature of a tusk; horizontal axis—the age of the animals (years). 1—Sevsk ($n = 14$); 2—Berelekh ($n = 23$).

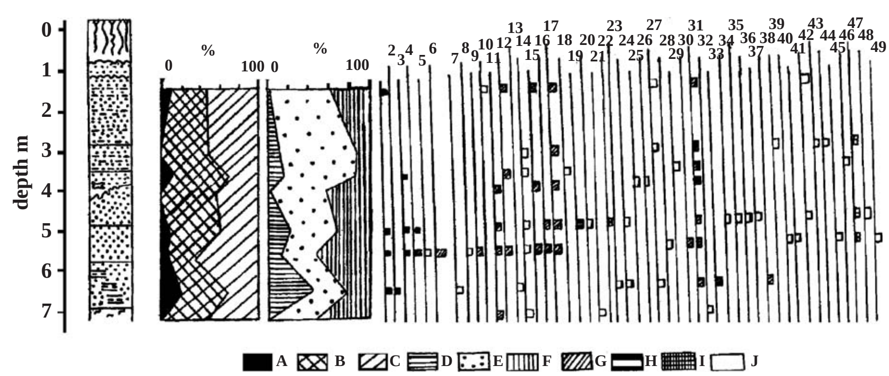

Fig. 3. Diagram showing distribution of diatoms in the Sevsk locality section. (A) plankton; (B) benthos; (C) epiphytes; (D) cold species; (E) boreal species; (F) ubiquitous species; (G) swamp and lacustrine-swamp species; (H) river species; (I) soil-dwelling species; (J) other benthos. 1—*Aulacosira italica* (Kütz.) Simonsen; 2—*Stephanodiscus minutulus* (Kütz.) Cleve and Mueller; 3—*Tabellaria fenestrata* (Lyngb.) Kütz.; 4—*T. flocculosa* (Roth.) Kütz.; 5—*Diatoma anceps* (Ehr.) Kirchn.; 6—*Fragilaria construens* var. *venter* (Ehr.) Grun.; 7—Fragilaria sp. 8—*Synedra ulna* (Nitzsch.) Ehr.; 9—*Eunotia faba* (Ehr.) Grun.; 10—*E. gracilis* (Ehr.) Rabenh.; 11—*E. lunaris* (Ehr.) Grun. et var.; 12—*E. monodon* Ehr. and var. *major* (W. Sm.) Hust.; 13—*E. parallela* Ehr.; 14—*E. pectinalis* var. *minor* (Kütz.) Rabenh.; 15—*E. praerupta* Ehr. and var.; 16—*E. sudetica* O. Müll.; 17—*Diploneis ovalis* (Hilse) Cl.; 18—*Stauroneis anceps* Ehr.; 19—*Navicula cryptocephala* Kütz.; 20—*N. seminulum* Grun.; 21—*Navicula* sp.; 22—*Pinnularia borealis* Ehr.; 23—*P. divergentissima* (Grun.) Cl.; 24—*P. gibba* Ehr. and var. *linearis* Hust.; 25—*P. major* (Kütz.) Cl.; 26—*P. mesolepta* var. *angustata* Cl.; 27—*P. microstauron* (Ehr.) Cl.; 28—P. savanensis Boye P.; 29—*P. spitzbergensis* Cl.; 30—*P. subcapitata* Greg.; 31—*P. viridis* (Nitz.) Ehr. et var. *intermedia* Cl.; 32—*Pinnularia* sp.; 33—*Neidium bisulcatum* (Lagerst) Cl.; 34—*Caloneis schumaniana* var. *biconstricta* Grun.; 35—*C. silicula* var. truncatula Grun.; 36—*Cymbella amphioxys* (Kütz.) Grun.; 37—*C. angustata* (W. Sm.) Cl.; 38—C. aspera (Ehr.) Cl.; 39—*C. heteropleura* var. *minor* Cl.; 40—*C. leptoceras* (Ehr.) Grun.; 41—*C. ventricosa* Kütz.; 42—*Gomphonema acuminatum* Ehr.; 43—*G. angustatum* var. *undulatum* Grun.; 44—*G. longiceps* var. *subclavatum* Grun.; 45—*G. parvulum* (Kütz.) Grun. and var. *lagenulum* (Kütz., Grun.) Hust.; 46—*Rhopalodia* sp.; 47—*Hantzschia amphioxys* (Ehr.) Grun.; 48—*Nitzschia palea* (Kütz.) W. Sm.; 49—*N. paleacea* Grun.

lower bone-bearing layer (Gablina, 1995). Among the swamp and lacustrine-swamp forms, *Tabellaria flocculosa* (Roth.) Kütz. and *Fragilaria construens* var. *venter* (Ehr.) Grun. dominate. Acidophilous species predominate in the lower bone-bearing layer.

Overall, cosmopolitan species make up 39.5%, boreal species 39.6%, and northern-alpine species 20.8% of the total types of diatoms in the section. The percentage of cryophilic elements is quite high for the temperate zone (Jousé, 1939). Cryophilic species decrease up the section.

The diatom complex below the bone-bearing layer suggests a shallow-water basin with a flow indicative of flood-plain conditions, in agreement with the lithological composition of the sediments (Fig. 1B). The low abundance of planktonic species, the high abundance of benthic and epiphytic forms, and the presence of rheophilous and soil-dwelling elements are typical characteristics of flood-plain conditions (Khursevich and Loginova, 1980). The relatively high number of swamp forms in this part of section suggests the swamping of the flood-plain.

Further overgrowing of the flood-plain was probably combined with its partial desiccation. Changes in both the lithological composition and the diatom assemblage of the bone-bearing layer, compared with the underlying beds, indicate the formation of a swampy, shallow-water distrophic basin with acid pH. The diatom assemblages from the deposits overlying the bone-bearing lens support the features of a distrophic basin. The relatively high number of north-alpine elements in the bone-bearing layer and underlying sediments suggests that the climate was colder than at present.

4. Palynology of the Sevsk locality

The palynological data are correlated with absolute dates from the locality. Pollen spectra are best represented for the bone-bearing layer and overlying strata (Fig. 4). Pollen of tree-shrubs (up to 53%) are predominant through the section. *Pinus silvestris* and *Pinus sibirica* (up to 94%) are most abundant. Pollen of *Betula pubescens* and *B. nana* is scarce. Pollen of other coniferous (*Larix*, *Abies*) and broad-leaved species (*Alnus*, *Quercus*, and *Fraxinus*) are represented by single grains. Compositae (up to 27%) and Poaceae (up to 21%) pollen dominant the herbaceous plants assemblage. Chenopodiaceae, Ericales, *Ephedra*, and Polygonaceae are also abundant. Spores are sparse; there are a few poorly preserved grains of *Botrychium*, *Lycopodium*, and Bryales.

Taiga species of both eastern Europe and western Siberia (*Larix*, *Picea*, *Abies*, *P. silvestris*, *P. sibirica*), subarctic species (*Betula nana*), and boreal-thermophilic species (*Quercus*, *Alnus*, *Fraxinus*) occur together in the locality. There is no analog for this vegetational assemblage in the modern flora. The center of maximum sympatric concentration of the species from the Sevsk locality lies hundreds of kilometers to the northeast of the study area. The Sevsk plant assemblage best correlates with the vegetation typical of the Late Pleistocene Interstadial (Grichuk, 1966, 1991; Grichuk and Zalikson, 1982). The presence of *Ephedra* and Chenopodiaceae suggests the Late Valdai Interstadial. Apparently, there was a predominance of a periglacial-steppe vegetation at the locality. The landscapes of meadow steppe in combination with pine-birch, and spruce forests with a small participation of broad-leaved species were widespread in the region. The radiocarbon data for Sevsk permit correlation of the vegetation with the Bolling Interstadial.

The Sevsk data are comparable with those from many localities in the Don River Basin (Spiridonova, 1991). Vegetation with a predominance of spruce-pine and broad-leaved forests and widespread meadow-steppe was identified there. The radiocarbon dates from that locality are $12,310 \pm 80$ (GIN 3161) and $12,350 \pm 50$ years BP (GIN 3160), and are immediately overlaid by Older Dryas sediments.

5. Analysis of the Sevsk microvertebrates

About 30 specimens of rodents were found by washing 500 kg of sediments from the main bone-bearing layer at Sevsk. Ten specimens of *Lagurus lagurus* (Pall.) and one specimen of *Microtus gregalis* (Pall.) were identified. Two other specimens identified as *Microtus* sp. probably belong to the same species.

Neither *L. lagurus* nor *M. gregalis* occurs in the modern fauna of the Bryansk region. The former presence of these species at Sevsk indicates that they were common in the small mammal fauna at the time of formation of the bone-bearing deposits. Elsewhere both species are widely represented in the late Pleistocene periglacial tundra-steppe faunas or in the mixed faunas of the region.

Both species were numerous in the areas adjacent to the Desna River Basin in northern Ukraine (Rekovets, 1988). Farther westward in Byelorussia and Poland, north of the Carpathian Mountains, *L. lagurus* is extremely rare in the late Pleistocene fauna, while *M. gregalis* was one of the dominant species (Kalinovskiy, 1983; Nadachowski, 1989). The latter is also abundant at the end of the late Pleistocene in the south and north of Germany (Storch, 1992).

The disappearance of *M. gregalis* from the small mammal fauna occurred due to climatic warming and afforestation of its territory. This process is noticeable in the Danube Basin (southern Germany) at the end of the Younger Dryas, about 10,000 years ago; in northern Germany it happened somewhat earlier, at the end of

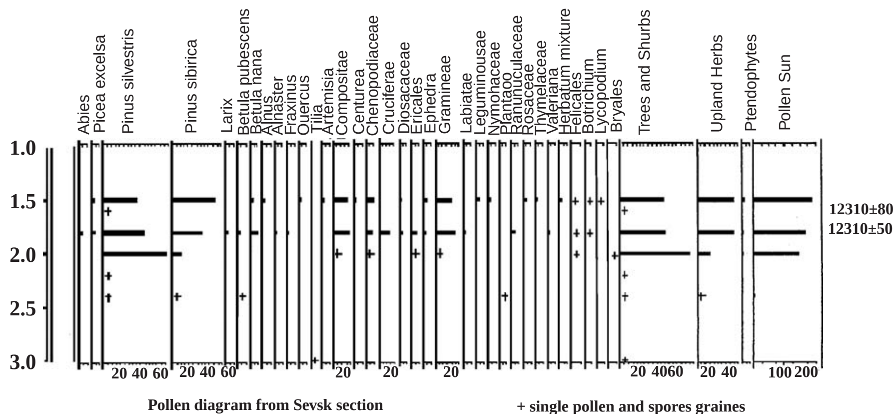

Fig. 4. Pollen diagram from the sevsk section (%).

the Allerød, about 11,000 years ago (Storch, 1992). *M. gregalis* was rare in Poland at the beginning of the Holocene, and appeared for the last time in the subboreal zone about 4000 years ago. *L. lagurus* disappeared in Poland during the late Vislaean about 18,000 years ago (Nadachowski, 1989).

While *L. lagurus* is still present in the terminal Pleistocene (youngest Dryas) small mammal fauna at Sevsk, the species had already disappeared from westernmost Europe. *M. gregalis* remained a common element of the rodent fauna at that time. This assemblage of species suggests that the typical conditions of arid, cool steppe environment had not yet been influenced by the consequences of Holocene climatic change. The co-occurrence of these two species is more common in eastern Eurasia. Both species are known up to the middle Holocene in faunas of the southern Ural Mountains (Smirnov et al., 1990) and in the modern fauna of the Trans-Urals and Northern Kazakhstan.

6. Archaeological materials at Sevsk

Sixteen worked flint pieces were found at Sevsk. All flint implements occur at the base of the main bone-bearing layer, primarily towards the center of the lens. However, there is no evidence of human processing of the mammoth remains, such as cut-marked bone. There are no hearths, no killing implements, no burned bones, and no activity areas for butchering or processing. Therefore, it is inferred that Paleolithic humans were not responsible for the accumulation of mammoth material at Sevsk.

7. Taphonomy of the mammoth bone bed

The entire excavation area encompassed nearly 1200 m^2, of which the bone-bearing lens occupied about 800 m^2, including the portion of the unit destroyed by commercial quarrying (Fig. 2A). The bone-bearing lens is elongate in plane view. The bones were distributed unevenly, both horizontally and vertically. In some instances, mammoth skulls, partial skeletons, and isolated bones were stacked vertically in two or three layers. Three nearly complete and two partially preserved skeletons of baby mammoths were found at the base of the accumulations. Their bones are well preserved (Fig. 5), while remains near the top of the upper bone-bearing layer (210–170 cm) are in poorer condition (Fig. 1B, 2B). Near the edge of the lens, the bone density decreases and the bones occur as isolated elements. More bone breakage is observed and preservation is poorer near the periphery of the lens than in the center. Fractured edges of broken bones are sharp and exhibit no traces of rounding. Articulated remains are absent at the periphery of the lens. Of the 3800 mammoth bones collected at Sevsk, only 10 to 12 show traces of gnaw-marks. There is little evidence of weathering on the bones.

Some redeposition of bones from the center of the lens is a likely cause for the differential preservation of elements noted between the main bone-bearing layer and the upper bone-bearing unit, and from the center of the main bone-bearing lens compared with its periphery. However, bone reworking inside the lens was not considerable, because eight large partial skeletons of adult individuals were found there in articulation, in addition to the articulated remains of the baby mammoth.

Several scattered bone fragments appear to represent one individual. The bones were not sorted by their size or weight and it is not possible to trace the direction of the paleocurrent in the ancient basin by either orientation of long bones or disposition of other skeletal fragments. Apparently, burial of most of the mammoth remains was very rapid, probably during one season of the year. This is suggested by homogeneous lithologic composition of the deposits in the main bone-bearing layer. The structure of the upper layer suggests that a

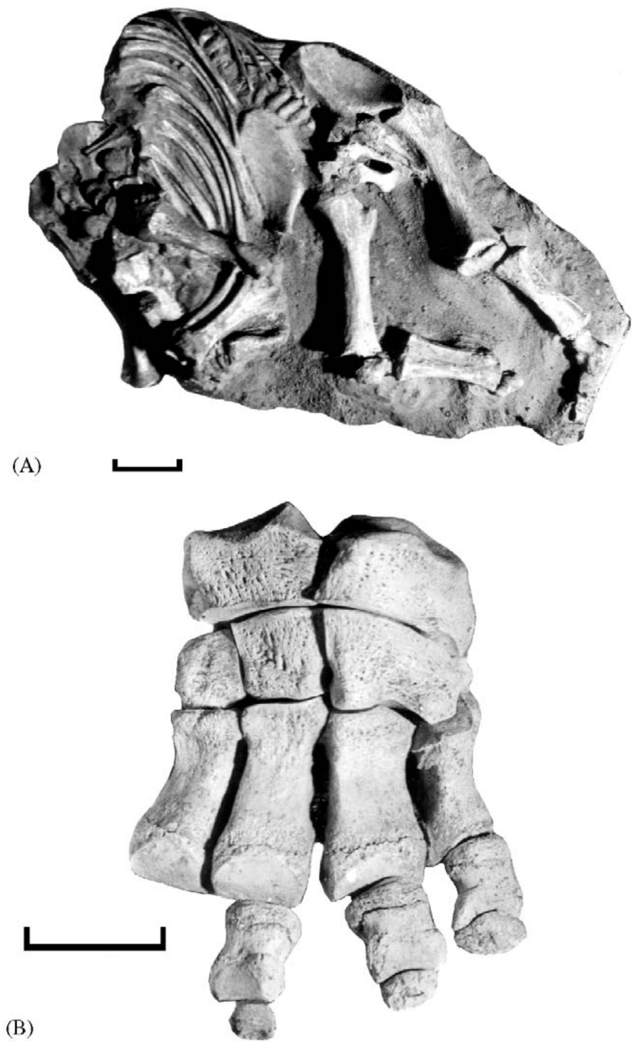

Fig. 5. Types of bone preservation in the Sevsk locality. Scales: 10 cm. (A) Skeleton of the 1-month-old baby mammoth in a rock-block in situ before preparation (PIN 4353-2619 to 4353-2704). The skull and lower jaw were at a distance of about 1 m from the skeleton. (B) Left manus of the adult animal preserving the anatomical position of bones (PIN 4353-2098 to 4353-2112).

periodic (seasonal) change of the sedimentary regime took place after the formation of the main bone-bearing layer. This change is indicated by alternation of loams and sands in the upper part of the section. In most places, the total thickness of lower and upper bone-bearing layers does not exceed 20–30 cm. In other places, however, because of deepening of the ancient basin bottom, the thickness increases to 35–50 cm.

Few bones of other large mammals occur at Sevsk: three bones of *Equus latipes* (PIN [Paleontological Institute, Russian Academy of Sciences] 4353-197-199), a rib of *Cervus* sp. (PIN 4353-301), a distal epiphysis of a tibia of *Bos* sp. (PIN 4353-343), and a humeral diaphysis of a juvenile *Coelodonta antiquitatis* (PIN 4353-3244). The scarcity of other large mammal species supports the interpretation that the mammoth remains accumulated in a brief period of time. By contrast, while the Berelekh locality (Yakutia) is also characterized by a predominance of mammoth bones, 18% of bones belong to other mammalian species (Vereshchagin, 1977). Moreover, the fossil assemblage at Berelekh accumulated over a long period of time (much more that one or two seasons of a year). Radiocarbon dates from Berelekh also provide these conclusions.

The skeletal elements found at Sevsk (Table 1) show that a minimum of 33 mammoths died there. Besides the remains of adult and juvenile mammoths, a humerus and femur were also found of a fetal mammoth, approximately 10–12 months of age (PIN 4353-3242, 3243; Fig. 6A).

Overall, the geologic, taphonomic, and paleontological data point to a single event (or catastrophic) formation of the main bone-bearing unit. As noted, this inference is predominantly based on the homogeneous lithology of the main bone-bearing unit, the scarcity of other large mammal bones, and generally good condition of preservation of the mammoth remains, particularly the high degree of articulation of juvenile mammoths. A subsequent depositional event completed the burial of the rest of the remains to form the bone-bearing unit.

8. Analysis of the mammoth bone assemblage

The minimum number of mammoths preserved at Sevsk was determined by identifying long bones from the right-hand side of the body and by counting crania, mandibles and pelvic elements. Six fairly complete skulls and 16 partial skulls exhibiting various degrees of preservation were identified. Tusks were preserved both separately (Fig. 6B–D) and in the alveoli of skulls (Fig. 7B, E, D). In tallying the long bones, epiphyses without diaphyses were viewed as complete elements in some cases.

Ribs, tarsals, metatarsals, phalanges, and carpals compose about 68% of the total number of bones found at the locality (Table 1). It is inferred from the lack of bone sorting and from the degree of articulation of remains throughout the bone-bearing deposits that the amount of material lost to commercial quarrying in 1988 could slightly increase the number of individuals. However, loss through quarrying most likely would not significantly change the age and sex profile of the Sevsk mammoth assemblage.

The method used to distinguish age and size groups among the Sevsk mammoths was developed at the Zoological Institute of the Russian Academy of Sciences by Baryshnikov et al. (1977) and Kuzmina and Maschenko (1999). Some modifications of the procedure were made related to epiphyseal growth and tooth

Table 1
Frequency of mammoth skeletal elements from the Sevsk and Berelekh (Yakutia) localities

Element	Number of bones		Percentage of the total number of mammoth bones	
	Sevsk	Berelekh	Sevsk	Berelekh
Tibia	52	169	1.4	2.01
Femur	52	179	1.4	2.12
Fibula	49	86	1.3	1.02
Humerus	53	184	1.4	1.85
Ulna	50	155	1.3	1.84
Radius	39	143	1.0	1.70
Pelvis	25	215	0.7	2.55
Scapula	30	156	0.8	1.85
Vertebra	740	1328	20.0	15.7
Cranium	24	—	0.6	—
Mandibula	23	128	0.6	1.44
Tusks	40	44	1.0	0.5
Total of all elements	3700	8431		
Number of individuals	33	156		

Berelekh numbers are from Vereshchagin, 1977.

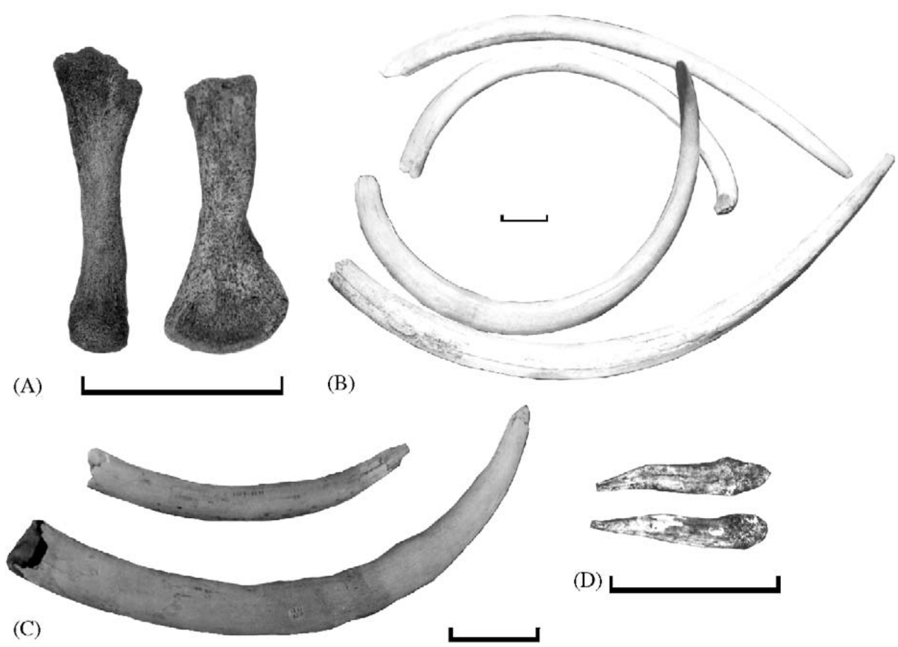

Fig. 6. Fetal bones and tusks from the Sevsk locality. Scales: 10 cm. (A) Fetal bones of the posterior end of *Mammuthus primigenius*. Left: right femur (upside down), PIN 4353-3243. Right: left humerus, PIN 4353-3242. (B) Two pairs of tusks of adult specimens. The internal pair is strongly curved (PIN 4353-3561, 4353-3562), while the external pair is less so (PIN 4353-3563, 4353-3664). The length of the largest tusk (outside curvature) is 1530 mm. (C) Tusks of young individuals. Above: a normal tusk of a 6-year-old mammoth. Below: a tusk of an 8- or 10-year-old individual (PIN 4353-320) with pathological nodes in the non-alveolar part. (D) Deciduous tusks of a mammoth calf. Above: tusk without wear (PIN 4353-3241). Below: wear tusk (PIN 4353-3240).

progression, and to sexual dimorphism in epiphyseal fusion, as suggested by Roth (1984) and Roth and Shoshani (1988). The length of the diaphysis and width of its proximal and distal ends were measured on the long bones of young and juvenile mammoths that had unfused epiphyses. In the case of fused distal epiphyses, total length was measured. The measurements were made using the method of Garutt (1954).

9. Age and sex profile

The 33 mammoths recovered at Sevsk are divided into five age groups. Group I includes animals from 1–2 months to 2 years old; group II from 2 years to 5–6 years old; group III from 6–7 to 11–13 years old, group IV from 13 to 35 years old; and group V over 40 years old. The determination of the boundaries of size variability

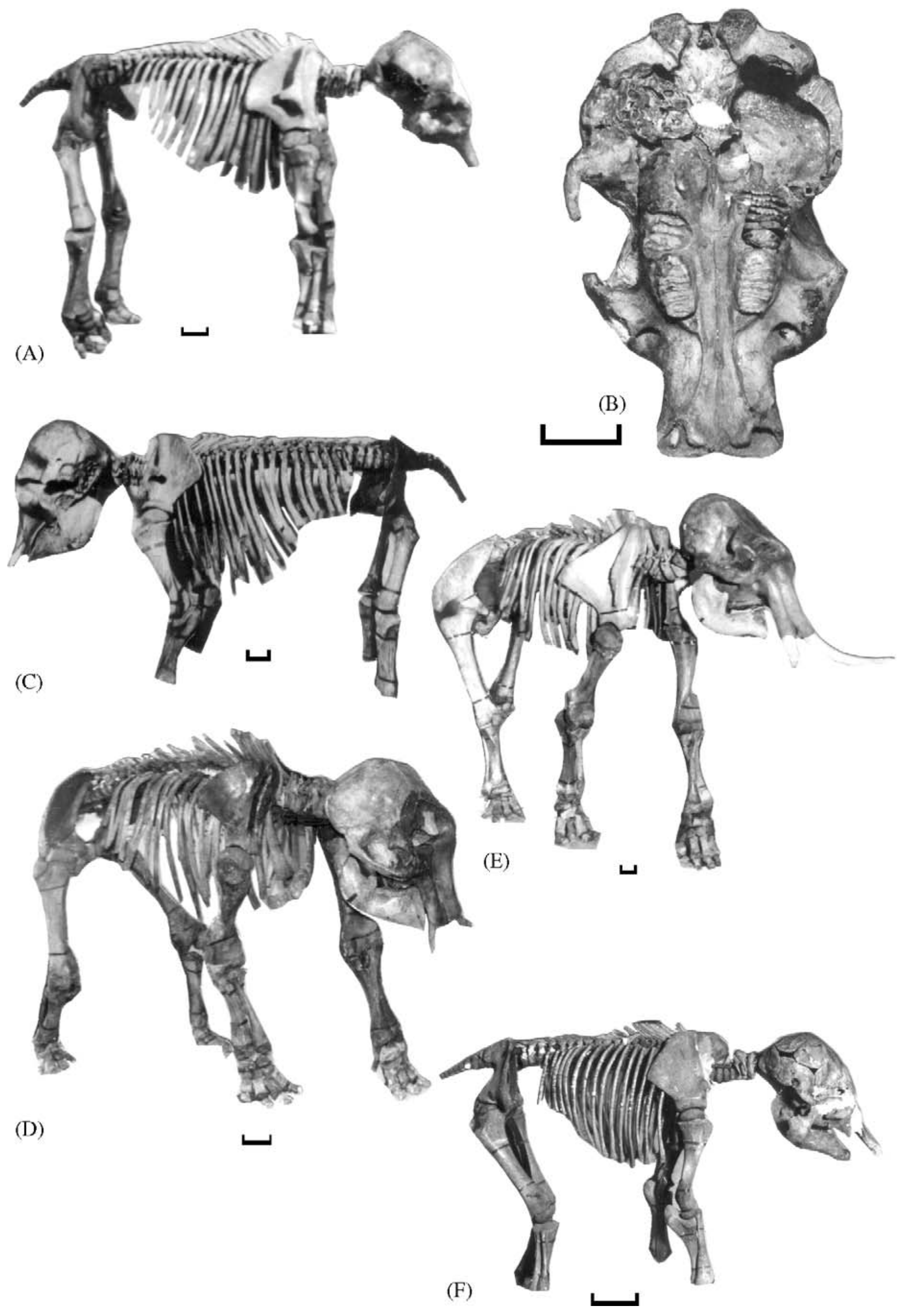

Fig. 7. Skeletons of mammoths of different ages from Sevsk. Scale: 10 cm. (A) Installed skeleton of the 1-year mammoth calf (PIN 4353-871-986). Mandible and right femur are plaster casts. Many bones of the distal part of the limbs are absent. The height of the skeleton is about 100 cm. (B) Skull of the skeleton of the 1-year mammoth calf (PIN 4353-933). The alveolus of dP2 anterior to dP3 is preserved; dP3 is worn all over the crown length; dP4 had almost completely formed, but had not yet erupted. There is a milk tusk in the left alveolus. (C) Skeleton of the 3 years old mammoth (PIN 4353-447-582). The height of the skeleton is about 125 cm. Most distal bones of the limbs are not preserved. The skull and the lower jaw were located at a distance of 2 and 3 m, respectively, from the postcranial skeleton, which laid in anatomically correct position. (D) Installed skeleton of the 6- or 7-year-old mammoth (PIN 4353). The height of the skeleton is 160 cm. The postcranial skeleton was not in anatomical position, but almost all the bones found were recovered within a limited area. About 50% of bones were absent: a femur and an ulna, bones of the distal part of the limbs, part of vertebrae, a lower jaw. The facial part of the skull (tooth generation dP3[?]) was at a distance of almost 3 m from the postcranial skeleton in situ. (E) Skeleton of the 14–17-year-old mammoth cow (PIN 4353). The height of the installed skeleton is 185 cm. About 40% of the postcranial skeleton was absent: part of vertebrae, half-part of pelvis and ribs, a scapula, part of a hind limb. The part of the vertebral column, the hind limbs with half-pelvis discovered in anatomical position (Fig. 2B). The skull retains tooth generation M1–M2. (F) Installed skeleton of the 1-month calf (PIN 4352-2614–2715). Many distal bones are absent. Tooth generation is dP2.

in group III posed the greatest difficulty. The most exact chart for this group was made from the tibia. For groups I, II, IV, and V, only the sizes of bones of the right-hand side of the skeleton were used. Some bones of the right-hand side together with the humerus, femur, and ulna were also used for the chart of group III. Puberty in mammoths, as well as that of modern elephants, apparently was reached in the range of 7–13 years old, followed by a growth acceleration (pubertal spurt) (Laws, 1966; Haynes, 1991). Differences in body size between males and females begin to appear in this age as well. Among the Sevsk mammoths, five individuals (15.5%) are assigned to Group I, four (12.3%) to Group II, five (15.1%) to Group III, nine (27.2%) to Group IV, and 10 (30.2%) to Group V. Proportionately, more old and prepubescent animals died at Sevsk than at other noted mammoth localities. Fig. 8A shows that at the Berelekh (Yakutia) and Mezin (Bryansk Region, Russia) Late Paleolithic sites 12–14% of the overall number are prepubertal animals. This percentage is similar to other Late Paleolithic sites of the Russian Plain and corresponds to the non-catastrophic death profiles of modern African elephant herds (Sikes, 1967; Urbanas, 1980). About 45% of individuals in the Sevsk locality are prepubertal and this probably reflects real differences between the various populations of mammoths inhabiting the Russian Plain at the end of the Pleistocene. The death of predominantly old and young mammoths suggests the existence of some unfavorable climatic conditions at Sevsk about 14,000 years ago. The presence of a fetal individual, the skeletons of two infants, a month old, and the skeleton of a 1 year old, suggest that the Sevsk mammoths may have died in the spring or early summer.

The distribution of hind limb bone sizes (maximum length and width of the lower or upper ends of diaphyses) enables us to distinguish roughly five age-size groups (Fig. 9A–D). Size variability is best established for groups I and II due to the presence of preserved skeletons with skulls, and also for group V because the fusion of long bone epiphyses and the obliteration of the epiphyseal suture lines are reliable criteria for age determination in male and female postcranial skeletons.

Three of the most complete skeletons of mammoth calves belonging to group I (Fig. 7A, C, F) were preserved in articulation. The sizes range of the long bones in this group (Fig. 9A–D) are presented in Table 2. The most complete skeleton of a young mammoth from group I (PIN 4353-2614 to 2715, Fig. 7F) was preserved in articulation. It has a well-preserved cranium and mandible (Fig. 10A, B). The DP2 and dp2 are not completely erupted from the bone. The DP3 and dp3 are not completely formed. The age of this individual is not more than 1 month based on tooth formation. The postcranial

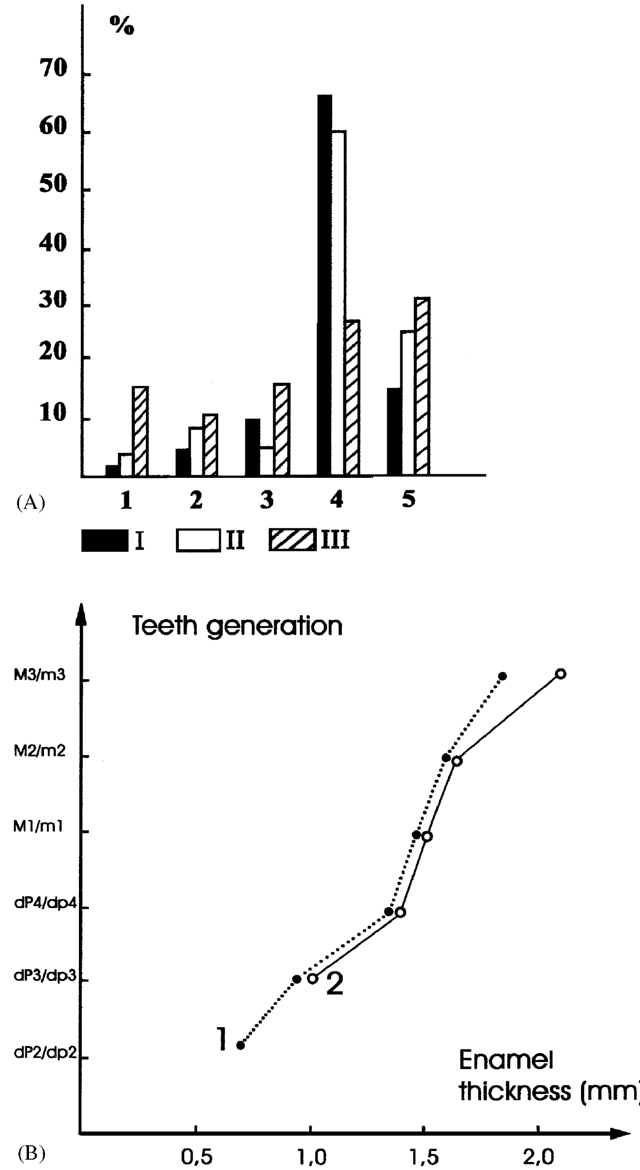

Fig. 8. Age composition of the mammoths group. The comparison of enamel thickness. (A) Chart of the age composition of the mammoths groups from Sevsk, Berelekh (Yakutia, Vereshchagin, 1977), and Mezin Late Paleolithic site (Vereshchagin, 1977). Vertical axis—percentage of total; horizontal axis—individual age (years). 1—Berelekh; 2—Mezin; 3—Sevsk; 4—new-born to 2 years old; 5—2 years old to 5 or 6 years old; 6–7 to 11 years old to 13 years old; 7–13 to 35 years old; 8—>40 years old. (B) Comparison of enamel thickness of the mammoth teeth from Sevsk and Berelekh (Zherekhova, 1977). Vertical axis—tooth generation; horizontal axis—thickness of enamel (mm). 1—Berelekh; 2—Sevsk.

skeleton is missing the left scapula and distal portions of the limbs.

The skeleton of the other mammoth calf, approximately the same age as the previous individual (DP2/dp2), was not preserved in articulation. Approximately 50% of its postcranial skeleton was recovered (PIN 4353-2355 to 4353-2364, 4353-2543 to 4353-2551, 4353-

2916 to 4353-2923, 4353-2451 to 4353-2464, 4353-3100 to 4353-3106). The mandible and fragments of the facial and cranial portions of the skull are absent. As mounted specimens, both of these baby mammoths are 70 cm in shoulder height.

A well-preserved skeleton of an 1-year-old baby mammoth is missing the distal portions of the limbs and the mandible (PIN 4353-871 to 4353-986; Fig. 7A, B). The alveolus of DP2 is present, the DP2 having been shed after full wear. The DP3 is present and dP4 is not completely formed. A deciduous tusk, not yet completely emerged from the alveolus, is present (Fig. 7B).

This most complete skeleton of a mammoth calf was found in situ in a flexed position with bent limbs (Fig. 5A). Another skeleton of an 1-year-old baby mammoth was found in situ on its right-hand side. The vertebral column was straight, so all spinous processes tightly overlaid one another. Each of the baby mammoth skulls (or their unfused parts) lay at some distance—from 10 cm to 1 m away—from the cervical vertebrae.

The skeleton of one 3-year-old mammoth calf is assigned to group II (PIN 4353-447 to 4353-585, Fig. 7C). The skeleton was preserved in anatomical position. The cranium, mandible, and some of the distal limbs elements were absent. The facial portion of the skull, adjacent to a functioning DP4 which may belong to another individual of approximately of the same age, was located 12 m from the skeleton. Although exact correspondence of this skull and postcranial skeleton was not established, they fit well together when mounted.

The size ranges of the long bones in group II are presented in Table 2. For the ulna (Fig. 9B), the proximal width of the diaphysis overlaps with group I, but the length of the diaphysis is always greater. For the tibia the boundaries between groups overlap in length, but in group II the proximal width of diaphysis is always greater. The reason for the overlap in both groups is evidently individual variability, with perhaps some sexual dimorphism reflected as well.

The fifth skeleton of a young mammoth, approximately 6–8 years of age, is assigned to group III (PIN 4353-334 to 4353-412, Fig. 7D). The bones were found in a limited area (1.5 m × 2 m) but not in anatomical position. Almost 40% of the postcranial bones and the lower jaw were absent. The cranium with highly worn DP4 probably belonging to this individual was located 2 m from the postcranial elements. After restoration of

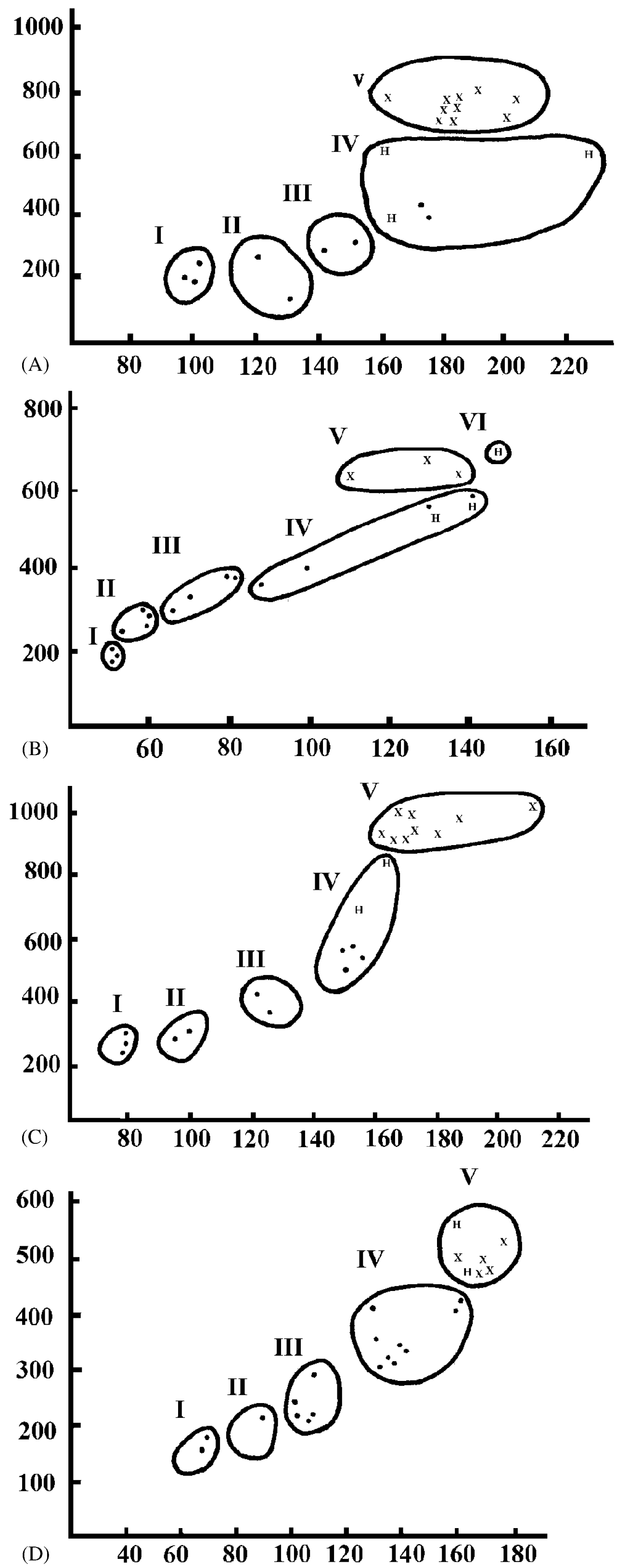

Fig. 9. Size of long bones of the mammoth limbs from the Sevsk locality. Vertical axis—maximum length of bone (mm); horizontal axis—width of distal epiphysis of humerus and femur and width of proximal epiphysis for ulna and tibia (mm). I—age group I (1 month to 2 years); II—age group II (2 to 5–6 years); III—age group III (from 7 to 11–13 years); IV—age group IV (from 13 to 35–40 years); V—age group V (over 40 years); +—bones with an unfused proximal and distal epiphyses; H—bones with unfused distal epiphysis; ×—bones with completely fused proximal and distal epiphyses; VI—one bone extremely large ulna, unfused proximal and distal epiphysis, perhaps belong to a male.

Table 2
Size comparison of mammoth limbs from Sevsk, Berelekh and Yuribei localities (Baryshnikov et al., 1977; Dubrovo, 1982)

Element	Maximum length			Width of distal epiphysis (humerus, femur) Width of proximal epiphysis (tibia, ulna)			Age group		
	Sevsk	Berelekh	Yuribei	Sevsk	Berelekh	Yuribei	Sevsk	Berelekh	Yuribei
	$n=5$	$n=2$		$n=5$	$n=2$				
Humerus	200–260	155–180	—	96–103	65–80	—			
Ulna	186–235	220–240	—	35–53	75–90	—	I. 1–24 months	I. Fetuses	—
Femur	240–350	190–230	—	75–79	30–35	—			
Tibia	153–204	135–150	—	65–75	45–55	—			
	$n=5$	$n=23$		$n=5$	$n=23$				
Humerus	250–310	250–490	—	123–130	115–170	—			
Ulna	243–290	290–400	—	45–63	110–145	—	II. 2–6 years	II. 1–10 years	—
Femur	320–359	350–610	—	94–100	50–90	—			
Tibia	200–235	200–340	—	75–97	75–135	—			
	$n=5$	$n=10$		$n=5$	$n=10$				
Humerus	375–430	480–620	760	135–150	160–180	214			
Ulna	282–330	380–550	547 (without lower epiphysis)	63–73	150–170	117	III. 7–13 years	III. 10–20 years	III. 10–12 years
Femur	374–470	600–720	—	100–125	80–100	197			
Tibia	250–325	320–450	475	102–120	130–160	169			
	$n=9$	$n=17$		$n=9$	$n=17$				
Humerus	405–620	640–750	—	158–185	170–215	—	IV. 13–35 years	IV. Adults up to 40 years	—
Ulna	350–380	500–650	—	87–98	170–210	—			
Femur	554–690	700–850	—	150–165	100–120	—			
Tibia	356–435	400–480	—	132–168	150–185	—			
	$n=10$	$n=9$		$n=10$	$n=9$				
Humerus	718–825	750–940	—	165–193	200–275	—	V. Over 40 years	V. Over 40 years	—
Ulna	532–672	600–780	—	128–165	180–225	—			
Femur	790–1010	850–1130	—	158–210	100–150	—			
Tibia	460–555	470–570	—	168–187	160–225	—			

Measurements in millimeters.

its occipital region, the cranium was used for the skeletal reconstruction. The shoulder height of the mounted skeleton is 160 cm. See Table 2 for size variation of group III limb bones.

Group IV includes the bones of mammoths with fused lower epiphyses in the humerus and femur as well as the ulna and tibia, of the corresponding size rank with incompletely fused or completely unfused epiphyses. Some parts of the humerus and femur with fused upper and lower epiphyses are in the same group and belong to females. In connection with birthing, the fusion of the epiphyses and termination of linear growth occurs earlier in females than in males (Roth, 1984). The size range of group IV long bones is present in Table 2.

An incomplete skeleton of a 15–17-year-old female mammoth is placed in group IV (Fig. 7E). Approximately 50% of the skeleton was preserved. Collection numbers of the skeleton are included as Appendix A The M1 and M2 are present, with the M2 beginning to wear. The height in shoulder of the reconstructed skeleton is about 190 cm. The proximal and distal epiphyses of the long bones of the limbs have not fused.

The comparison of individual skeletal sizes from Sevsk groups III and IV with those of the mammoths from Eastern Siberia (Table 2) shows that the Sevsk mammoths are smaller than Siberian animals of corresponding age. For example, based on long bone measurements a female specimen from the Yuribei locality (PIN 3941-1-130) would be assigned to Sevsk group IV, but based on the age determined by tooth generation and its wearing the Yuribei mammoth relates to group III (Dubrovo, 1982).

Two large specimens from group IV with incompletely fused epiphyses correspond to group V based on

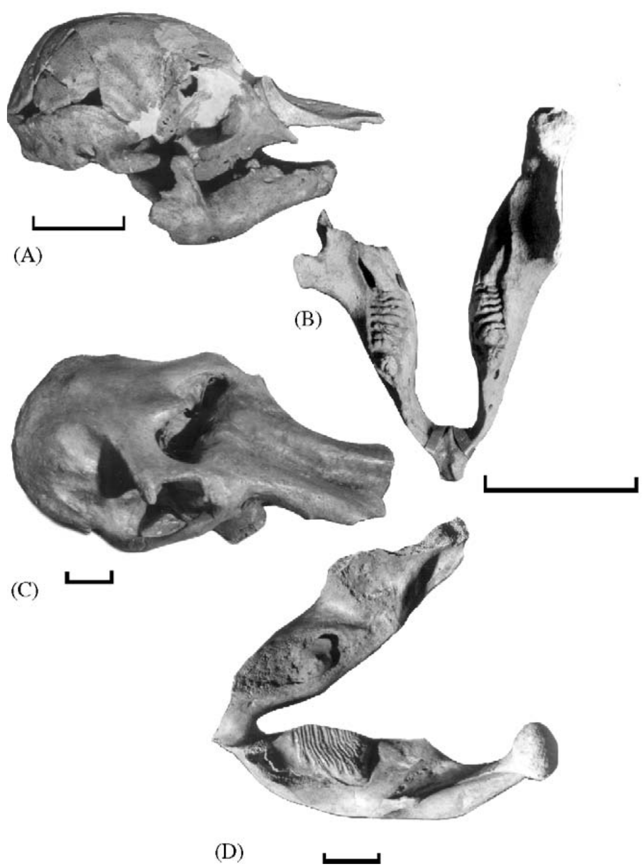

Fig. 10. Skulls and lower jaws of the mammoths from Sevsk. Scales: 10 cm. (A) The skull and mandible of the 1-month-old baby mammoth, lateral view (PIN 4353-2614). (B) Lower jaw, upper view (PIN 4353-2615); dP2 is practically affected by attrition; dP3 has completely formed, but is not yet erupted. The last enamel plates of this tooth are not yet completely knitted. (C) Right view of the skull of an adult male (PIN 4353-3570). The tooth generation is M3. An individual age is about 50 years old. The tooth of the last generation is worn more than one-third. (D) The lower jaw of the old mammoth from Sevsk (PIN 4353-442). The individual's age is about 60 years. The right M3 is completely worn out.

long bone size. However, all specimens in group V exhibit completely fused epiphyses while some specimens still have incompletely fused epiphyseal sutures. It is likely that the two large specimens with unfused epiphyses are males and all other specimens, which are smaller with fused epiphyses, are females. The differences in size are explained by appreciable sexual dimorphism (Laws, 1966; Sikes, 1967). The dimensions of the long bones in group V are present in Table 2.

The shoulder height of the largest mounted skeleton from Sevsk is about 235 cm. About 50% of the skeleton is preserved, including the cranium (Fig. 10C), tusks, mandible, and parts of the postcranial skeleton. Reconstruction of the skeleton was completed by bones of the same size class collected from the adjacent parts of the excavation, which may belong to the same individual. The degree of wear of M3 indicates that the individual is at least 50 years old. Some features of the skull and the large size of the bones and tusks as well as the shape of premaxillar bones indicate that this is the skeleton of an old male. The length of the femur is 97 cm; the maximum length of the tusks along the curvature is 150 cm, and their diameter is 10 cm.

The height of the largest adult Sevsk mammoth, including soft tissues during life, was about 240–245 cm at the shoulder. This is shorter than the largest specimens from the Berelekh locality and is considerably less than the size of adult mammoths from other localities in Eastern Siberia (Vereshchagin and Nikolayev, 1982). Mammoth remains of similar radiocarbon age found in Shrewsbury (England) are also from fairly large mammoths, with a skeletal height of 3 m (Coope and Lister, 1987). A 10-year-old female from the Yuribei locality, of a younger radiocarbon age than that from Sevsk, is also comparatively larger than adult Sevsk mammoths (except the largest one). The height of its skeleton is about 230 cm (Dubrovo, 1982). Large variability in stature is typical for modern elephants (Haynes, 1991). However, we propose that in the case of the four localities mentioned above the differences in body height from various regions (Western and Eastern Europe, Western and Eastern Siberia) reflect true differences in stature among isolated populations of *M. primigenius* at the end of the Pleistocene. These differences are expressed not only in the size of animals, but also, in the example of Sevsk mammoths, in some morphological features.

Considerable difference in the size of the premaxillary bones was noted during comparison of the skull of the largest Sevsk mammoth (PIN 4353-3570; Fig. 10C) with that of the Berezovka (Zalensky, 1903: ZIN [Zoological Institute of Russian Academy of Sciences] 3515) (Table 3). The skull of the old male from Sevsk is similar to the Berezovka mammoth in most other proportions and characters. The difference in the size of the premaxillary bones is explained by the small size of the male tusks from Sevsk. The small size of Sevsk mammoth tusks is noted in comparison with specimens from Eastern Siberia (Fig. 2C). Only one pair of tusks in the Sevsk population belongs to a male, the others represent females. Almost 30% of the females from Siberia more than 40 years old have tusks larger than those of the Sevsk male. A coefficient of curvature radius used for identification of sex in mammoths from Siberia (Vereshchagin and Tikhonov, 1986) cannot be used for this purpose in the population from Sevsk. The mean curvature radius for female tusks in Siberia is 31.7, whereas for males it is always much greater. The mean coefficient of curvature radius is 76.2 at Sevsk (Table 4). This means that among the females from Sevsk there were specimens with both straight and curved tusks (Fig. 6B). The male tusks (PIN 4353-3565-3566) have an

Table 3
Comparison of skull sizes of the Berezovka river specimen (Zalensky, 1903) and the largest male from Sevsk

Measurement	Beryozovka, ZIN 5315 (individual age is about 30 years old)	Sevsk, PIN 353-3570 (individual age is over 50 years old)
1. Length from the distal edge of premaxillary bones to the vertex of skull	1260	1000
2. Length from the occipital condyle to the distal edge of the alveolus of the tusk	845	850
3. Length from vertex to bottom of nasal bones	345	470
4. Length of frontal bones with nasal foramen	478	510
5. Length of premaxillary	642	500
6. Maximum length and width of nasal foramen	420/113	340/90
7. Maximum distance between left and right zygomatic bones	657	570
8. Maximum distance between left and right occipital bones	720	580
9. Width of premaxillary on the infraorbital foramen level	298	320
10. Width of premaxillary (lower) on the level of the distal edge	446	—
11. Minimum width of frontal bones	327	290
12. Height from condyle to a level of a masticatory surface of the teeth	266	370
13. Height of a skull from vertex to the level of a masticatory surface	720	740
14. Height from vertex to a lower edge of a condyle	456	410
15. Minimum and maximum height of a zygomatic arch	42/73	40/80
16. Length of a zygomatic arch	349	330

Measurements in millimeters. Characteristics measured follow Garutt (1954).

index of curvature of 0.66, but differ from the other Sevsk tusks in their larger diameter. Their relatively short curve length (about 150 cm) is accounted for by strong attrition. The size of the pulp cavity can be used as a secondary character for sex determination. It is largest in young and adult (up to 40 years old) mammoths from Sevsk (Table 4). It is reported for recent *Loxodonta africana* that the size of the pulp cavity in males increases with the growth of tusks progressively throughout life, but in females this process ceases at reproductive age and the pulp cavity begins to fill in (Haynes, 1991). One cannot use this feature for sex determination in the Sevsk population, because the tusks belong to males younger than 40 years old.

It is possible to show that reduction in depth of the pulp cavity with increasing age took place in mammoth tusks from other localities, too. The depth of the pulp cavity of the biggest tusk stored in the Paleontological Institute (diameter 16 cm, length along the outside curvature 2.8 m) is 150 mm. The depth of the pulp cavity on a smaller tusk also pertaining to a younger male is about 400 mm.

Attrition on the edges of tusks and formation of abrasion facets in the mammoths from Sevsk which were up to 30 years old is similar to the condition seen in mammoths from Eastern Siberia (Vereshchagin and Tikhonov, 1986; Haynes, 1991). The edges of all tusks of mammoths that were probably younger than 40 years old are broken and the surfaces are rounded as described for *L. africana* (Haynes, 1991). Tusk attrition in old adult specimens is very strong. The tusk attrition is over 40% on specimen PIN 4353-3567, from a 50+ years old individual. The surface of attrition resembles the secondary type of attrition formed after the tusk tip has been broken.

The proportions and size of the lower jaws of the mammoths from the Sevsk and Kostenki-I (Urbanas, 1980) localities differ mainly in the smaller sizes of the Sevsk specimens (Table 5). The large angle of divergence between the horizontal rami and the short length of the symphyseal region are characteristics of Sevsk mammoths and are not dependent on the size-class of animals. For adult specimens the maximum angle is 51° and the minimum is 32°.

It was not possible to separate the jaws of males and females from Sevsk according to the proportions of the corpus mandibulae and processus coronoideus and the shape of the processus mandibularis. These criteria were first used by Korniets (1959) for sex determination of lower jaws from the Mezin locality (Bryansk Region). It was presumed that low, elongated jaws with long mandibularis processes belonged to males, while shorter and higher ones with short mandibular processes belonged to females (Table 5). According to this classification, all lower jaws of the adult specimens from Sevsk (with m1, m2, or m3 in wear) are attributable to females. The jaw of the largest mammoth (PIN 4353-3559) also relates to females according to these criteria.

Another age characteristic is evident in the lower jaws from Sevsk. The height of the ramus in older specimens having a highly worn m3 is less than that of younger specimens with m2–m3 in position, whereas some other parameters are similar. The height of the ramus (behind m3) in the 60-year-old individual (PIN 4353-442; Fig. 10D) is 108 mm. In another lower jaw from a 40–50 year

Table 4
Sizes of mammoth tusks from Sevsk

Measurement	Specimen Catalogue number (PIN)													
	4353-687	4353-3567	4353-1502	4353-320	4353-1098	4353-3564	4353-3569	4353-3562	4353-3566	4353-3565	4353-445	4353-3563	4353-3561	4353-1213
1. Maximum diameter	57	89	41	63	83	75	75	73	101	96	27	64	68	43
2. Length of outside curvature	770	1260	445	713	1360	1528	1590	1524	1430	1480	244	1042	1156	387
3. Straight-line (Chord) length from base to tip	656	856	410	560	920	1220	1080	770	940	970	227	745	1063	353
4. Index of curvature (3/2)	0.85	0.68	0.90	0.79	0.68	0.79	0.68	0.50	0.66	0.66	0.93	0.71	0.91	0.91
5. Length of alveolar part of the tusk	280	480	—	247	364	—	500	490	590	—	155(?)	-	-	-
6. Age (years)	17	60(?)	7	12(?)	50(?)	30(?)	35(?)	40(?)	50	50	5	35(?)	30(?)	6
7. Sex	Female	Female	Female	Female	Female (?)	Female	Female	Female	Male	Male	Female	Female	Female	Female (?)
8. Depth of pulp cavities	—	236	—	205	162	150	130	127	—	—	—	—	98	—

Measurements in millimeters. All specimens are catalogued into the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN).

old with m2–m3, this parameter changes within the limits 125–150 mm. The height of the ramus was reduced by the attrition of the last molar.

Comparison of mammoth teeth from Berelekh, Eliseevichi, Kostenki-XI (Urbanas, 1980) and Sevsk shows that the mammoths from these localities are similar in the number of enamel plates on M3 and m3 (Table 6). In general, the number of plates varies in later representatives of *M. primigenius* Blum. The shorter distance between the plates and the slightly greater thickness of the enamel on M3 and m3 (Fig. 8B) are features typical of the mammoths from Sevsk in comparison with other populations. The enamel plate is enlarged to form a sinus on some mandibular teeth (lower jaws: PIN 4353-2789, 3558). This enamel sinus appears on the anterior edges of plates IV–VI on these teeth. Such enlargement of the posterior edges of plates is absent or is only weakly developed.

Sevsk mammoth bones exhibit a few pathologies. The skeleton of a 3 year old shows fractures of two right ribs that healed despite the dislocation of the rib heads. A curvature of the coronoid processes is noticeable on two skeletons of young individuals. A rib head with a lesion or healed fracture (Fig. 11B) and an adult radius exhibiting hypertrophy where it has fused to the cuboid (PIN 4353-969) are notable pathologies. Also, there is fusion of two or three thoracic and lumbar vertebrae, such as that occuring on skeletons of some modern captive elephants. One tusk, referred to an 8- or 10-year-old animal, shows enlargements on the non-alveolar surface (Fig. 6C).

Sex determination of adult mammoths from Sevsk shows that 16 of the 19 postpubertal individuals are females. At least nine of these 16 females have completely fused epiphyses and obliterated epiphyseal sutures. Six animals have incompletely fused epiphyseal sutures or totally unfused upper or lower epiphyses. The remains of the male over 50 years old and at least one male with unfused epiphyses on femur and humerus were identified among the adult specimens. The identification of males was difficult because of the small sizes of mammoths from Sevsk.

The long bones of a single adult specimen identified as a male can be readily separated from the other bones of adult females (Fig. 10C; group V, the largest value). However, comparison with a single complete skeleton most likely to be a female *M. primigenius* from the Oyesh River, stored in the Novosibirsk Museum of Ethnography, showed close agreement in size (Table 7). Nevertheless, different proportions of the Sevsk mammoth bones can be used to identify the individual sex as male. The most important osteological indications that it is a male are the width of the lower epiphysis of the humerus, indicating its robust proportions, and the greater minimum width of the femur. The diameter of the tusks and the size of the premaxillar bones are also

Table 5
Size comparison of mammoth lower jaws from Kostenki I (Voronezh region (Urbanas, 1980), Mezin (Bryansk region) (Korniets, 1959), and Sevsk

Measurement	m1—m2		m2—m3		m3		Mezin (females)
	Kostenki I	Sevsk	Kostenki I	Sevsk	Kostenki I	Sevsk	
1. Maximum width	363	323	456–489	446	—	450–500	—
2. Height of a coronoid processus in posterior edge of the alveolus	98	91–140	133–146	123	141–161	108–140	121–153
3. Thickness of corpus mandibulae in posterior edge of alveolus	103	95–136	127–146	122	144–159	127–134	93–127
4. Minimum width of the ascending ramus	—	195	—	204	257	202–230	—
5. Distance from end of mental process to the edge of the alveolus	—	122–136	150–157	142	135–247	130–150	—
6. Length of symphysis	—	65–79	97–111	108	108–149	75–98	—
7. Size of glenoid head (length/width)	—	48–52	—	54	92	50–79	—
8. Distance between teeth (anteriorly/posteriorly)	79/121	46–64/83–92	108–125/ 88–194	68/150	116/181	75–78/ 116–200	57–95/ 116–200
9. Height/length of jaw	—	73–86	—	—	—	76	85.8

Measurements in millimeters.

important distinguishing characters for sex determination.

Overall, the sex profile and the age structure of the adult Sevsk mammoth assemblage correlate well with a herd-family of *L. africana* (Laws, 1966; Sikes, 1967), where females dominate among adult animals. However, the great number of prepubertal animals (14, or about 45% of the total number of animals) distinguishes the Sevsk locality from other localities of the Russian Plain. Sex could not be determined in prepubertal mammoths.

10. Summary

Sevsk mammoths are characterized by small size and weak sexual dimorphism. Sexually related size variability in *L. africana* can sometimes reach 40% (Haynes, 1991). The smallest tibia from Sevsk (Fig. 11A) that has completely fused epiphyseal sutures is 42 cm long and belongs to a female. The skeletal height of this smallest adult specimen does not exceed 190 cm. Thus, the range of body-size variability between the largest and smallest animals from Sevsk is about 20%.

It is likely that most of the mammoths that died at Sevsk were from one family group. The age and sexual structure of the death assemblage, the similarity in body sizes, and some morphological features of the skeleton and dentition of adult females support this. In the tables of long bone sizes, the group of adult mammoths (group V) shows the smallest variation in size (Fig. 9). At least four individuals, three prepubertal and one young pubertal, have foramina on the spinous processes of the thoracic vertebrae (Fig. 11C). Such features are usually genetically determined and it may be that all the baby mammoths were descended from one female or her female relatives. The transfer of similar characters in family lines of other mammal species, including human, also have been observed in the archaeological record.

Similar foramina in mammoth vertebrae from other localities were reported for the Yudinovo Late Paleolithic site (Bryansk Region), the radiocarbon age of which is about 13,000 years (Z. Abramova, pers. comm.) and Shestakovo site (Kemerovo Region) (Derevianko et al., 2000). Similar foramina in mammoth spinous processes is also present for the Krakow Spadista Street (B) site, whose radiocarbon ages are 20,600 + 1050−23040 + 170 years (P. Wojtal, pers. comm., 1999).

All aforementioned data suggest that, similar to modern *L. africana*, the stable structure of the herd of *M. primigenius* may have been due to their membership in a family group consisting of one or few females and their offspring of different ages. At Sevsk the herd consisted of at least 33 members. Postpubertal individuals (mammoth bulls), probably, were not permanent members of such a family group. The age and sex ratio of the group also supports this inference. A ratio of prepubertal animals approaching 45% is typical for the composition of a family herd in African elephants. Most likely, this also supports the speculation of a catastrophic death of a single mammoth group in the region of Sevsk during the late Valdaian glaciations.

Table 6
Comparison of tooth dimensions of mammoths from Berelekh, Eliseevichi (Bryansk region), Kostenki XI (Voronezh region) (Urbanas, 1980) and Sevsk

Dental element	Measurement	Locality			
		Berelekh	Eliseevichi	Kostenki XI	Sevsk
	Length of crown	14.3 – 18 / 14	14.1 – 15 / 11.3 – 14.5	—	12.6 – 15 / 13 – 13.5
	Width of crown	13.5 – 17.8 / 11.2	12.0 – 13.0 / 7.3 – 9.0	—	11.5 – 12.2 / 8 – 11
d P2 / d p2	Number of plates	5 / 5	5 / 4 – 5	—	3 – 4 / 4
	Average length of plate	3 – 3.6 / 2.8	3 / 2.8 – 3.4	—	—
	Thickness of enamel	0.7 – 0.8 / 0.7	3 0.4 – 0.5 / —	—	—
	Length of crown	41 – 61 / 48.5 – 54	53 – 56.5 / 52.3	—	52 – 57 / —
	Width of crown	33 – 37 / 32 – 37.2	35.5 – 40 / 34	—	32 – 35 / —
d P3 / d p3	Number of plates	8 – 10 / 9 – 10	7 – 10 / 7	—	7 – 8 / —
	Average length of plate	6.6 – 7.9 / 7.2 – 7.6	5.5 – 8 / —	—	3 / —
	Thickness of enamel	0.7 – 1.3 / 0.7 – 1.0	0.9 – 1.2 / 0.9	—	1.2 / —
	Length of crown	75 – 140 / 100 – 130	64.7 – 121.6 / 112.2 – 122.7	101 – 125 / 113 – 144	— / 102 – 138
	Width of crown	48 – 68 / 43 – 67	53.5 – 64.7 / 60 – 65.5	56 – 57 / 59 – 67	68 / 45 – 67
d P4 / d p4	Number of plates	13 – 16 / 11 – 15	7 – 13 / 10 – 14	12 / 14	— / 9 – 12
	Average length of plate	7.2 – 10 / 7.5 – 12.2	8.7 – 10.1 / 8.9 – 11.6	8.6 – 9.6 / 9.5 – 10.8	3.5 – 3.8 / 4
	Thickness of enamel	0.7 – 1.3 / 0.6 – 1.3	0.7 – 1.2 / 1.0 – 1.2	1.0 – 1.5 / 1.0 – 1.8	0.8 – 0.2 / 1.2 – 1.5
	Length of crown	193 – 238 / 170 – 250	—	— / 268	210 – 220 / 190 – 250
	Width of crown	60 – 90 / 72 – 96	82 / 86 – 88	— / 82.5 – 100	92 / 82 – 93
M3 / m3	Number of plates	22 – 26 / 24 – 26	23 / —	— / 25	— / 20 – 22
	Average length of plate	7.4 – 10.7 / 9.4 – 11.5	11.6 / 11.7 – 12.2	— / 11.1 – 12.5	5 – 6.5 / 2.2 – 6
	Thickness of enamel	1.5 – 2.1 / 1.6 – 2.0	1.8 / 1.5	— / 1.6 – 2.0	2.2 – 2.5 / 1.8 – 2.2

Measurements in millimeters.

11. Conclusions

The unique materials from the Sevsk locality provide a special opportunity for the studies of biology and natural history of the woolly mammoth. It particular, some important features of mammoth ecology and ethology become clear.

Owing to specific geological conditions, it is reliably established that the Sevsk mammoths died simultaneously, during one season. The main bone-bearing layer of the locality is homogeneous and preserved most of the mammoth remains in situ. Only a minor part of the bones is redeposited. This makes possible a reconstruction of age composition of the group buried in the Sevsk locality. According to this reconstruction, Late Pleistocene mammoth groups in the Russian Plain were structured similarly to modern elephant groups and most likely consisted of close relatives. These features could not be observed in mammoth remains from numerous other localities in the Russian Plain and Siberia, because those localities eroded during the Pleistocene and Holocene, and the bones were not strictly in situ. Moreover, many of the mammoth remains from the Russian Plain are known from Late Pleistocene archaeological sites, where they were collected purposely, and thus do not represent natural accumulations, so no reliable conclusions regarding specific aspects of mammoth biology may be made on those materials.

The skeletons of calves of different ages preserved at Sevsk provide a unique opportunity to study early ontogenetic development (before subadalt age) of *M. primigenius*. Owing to five almost complete calf skeletons from Sevsk, the formation of the skeleton in early postnatal stages has been studied almost as thoroughly as in modern elephants.

The taphonomy of the Sevsk locality provides evidence that mammoths inhabited river valleys during the spring (the time of death of the Sevsk group) and summer. Because of catastrophic floods some groups evidently were unable to escape dangerous places in the river valleys of the Russian Plain. Erosion and other destructive events in the river valleys during the Late Pleistocene and Holocene made localities of this kind

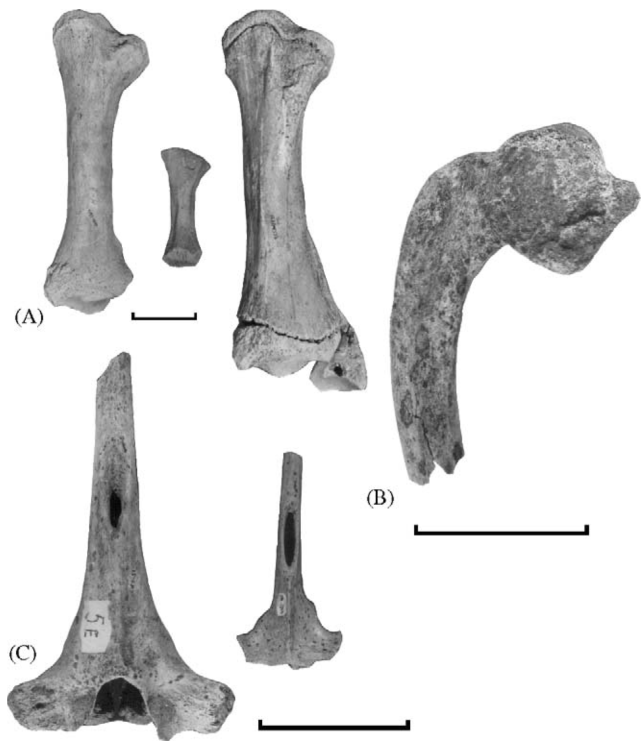

Fig. 11. Bones of the mammoth from the Sevsk locality. (A) Tibia of mammoths from Sevsk. Left: adult female, age about 35 years (epiphyseal sutures have completely fused). Center: baby mammoth, age 1.5–2 years old. Right: young male, age about 15–20 years old. (B) Rib of an adult animal with an hypertrophic development of the head. (C) Processus spinosus of thoracic vertebrae of the 10–15 years old mammoth (PIN 4353-845) and the 1.5–2 years old animal (PIN 4353-400). Scale bar is 10 cm.

Table 7
Comparison of the cranium and postcranial elements of a female mammoth from the Oyesh River (Novosibirsk region) locality and a male mammoth from Sevsk

Measurement	Oyesh River Female	Sevsk Male
1. Length of humerus	730	825
2. Width of lower epiphysis of humerus	176	210
3. Length of femur	930	965
4. Width of distal epiphysis of femur	175	180
5. Minimum width of femur	110	140
6. Length from distal edge of premaxillary bones to vertex of skull	920	1000
7. Height of skull from vertex to the level of the masticatory surface of the teeth	710	740
8. Width of premaxillary on the level of alveolus	320	360(?)
9. Width of premaxillary on the level of foramen infraorbitale	240	280
10. Length of tusk on outside curvature	1400	1480
11. Diameter of tusk	74	101
12. Height of reconstructed skeleton	2150	2350

Measurements in millimeters.

scarce: in fact, the Sevsk locality is the only known locality of this kind in the world.

The data on the small mammal assemblage, and on spores, pollen, and the composition of the diatom flora from the ancient river bed where the bone-bearing layer was formed, all suggest that the late Pleistocene conditions in this area differed greatly from modern ones. Conditions also differed from those typical of mammoth populations in Eastern Siberia. Unlike the tundra-steppe with its typical mosaic landscape and vegetation, the Sevsk landscape was of a transitive type. Together with changing environment, the pressure of humans (but not overkill) who had long before colonized the Russian Plain made the Sevsk population among the last survivors of *M. primigenius* in the Russian Plain about 14 thousands years ago.

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Appendix A

An incomplete skeleton of a 15–17-year-old female mammoth placed into the group IV. Approximately 50% of the skeleton was preserved. Collection numbers: PIN 4353-4, 5, 8, 9, 24, 34, 39, 52, 54, 56, 60, 61, 86, 102, 119, 120, 123-127, 131, 132, 139, 142, 192, 221, 227, 242, 244, 245, 247, 248, 250, 251, 265, 268, 275, 280, 286, 270, 290, 316, 327, 332, 367, 368, 374, 375, 404, 412, 413, 416, 417, 419, 427, 429, 430, 436, 587, 593, 601, 710, 724, 737, 772, 782, 784, 793, 794, 808, 812, 822, 827, 828, 829, 832, 851, 857, 858, 861, 862, 969, 984, 985, 996, 1004-1006, 1009, 1012, 1013, 1020, 1023, 1045, 1060, 1063, 1068, 1077, 1079, 1086, 1095, 1139, 1171, 1175, 1222, 1227, 1252, 1255, 1298, 1453, 1454, 1462, 1469, 1555, 1156, 1599, 1600, 1601, 1634, 1670, 1674, 1698, 1754, 1757, 1777, 1782, 1859, 1862, 1935, 1941, 1958, 1982, 1989, 1992, 1995-1998, 2000-2002, 2031, 2085, 2086, 2091, 2150, 2211, 2267, 2276, 2297, 2298, 2331, 2448, 2472, 2475, 2611, 2821, 2939, 3010, 3027, 3052, 3069, 3118, 3121, 3137, 3156, 3171, 3172, 3176, 3230, 3235, 3236, 3359, 3363, 3372, 3433, 3568, 3573.

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