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Mammuthus intermedius (Proboscidea, Elephantidae) from the late Middle Pleistocene of the southern Western and Central Siberia, Russia: the problem of intermediate elements in the mammoth lineage

I.V. Foronova

ABSTRACT. A peculiar form of the thick-enamel mammoth from late Middle Pleistocene of the Kuznetsk Basin (South of Western Siberia) and from the Acheulian-Mousterian site Ust'-Izhul'1 with a unique faunal assemblage (North-Minusinsk Basin, Kurtak, Yenisei River, south of Central Siberia) is described. It is compared to *Mammuthus intermedius* (Jourdan, 1861) from Western Europe. The stratigraphic position and morphometric features of molars, defining the position of this form in the mammoth lineage, characterize it as an intermediate link in the transition from *M. trogontherii* to *M. primigenius*. *Mammuthus intermedius* inhabited interstadial/interglacial environments of late Middle Pleistocene and had a vast Eurasian range.

KEY WORDS: Middle Pleistocene, Early Paleolithic, *Mammuthus intermedius*, mammoth lineage, south of Siberia, Russia.

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Mammuthus intermedius (Proboscidea, Elephantidae) второй половины среднего плейстоцена на юге Западной и Средней Сибири (Россия): к вопросу о промежуточных звеньях в мамонтовой линии

И.В. Форонова

РЕЗЮМЕ. Своеобразный толстоэмалевый мамонт, известный из отложений второй половины среднего плейстоцена в Кузнецкой котловине (юг Западной Сибири) и ашель-мустьерского памятника Усть-Ижуль 1 с уникальным скоплением фауны (Северо-Минусинская котловина, Куртак, р. Енисей, юг Центральной Сибири), описан в сравнении с *Mammuthus intermedius* (Jourdan, 1861) Западной Европы. Стратиграфическая позиция и морфометрические особенности коренных зубов, определившие положение этой формы в мамонтовой линии, характеризуют ее, как одно из промежуточных звеньев, на переходном этапе филетической линии от *M. trogontherii* к *M. primigenius*. *Mammuthus intermedius* существовал в межстадиальных/межледниковых условиях второй половины среднего плейстоцена и имел обширный евразиатский ареал.

КЛЮЧЕВЫЕ СЛОВА: средний плейстоцен, ранний палеолит, *Mammuthus intermedius*, мамонтовая линия, юг Сибири, Россия.

Introduction

Proboscideans have a long history of study. The taxonomic definitions based on the traditional methods of dental analysis are, however, strongly impeded by the transgression of teeth characters. The taxonomy of the group still remains unclear and requires revision. This often and inevitably causes problems in biostratigraphic definitions and paleoclimatic reconstructions.

In order to obtain more precise taxonomical definitions and override the transgression, a more complex statistical approach was suggested using traditional morphometric molar features in an untraditional way. It was a method of so called "optimal parameters" (Garutt & Foronova, 1976), and a multiple stage method of cluster analysis of large series of M3. It allowed constructing multidimensional models of the *Archidiskodon-Mammuthus* lineage in Northern Eurasia (Foronova & Zudin, 1986, 1995, 1999, 2001; Foronova, 2001a, b, 2007, 2014) (see Figs. 4, 5).

This method clearly shows the structure of the mammoth lineage to be more complex than a simple gradualistic sequence presumed before. It illustrates evolutionary trends and discreteness of processes in the mam-

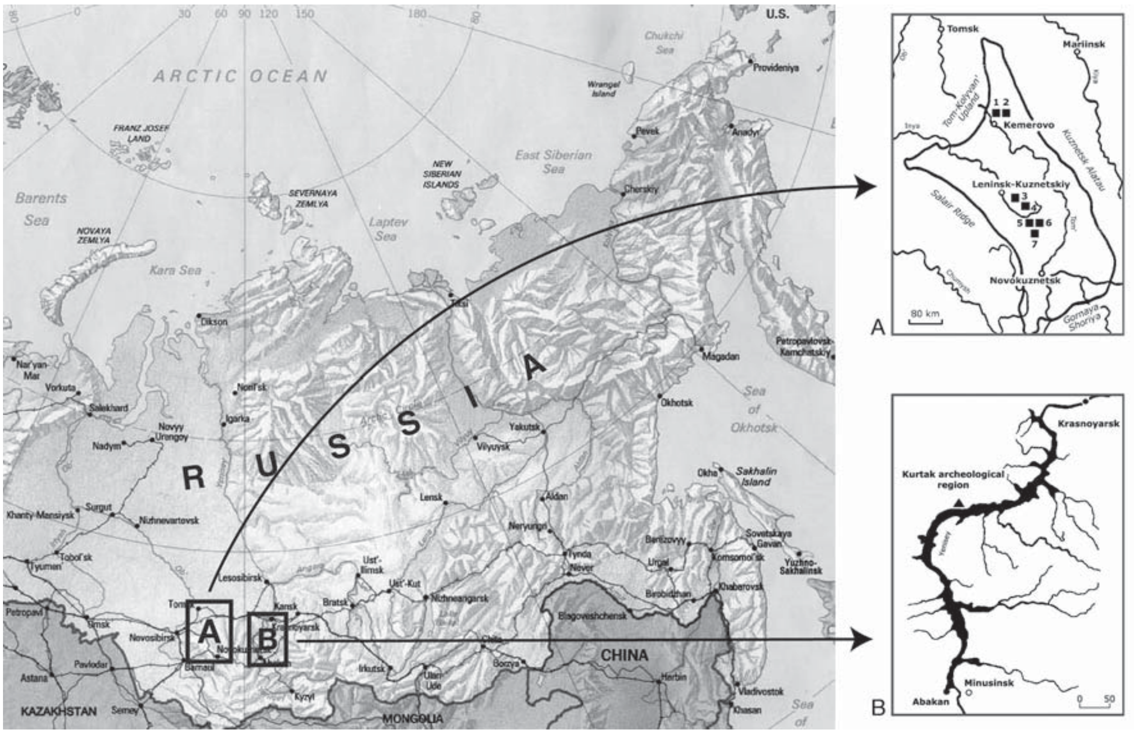

Fig. 1. Location of the Kuznetsk Basin (Southwestern Siberia) and North-Minusinsk Basin, Kurtak archaeological region (South-Central Siberia). A: Kuznetsk Basin. Locations of coal-mining pits (fossil mammal localities): 1 — Kedrovka, 2 — Chernigovo, 3 — Mokhovo, 4 — Gramoteino, 5 — Bachatsk, 6 — Novosergeevo, 7 — Krasnobrodsk. B: North-Minusinsk Basin. Kurtak archaeological region.

moth lineage. Moreover, the method may provide a solution to many pending problems, including the main ones: revealing intermediate elements (Garutt, 1971), revision of old taxa, and determining new ones within the lineage.

The present paper is devoted to one of such taxa, a peculiar *Mammuthus intermedius* (Jourdan, 1861) widely spread in Northern Eurasia at the end of Middle Pleistocene. The structure of its teeth gives it a definite position in the mammoth lineage among other intermediate forms between *Mammuthus trogontherii* (Pohlig, 1885) and *Mammuthus primigenius* (Blumenbach, 1799). Originally, this form was described in Western Europe (Lyon Plateau in the Rhône Valley, France) as *Elephas intermedius* (Jourdan, 1861; Lortet & Chantre, 1872). For a long time it was recognized as valid (Osborn, 1942; Aguirre, 1969; Beden & Guérin, 1975). But later the validity of this species was questioned (Lister, 1996). Recently French scientists revived *M. intermedius* and supplemented its diagnostics with molars from Abîmes de La Fage (Corrèze, France) (Beden & Guérin, 1975; Labe & Guérin, 2005).

In Russia, it was Baygusheva (1980) who described specific features of this unusual mammoth based on a record from the left bank of Severskiy Donets River (Kamensk, Rostov Region). She defined this form to be very close to *Mammuthus chosaricus* Dubrovo, 1966. In her opinion some of its distinctive features support establishing a separate subspecies within *M. primigenius*. Later, while developing the method and constructing diagrams based on the material from Europe, Eastern and Western Siberia (Foronova & Zudin, 1986), a prominent adaptive peak was recognized on each of the diagrams. Its center nearly matched the parameters of *M. intermedius* from France (according to data of Osborn, 1942) (see Figs 4, 5). Mammoths of similar morphological structure and geological age were also found in the Volga region (Kamskoe Ust'e and Mysy-Mansurovo) and described as a part of the Volga fauna (Averianov *et al*., 1992). Based on cranial and postcranial material Averianov attributed them to the so-called 'post-Khozar mammoth', following Baygusheva (1980) who placed the mammoth from Kamensk to this form.

Thus, the analysis of extensive Eurasian materials using the above mentioned method confirmed the existence of the specific mammoth form and showed its distribution from Western and Eastern Europe to Asia (in Western and Central Siberia) (Foronova & Zudin, 1986, 1995, 1999, 2001; Drozdov *et al*., 1990; Foronova, 2001a, b).

Despite the early discovery of this mammoth form in Siberia, the cited publications refer to it using the open nomenclature: *M. primigenius* ssp., thick-enamel form, intermediate between *M. chosaricus* and early *M. primigenius*; *M.* ex gr. *trogontherii–intermedius and M.* cf. *intermedius,* etc. We follow Baygusheva (1980, 1999) in considering this peculiar form of "post-chosaricus" thick-enamel early mammoth as a separate taxon.

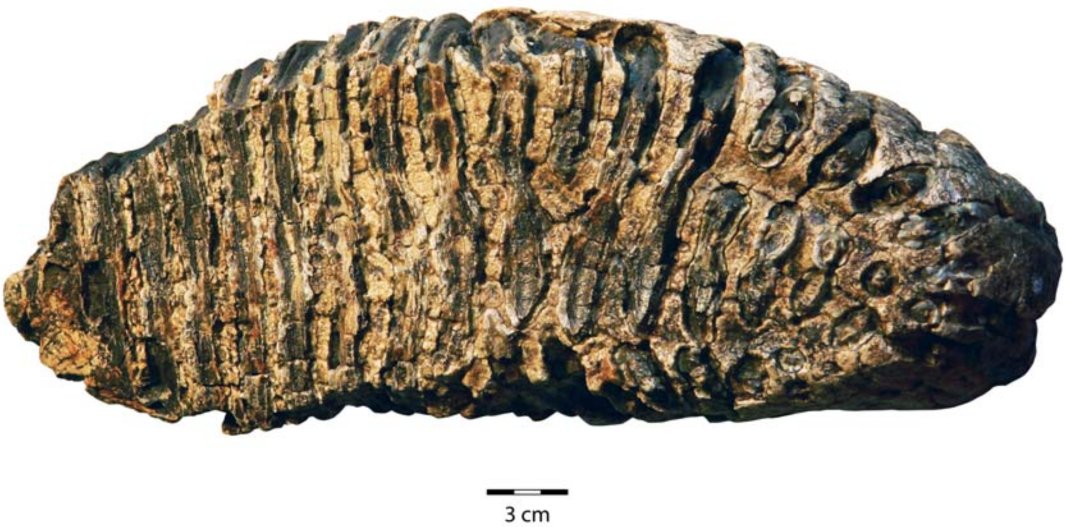

Fig. 2. *Mammuthus intermedius* (Jourdan, 1861): M^3 sin, IGM SB RAS #755. Krasogolovo layers of Kedrovka Formation, Bachatsk pit, Kuznetsk Basin. Occlusal view.

Below we provide a systematical description of this mammoth's molars from two major stratigraphic regions in southern Siberia, the Kuznetsk and North-Minusinsk Basins (Fig. 1), and justify its attribution to *M. intermedius* (Jourdan, 1861).

Abbreviations. IGM SB RAS — V.S. Sobolev Institute of Geology and Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk; IAE SB RAS — Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences, Novosibirsk.

Localities and material

The Kuznetsk Basin and Kurtak archaeological district are the largest South-Siberian stratigraphic regions that represent almost continuous sequence of Quaternary sediments and faunas (Fig. 1). The examination of rich paleontological collections from these regions allowed us to trace the development of Proboscidea through the entire Pleistocene (Foronova, 1986, 1998, 2001a, b, 2010).

Kuznetsk Basin (54°13′ N, 86°20′ E) is a vast intermountain depression situated in the South-East of Western Siberia. It is surrounded by Kuznetsk Alatau Ridge from the East, Mountainous Shoriya from the South, Salair Ridge in the West and Kolyvan-Tomsk Upland from the North-East (Fig. 1A). Eight of Russia's largest coal-mining pits located here expose a thick (over 100 m) layer of Neogene-Quaternary sediments. This creates unique possibilities for collecting abundant paleontological material characterizing almost every period of Pleistocene. The coal-mine exposures also facilitate complex geological and taphonomical observations. A detailed biostratigraphic subdivision of the Quaternary in the region was performed on the basis of the multimethod study of the large mammal fauna. It resulted in a refined regional stratigraphic scale of the Kuznetsk Basin, including important refinement of stratigraphical ranges of the Kedrovka and Bachatsk Formations, and establishing the Berezovo and Chernigovo Formations (Foronova, 2001b).

The material under study (18 last mammoth molars) was excavated in situ in Bachatsk, Novosergeevo, Mokhovo, and Kedrovka coal pits, from Krasogolovo beds in the upper part of fluviatile Kedrovka Formation. Molars of the peculiar form under study (Fig. 2) constitute the majority of mammoth teeth found in the entire Kedrovka Formation. The Krasogolovo beds also yielded remains of *Ursus rossicus* Borissiak, 1930, *Panthera spelaea* Goldfuss, 1810, *Equus* cf. *germanicus* Nehring, 1884, *Cervus elaphus* Linnaeus, 1758, *Megaloceros giganteus* Blumenbach, 1803, *Alces* cf. *alces* Linnaeus, 1758, and *Bison priscus* Bojanus, 1827.

Two additional teeth of similar structure were found in the Mokhovo pit, in loess-like loams of the overlying Berezovo Formation, particulary, in its lower part with a paleosol. These deposits also yielded remains of *Ursus* cf. *arctos* Linnaeus, 1758, *Panthera spelaea, Stephanorhinus kirchbergensis* (Jäger, 1839) (=*Dicerorhinus mercki* (Jäger, 1839)), *Equus* sp., *Cervus elaphus*, *Megalocerus giganteus*, *Bison priscus.* Paleontological characteristic of this series can be supplemented with a complex of small mammals. According to Galkina (Zudin *et al.*, 1982), it is represented by: *Lagurus* cf. *lagurus*, *Microtus* (*Stenocranius*) cf. *gregalis*, *Myospalax* cf. *myospalax*, *Dicrostonyx simplicior-henseli*.

The species composition of large and small mammals and a clear geological position within a nearly continuous sequence of Quaternary deposits in the Kuznetsk Basin, indicate late Middle Pleistocene and the

Shirta Interglacial/Interstadial (inter-Saalian) as the time of sedimentation of the upper part of Kedrovka Formation (Krasogolovo layers) and Berezovo Formation (Foronova, 2001b).

North-Minusinsk Basin (55°09′ N, 91°32′ E) is situated in the south of Central Siberia and represents one of intermountain depressions in the eastern part of Altai-Sayan mountainous region (Fig. 1B). From east and west it is bounded by the ridges of Kuznetsk Alatau and Eastern Sayan. The main water artery of the Basin is the Yenisei River. Its valley is presently filled by the Krasnoyarsk Reservoir. The erosional coastal cliffs of the reservoir hosted the most important archaeological sites of Siberia. 20-km long coastal zone is known as the Kurtak archeological district with numerous sites and localities of Quaternary mammals (Drozdov *et al.*, 1990). The local sections of the Quaternary are among the best in south Siberia. They comprise the 60–100 m thick loess-paleosol sequence and alluvial sediments of high terraces (Krukover & Chekha, 1999; Haesaerts *et al.*, 2009; etc.).

In this south Siberian region, mammoths were found in the Ust'-Izhul'1 locality. It is one of the well-known Paleolithic sites occurring in the eastern part of Kurtak archaeological district, at the left bank of the Krasnoyarsk Reservoir. The locality is famous for the immense amount of animal remains and human artifacts that have been described in numerous publications (Drozdov *et al.*, 1990; Ovodov, 1995; Laukhin *et al.*, 1999; etc.).

The mass burial of mammal bones (beds 25 and 26) occurred at the depth of 18–20 m at the base of mostly loamy member overlying the eroded terrace alluvium. The fossiliferous beds are represented by cherry-terracotta colored clays of bed 25 (with interbeds of loamy sand) changing to dark nonstratified humus-rich clays of bed 26. The major part of the fossil accumulation is represented by hundreds of mammoth bones and more than 40 teeth of various generations, from dP4 to M3. It was established that these remains belonged to approximately 16 individuals of presumed age from 2 to 40–60 years. Other finds included badger, marmot, mole vole, broad-toed horse, rhinoceros, red deer, and small bison. The fact that some bones were found in anatomical order implies in situ accumulation (Ovodov, 1995). Eight molars of last generation (4 uppers and 4 lowers) are used in the present study (Fig. 3).

These faunal remains co-occurred with Acheulian-Mousterian implements. Numerous artifacts with characters of the Levallois technique occurred among the animal remains. The composition of rock material used for these tools is identical to Early-Paleolithic and Mousterian assemblages of the Kutrak archaeological district. Human activity is also evidenced by fire spots and abundant charcoal pieces on the surface of a paleosol in the layer 26. In addition, some bones have cut-marks and signs of breaking easily distinguishable from bites of carnivores (Laukhin *et al.*, 1999).

Along with archaeological data and other dating information, the age Ust'-Izhul' 1 site was significantly constrained by the author using its faunal composition. Broad-legged horse attributed to *E.* ex gr. *mosbachensis-germanicus* occurred in Siberia in the Middle Pleistocene. Mammoths, similar to *M. intermedius*, are represented by a thick-enamel form transitional between Middle Pleistocene *M. chosaricus* and the typical Late Pleistocene *M. primigenius* (Drozdov *et al.*, 1990; Foronova & Zudin, 1995). These data were later used for refining the age of the site (Ovodov, 1995; Laukhin *et al.*, 1999; Foronova, 2000).

Methods

The methodology used in this contribution has been elaborated and described in detail by Foronova & Zudin (1986, 1999) and discussed in subsequent publications (Foronova & Zudin, 1995, 2001; Foronova, 2001a, b, 2003, 2007, 2014). It was based on plotting and analyzing multi-dimensional diagrams based on values of enamel thickness (E), plate frequency (PF) per 100 mm of crown length and average plate length (PL) of several thousands of molars (M3) representing the *Archidiskodon-Mammuthus* lineage from numerous Quaternary localities and archaeological sites in Northern Eurasia (Western and Eastern Europe, Western, Central, and Eastern Siberia) (Figs. 4, 5). These features show directed evolution and are traditionally regarded as the most important for defining taxonomic position of mammothoid elephants. The isolines of abundance plotted against bivariate graphs revealed a complex and nonlinear morphospace. It is believed that in the giant data set as we used the major peaks of the morphospace correspond to non-random adaptive zones of dental evolution in the mammoth lineage. The detailed description of the methods is provided in above mentioned publications.

In the course of analysis of two-dimensional diagrams, additional dental parameters were also used for comparison of individual clusters and evaluation of distribution pattern of molars. Crown width, total number of plates, hypsodonty index, angle of molar eruption, and angle of abrasive wear were analyzed using Kolmogorov-Smirnov's criterion (Miller & Kahn, 1963). Shape of enamel loops on the masticatory surface and ratios of plate cement, dentine, and enamel in molars were also included in the analysis (Foronova & Zudin, 1986).

Variability

The samples included into the analysis were selected on the basis of their relative uniformity: different types of variability, except intraspecific variability, were excluded. The age variability of teeth was excluded because only the molars of last generation (M3) were analyzed. The dentition asymmetry was analyzed using the subset of European mammoths. Separate diagrams for lower, upper, right and left M3 are virtually indistinguishable, the number, position and parameters of clus-

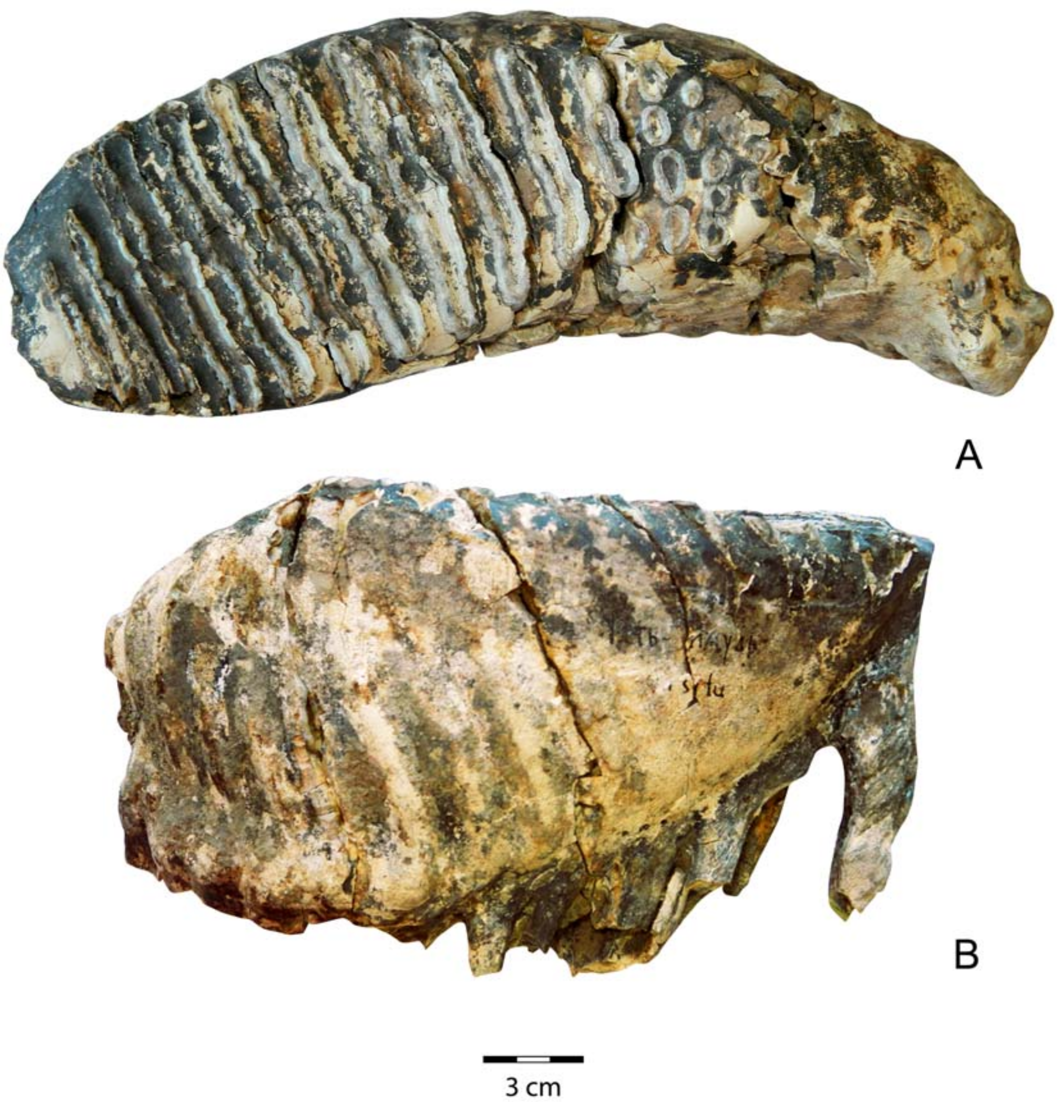

Fig. 3. *Mammuthus intermedius* (Jourdan, 1861): M_3 sin, IAE SB RAS #25, Ust'-Izhul'1 site, Kurtak archaeological region. A — occlusal view; B — lingual view.

ters do not change (Foronova & Zudin, 1986, 1999, 2001; Foronova, 2007). Variations of features from different stages of abrasive wear of a crown were excluded due to technique for measuring enamel thickness (along the entire chewing surface), described above. Pathological teeth were extremely rare. However, their key features appeared to be similar to those of normal teeth. Geographical variability was excluded by plotting diagrams separately for Europe, Western and Eastern Siberia. These graphs showed both similarity of the general structure and the presence of the overwhelming majority of elements, analogous in position and structure.

Analysis of distribution structure

Separate diagrams were built for Europe, Western and Eastern Siberia. They appeared to be extremely informative and clearly demonstrated the lineage structure to be far more complex than a traditional gradualistic sequence still in use.

Generally, the variability area (from archaic forms to the latest mammoth) reflects canalizing selection in the lineage due to global natural changes of the Quaternary (Figs. 4, 5). However, the most important and innovative result is that selection of combinations of the features under study (i.e. of levels of dental system specialization, most optimal for different stages of lineage development) was observed to be discrete. The structure consists of subordinated "adaptive peaks" (zones of high distribution density) and depressions, and resembles the "Wright's symbolic picture" (in terminology of Dobzhansky, 1951). The peaks group into ensembles, so a hierarchy of marginal depressions can be seen. One of the large

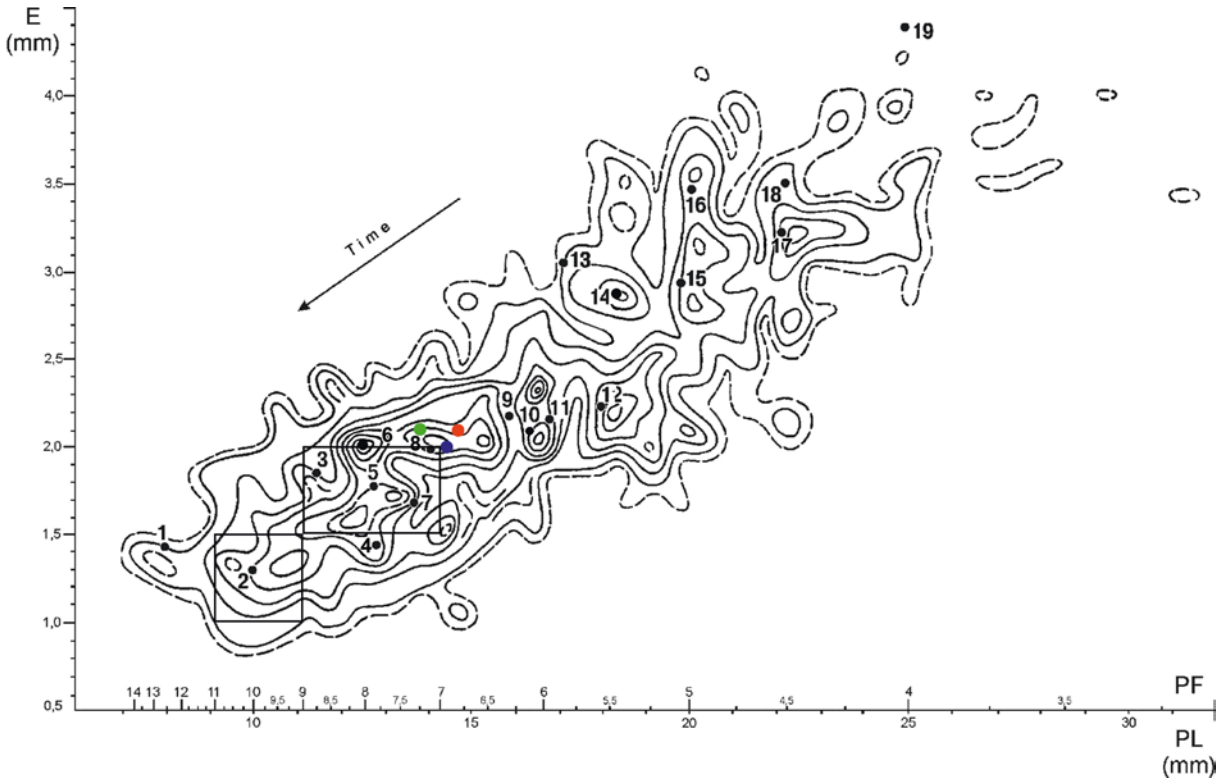

Fig. 4. Variability of characters of M3 in elephants of the mammoth lineage in Europe (by materials from Western and Eastern Europe) (modified after Foronova & Zudin, 1999).

Coordinate axes: E — enamel thickness; PF — plate frequency per 100 mm; PL — length of one plate. Continuous isolines of distribution density are drawn with increment of 0.5 Uniform Density Units, punctuated isolines, 0.25 Units, outer isoline corresponds to 0.25. **Punctuated lines** show assumed direction of lineage development due to selection pressure. **Rectangles** show variability limits for features of early and late form of *M. primigenius* (according to Vangengeim, 1961).

Dots are the coordinates of typical specimens of taxa distinguished in the lineage and some peculiar forms: 1 — *M. primigenius sibiricus*; 2 — *M. primigenius primigenius*, neotype; 3 — *M. primigenius jatzkovi,* holotype; 4 — *M. primigenius fraasi,* holotype; 5 — *M. primigenius*, early form, average parameter values; 6 — *M. primigenius* (Chokurcha site); 7 — *M. primigenius,* lectotype; 8 — *M. intermedius* (after Osborn, 1942); 9 — *M. trogontherii chosaricus*, holotype; 10 — *M. trogontherii chosaricus,* holotype (authors' measurements); 11 — *M. trogontherii trogontherii*, lectotype; 12 — *M. trogontherii* (Azov Museum; authors' measurements) = *A. wuesti*; 13 — *A. meridionalis cromerensis*, holotype; 14 — *A. m. voigtstedtensis,* holotype; 15 — *A. m. tamanensis*, holotype; 16 — *A. meridionalis*; 17 — *A. m. meridionalis*, holotype; 18 — *A. gromovi*; 19 — *A. m. taribanensis.*

Color dots stand for mean values: red — *M. intermedius* (Jourdan, 1861), Rhône, France, after Labe & Guérin (2005); green — *M. primigenius* from Kamensk town, Rostov Region, after Baygusheva (1980, 1999); blue — *M. primigenius* from Kamensk town, Rostov Region, measurements of I. Foronova and A. Zudin.

ensembles corresponds to the final stage of lineage development within the genus *Mammuthus*. In addition to adaptive peaks of axial zone, we pioneered to find series of peaks in "thick-enamel" and "thin-enamel" areas of distribution. They are oppositely oriented and clinally linked with the axial zone peaks. These peaks are entirely new elements, significantly differing the structure from traditional gradualistic model. Thick-enamel peaks are represented by the forms with thickened folded enamel, medial sinuses, and low hypsodonty of a crown, whereas high hypsodonty, rare narrow plates with thin and weakly folded enamel are typical of thin-enamel forms.

The comparison of regional diagrams shows transcontinental distribution of the majority of phenotypes and chiefly autochthonous development at the continental scale. Slight difference between the parameters of analogous phenotypes from various regions implies geographical clinal variability due to different responses of regional environments to global climatic changes. Thick-enamel and thin-enamel adaptive peaks are regarded as forms with different ecological adaptations. Morpho-functional differences, accompanying fauna and flora, different habitats, physical parameters, and certain agreement between the sequence of these forms and marine oxygen-isotope stages provide grounds to link thick-enamel and thin-enamel adaptations with interglacial and periglacial environments respectively. It makes forms of the mammoth lineage significant for paleoecologic reconstructions.

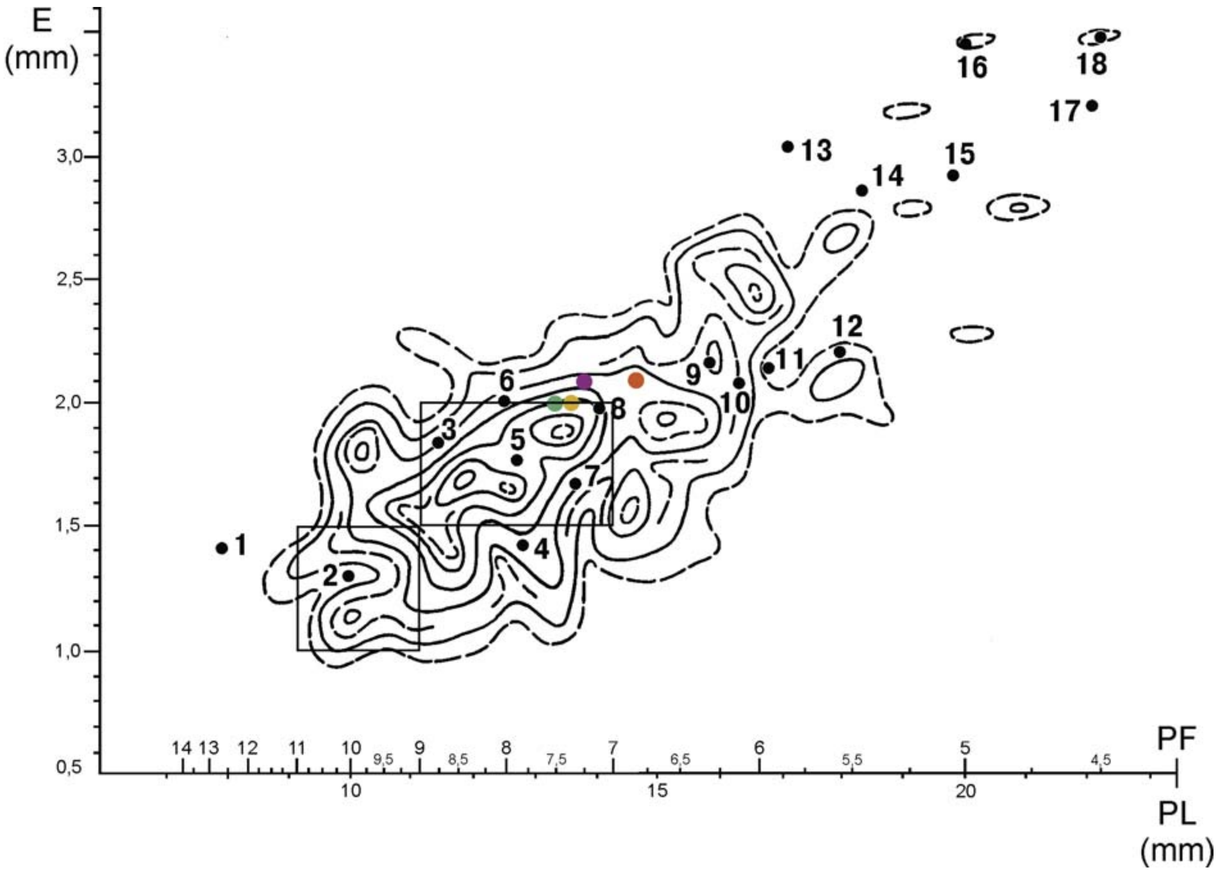

Fig. 5. Variability of characters of M3 in elephants of the mammoth lineage from Kuznetsk Basin (south of Western Siberia). See Fig. 4 for details.

Color dots stand for mean values of *M. intermedius*: red — after Labe & Guerin (2005); yellow — Kuznetsk Basin, after Foronova (2001b); violet — Ust'-Izhul' 1, Kurtak, after Zudin & Foronova, 1995; Foronova, 2000; green — Oyash River, Novosibirsk Region, measurements of V.E. Garutt and I. Foronova.

Results

Systematic Paleontology

Order Proboscidea Illyger, 1811
Family Elephantidae Gray, 1821
Genus *Mammuthus* Brookes, 1828
Mammuthus intermedius (Jourdan, 1861)
Figs. 2, 3; Tab.1.

1861: *Elephas intermedius*: C. Jourdan, Des terrains sidérolitiques: 1013.

1990: *Mammuthus primigenius* ssp. (thick-enamel form, intermediate between *M. chosaricus* and early form of *M. primigenius*): Drozdov *et al*., Chronostratigraphy of the Paleolithic Sites…: 111, Table 5.

1995: *Mammuthus* ex gr. *trogontherii – intermedius*: I.V. Foronova & A.N. Zudin, O novom metode izucheniya…: 132, fig. 1.

1999: *Mammuthus* cf. *intermedius*: I.V. Foronova, Quaternary mammals….: 86, fig. 9(2), # 575.

2001a: *Mammuthus* cf. *intermedius*: I.V. Foronova, History of Quaternary proboscideans of south…: 110–111, figs.1, 2.

2001b: *Mammuthus* cf. *intermedius*: I.V. Foronova, Quaternary mammals of the South-East…: 86–87, 208–209, Table X, fig. 2.

TYPE MATERIAL. The species was originally based on check teeth found in the vicinity of Lyon, France (Jourdan, 1861). **Neotype**: right hemimandible No.42341 (Beden & Guérin, 1975, pl. 8). **Paratypes**: four third molars from Abîmes de La Fage (Corrèze, France): lower M_3 No.42303 and 42329, upper M^3 No.42302 and No.42312 (Labe & Guerin, 2005).

TYPE LOCALITY. Karst filling of Aven I des Abîmes de La Fage, at Noailles (Corrèze, France), upper Middle Pleistocene (Labe & Guerin, 2005).

MATERIAL

Kuznetsk Basin, Southeast of Western Siberia. *Upper molars:* M^3 dex and M^3 sin, paired, complete, #6240; M^3 dex, #6007; M^3 dex, #6021; M^3 dex, #5042, Mokhovo coal-mining pit, Krasogolovo layers of Kedrovka Formation, basal part of Berezovo Formation. M^3 dex, #4038; M^3 sin, #766, Kedrovka coal-mining pit. M^3 dex, #11; M^3 dex, #7000, Novosergeevo coal-mining pit. M^3 sin #755, Bachatsk coal-mining pit, Krasogolovo layers of Kedrovka Formation.

Lower molars: M_3 sin, complete, #9075; M_3 sin, #6258, Novosergeevo coal-mining pit, Krasogolovo layers of Kedrovka Formation. M_3 dex, complete, ##

Table 1. Molars (M3) of mammoths from the late Middle Pleistocene of Europe, Western and Central Siberia.

Measurements, mm	*M. intermedius* (Jourdan, 1861) Rhône, Lion, France, (Labe B., Guérin C., 2005)		*M. intermedius* Kuznetsk Basin, IGM SB RAS, (Foronova & Zudin, 1986, 1995, 1999; Foronova, 1990, 2001)		*M. intermedius* Ust'-Izhul' 1, Kurtak, IAE SB RAS (Foronova & Zudin, 1995; Foronova, 2000, 2001)	
	M^3 n=2	M_3 n=10	M^3 n=6	M_3 n=9	M^3 n=4	M_3 n=4
1. Crown length	300–305	+138–305	240–285	245–365	280–300	257–290
2. Crown width	96–102	80–96	90–106	80–108	89–94	81–88
3. Crown height	158	122–154	180–186	130–144	160–190	130–140
4. Plate number	24	–	23+	24–25	22–24	20–23
5. Plate frequency / 100 mm	6.4–6.7	6.5–7.5	7.0–8.0	6.5–8.0	7.5–8.5	6.5–8.0
	(mean 6.75)		(mean 7.3)		(mean 7.25)	
6. Average length of a plate	–	–	13.1–14.6	13.0–14.4	12.5–13.5	12.5–14.8
			(mean 13.6)		(mean 13.4)	
7. Enamel thickness	1.7–2.0	1.9–2.4	1.8–2.3	1.7–2.3	2,0–2,2	2,0–2,2
	(mean 2.1)		(mean 2.0)		(mean 2.1)	
	M. intermedius Novosibirsk Region, Oyash river, Novosibirsk Regional Studies Museum (measurements by V. Garutt, I. Foronova; Foronova, 2001)		*M. primigenius* Kamensk, Rostov Region, Collection of Novocherkassk Regional Studies Museum (Baygusheva, 1980, 1999)		*M. primigenius* Kamensk, Rostov Region, Collection of Novocherkassk Regional Studies Museum (measurements by I. Foronova and A. Zudin)	
	M^3 n=2	M_3 n=2	M^3 n=4	M_3 n=3	M^3 n=3	M_3 n=2
1. Crown length	195+	225+	303–310	280	245–310	260–265
2. Crown width	93–94	88	95–97.6	91.8	93–98	92–94
3. Crown height	190+	–	170	–	175	–
4. Plate number	23–24	15+	24–25	18+	23+	18+
5. Plate frequency / 100 mm	7.0–8.0	7.5	7.35–7.75	6.75–7.25	7.0–8.0	6.0–6.5
	(mean 7.5)		(mean 7.25)		(mean 6.9)	
6. Average length of a plate	13.0–13,5	–	–	1.6–13.6	15.0–15.9	13.0–13,5
	(mean 13.8)				(mean 14.3)	
7. Enamel thickness	1.8–2.0	1.85–2.2	2.1–2.2	1.7–2.2	1.9–2.3	1.8–2.0
	(mean 2.0)		(mean 2.1)		(mean 2.0)	

3186, 8016; M_3 dex, #8254, Mokhovo coal-mining pit. M_3 dex, #3432; M_3 dex, #604. Bachatsk coal-mining pit. M_3 dex, #8009, Sartaki Krasogolovo layers of Kedrovka Formation. Collection of IGM SB RAS.

North-Minusinsk Basin, Kurtak archaeological district, South of Central Siberia.

Upper molars: M^3, ## 10, 11, 12, 13. *Lower molars*: M_3, ## 25, 26, 27, 28.

Ust'-Izhul'1 Paleolithic site, beds 25–26, left bank of Krasnoyarsk Reservoir. Collection of IAE SB RAS.

Geological age. Late Middle Pleistocene, Shirta horizon of Western Siberia, Odintsovo horizon of Eastern Europe, second half of Saalian of Western Europe, ca. 200-160 ka.

Description and comparison

Molars (M3) of this Siberian mammoth are relatively large: upper molars are 240–300 mm long, 89–106 mm wide, and 160–190 mm high; lower molars are 245–365 mm long, 80–108 mm wide and 130–144 mm high. Mean plate length (PL), 13.4–13.8 mm; mean plate frequency (PF), 7.25–7.5; mean enamel thickness (E), 2.0–2.1 mm (calculated for upper and lower molars) (Tab. 1).

In values of PF, PL and E the mammoth under study significantly differs from the neotype of *M. primigenius* (Blumenbach, 1799) corresponding to the late form of the species (Figs. 4, 5). On the basis of traditional morphometric analysis this mammoth could be regarded as one of the earliest representatives of *M. primigenius* of the early type, since the provided values partly correspond to extreme "archaic" values of the early form of mammoth (according to the variability range given by Vangengeim, 1961). Alternatively, diagrams based on our method (Figs. 4, 5) demonstrate that a significantly compact group (a distinct adaptive peak near the point 8) can be observed at this stage of mammoth lineage development. Partly, it is situated in "archaic" upper right corner of *M. primigenius* (see the right rectangle on the diagrams). However it can be clearly seen that variability limits of this form are much broader and overlap the conventional limits proposed for early *M. primigenius* by Vangengeim (1961) reaching even more "archaic" values (Tab. 1). Obviously this form has an intermediate position between so-called "Khosar" and "early" mammoths. To be more precise, it differs from *M. chosaricus* Dubrovo in higher (more progressive) plate frequency and from *M. primigenius* of early type in somewhat thicker enamel.

Dental parameters of the Siberian mammoths attributed to this form are rather similar (Tab. 1). Apart from the materials from Kuznetsk and North-Minusinsk Basins, this group of finds includes a full skeleton of female mammoth, found in blue clays of a coastal exposure of Oyash River near the city of Novosibirsk (exhibited in Novosibirsk Regional Studies Museum). Measurements of its skull and post-cranial skeleton were published by V.E. Garutt (Averianov *et al.*, 1992: 31–54). This material corresponds to all morphological features of the genus *Mammuthus* and differs only in small dimensions. Dots corresponding to average values of PF and E of these Siberian forms are densely spaced within the mentioned adaptive peak (Fig. 5). The only exception is slightly increased enamel thickness of mammoths from Ust'-Izhul'1 locality, which is more similar to the values of European representatives of the group and implies mild environmental conditions of these mammoths' habitat in Siberia.

In addition, characteristic features of these mammoths' M3 include lower hypsodonty, rare medial widening of plates, in most cases roughly folded and (as mentioned above) thickened enamel. These features are typical of teeth from the so-called "thick-enamel" and partly "axial" zones of distribution. Sequence of forms with such a specialization of molars, distinguishing them from thin-enamel type, has been traced from the archaic to the latest forms of elephants (Foronova & Zudin, 1986, 1999, 2001; Foronova, 2001a, b).

The listed morpho-functional dental features, coupled with geological data and other data, indicate a habitat with reltively mild conditions in the late Middle Pleistocene, corresponding to the intra-Riss/intra-Saalian Shirta interstadial horizon of the West Siberian stratigraphic chart (Foronova, 2001b).

In Europe, *Mammuthus intermedius* (Jourdan, 1861) from interglacial loess of Lyon Plateau in France corresponds to the same stratigraphical interval. This species has a long history of definitions, descriptions, denials and later revivals (Osborn, 1942; Aguirre, 1969; Beden & Guérin, 1975; Labe & Guérin, 2005). The morphological and chronological characters of this species correspond to the distinct adaptive peak in the diagrams and define its position in the lineage. Previously, we have shown (Foronova & Zudin, 1986, 1999; Foronova, 2001) that the mean values of PF and E in topotypic forms nearly coincide with the center of the distinct adaptive peak in the diagrams (Figs. 4, 5; black dot 8) and are very similar to the available Siberian data. A recent contribution (Labe & Guérin, 2005) revisiting *M. intermedius* provided somewhat different values for this form. The diagrams show that revised mean values (red dot) are slightly shifted towards the "archaic" area, but its variability range still closely corresponds to that of the Siberian form under study.

In European Russia, Baygusheva (1980, 1999) has long since described similar mammoths in Kamensk town, Rostov Region. They deserve a special attention, because their values of PF, PL and E, similar to *M. intermedius* from France, closely match the grouping center of the corresponding adaptive peak (Tab. 1; Fig. 4). In course of her study Baygusheva concluded the position of this so-called "early mammoth" to be conterminal with *M. chosaricus* and proposed to distinguish it as a subspecies within *M. primigenius*. Our study demonstrates that this mammoth from southern Russia hardly differs in its parameters from the southern Siberian mammoth studied in the present paper. (Tab. 1; Fig. 4).

Two mammoth skeletons from Kamskoe Ust'e and Mysy-Mansurovo sites in the Volga region may be conspecific with the form under study. It is important that Averianov, who studied the molars, cranial and post-cranial material of the Volga mammoths, attributed them to the so-called 'post-Khozar mammoth'. Moreover, Averianov emphasized that in dental characters the mammoths from Mysy-Mansurovo characterize the

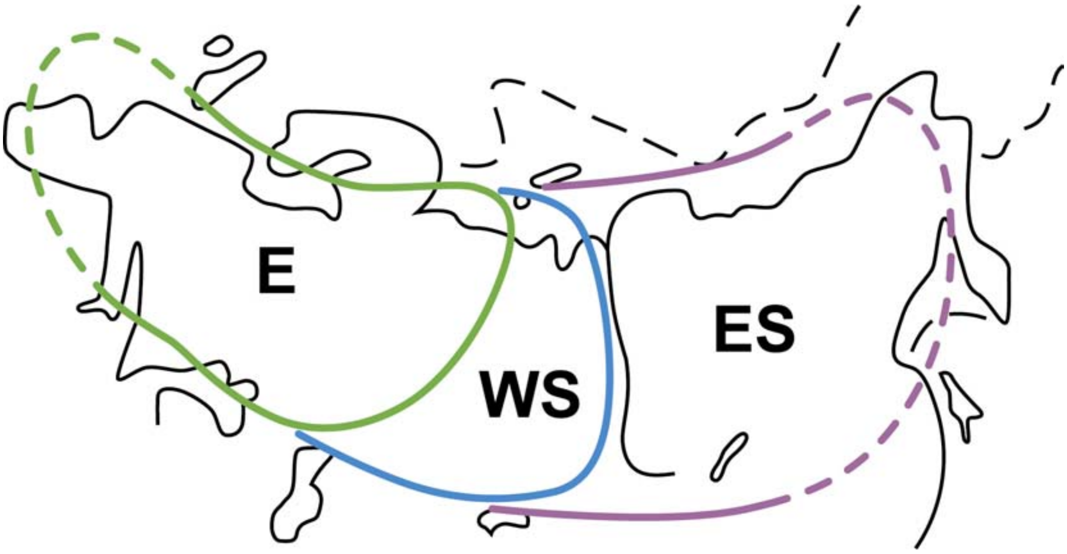

Fig. 6. Schematic distribution of *M. intermedius* (Jourdan, 1861) in the late Middle Pleistocene in Eurasia. Range borders are given according to geographical distribution of material used (after Foronova & Zudin, 1986; Foronova, 2007, with modifications). E — Europe; WS — Western Siberia; ES — Eastern Siberia.

same 'stage of phenotype stabilization' (in terminology of Foronova & Zudin, 1986) as the Kamensk mammoth described by Baygusheva (1980, 1999) (Averianov *et al*., 1992: 74).

Hence, all provided data and comparison make us refer the late Middle Pleistocene mammoth form of south of Western and Central Siberia to *Mammuthus intermedius* (Jourdan, 1861).

Comments

Comparison of European and Siberian diagrams demonstrates that the analyzed adaptive peak is more pronounced and advanced in its parameters in the Siberian diagram (Figs. 4, 5). This effect was noted at the beginning of our work with the method (Foronova & Zudin, 1986, 1999, 2001), when a slight displacement of all similar adaptive peaks of mammoth lineage occurred while superimposing the diagrams of Europe and Siberia. We believe that this is a reflection of clinal variability of the lineage, which was caused by different reaction of regional environments (changes in landscape and vegetation zones) to global climatic changes. This is also illustrated by Fig. 6 which shows schematic distribution of *M. intermedius* (Jourdan, 1861) in late Middle Pleistocene in Eurasia. Range boundaries are given according to geographical distribution of extensive materials from Europe, Western and Eastern Siberia (Foronova & Zudin, 1986).

Distribution

The large factual material (measurements of thousands of M3 from numerous localities of Western and Eastern Europe, and entire Siberia) collected and used for compilation of diagrams, as well as numerous literature data indicate a fairly large geographic range of *M. intermedius* (Fig. 6) covering almost the entire northern latitudes of Eurasia (Foronova & Zudin, 1986, 1999).

Discussion

The materials provided and discussed in this paper refer to one of the most long-lasting and complicated problems in Quaternary paleontology, the distinguishing and determining of the so-called "intermediate elements" in the *Archidiskodon-Mammuthus* lineage (Pohlig, 1885; Dubrovo, 1966; Garutt, 1971, and others).

Considerable climatic and environmental changes at the end of Early and especially in Middle Pleistocene have conditioned further development of the mammoth lineage. Periodic changes of landscape and vegetation have caused an increase of plate number and frequency in the tooth crown, and decrease of plate length and enamel thickness. The obtained diagrams clearly show these changes to be successive stages of elephants' adaptation to periodic environmental changes. A number of transitional forms (well-pronounced adaptive peaks) between *M. trogontherii* and *M. primigenius* s.l. can be seen on all regional diagrams (including the one for Kuznetsk Basin) in the major part of the late Middle Pleistocene (Tobol, Samarovo, and Shirta horizons of West Siberian stratigraphic scale (= Holstenian and major part of Saalian of Western Europe).

One of such intermediate forms is undoubtedly *M. intermedius* first described by Jourdan (1861) as *Elephas intermedius* whose numerous cheek teeth were found near Lyons (Rhône, France). Labe & Guérin (2005) provided a brief history of study of this species, reestablished it as *M. intermedius* (Jourdan, 1861) and proposed the inclusion of all described forms spanning the interval between *M. trogontherii* and *M. primige-*

nius to this species. These authors estimated a chronological range of *M. intermedius* within the zone MNQ24 of C. Guérin biochronological scale, from 305 to 105 ky. All forms more advanced than *M. trogonterii,* including *M. t. chosaricus* (Dubrovo, 1966, Garutt, 1972), *M. primigenius-trogontherii* (Guenther, 1969) and others, are regarded as synonyms to *M. intermedius*.

Another related issue is the status of the species *M. chosaricus* Dubrovo, 1966. In the stratigraphical scheme, this form spans the interval between 400–300 ka and corresponds to Singil/Tobol faunal complexes of the Russian continental scale (Holstenian of Western Europe). Thus the upper boundary of *M. trogonterii* is restricted to 400 ka or the mid Middle Pleistocene. The recognizing of *M. chosaricus* is usually a much more difficult problem than in case of other species. As we have already noted (Foronova, 2001b) this form lacks a clear morphological definition. The Khosar mammoth was initially described as a late subspecies of *M. trogontherii*, *M. trogontherii chosaricus* (Dubrovo, 1966), but later raised to a species level (Garutt, 1972). Rationalizing the taxonomic validity of theses two subspecies Dubrovo provided the variability range of plate frequency of *M. t. trogontherii* as 5.0–7.0, but it appears to be the same for *M. t. chosaricus.* The enamel thickness varies from 2 to 3.5 in *M. t. trogontherii* and from 2.0 to 2.5 in *M. t. chosaricus.* When the mean values of the lectotype of *M. trogontherii* (PF: 6.25; E: 2.1) are compared to values in *M. t. chosaricus* (PF: 6, 25, E: 2, 5), it becomes clear that the two forms are hard to distinguish. In other words, when a variability range of a taxon is nested within variability range of another taxon, that Dubrovo's diagnostics is obviously incorrect. The described situation is vividly reflected in the European and Siberian diagrams which demonstrate the proximity of dots 9, 10 and 11 corresponding to the typical specimens of these two forms (Figs. 4, 5).

In addition, the diagrams, especially the Siberian one, demonstrate one extra adaptive peak different from *M. intermedius* that occupies a substantial interval from the "typical" *M. trogontherii-chosaricus* to *M. intermedius.* Obviously, it was this form (probably a subspecies), and not a vague *M. chosaricus*, that could be a predecessor of *M. intermedius*. Moreover, Labe & Guérin (2005) spreading the boundaries of *M. intermedius* to this entire interval (down to *M. trogontherii*) and including into it "*M. chosaricus*", date its lower boundary at 305 ka.

Our previous studies (Foronova & Zudin, 1986, 1999, 2001; Foronova, 2001a, b, 2007, 2014) have shown that thick- and thin-enamel forms (perhaps, in rank of subspecies) could correspond to the second half of Middle Pleistocene, beginning from 400 ka as shown by provided diagrams and results of other studies. Forms with thin enamel inhabited severe periglacial environments, while thick-enamel forms lived in interstadial and interglacial climatic conditions. Two thin-enamel forms correspond to the time-span of 400–130 ka or the late Middle Pleistocene. The first form, identified as *Mammuthus* sp., occurred in late Middle Pleistocene (Khazar and Samarovo horizons of the Russian timescale, or Early Saalian in Western Europe). The second form, described as *M. primigenius* cf. *fraasi* Dietrich 1912 (Figs. 4, 5; dot 4), corresponds to the very end of Middle Pleistocene (Tazovo horizon of the West-Siberian Stratigraphic Scale of Russia, or Late Saalian in Western Europe) (Foronova, 2007, 2014).

The form *M. intermedius* (Jourdan, 1861) described in this paper as judged by its dental characters inhabited mild and relatively warm environment of inter-Saalian, late Middle Pleistocene, Shirta Interglacial/Interstadial of Southern Siberia, ca. 200–160 ka.

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References

Aguirre E. 1969. Revision sistematica de los Elephantidae por su morfologia y morfometria dentaria // Estudios Geologicos. Madrid. Vol.24. P.123–177; Vol.25. P.317–367.

Averianov A.O., Baryshnikov G.F., Garutt V.E., Garutt N.V. & Fomitcheva N.L. 1992. [The fauna of Pleistocene mammals from the Volga Basin in the Museum of Geology and Mineralogy of the Kazan University]. Kazan. P.66–75 [in Russian].

Baygusheva V.S. 1980. [Mammoth *Mammuthus primigenius* Blum. from the left bank of Severskiy Donets] // Trudy Zoologicheskogo Instituta AN SSSR. Vol.93. P.75–80 [in Russian].

Baygusheva V.S. 1999. [Some paleontological finds from the collection of Don Cossack Museum] // Kraevedcheskie Zapiski. Sbornik Nauchnykh Trudov. Novocherkassk. Vol.4. P.94–115 [in Russian].

Beden M. & Guérin C. 1975. Les Proboscidiens du gisement pléistocène moyen des Abîmes de La Fage à Noailles (Corrèze) // Nouvelles Archives du Museum d'Histoire Naturelle. Lyon. Vol.13. P.69–87.

Dobzhansky T. 1951. Genetics and the Origin of Species. New York: Columbia University Press. 364 p.

Drozdov N.I., Chekha V.P.; Laukhin S. A., Koltsova V.G., Akimova E.V., Ermolaev A.V., Leontiev V.P., Vasiliev S.A., Yamskikh A.F., Demidenko G.A., Artemiev E.V., Vikulov A.A., Bokarev A.A., Foronova I.V. & Sidoras S.D. 1990. [Chronostratigraphy of the Paleolithic Sites in Middle Siberia (Yenisei River Basin)]. Novosibirsk. 184 p. [in Russian]

Dubrovo I.A. 1966. [Systematic position of an elephant from the Khozar faunal assemblage] // Byulleten' Komissii po Izucheniyu Chetvertichnogo Perioda. Vol.32. P.63–74 [in Russian].

Foronova I.V. 1986. Elephants of the genus *Archidiskodon* from the Late Pliocene and Pleistocene of the Kuznetsk Basin (southeastern West Siberia) // Quartärpaläontologie. No.6. P.29–42.

Foronova I.V. 1998. Early Quaternary mammals from the Kuznetsk Basin, south of Western Siberia // Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO. Vol.60. P.353–374.

Foronova I.V. 1999. Quaternary mammals and stratigraphy of the Kuznetsk Basin (southwestern Siberia) // Antropozoikum "Quaternary of Siberia". Vol.23. P.71–98.

Foronova I.V. 2000. [Morphology, systematic position and age of the mammoth from the site Ust'-Izhul'1] // Paleogeografiya kamennogo veka. Korreliatsiya prirodnyh sobytiy i arkheologicheskikh kultur paleolita Severnoy Azii i sopredelnykh territoriy. Krasnoyarsk. P.134–137 [in Russian].

Foronova I.V. 2001a. History of Quaternary proboscideans of the south of Western Siberia inferred from dental system analysis // Cavarretta G., Gioia P., Mussi M. & Palombo M.R. (eds.). The World of Elephants. Rome. P.109–114.

Foronova I.V. 2001b. [Quaternary Mammals of the South-East of Western Siberia (Kuznetsk Basin): Phylogeny, Biostratigraphy, and Palaeoecology]. Novosibirsk: Publishing House of Siberian Branch, Russian Academy of Sciences. 243 p. [in Russian]

Foronova I.V. 2003. History of mammoth lineage in the Southern part of Central Siberia // Third International Mammoth Conference, Dawson City and Whitehorse, Yukon. Occasional Papers in Earth Sciences. No.5. P.35–36.

Foronova I.V. 2007. Thin-enamel dental specialization in mammoth evolution: an example of direction selection // Quaternary International. Vol.69–70. P.95–104.

Foronova I.V. 2010. Pleistocene history of mammoth lineage in Southern Siberia // Quaternaire, Hors Ser. Vol.3. P.17–18.

Foronova I.V. 2014. Mammoths of the Molodova V Paleolithic site (Dniester Basin): The case of dental thin-enamel specialization and paleoecological adaptation // Quaternary International. Vol.326–327. P.235–242.

Foronova I.V. & Zudin A.N. 1986. [A new approach to the study of north Eurasian fossil elephants of the *Archidiskodon-Mammuthus* lineage] // Arkhipov S.A. (ed.). [Biostratigraphy and Paleoclimates of the Pleistocene in Siberia]. Novosibirsk. P.6–31 [in Russian].

Foronova I.V. & Zudin A.N. 1995. [A new method for the study of fossil Proboscideans and Perspectives of its application in archaeology] // Metody Estestvennykh Nauk v Arkheologitcheskikh Rekonstruktsiyakh. Novosibirsk. P.129–135 [in Russian].

Foronova I.V. & Zudin A.N. 1999. The structure of the lineage *Archidiskodon* – *Mammuthus* in Eurasia and peculiarities of its evolution // Haynes G., Klimovicz J. & Reumer J.W.F. (eds.). Mammoths and the Mammoth Fauna. Deinsea. Vol.6. P.103–118.

Foronova I.V. & Zudin A.N. 2001. Discreteness of evolution and variability in mammoth lineage: method for group study // Cavarretta G., Gioia P., Mussi M. & Palombo M.R. (eds.). The World of Elephants. Rome. P.540–543.

Garutt V.E. 1971. [History of distinguishing of intermediate elements in the lineage *Archidiskodon* – *Mammuthus*] // Khronologiya Lednikovogo Veka. Moskva. P.78–88 [in Russian].

Garutt V.E. 1972. [Skeleton of Khozarian mammoth *Mammuthus* cf. *chosaricus* Dubrovo from the Middle Pleistocene deposit of Oria (Kama Basin)] // Voprosy Stratigrafii i Korellyatsii Pliotsenovykh i Pleistotsenovykh Otlozhenii Severnoi i Yuzhnoi Chasti Preduraliya. Vol.2. P.35–55 [in Russian].

Garutt V.E. & Foronova I.V. 1976. [Research on the Teeth of Extant Elephants: Methodological Recommendations]. Novosibirsk: Institute for Geology and Geophysics. 36 p. [in Russian]

Guenther E.W. 1969. Die Elefanten Molaren aus den Kiesen von Süssenborn bei Weimar // Paläontologie, Abhandlungen. Vol.3. No.4. P.711–734.

Haesaerts P., Borziac I., Chekha V.P., Chirica V., Damblo F., Drozdov N.I., Orlova L.A., Pirson S. & van der Plicht J. 2009. Climatic signature and radiocarbon chronology of middle and late pleniglacial loess from Eurasia: comparison with the marine and greenland records // Radiocarbon. Vol.51. No.1. P.301–318.

Jourdan C. 1861. Des terrains sidérolitiques. Comptes Rendus de l'Academie des Sciences. Paris. Vol.53. P.1009–1014.

Krukover A.A. & Chekha V.P. 1999. Small fossil mammals from the Kurtak archaeological region (Kranoyarsk District) // Antropozoikum "Quaternary of Siberia". Vol.23. P.71–98.

Labe B. & Guérin C. 2005. Réhabilitation de *Mammuthus intermedius* (Jourdan, 1861), un mammouth (Mammalia, Elephantidae) du Pléistocène moyen récent d'Europe // Comptes Rendus Palevol. Vol.4. P.235–242.

Laukhin S.A., Akimova E.V., Ovodov N.D., Drozdov N.I., Stasiuk I.V. & Tomilova E.A. 1999. [Geological setting of Middle Pleistocene Paleolithic site Ust'-Izhul' (south of Central Siberia)] // Vestnik Arkheologii, Antropologii i Etnografii. Tyumen: IPOS SO RAN. Vol.2. P.105–114 [in Russian].

Lister A. 1996. Evolution and taxonomy of Eurasian mammoths // Shoshani J. & Tassy P. (eds.). The Proboscidea. Oxford University Press. P.203–213.

Lortet L. & Chantre E. 1872. Études paléontologiques dans le basin du Rhône. Période quaternaire // Archives du Museum d'Histoire Naturelle. Lyon 1. P. 59–130.

Miller R.L., Kahn J.S. 1963. Statistical analysis in the geological sciences. New York and London: John Wiley & Sons. 483 p.

Osborn H.F. 1942. Proboscidea. A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World. New York: Vol.2. P.805–1676.

Ovodov N.D. 1995. [Ust'-Izhul' mammoth paradox (Yenisei River, 55ºNL)] // Tezisy 1-go Mezhdunarodnogo Mamontovogo Soveschaniya. Sankt-Peterburg. P.632 [in Russian].

Pohlig H. 1885. Ueber eine Hipparionen-Fauna von Maragha in Nordpersien // Zeitschrift der Deutschen Geologischen Gesellschaft. Vol.37. P.1022–1027.

Vangengeim E.A. 1961. [Paleontological foundation of the Anthropogene stratigraphy of northeastern Siberia (on mammals)] // Trudy Geologicheskogo Instituta Akademii Nauk SSSR. Vol.48. P.1–182 [in Russian].

Zudin A.N., Nikolaev S.V., Galkina L.I., Butkeeva O.Yu., Efimova L.I., Panychev V.A. & Ponomareva E.A. 1982. [Foundation of the stratigraphical scheme of the Neogene and Quaternary deposits in the Kuznetsk Basin] // Problemy Stratigrafii i Paleogeografii Pleistotsena Sibiri. Novosibirsk: Nauka. P.133–149 [in Russian].