

Irina V. Foronova & Alexander N. Zudin
Russian Academy of Science, Novosibirsk

The structure of the lineage *Archidiskodon-Mammuthus* in Eurasia and peculiarities of its evolution

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An original method was proposed to study the elephants of the *Archidiskodon-Mammuthus* lineage (using materials from numerous Eurasian localities). As a result, a multidimensional model was created for the lineage. The enamel thickness and plate frequency of the last molars of the taxa known in the lineage were analyzed. The model is a multiple-level structure of adaptive peaks and depressions, organized like 'Wright's symbolic picture'. Generally, it reflects anagenesis and canalized selection associated with the progressing increase of cold and aridification of Quaternary climates. Also, it illustrates the microevolutionary process. The discreteness of adaptive peaks reflects the selection of optimal phenotypes and intraspecific variability. The sequences of adaptive peaks in thin-enamel and thick-enamel limits of distribution (all along the lineage) are entirely new elements making the structure different from traditional gradualistic model. The data complex allows us to interpret these forms as 'adaptations' to alternating glacial and interglacial conditions. An analysis of regional graphs shows: (1) transcontinental spreading of the majority of phenotypes (forms); (2) chronological, geographical (clinal), and paleogeographical variability; (3) two speciation 'directions' at different stages of the lineage development; and (4) the possibility of comparing depressions with the variability limits of different ranged taxa. The method provides new information on lineage development in general, and on microevolutionary and macroevolutionary processes.

De structuur van de lijn Archidiskodon-Mammuthus in Eurazië en bijzonderheden aangaande de evolutie ervan - In dit artikel wordt een originele methode voorgesteld om de olifanten van de *Archidiskodon-Mammuthus* lijn te bestuderen, uitgaande van materiaal uit een groot aantal vindplaatsen in Europa en Azië. De emaildikte en de lamellenfrequentie van de laatste molaren zijn het uitgangspunt. Het resultaat is een multidimensionaal model. Het model is een structuur van meerdere niveaus, georganiseerd als een 'Wright's symbolic picture', met adaptieve 'pieken' en 'dalen'. Het weerspiegelt (micro)evolutionaire fenomenen in verband met voortschrijdende afkoeling en verdroging tijdens het Pleistoceen. De duidelijke pieken in het model zijn een gevolg van selectie van optimale fenotypen en van intraspecificke variatie. De opeenvolgingen van pieken in 'dun email' en 'dik email' zijn nieuwe elementen in het model dat daardoor afwijkt van het traditionele gradualistische model. Deze vormen kunnen worden verklaard als aanpassingen aan afwisselende koude (glaciale) en warme (interglaciale) omstandigheden. Uit de bestudering van de regionale grafieken volgt: (1) een transcontinentale verspreiding van de meeste fenotypen, (2) chronologische, geografische en paleogeografische variatie, (3) twee speciatie-'richtingen' tijdens verschillende stadia van de evolutie van de lijn, en (4) de mogelijkheid om de 'dalen' te vergelijken met de uitersten in de variatie van de verschillende taxa. Er ontstaat aldus een beter zicht op de ontwikkeling van de lijn, en op micro- en macroevolutionaire processen.

Correspondence: Irina V. Foronova & Alexander N. Zudin, United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of the Russian Academy of Science, Universitetskiy pr. 3, Novosibirsk 630090, Russia.

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INTRODUCTION

The elephants of the *Archidiskodon-Mammuthus* lineage are traditionally considered to be the main group in Quaternary paleontology and biostratigraphy. Permanent improvement of the dental system and the ability for long-distance migration had shaped a relatively rapid rate of evolutionary change and wide adaptive radiation in geographically different and frequently changing paleoclimatic conditions. The transformations in the dental system clearly traced from the more archaic to the latest forms included changes in tooth proportions, simplification of plate structure, increase of plate quantity and frequency in the crown, and decrease of plate length and enamel thickness. The most efficient processing of vegetation was being achieved by means of dental structures such as enamel, cement, and dentine, as well as of each file-like tooth as a whole.

The wide dispersal of elephants into the vast territories of Eurasia and North America in the Pliocene and Pleistocene led to the appearance of a large variety of forms. The group systematics, based partly on cranial features and mainly on molar structure, are complicated and often confused. According to the opinions of different researches, representatives of the lineage are to be attributed either to two genera (*Archidiskodon* POHLIG, 1885 and *Mammuthus* BROOKES, 1828) or only to the genus *Mammuthus*. Numerous species and subspecies are commonly distinguished within these genera. However, the taxonomical definitions are impeded by a wide range of variability of the mentioned features. Despite the fact that many authors emphasize variability, the proposed methods for statistical processing of the parameters (Guenther 1954, 1969, Dietrich 1958, Dubrovo 1960, 1964, Vangengeim 1961, Musil 1968, Aguirre 1969, Agadzhanian 1972, Garutt 1972, Garutt & Foronova 1976, etc.) did not allow the establishment of exact boundaries between species. The method proposed by the authors

(Foronova & Zudin 1986, 1995a, b, c) partly resolves the problem and provides new information on the development of a whole lineage, as well as on intraspecific, geographical, and paleoecological variability. The method's advantages include graphical and visual results, and the ability to use enormous amounts of data.

MATERIALS AND METHODS

Attention was directed to the last molars (M3/m3) of representatives of all known taxa of the lineage under study from numerous localities of Europe, Eastern and Western Siberia. The material - more than 1500 pieces - is stored in the collections of the United Institute of Geology, Geophysics and Mineralogy (UIGGM), RAS, Siberian Branch, Novosibirsk; the Zoological Institute (ZIN), RAS, St. Petersburg; the Paleontology Institute (PIN), RAS, Moscow; the Moscow Geological Prospecting Institute (MGPI), Moscow; the Institut für Quartärpaläontologie, Weimar, Germany; and the Universities of Tomsk, Rostov-on-Don, and Odessa (Ukraine). Also studied were dated samples from the Kuznetsk basin, West Siberia, the Kurtak archaeological region, Enisey River, Middle Siberia (in the UIGGM, Novosibirsk); paleolithic sites of the Kostenki group, Don River, Voronezh region (in the ZIN, St. Petersburg); Khotylevo 1 and 2, Desna River, Bryansk region (in the collection of the Bryansk Museum of Regional Studies); and Dolni Vestonitse and Predmosti, Czech Republic (in the collection of the Moravian Museum, Brno). The materials of many Regional Museums of Russia were also used in the study. Published materials were added to the analyses, as well. The teeth of contemporary Asian and African elephants from the collections of the ZIN(RAS) were analyzed using measurements kindly offered by Dr. Vadim E. Garutt. The study is based on the building of two-dimensional distribution of the coordinates of plate frequency on a 100 mm stretch of crown length (average length of a plate is marked on the parallel scale) and

enamel thickness. These features are considered to be the major ones for defining the taxonomical position of the mammoth-lineage elephants.

Plate frequency

A general average value of plate frequency was calculated based on average data obtained by the means of three methods:

- (1) traditional method – the number of plates on 100 mm of crown length is counted on the level of half the height of the side surface, on both sides of the crown;
- (2) a length of 3-5 plates was measured on both sides of the crown, at the level of half the tooth height;
- (3) the length of a crown is divided by the total number of plates.

Values of average plate length obtained by means of (2) and (3) are used in each case to calculate plate frequency (100 mm is divided by average plate length).

Enamel thickness

10-20 measurements of enamel thickness were made all over the occlusal surface (most preferably on straight enamel stretches). Then the average value of enamel thickness was calculated for every M3/m3. The proposed algorithm for data processing and graph building (noncomputer version) is applied for the first time in paleontology. Such an approach permitted us to derive a maximal amount of information from morphological features and to analyze vast complexes of material from the whole lineage and its regional variations. The operating sequence of the method is the following:

- (1) building punctuated diffusion diagrams;
- (2) converting 'point clouds' into numeric values of distribution density, and simultaneous sliding averaging (replacing of a single square-platform to half its side);
- (3) building distribution density isolines and normalizing distribution density values in units of the Law of Uniform Density (division of the sample volume by the variability range square).

It is important to note that the sliding averaging and normalization theoretically should have adjusted the structure under study to the traditional lineage model currently used, i.e. to the subuniform type of distribution. The results, however, appeared to be utterly different. Step 4 is the hierarchic procedures that imply the varying of the sizes of the averaging square-platform. With the help of this procedure we succeeded in revealing a range (0.8 - 1.0 - 1.5) in which the character of distribution does not depend on a building technique. Dependence of the structure on sample size was also analyzed. It was established that 30 - 50 'casual' samples are enough for its stabilization. The influence of possible nongenetic variability on the character of the structure is excluded. The age variability is also excluded because only the teeth of the last generation are analyzed. Feature variations on different stages of crown wear are excluded by the measuring method described above. Pathological teeth are extremely rare, their feature values, however, are similar to those of normal teeth. The principle of geographical uniformity of the material on a subcontinental scale had been followed while forming the samples.

During the analysis of two-dimensional distributions, other dental system parameters were used for a comparison of single peaks and for an evaluation of common regularities in multi-dimensional space. Width of a crown, total number of plates, hypsodonty index, the angles of cutting and rubbing were analyzed according to the Kholmogorov-Smirnov's test (Miller & Kan 1965). The configuration of occlusion and the cement-dentine-enamel dimensional ratio were also involved in the analysis (Foronova & Zudin 1986).

RESULTS AND DISCUSSION

Separate graphs for Europe, Western and Eastern Siberia (Figs. 1 - 4) reveal the lineage structure to be far more complicated than a simple phyletic (gradualistic) sequence. The distributions clearly show that in the range

from minimal to maximal values of last molars' plate frequency and enamel thickness not all of the possible combinations of these values become realized. The variability area lies diagonally from the most archaic forms to the latest *Mammuthus primigenius* on the coordinate grid. On the one hand, it is generally indicative of anagenetic evolution and canalizing selection in the lineage, the direction of which corresponds to the traditional notion of group development. On the other hand, the far more important result is that discrete selection of combinations of features under study was revealed. These combinations correspond to the levels of dental system specialization, most optimal on certain stages of the lineage development. The structure consists of subordinated 'adaptive peaks' (zones of heightened distribution density) and depressions, and is organized like 'Wright's symbolic picture' (Dobzhansky 1951). It resembles a mountain sierra on a topographic map. Adaptive peaks are asymmetric in variable extents. The sizes of the peaks are close within outlining isolines and vary only within a small range. Exceeding of distribution density values in the optimums over adjoining depressions is different but always significant (0.5 - 2.5 Uniform Density units). The peaks of different size and statistical significance are united into 'ensembles'. Thus the hierarchy of boundary depressions is established. One of the largest ensembles corresponds to the last stage of the lineage development within the genus *Mammuthus*. In addition to the peaks of the axial zone, a series of adaptive peaks in thin-enamel and thick-enamel areas was established for the first time. These peaks are oppositely oriented and clinally linked with axial zone peaks. It can be seen most distinctly on the Siberian graphs (Figs. 2, 3, and 4).

Beginning the analysis of graph structure, it is important to specify the character of the variability revealed. Continuous individual variability caused by slight genetic differences between individuals, together with the

stabilizing feature of population, always leads to a normal (single-cone) distribution (Mayr 1969). In our case the variability apparently does not go over single-cone clusters. First of all, the graphs illustrate the variability of another type. All along the lineage this variability is manifested in the fact that the graphs are multiple-cone, that is indicative of discrete selections of evolutionary features and, therefore, of species polymorphism. The features we considered are the most important elements of the elephant phenotype. Unlike in morphotypical studies where phenes and morphotypes are used as elementary indivisible particles whose discreteness is postulated, the discreteness discussed here is only to be established after certain consequent procedures of graph building. We believe, however, that the present research is to be attributed to phenetics, or more exactly to the section of population morphophysiology that deals with similarities and affinities between populations and population groups within a species. Such research is possible by means of a large number of phenes, their groups, and other features more complex than phenes (Sarycheva & Yablokov 1973, Timofeev-Ressovskiy *et al.* 1973, 1977). We study the morphological and quantitative expression of an aggregate of complex features whose functional meaning is obvious. Therefore, adaptive peaks may be apparently considered as the stages of phenotype stabilization (or phenotypes), which the variability area of the species under study was divided onto. Taking into account the certain positions of these stages in the evolutionary sequence, we believe that they correspond to an elementary evolving structure. In one contemporary theory of species formation a population is agreed to be considered as the latter (Mayr 1970). Since we are unable to reconstruct the borders of populations that existed in the past, we assume that each stage of a phenotype represents the individuals of adjacent populations separated by major orohydrographic boundaries (Urals and Yenisey River). These boundaries have been unchanged during the major part of

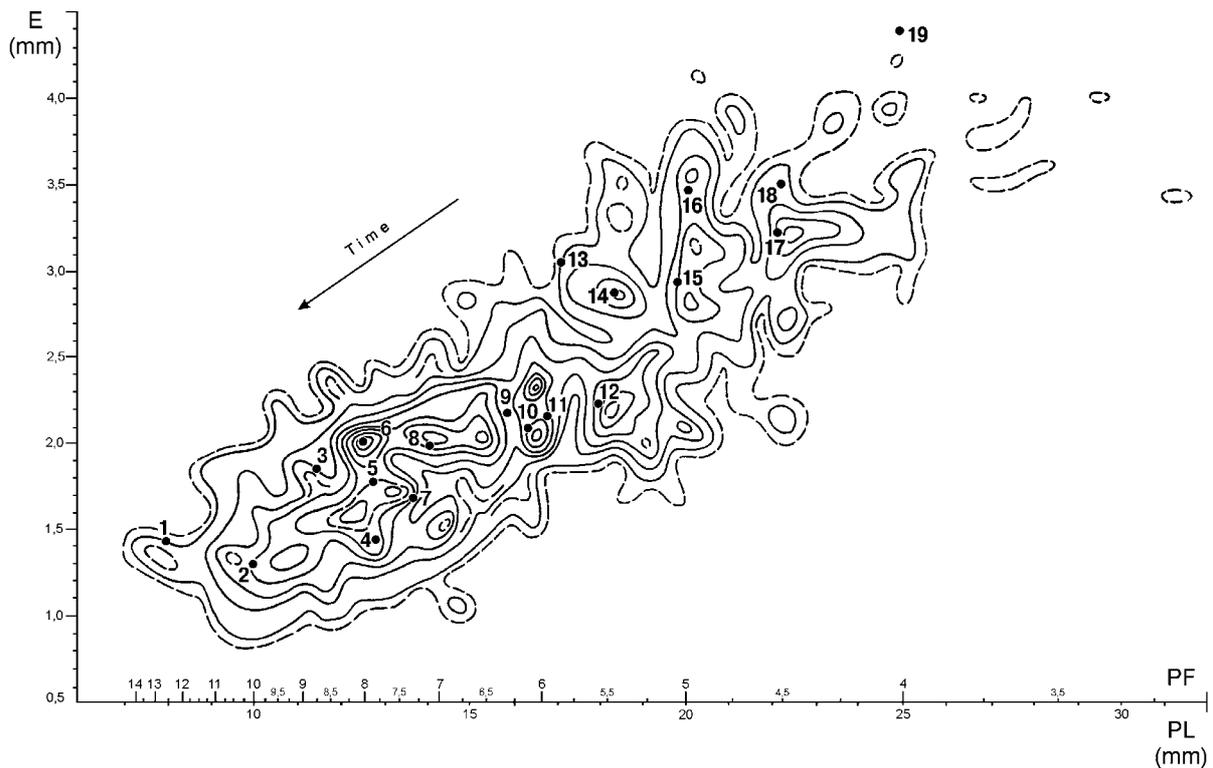


Figure 1 The variability of the elephants of the *Archidiskodon-Mammuthus* lineage in Europe (according to M3 parameters). Coordinate axis: E - enamel thickness; PF - plate frequency on 100 mm stretch; PL - length of one plate. Continuous isolines of distribution density are drawn through 0.5 Unifom Density Units, punctuated isolines are drawn through 0.25 Units, outer isoline corresponds to 0.25. Points are the coordinates of type-samples of taxa distinguished in the lineage and some peculiar forms:

- 1 *Mammuthus primigenius sibiricus*, according to L. Mayet & Ch. Deperet (Gromova 1965)
- 2 *M. primigenius primigenius*, neotype (Garutt et al. 1990)
- 3 *M. primigenius jatzkovi*, holotype (Golovko 1958)
- 4 *M. primigenius fraasi*, holotype (Dietrich 1912)
- 5 *M. primigenius*, average parameter values (Vangengeim 1961)
- 6 *M. primigenius* (Chokurcha site, Crimea; Vereshchagin 1959)
- 7 *M. primigenius*, lectotype (Osborn 1942)
- 8 *M. intermedius* Jourd, holotype, according to L. Mayet & Ch. Deperet (Osborn 1942)
- 9 *M. trogontherii chosaiicus*, holotype (Dubrovo 1966)
- 10 *M. trogontherii chosaiicus*, holotype (authors' measurements)
- 11 *M. trogontherii trogontherii*, lectotype (Dubrovo 1966)
- 12 *A. trogontherii*, average parameter values of the teeth of the skeleton from Azov museum (authors' measurements) = *A. wusti* Pavlova (according to Alekseeva 1977)
- 13 *A. meridionalis cromerensis*, holotype (Mayet et al. 1923)
- 14 *A. m. voigtstedtensis*, holotype (Dietrich 1958)
- 15 *A. m. tamanensis*, holotype (Dubrovo 1964)
- 16 *A. meridionalis*, average parameter values, Psekups River; Northern Caucasus (Vereshchagin 1959)
- 17 *A. m. meridionalis*, holotype (Dubrovo 1964)
- 18 *A. gromovi* Garutt et Alexeeva (Alekseeva 1977)
- 19 *A. m. taiibanensis* Gabounia et Vekua (Alekseeva 1977).

the Quaternary (in interglacial and transitional periods).

Thus, there are no serious obstacles for the study of the dynamics of population processes. Furthermore, even in phenetic studies of contemporary faunas one has to deal with 'a morphophysiological aggregate of individuals attributed to different populations'

(Timofeev-Ressovskiy *et al.* 1973: 153).

Besides that, the data on daily (20 - 30 km) and seasonal (several hundreds km) migrations of contemporary African elephants (Nasimovitch 1975) provide grounds to believe that on every stage of formation of the fossil elephants' phenotypes a wide genetic exchange (panmixia) took place between adjacent populations of subcontinental groups (Averianov 1992).

Variability in isochronous populational groups and the influence of dental system

asymmetry need to be taken into account while analyzing the structures described, since it is known that the parameters of upper and lower teeth may differ, thus causing the scatter on the graphs. Earlier, based on the materials from localities of a wide stratigraphical range, we have concluded that the distribution structure may be related to polymorphism and polytypism of taxa, whereas dental system asymmetry does not influence the distribution structure significantly (Foronova & Zudin 1986). These data currently are amended by the results of a study of contemporary Asian and African elephants and apparently isochronous samples from several archaeological sites. Wide polymorphism is characteristic for contemporary elephants and mammoths from Berelekh (Yakutia) and Dolni Vestonitse, while the populations of Predmosti, Khotylevo 2, and Kostenki 1 and 2 are more or less monomorphous.

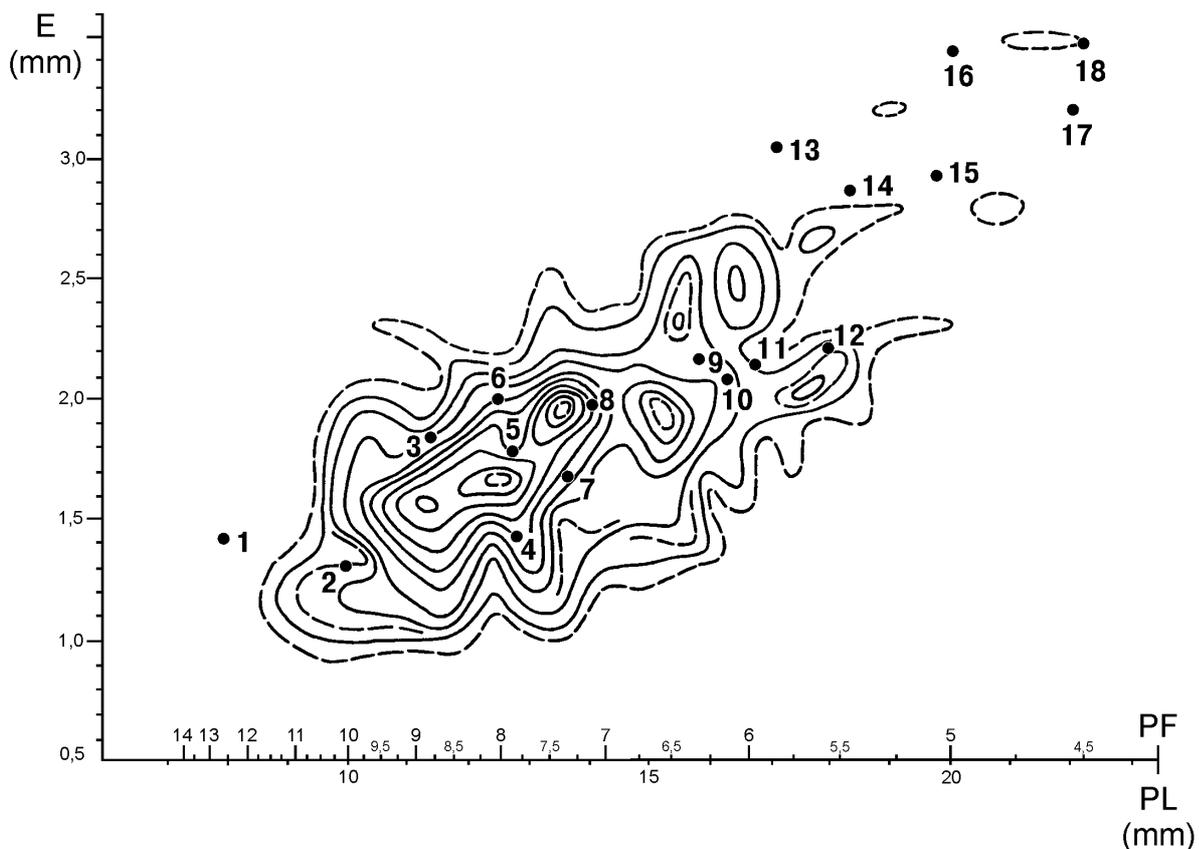


Figure 2 Variability of the elephants of the lineage *Archidiskodon-Mammuthus* in West Siberia. See Figure 1 for legend.

Quantitative predominance of one, sometimes two, phenotype(s) is observed in all samples. The scatter between lower and upper teeth, though different in direction, takes place with contemporary mammoths. In Khotylevo 2 asymmetry does not make any impact on distribution, while in Predmosti, Dolni Vestonitse, and Berelekh populations the teeth deviate to archaic phenotypes. The degree of this deviation varies in geographically and chronologically different populations. Thus, the previous supposition that dental system asymmetry does not make a regular impact on the lineage structure is now confirmed. The predominance of one of the phenotypes in isochronous populations allows us to assume the chronological and paleogeographical interpretation of lineage variability in general. The very existence of isochronous polymorphism, however, increases the probability base for such interpretations and is indicative of

possibility of making mistakes when working with small samples or single specimens.

A comparison of regional graphs shows the general similarity of the structure. Besides that, on every graph the presence of an overwhelming majority of adaptive peaks analogous by their position in the structure was revealed. This fact suggests autochthonous speciation nearly in the entire area. The differences can be seen in the character of graph depression and in the grouping of the peaks into ensembles. Furthermore, while superimposing the graphs one can easily see that analogous peaks (regional versions of phenotypes) almost completely matching (no less than 75%) appear to be somewhat off-set from each other. Formally they are attributed to one subspecies. This is how the geographical clinal variability within every phenotype is fixed.

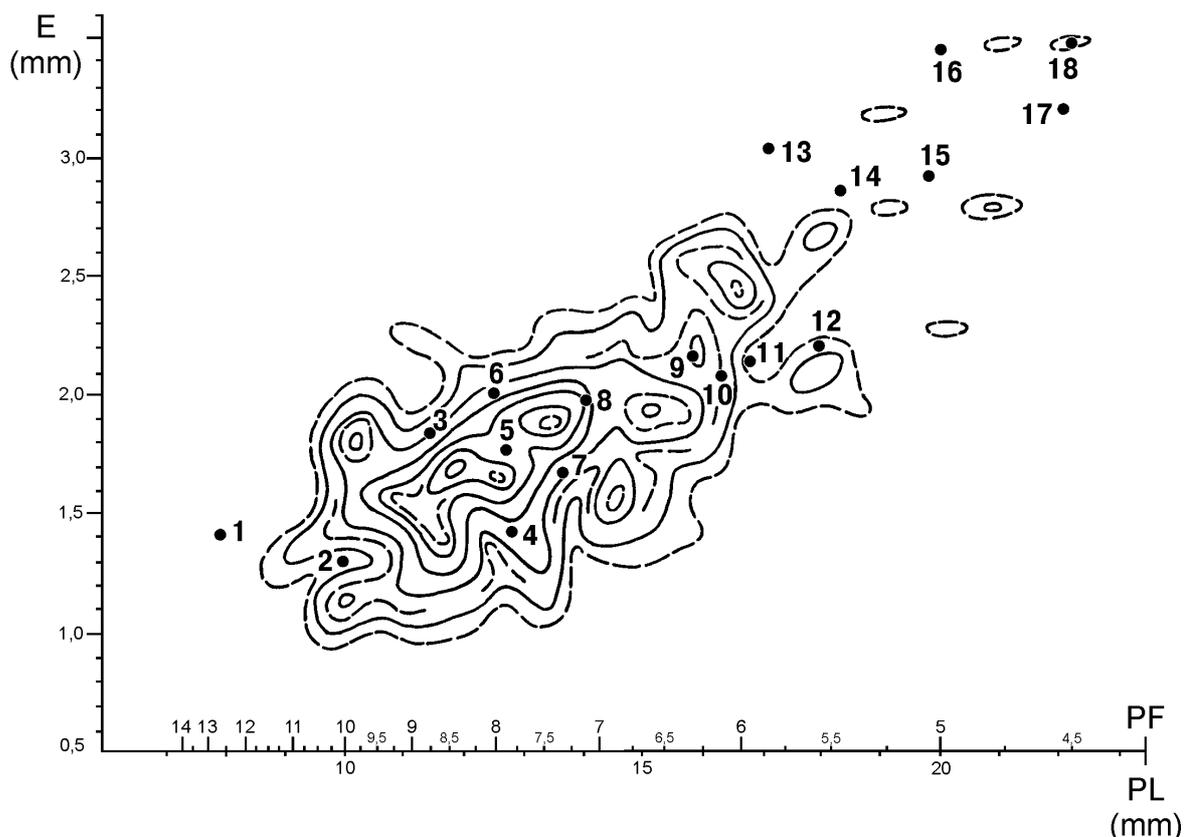


Figure 3 Variability of the elephants of the lineage *Archidiskodon/Mammuthus* in Kuznetsk Basin (Southern West Siberia). See Figure 1 for legend.

Marginal 'thick-enamel and thin-enamel' adaptive peaks (Figs. 1-4) are very interesting and entirely new elements of the structure. The first ones are represented by forms with thickened folded enamel, a medial sinus on a plate, a lowered hypsodonty index and a wider crown. Teeth of the opposite 'thin-enamel specialization' are characterized by a somewhat heightened hypsodonty index, a relatively larger interval between plates that are more narrow, and weakly folded enamel. A medial sinus is hardly manifested in the European and West Siberian mammoths, while it is present in the mammoths from East Siberia. The functional difference of the above mentioned morphological features of the opposite marginal (regarding their positions on graphs) forms is traditionally consi-

dered as the following: thick-enamel forms are adapted for soft vegetation; thin-enamel forms having increased cutting ability are adapted to abrasions from arid landscapes. The facts described above - as well as data on accompanying fauna and flora, physical datings, and agreement between the sequence of adaptive peaks, the stages of the oxygen-isotope ocean scale (Bowen 1981), up to the borders dated by the paleomagnetic method - give reasons to relate 'thick-enamel adaptations' to interglacial environments, while 'thin-enamel adaptations' are to be related to periglacial habitats.

It is important to note that type samples parameters of the majority of the taxa distinguished in the lineage correspond with the optima

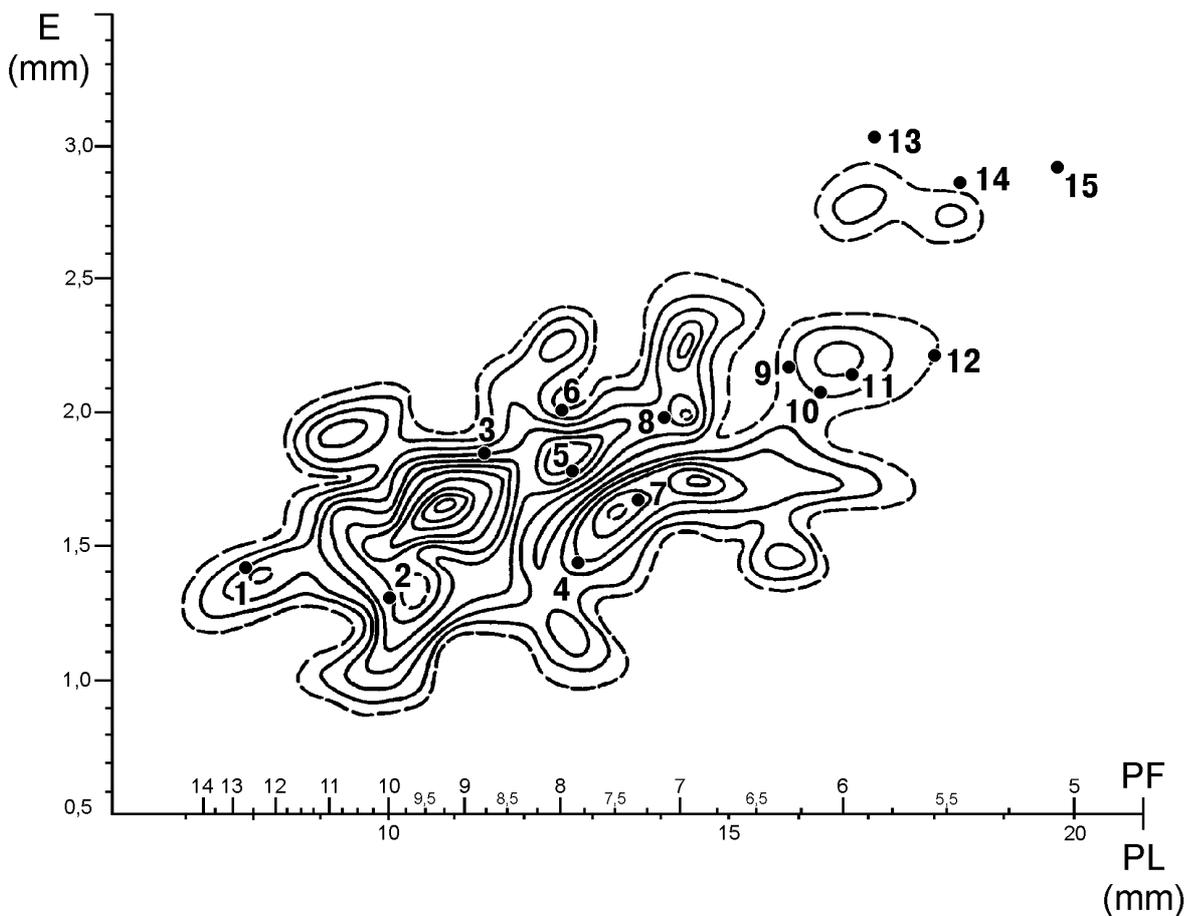


Figure 4 Variability of the elephants of the lineage *Archidiskodon-Mammuthus* in East Siberia. See Figure 1 for legend.

of some adaptive peaks of every sequence (Figs. 1-4). For example, four peaks were established in the 'thick-enamel' variability area of *M. primigenius*. The form analogous to *M. primigenius* from the Early Mousterian Chokurcha site (Crimea) (Figs. 1-4, no. 6) corresponds to one of them. The next one correlates with the parameters of the thick-enamel *M. p. jatzkovi* GOL. from Ukraine (Figs. 1-4, no. 3). The later peak apparently corresponds with *M. p. leith-adamsi* POHL. from interglacial Thuringian travertines and with representatives of the thick-enamel variation of the *M. primigenius* intermediate form (Vangengeim 1961). The teeth of these mammoths from Kuznetsk Basin (Southern West Siberia) are radiocarbon-dated $39,100 \pm 240$ and $28,900 \pm 600$ years (Foronova 1990). The final stage of the lineage development conforms the last thick-enamel peak, which *M. p. sibiricus* DEPERET ET MAYET (Figs. 1-4, no. 1) corresponds to. The analysis of the data complex allows to assume a link between the mentioned 'adaptations' (forms) with Inter-Riss, Riss-Würm, Inter-Würm, and Holocene of the Alpine scale.

In the 'thin-enamel' variability area of *M. primigenius*, parameters of *M. p. fraasi* DIETRICH from Riss layers of Steinheim (Germany) correspond to one of the well-developed peaks (Figs. 1-4, no. 4). The analog of this form (from Novotroitskoe locality, Irtysh River, West Siberia) was found in deposits dated by EPR to 174.2 ka (Arkhipov & Linke 1987). It is possible to compare this form with stage 6 (128 - 195 ka) of the oxygen-isotope curve V28 - 238 (Shackleton & Opdyke 1976).

The area of elephants with thin-enamel phenotypes lies in a relatively narrow transcontinental zone (1/3 of *M. primigenius* sensu lato maximal area approx.). Superimposition of this narrow area on the paleogeographical scheme for maximal penetration of Quaternary glaciers (from Flint 1963, Markov *et al.* 1968, Bowen 1981) showed that all

localities, with rare exceptions, are situated in the zone that is free of glaciers. In East Siberia, they are linked to the narrow space between mountain glaciers and ice-seas (Fig. 5, A & B). The forms with thick-enamel and axial phenotypes are spread considerably wider. Their areas overlap the previous one and cover the territory of former glaciers (Fig. 5, C). Orthogonal transformation of river-systems in glacial and interglacial periods of the Quaternary also played a significant role in the different distribution of these forms. The data submitted serve as additional arguments in favor of the assumed linkage of thin-enamel forms with periglacial habitats of the Quaternary, thick-enamel and main forms being linked with interglacial and transitional environments of the period. Depressions in the lineage structure could be ranged according to their statistical significance (relative depth). In this connection, dynamics of other teeth parameters on these borders and the possible taxonomic status of these borders are of big interest.

According to phenogeographical data, the representatives of the genus *Archidiskodon* (*A. gromovi* GARUTT ET ALEXEEVA, *A. meridionalis meridionalis* (NESTI), *A. m. tamanensis* DUBROVO, *A. m. voigtstedtensis* DIETRICH, *A. m. cromerensis* DEPERET, MAYET ET ROMAN) were less advanced in Europe than in Asia on the early stages of the lineage development (Foronova 1990). It is important to note that the earliest archidiskodonts had considerable variability in enamel thickness already (Figs. 1-4). First forms with relatively thin enamel appear and dominate in quantity (that is, they form adaptive peaks) in the South of Europe, from where they spread to the South of Western Siberia and further into Asia. Probably it was the thin-enamel forms that pioneered new adaptive zones.

On the early stretch of the lineage, the width of a crown gradually changes, slightly decreasing from the archaic to the later forms, whereas the hypsodonty index increases

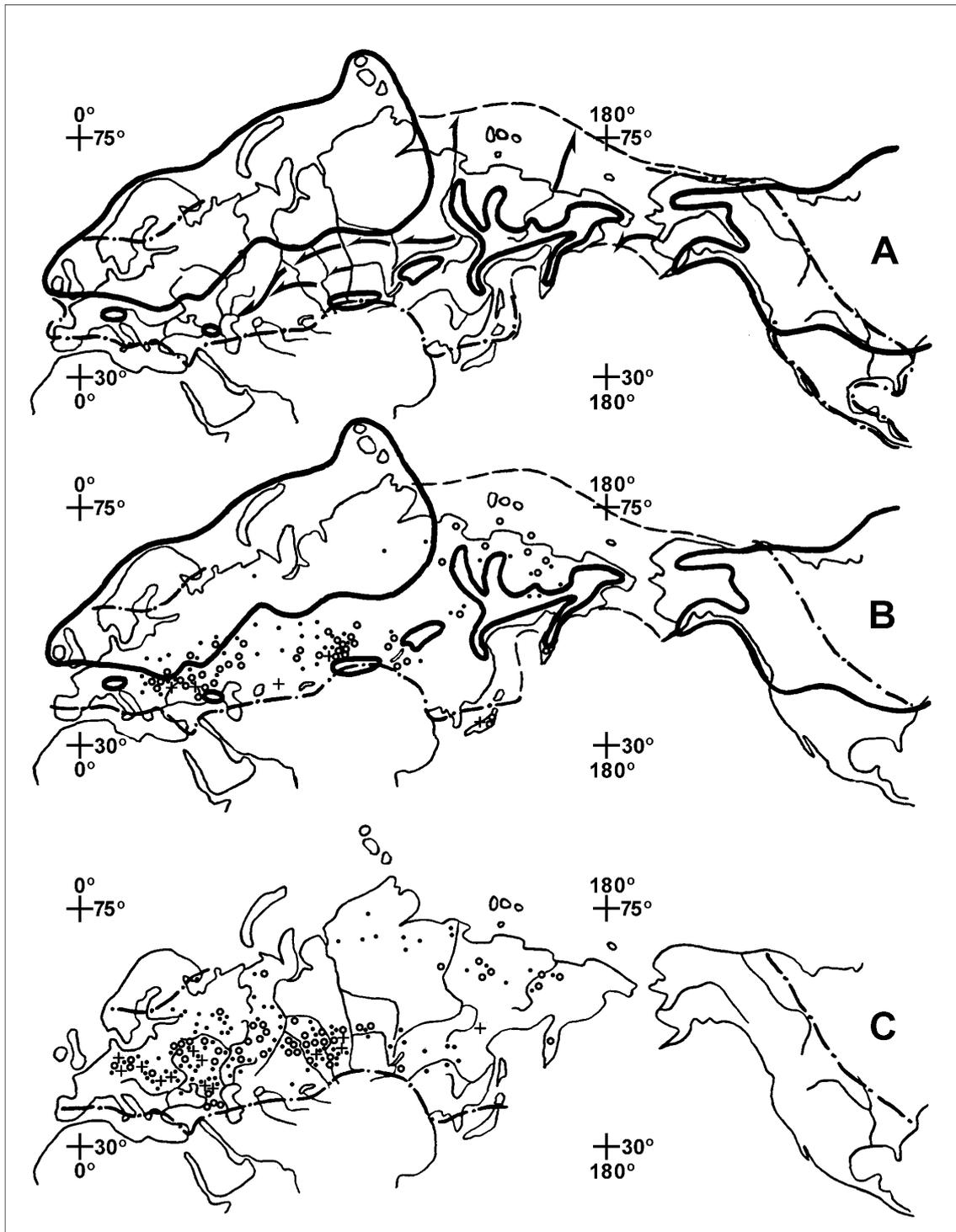


Figure 5 The paleogeographic situation in the period of maximal penetration of glaciers (A) (according to Flint 1963, Markov *et al.* 1968, Bowen 1981) and geographic locations of thin-enamel (B) and thick-enamel (C) forms of elephants. Legend: thick line: glacier border; arrows: paleorivers; dot-and-dash line: border of *M. primigenius* s.l. area; punctuated line: shore line of Beringia (maximal ocean regression); points: localities of *M. p. primigenius* s.l.; circles: localities of transitional forms from *A. trogontheii* (= *A. wüsti*) to *M. intermedius*; crosses: localities of *A. meridionalis* s.l.

‘leap-like’ on the borders of the adaptive peak ensembles (Fig. 1). The first such leap coincides with the border between the ensembles, which include *A. m. meridionalis* with its thin-enamel and thick-enamel phenotypes on the one hand, and *A. m. tamanensis* with analogous phenotypes on the other hand. The next border is remarkable for the biggest leap of the hypsodonty index in the lineage (Foronova & Zudin 1986, Lister 1993). This fact may be indicative of its taxonomical status. The border separates the above mentioned forms and two distinct ensembles approximately in one plate frequency range, but differing in enamel thickness. The first one is in the thick-enamel area, with *A. m. voigtstedtensis* and *A. m. cromerensis*; the second one is in the thin-enamel area, with *A. trogontherii* (the skeleton of the Asov museum described by Baygusheva & Garutt 1987) and *A. wüsti* (teeth from M. Pavlova's collection, MGPI, Moscow). Such changes in the teeth of the archidiskodonts, undoubtedly adaptive in their nature, were accompanied by corresponding changes in cranial proportions (Osborn 1942, Garutt 1954, Azzaroli 1977, etc.). A distinct specialization by enamel thickness fixed in this part of the graph and an isolation of corresponding forms of late archidiskodonts correspond with the global nature and climate fluctuations in the beginning of the Quaternary. No less significant statistically is the border between the above mentioned forms and the adaptive peak with the parameters of the lectotype *M. trogontherii trogontherii* from Süssenborn. The crown width and hypsodonty index almost does not change here. This border, however, is very important in terms of statistics, since it is this border that is marked by the wide spreading of the early representatives of the genus *Mammuthus* to the higher latitudes. This stage is associated with the problems still widely discussed, such as the border between the genera *Archidiskodon* and *Mammuthus*, and the intermediate and ancestral forms of the elephants of the mammoth group.

The European structure allows us to consider the controversial question of the range of a wide species *Elephas trogontherii* H. POHLIG, 1885. Pohlig (1885) has noted that this species had had an intermediate position zoologically as well as geologically, i.e. had represented a real ‘bridge’ between the Southern elephant and the mammoth. The distinct border mentioned above separates the ensemble with *A. wüsti* parameters from the group of the adaptive peaks with *M. t. trogontherii*. These peaks are located in the beginning of the biggest ensemble uniting the representatives of the genus *Mammuthus* and appear to be tightly linked with them. It is known that the species *E. wüsti* was derived on the basis of the archaic variation of *E. (meridionalis) trogontherii* of H. Pohlig and teeth from Tiraspol (Moldavia; Pavlow 1910). Later, I.A. Dubrovo (1963) considered it to be only a synonym of Pohlig's *E. trogontherii* and described its earlier variation as a nominative subspecies of *M. t. trogontherii* within the genus *Mammuthus* (Dubrovo 1966). Taking into account everything written above, we consider the following point of view to be the most realistic. The earlier form of *trogontherii* elephant is an independent form, and it is attributed to the genus *Archidiskodon* (Pavlow 1910, Yatzko 1948, Sher 1971, Alekseeva 1977). Thus, we can assume a generic status of the border. Apparently, this form, unlike the thick-enamel phenotypes of the late *meridionalis* subspecies that look isolated on the graphs (Fig. 1), has been the ‘bridge’ between Southern elephants and mammoths, which Pohlig (1885) wrote about.

Beyond this border, on the mammoth stretch of the lineage development, marked with even wider polymorphism on the graphs, the evolutionary processes embraced all Eurasia, with considerable regional differences, however. The character of these events in Eastern Siberia gives grounds to suppose the influence of Beringian and, probably, North American populations, as was assumed by Garutt (1995). The phenogram (Fig. 4) fixes a

deep length-wise depression here dividing 'thick-enamel' and 'thin-enamel' phenotypes beginning from the forms likely with *A. m. voigtstedtensis* and *M. trogontherii* up to the late *M. primigenius*. On the graph for Europe this depression is manifested weakly and can be traced only on *M. intermedius* stretch and on the early forms of *M. primigenius*. In Siberia the thin-enamel 'adaptations' of early *Mammuthus* s.l. are manifested as the clines of the 'axial' phenotypes. In accordance with clinal geographical variability East Siberian mammoths appear to be more archaic on the considered stage, whereas West Siberian and European mammoths seem to be more advanced. In addition, this is accompanied by some morphological peculiarity of East Siberian forms. Their thin-enamel representatives (much more than thick-enamel ones) are characterized by a 'meridionaloid – wustoid' rubbing configuration of plates. They have a smaller size and higher hypsodonty index, when compared with West Siberian forms. It was Sher (1971) who first pointed out peculiarity of East Siberian elephants, while describing the Olyorian *Archidiskodon* (aut *Mammuthus*) sp., having emphasized the 'wustoid' type of plate rubbing. The parameters of this elephant correspond to the adaptive peak with *M. trogontherii trogontherii* lectotype on our diagrams. Obviously, this peak, the linkage of which with *A. wusti* discussed before is well seen on the European graph (Fig. 1), begins the sequence of East Siberian thin-enamel forms.

On the basis of all above mentioned we can assume that the parallel development of Early mammoths took place in East Siberia. Probably these mammoths had originated from sister-forms that strongly diverged in the period of isolation of Eurasian and North American populations. The role of Beringia in the formation of a Holarctic fauna, the peculiarity of North-Eastern elephants, and their phylogenetic links with other representatives of the mammoth lineage are described in detail in special papers (Sher 1971, Sher *et*

al. 1995, etc.). Two more depressions correspond to the further borders of the lineage (Figs. 1-4). The first one, between *M. intermedius* and early form of *M. primigenius* (from Vangengeim 1961), seems to be more significant. Another border lies in the bottom of the adaptive peak with the parameters of the *M. primigenius primigenius* nominative subspecies (Figs. 1-4). Both depressions are marked by the decrease of crown width. In addition, the last one has a considerable increase of hypsodonty index. The European phenotypes appear to be less advanced than the East Siberian and West Siberian at this stage, as well as at the earlier stages of the lineage development. The mammoth stage of the lineage development together with detailed characteristics of phenotypes and their interregional comparison has been already described (Foronova & Zudin 1986).

CONCLUSION

This analytical method substantially increases the information available from the traditional morphometrical features of elephant teeth and visually demonstrates its results. The structures analyzed illustrate the microevolutionary and macroevolutionary processes in the lineage. It is still difficult to say exactly how the polymorphism of isochronous populations was manifested in these structures. Currently, the chronological and paleogeographical interpretation of the results seems to be well justified, although we concede that like any other statistical research, our results are to be thought of as probabilities, not certainties. We assume that the process of the lineage development was more complicated than a simple phyletic sequence (Foronova & Zudin 1986, 1995a, b, c). Apparently, we are dealing with consecutive (populational) speciation, but strongly complicated by the selective impact of environment (selection pressure increasing the diversity) in accordance with the dynamics of oscillating climatic changes during the Quaternary.

Transcontinental spreading of adaptive peaks

(optimal phenotypes), in conjunction with other data (presence of ruptures or depressions, agreement of type-specimens of the majority of the taxa with optimums of peaks), allows us to suppose at least subspecific taxonomical status of these peaks. This is indicative of chiefly autochthonous speciation in the lineage. Geographical clinal variability within analogous phenotypes allows us to suppose two 'directions' of speciation (European - Asian and East Siberian - European) on different stages of the lineage development. A significance of a paleogeographical factor in the lineage development is emphasized by the special role of thin-enamel (periglacial) adaptations. In addition, the existence of an independent branch of thin-enamel Northeastern elephants is possible. The predominance of the thin-enamel forms could have conditioned two large waves of the lineage area expansion: first, to the middle latitudes, and then to the extremely high latitudes of Eurasia. Probably, it is reflected in the European structure. The latter demonstrates some crucial events in the lineage (Fig. 1) which deviates from its main direction, moves to the lower 'step' by enamel thickness, and continues to develop further from it. The first of such events is fixed before the generic border at the stage of the late archidiskodonts (1.0 - 0.7 MyBP approx.). The second one is traced before the border between the early and late forms of *M. primigenius* (according to Vangengeim 1961) at the stage of the early one (0.2 MyBP approx.). Besides, it is these mammoths that are characterized by the maximal plate counts in the lineage (30). This boundary is remarkable by its outstanding paleogeographic events. The area of the early *M. primigenius* embraced all of Northern Eurasia, but the differences between East Siberian and West Siberian mammoths were so substantial that they may be attributed to different subspecies. These adaptive peculiarities, still not completely described, shaped considerable taxonomic polymorphism and polytypism which provided this group with flexibility and predominance among North

Eurasian Quaternary faunas. Undoubtedly, the real history of the lineage was more complex and diverse, and requires further reflection.

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