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Evolution of the mammoth lineage in Eurasia

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Abstract: The evolution and adaptive radiation of the mammoth-lineage elephants occurred in various environments throughout the Quaternary of Eurasia. Traditional methods have failed to reveal the peculiarities of development of this group and its significance for Pleistocene biostratigraphy and palaeoecology.

An original method of study of elephants of the *Archidiskodon-Mammuthus* lineage is outlined in this paper. A multidimensional model, based on the enamel thickness and plate frequency of last-shift molars (more than 1,500 analyzed specimens) is presented. The model is founded on a multiple-level structure of adaptive peaks and depressions, organized like "Wright's symbolic picture", reflecting the anagenesis and canalized selection associated with the progressing cooling and aridization of the Quaternary climate, and illustrates the microevolutionary process. The adaptive-peaks' discreteness shows the selection of optimal phenotypes and interspecific variability. The data base allows these forms to be interpreted as "adaptations" to alternating glacial and interglacial conditions. It is supposed that the thin-enamel forms pioneered, inhabiting new adaptive zones and providing progressive development of the lineage. Analysis of regional graphs shows transcontinental spreading of the majority of phenotypes (forms), chronological, geographical and palaeogeographical variability and two "directions" of different stages of the lineage development. The method provides the possibility for obtainment of new information on the lineage development in general, as well as local macroevolutionary and microevolutionary processes.

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INTRODUCTION

The elephants of the *Archidiskodon-Mammuthus* lineage are traditionally considered to be the main fossil faunal group in Quaternary palaeontology and biostratigraphy. A continuous improvement of the dental system and ability of broad geographical migrations enabled a relatively high evolution rate and a wide adaptive radiation in geographically different ecotomes and frequently changing palaeoclimatic conditions. The transformations in the dental system, well traced from the archaic to the latest forms, included changes in teeth proportions, simplification of plate structure, increase of plate quantity and frequency in a crown, and decrease of plate length and enamel thickness. The most efficient processing of vegetation was achieved by means of the dental structures such as enamel, cement and dentine, as well as a file-like tooth accommodation.

The wide spread of elephants over the vast territories of Eurasia and North America in the Pliocene and Pleistocene led to the emergence of a large variety of forms. The group systematics is, however, rather complex and often confused. According to the opinions of different researchers, 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 distinguished within these genera. However, the taxonomical definitions are impeded by a wide transgression of variability limits of particular features.

Despite the fact that many authors have emphasized the species variability, the proposed methods used for the statistical interpretation of parameters (GUENTHER 1954, 1969, DIETRICH 1958, DUBROVO 1960, 1964, VANGENGEIM 1961, MUSIL 1968, AGUIRRE 1969, AGAGZHANIAN 1972, GARUTT 1972, GARUTT - FORONOVA 1976, etc.) do not allow the establishment of exact boundaries between single species.

The method proposed by the authors (FORONOVA - ZUDIN 1986, 1995a, b, c) partly resolves this problem and allows new information to be obtained on the development of the entire lineage, as well as on its intraspecific, geographical and palaeoecological variability. Illustrativeness of results and ability to operate with large databases are the principal advantages of this technique.

MATERIAL AND METHOD

Comparative analysis was undertaken of the last-shift molars (M3/3) of the representatives of all known taxa of the *Archidiskodon-Mammuthus* lineage (more than 1,500 pieces) from numerous localities of Europe, and Eastern and Western Siberia, including collections of

the IUGGM Siberian Branch of RAS, Novosibirsk; Zoological Institute (ZIN) RAS, St. Petersburg; Palaeontological Institute (PIN), RAS, Moscow; Moscow Geological Prospecting Institute (MGPI), Moscow; Institute für Quartärpaläontologie, Weimar, Germany; Universities of Tomsk, Rostov on Don and Odessa. The following were also used for the study: dated Eurasian assemblages (from the Kuznetsk Basin, West Siberia), the Kurtak archaeological region in the Yenisey River Basin (collection of IUGGM, Novosibirsk); from palaeolithic sites of the Kostenki complex, Don River and from the Voronezh region (collection of ZIN, St. Petersburg); Khotylevo Site 1 and 2, from the Desna River valley; the Bryansk region-collection of the Bryansk Museum of Regional Studies; Dolní Věstonice and Předmostí, Czech Republic (collection of the Moravian Museum, Brno) and other materials from many regional museums of Russia as well as published data. Finally, teeth of contemporary Asian and African elephants from collections of ZIN RAS were analysed.

The study is based on two-dimensional coordinate distribution of plate frequency on the 100 mm stretch of the crown length (with average length of a plate marked on the horizontal scale) and the enamel thickness on the vertical scale. These are considered to be the major features for defining the taxonomical position of the mammoth-lineage elephants. The values of these features may significantly differ even with a single tooth. In order to avoid occasional deviations, the maximum number of measurements on one M3 was used to get the average values.

Plate frequency: A general average value of plate frequency was calculated basing on average data received by means of 3 methods:

a) traditional method – a number of plates on 100 mm of crown length is counted (on the level of 1/2 height of side-surface on both sides of a crown);

b) a length of 3–5 plates was measured on both sides of a crown (on the level of 1/2 of a tooth height);

c) a length of a crown is divided to a total number of plates.

Values of average plate length obtained by means of operations “b” and “c” are used in each case to calculate frequency (100 mm is divided to average plate length).

Enamel thickness: 10–20 measurements of enamel thickness were made all over the chewing surface (most advisable on straight enamel stretches). Then the average value of enamel thickness was calculated for each M3.

The proposed algorithm for data processing and graphic illustration is applied for the first time in palaeontology. Such an approach permits the maximum amount of information to be derived from morphological features and the analysis of large complexes of fossil material throughout the lineage and their regional variations.

The operating sequence of the methods is as follows:

1. Formation of punctuated diffusion diagrams.

2. Conversion of “point clouds” into numerical values of a specific distribution density, and a simultaneous averaging (replacing of a single square-platform to half of its side).

3. Building the distribution density isolines and normalizing the distribution density values in the units of the Law of Uniform Density (division of the exception volume to 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 a subuniform type of distribution. The results, however, appeared to be completely different.

4. Establishment of hierarchical procedures based on the size variation of the averaging square-platform, with a range of 0.8–1.0–1.5 in which the distribution does not depend on the building technique.

Dependence of the structure on the exception volume was also analyzed by 30–50 randomly chosen samples. The influence of a 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 (M3/3) are analyzed. Feature variations on different stages of the crown rubbing 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 was applied while forming the exceptions.

During the analysis of the two-dimensional distributions, other dental system parameters were used for comparison of single peaks and for the evaluation of common regularities in the multi-dimensional diagrams. The width of a crown, the total number of plates, the hypsodonty index and the angles of cutting and rubbing were analyzed according to Kolmogorov-Smirnov's criterion (MILLER - KAN 1965). The configuration of rubbing and the cement-dentine-enamel dimensional ratio were also included in the analysis (FORONOVA - ZUDIN 1986).

RESULTS AND DISCUSSION

Separate diagrams for Europe, Western and Eastern Siberia (Fig. 1–4) reveal the lineage structure to be far more complicated than a simple phylogenetic gradualistic sequence traditionally used. The distributions clearly show that, in the range from minimum to maximum values of the molar's plate frequency and enamel thickness, not all possible combinations of these values occur. The variability area lies diagonally from the most archaic forms to the latest *Mammuthus primigenius* BLUM. on the coordinate grid.

In general, it is indicative of anagenetic evolution and canalizing selection in the lineage, the direction of which corresponds to the traditional notion of the group development. On the other hand, the far more important

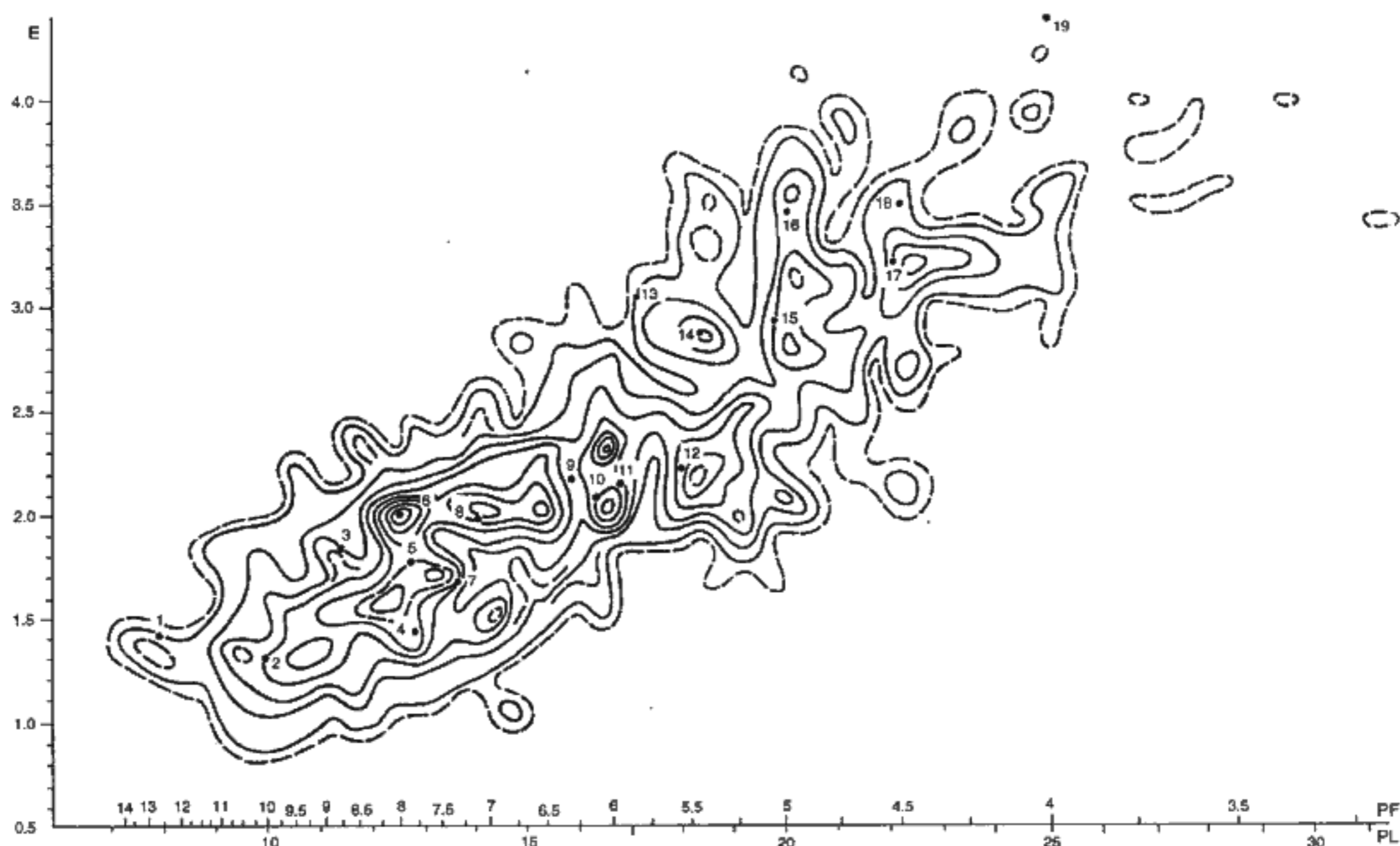


Fig. 1. Variability of elephants of the *Archidiskodon-Mammuthus* lineage in Europe (according to M3 parameters) Coordinate axis: E – enamel thickness; PF – plate frequency on 100 mm stretch; PL – length of one plate. Continuous isolines of distribution density are drawn through 0.5 Uniform Density Units, 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 MAYET - DEPERET, GROMOVA 1965); 2. *Mammuthus primigenius*, neotype GARUTT et al. 1990); 3. *Mammuthus primigenius jatzkovi*, holotype (GOLOVKO 1958); 4. *Mammuthus primigenius fraasi*, holotype (DIETRICH 1912); 5. *M. primigenius* (early form), 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 MAYET and DEPERET (OSBORN 1942); 9. *M. trogontherii chosaricus*, holotype (DUBROVO 1966); 10. *M. trogontherii chosaricus*, holotype (author's measurements); 11. *M. trogontherii trogontherii*, lectotype (DUBROVO 1966); 12. *Archidiskodon trogontherii*, average values (Azov museum – author's measurements) = *A. wuesti* (according to ALEKSEEVA 1977); 13. *A. meridionalis cromerensis*, holotype (DEPERET et al. 1923); 14. *A. m. voigtstedtensis*, holotype (DIETRICH 1958); 15. *A. m. tamanensis*, holotype (DUBROVO 1964); 16. *A. m.*, average values, Psekups River, N. Caucasus (VERESHCHAGIN 1959); 17. *A. m. meridionalis*, holotype (DUBROVO 1964); 18. *A. gromovi* GARUTT et ALEXEEVA (ALEKSEEVA 1977); 19. *A. m. taribanensis* GABOUNIA et VEKUA (ALEKSEEVA 1977).

result is that the selection discreteness 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 range on the topographic map. Adaptive peaks are asymmetric to variable extents. The sizes of the peaks are close within outlining isolines and vary over a small range. The peaks of different size and statistical significance are united into "clusters". Thus, the hierarchy of boundary depressions is established. One of the largest clusters corresponds to the last stage of the lineage development within the genus *Mammuthus*.

In addition to the peaks of the axial zone, series of

adaptive peaks in thin-enamel and thick-enamel areas were established for the first time. These peaks are oppositely oriented and clinally linked with the axial zone peaks, best manifested in the Siberian assemblages (Figs. 2, 3, 4).

Beginning the analysis of the graphic structure, it is important to specify the character of the variability revealed. A continuous individual variability caused by minor genetic differences between individuals, together with a stabilizing property 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 diagrams illustrate the variability of a different type. All along the lineage, this variability is manifested in the fact that the diagrams are multiple-cone, that is indicative of discrete selections of evolutionary features and, therefore, of a species polymorphism.

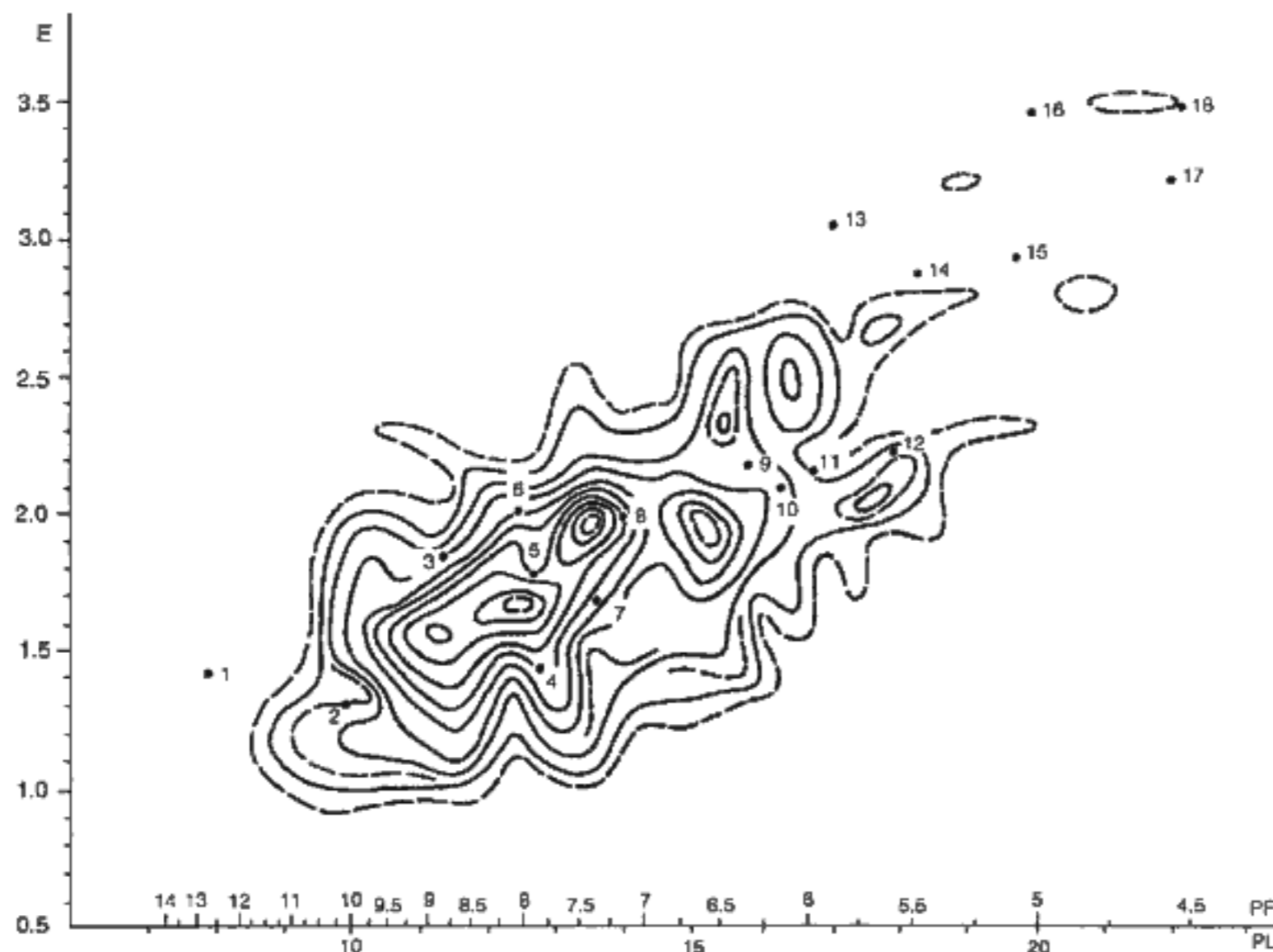


Fig. 2. Variability of elephants of the lineage *Archidiskodon-Mammuthus* in West Siberia. For legend see Fig. 1.

The considered features are the most important elements of the elephants phenotype. Unlike in morphotypical studies, where phenes and morphotypes are used as elementary indivisible particles whose discreteness is postulated, the discreteness discussed here can only be established after certain procedures of diagram-building. It is believed, however, that the present research is to be attributed to the section of population morphophysiology that deals with similarities and affinities between 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 (SARYTCHEVA - YABLOKOV 1973, TIMOFEEV - RESSOVKIY

et al. 1973, 1977). A functional meaning for the morphological and quantitative expression of aggregate of complex features is obvious. Therefore, adaptive peaks may be considered apparently as the stages of phenotype stabilization (or phenotypes), which were divided by the variability area of the species under study.

The positions of these stages in the evolutionary sequence are considered to correspond to an elementary evolution structure. Each stage of a phenotype is thought to represent individuals of adjacent populations delimited in accordance with the major orohydrographic boundaries (Urals and Yenisey River), which have been fixed during the Quaternary. Thus, there are no serious

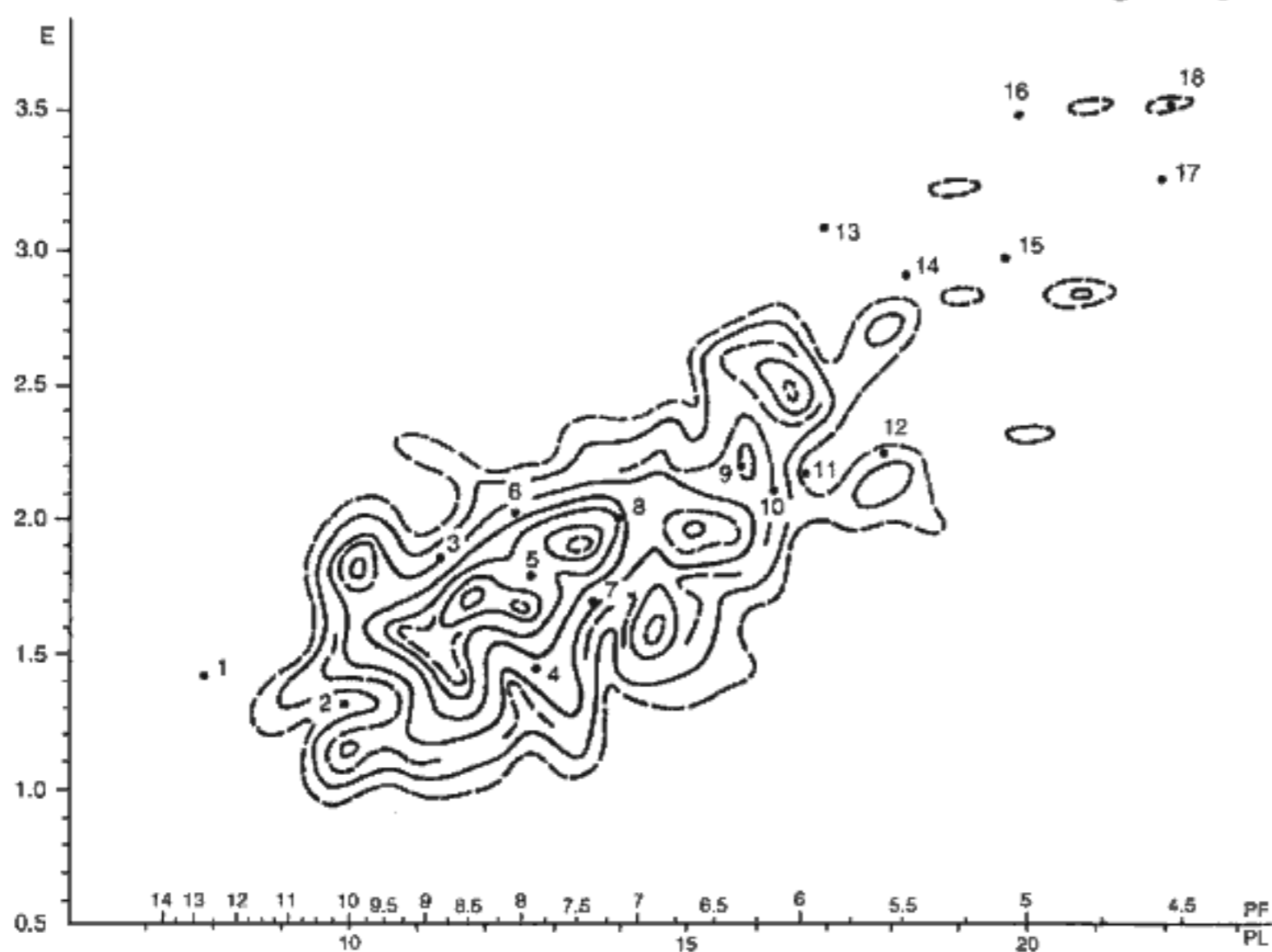


Fig. 3. Variability of elephants of the *Archidiskodon-Mammuthus* lineage in the Kuznetsk Basin (southern West Siberia). For legend see Fig. 1.

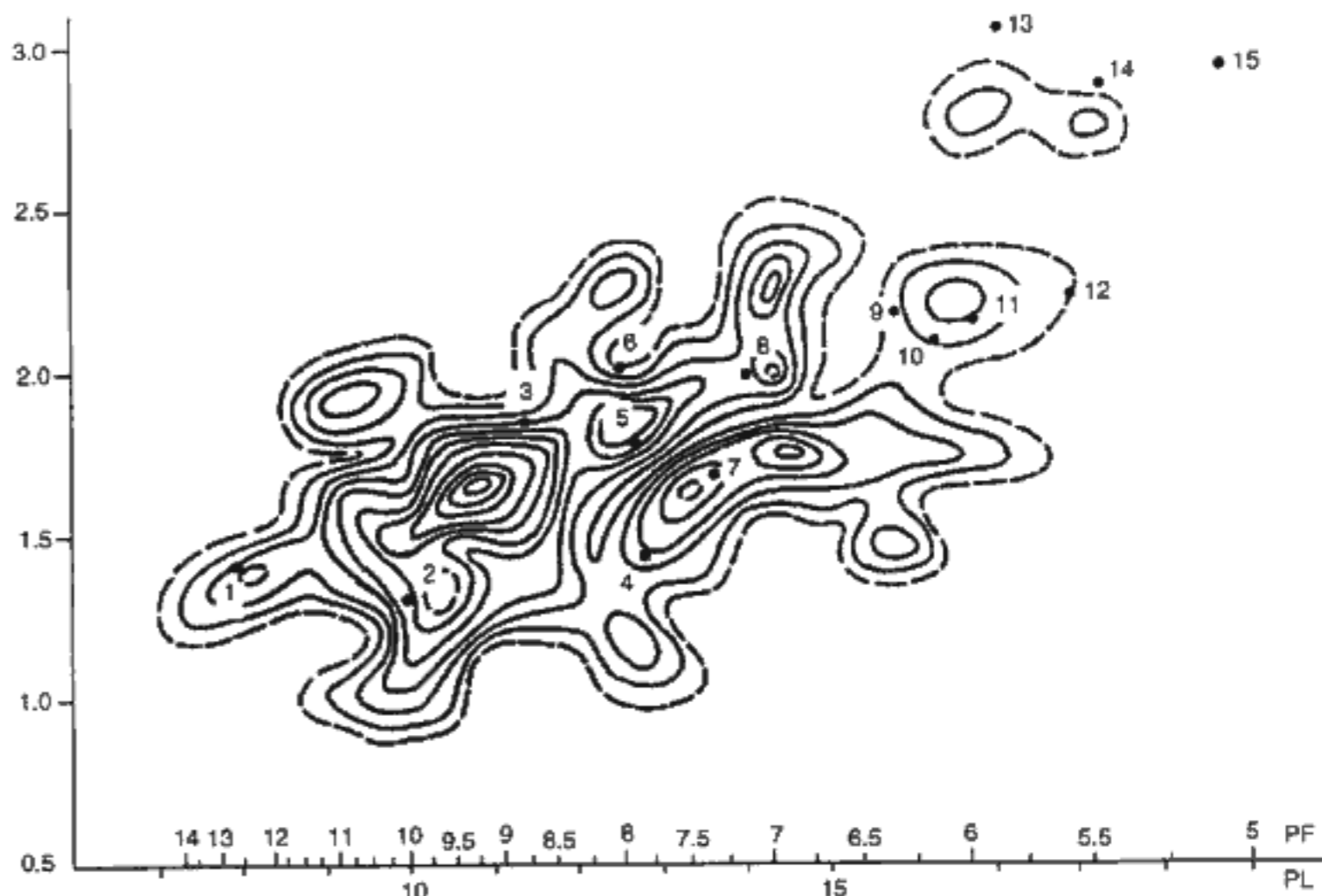


Fig. 4. Variability of elephants of the *Archidiskodon-Mammuthus* lineage in East Siberia. For legend see Fig. 1.

obstacles for the study of the dynamics of population processes. The modern data on daily (20–30 km) and seasonal (several hundreds km) migrations of contemporary African elephants suggest that at every stage of formation of the fossil elephants' phenotypes, a wide genetic exchange took place between adjacent populations of subcontinental groups.

Variability in isochronous populational groups and influence of the 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 a scatter on diagrams. Earlier, on materials from localities of a wide stratigraphical range, it was concluded that the distribution structure may be related to polymorphism and polytypism of taxa, whereas the dental system asymmetry does not significantly influence the distribution structure (FORONOVA - ZUDIN 1986). These data are currently amended by the results of a study of contemporary Asian and African elephants and apparently isochronous excursions from several archaeological sites. The wide polymorphism range is characteristic of contemporary elephants and late Pleistocene mammoths from Dolní Věstonice and Berelekh (Yakutia), whilst the latter populations from Předmostí, Khotylevo 2 and Kostenki 1 and 2 are more or less monomorphous (Fig. 5). A quantitative predominance of one phenotype (sometimes two phenotypes) is observed in all excursions. In Khotylevo 2 asymmetry does not have any influence on distribution, while in Předmostí, Dolní Věstonice and Berelekh, the teeth populations deviate to archaic phenotypes. The degree of this deviation varies geographically and chronologically.

In summary, the previous assumption that the dental system asymmetry does not make a regular impact on the lineage structure is now confirmed. The predomi-

nance of one of the phenotypes in isochronous population allows a chronological and palaeogeographical interpretation of lineage variability. The very existence of the isochronous polymorphism, however, increases the probability base for such interpretations and is indicative of possible mistakes when working with small excursions and single samples.

The comparison of regional diagrams shows the general similarity of the structure. The presence of an overwhelming majority of adaptive peaks, analogous by their position in the structure, is evident in every diagram. This fact allows the assumption of autochthonous speciation nearly across the entire area. The differences are expressed by the grouping of peaks into clusters. Furthermore, while superimposing the diagrams the analogous peaks partly off-set from another (regional versions of phenotypes) almost completely match (no less than 75%). They are formally attributed to one subspecies, thus fixing the geographical clinal variability within every phenotype.

Marginal "thick-enamel and thin-enamel" adaptive peaks (Fig. 1–4) are very interesting and entirely new elements of the structure. The first ones are represented by the 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 an increased hypsodonty index, a relatively larger interval between plates which are narrower and have weakly folded enamel. Medial sinus is hardly manifested in the European and West Siberian mammoths, while it is present in the mammoth assemblages from East Siberia. The functional difference of the above mentioned morphological features of this opposite marginal forms is traditionally considered as following: thick-enamel forms are adapted for soft vegetation of a forest environment; thin-enamel forms with an increased

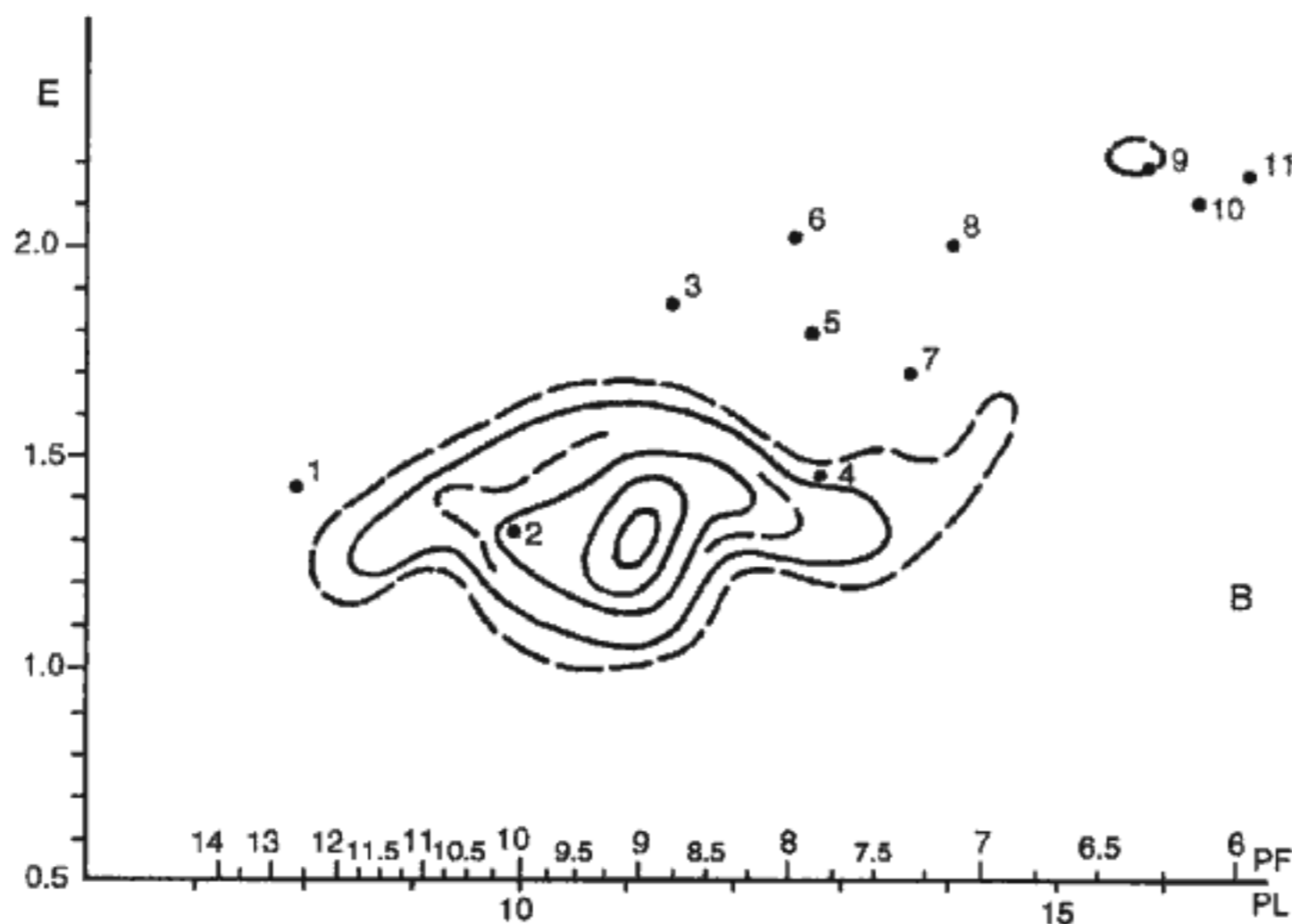
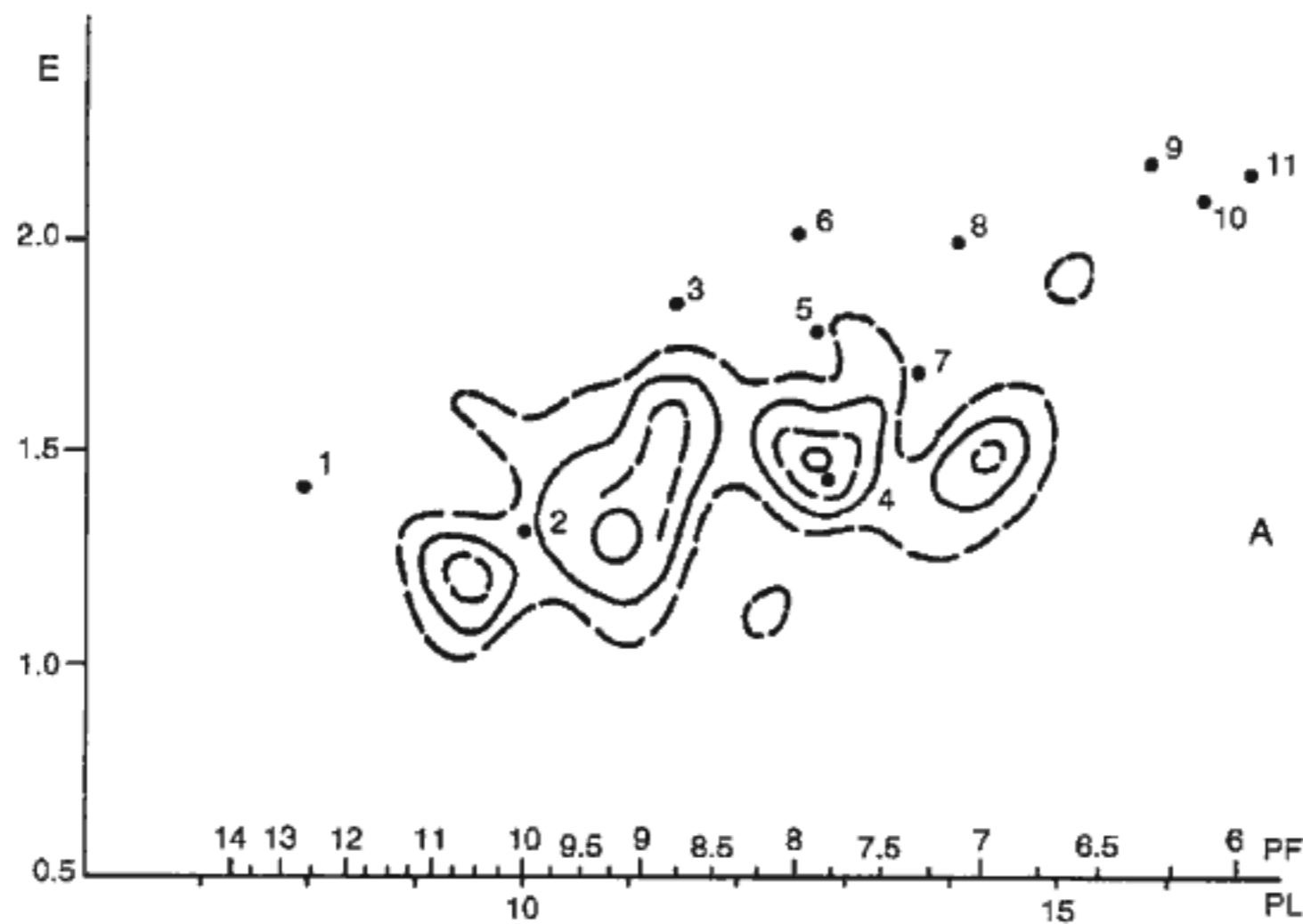


Fig. 5. Variability of *M. primigenius* in the population from the Czech Republic. A – Dolní Věstonice (redeposition is possible); B – Předmostí.

cutting/grinding ability are adapted for hard-tissue of arid landscapes. The facts described above, as well as data on the accompanying fauna and flora, the chronostratigraphic correlation between the sequence of adaptive peaks and the oxygen-isotope record (BOWEN 1981) indicate that the “thick-enamel adaptations” are associated with interglacial environments, while the “thin-enamel adaptations” are related to periglacial habitats.

It is important to note that the type sample parameters of the majority of taxa distinguished in the lineage correspond with the optima of adaptive peaks of every sequence (Fig. 1–4). For example, four peaks were established in “thick-enamel” variability of *M. primigenius* BLUM. The former, analogous to *M. primigenius* from the Early Mousterian Chokurcha site (Crimea – Fig. 1–4, 6), correspond to one of them. The next peak corre-

lates with the parameters of the thick enamel *M. primigenius jatzkovi* GOL. from Ukraine (Fig. 1–4, 3). The following peak apparently corresponds to *M. p. leith-adamsi* POHL. from the Thuringian interglacial travertines and representatives of the thick enamel variation of *M. primigenius* intermediate form (VANGENGEIM 1961). The teeth of these mammoths from the Kuznetsk Basin (Southern West Siberia) are radiocarbon dated to $39\,100 \pm 240$ and $28\,900 \pm 600$ yr. BP (FORONOVA 1990). The final stage of the lineage development conforms with the last thick-enamel peak, representing *M. p. sibiricus* DEPRET et MAYET (Fig. 1, 4, 1). The analysis of the data allows the linkage of mentioned “adaptations” with the inter-Riss, Riss-Würm, inter-Würm, and Holocene age respectively, according to the Alpine scale. In the “thin-enamel” variability area of *M. primigenius*, pa-

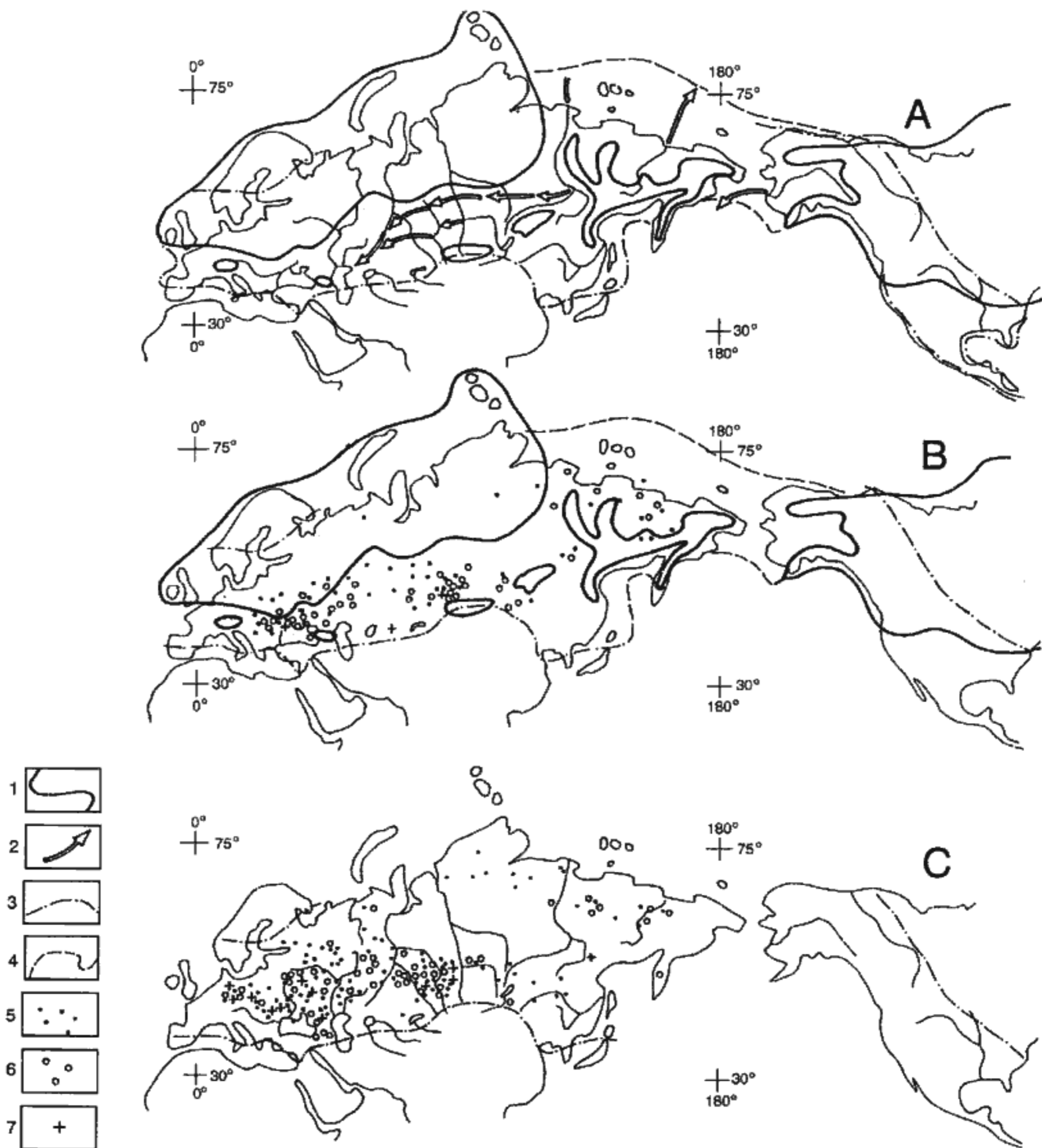


Fig. 6. Palaeogeographic situation during the maximum Quaternary glaciation of northern Eurasia (according to FLINT 1963, MARKOV et al. 1968, BOWEN 1981) and geography of localities of thin-enamel (B), and thick-enamel (C) forms.
 1 – ice sheet limit; 2 – palaeorivers; 3 – distribution limit of *M. primigenius* s.l.; 4 – the shoreline of Beringia during the maximum regression; 5 – localities of *M. primigenius* s.l.; 6 – localities of transitional forms from *A. trogontherii* = *A. wuesti* to *M. intermedius*; 7 – localities of *A. meridionalis* s.l.

rameters of *M. p. fraasi* DIETR. from the Riss layers of Steinheim (Germany) correspond to one of the well-developed peaks (Fig. 1–4, 4). The analogue of this form (from the Novotroitskoe locality, Irtysh River, West Siberia) was found in deposits dated by ESR to 174.2 ka BP (ARKHIPOV - LINKE 1987). Accordingly, this form can

be correlated with Stage 6 (128–195 ka BP) of the oxygen-isotope record V28–238 (SHACKLETON - OPDYKE 1973). The area of elephants with the thin-enamel phenotypes lies in a relatively narrow transcontinental zone (1/3 of *M. primigenius* s.l. maximal area approx. – KAHLKE 1993). Superimposition of this area with the

palaeogeographical scheme of the maximum Quaternary glaciation of northern Eurasia (FLINT 1963, MARKOV et al. 1968, BOWEN 1981) shows that all localities, with rare exceptions, are situated in ice-free zone. In East Siberia, they are linked within a narrow periglacial belt between the mountain and lowland glaciers (Fig. 6A, B). The forms with a thick-enamel and axial phenotypes are spread considerably wider. Their distribution areas overlap the previous one and cover the formerly glaciated territory (Fig. 6C). The orthogonal transformation of river-systems in glacials and interglacials also played a significant role in a particular distribution of these forms. The results support the assumed linkage of the thin-enamel forms with periglacial Quaternary habitats and the thick-enamel and main forms with interglacial and transitional environments.

Depressions in the lineage structure could range according to their statistical significance (relative depth). In this connection, dynamics of other teeth parameters on these borders and their possible taxonomic status are of a major interest.

According to phenogeographical data, the representatives of genus *Archidiskodon* (*A. gromovi* GARUTT and ALEXEEVA, *A. 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 during the early stages of the lineage development (FORONOVA 1990). It is important to note that the earliest *Archidiskodons* already had a very considerable variability in the enamel thickness (Fig. 1-4). First forms with a relatively thin enamel appeared and dominated in quantity (form adaptive peaks) in southern Europe, from where they spread to the south of Western Siberia and further east into Asia. Probably the thin-enamel forms pioneered the new adaptive zones.

SUMMARY

Since the early stage of the lineage, the crown width had gradually changed, decreasing from the archaic to the later forms, whereas the hypsodonty index increased "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 thin-enamel and thick-enamel phenotypes on one side and *A. m. tamanensis* with analagous phenotypes on another side. The next border is remarkable for the major leap of the hypsodonty index in the lineage (FORONOVA - ZUDIN 1986, LISTER 1993). This fact may be indicative of its definite 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 the thick-enamel area, with *A. m. voigtstedtensis* and *A. m. cromerensis*; the second in the thin-enamel area, with

A. trogontherii (POHLIG), the skeleton of which in the Azov Museum was described by V. BAYGUSHEVA and V. GARUTT in 1987, and *A. wuesti* (M. PAVLOVA) - teeth from the M. PAVLOVA collection are in MGPI, Moscow. Such changes in the teeth constitution of *Archidiskodons*, undoubtedly adaptive in their nature, were accompanied by corresponding changes in cranial proportions (OSBORN 1942, GARUTT 1954, AZZAROLLI 1977). A distinct specialization by the enamel thickness fixed in this part of the diagram and isolation of corresponding forms of late *Archidiskodons* correspond with the global climate changes at the beginning of Quaternary.

No less statistically significant is the border between the above forms and the adaptive peak with the parameters of the lectotype *M. trogontherii* from Süssenborn, with the crown width and hypsodonty index almost stable. This border, however, is very important in terms of statistics, since it is marked by the wide geographical spread of the early representatives of the genus *Mammuthus* to higher latitudes.

This evolution is associated with the widely discussed problem such as the border between the genera *Archidiskodon* and *Mammuthus* and the intermediate and ancestry forms for elephants of the Mammoth group.

The European structure allows the question of the volume of a wide species *Elephas trogontherii* (POHLIG, 1885) to be addressed. This author has noted that this species had zoologically, as well as geologically, an intermediate position representing a "bridge" between the southern Elephant and Mammoth. The distinct border mentioned above separates the ensemble with *A. wuesti* parameters from the group of adaptive peaks with *M. t. trogontherii*. The peaks are located at the beginning of the largest ensemble uniting the representatives of genus *Mammuthus*. It is known that the species *E. wuesti* was derived on the basis of the archaic variation of *E. (meridionalis) trogontherii* of Pohligh and teeth from Tiraspol (Moldavia - PAWLOW 1910). Later, it is considered by DUBROVO (1963) to be only a synonym of *E. trogontherii* of POHLIG and describes its earlier variation as a nominative subspecies of *M. t. trogontherii* within the genus *Mammuthus* (DUBROVO 1966). According to the present authors, the earlier form of *Trogontherii* elephant is an independent form, and it is attributed to the genus *Archidiskodon* (PAWLOW 1910, YATZKO 1948, SHER 1971, ALEKSEEVA 1977). Thus, a generic status of the border can be assumed. Apparently, this form, unlike the thick-enamel phenotypes of the late *meridionalis* subspecies, being rather isolated in the diagrams (Fig. 1), provided the gene-flow "bridge" between the southern elephants and mammoths originally postulated by H. POHLIG (1885).

The mammoth part of the lineage development, marked by even a wider polymorphism embraced in the evolutionary process all Eurasia with considerable re-

gional differences. The character of these events in Eastern Siberia gives grounds to suppose the influence of the Beringian and, probably, North American population assumed by GARUTT (1995). The phenogram (Fig. 4) fixes a deep length-wise depression dividing "thick-enamel and thin-enamel" phenotypes, beginning with forms of *A. voigtstedtensis* and *M. trogontherii* up to the late *M. primigenius*. On the diagram for Europe, this depression is weakly manifested and can be traced only on the *M. intermedius* stretch and the early forms of *M. primigenius*. In Siberia, the thin-enamel "adaptations" of early *Mammuthus* s.l. are manifested as the clinas of the "axial" phenotypes.

In accordance with the clinal geographical variability, the East Siberian mammoths appear to be more archaic, whereas West Siberian and European forms seem to be more advanced at the particular stage. In addition, this is accompanied by some morphological peculiarity of the East Siberian forms. Their thin-enamel representatives (much more than thick-enamel ones) are characterized by "meridionaloid-wuestoid" rubbing configuration of plates; they have a smaller size, as well as the higher hypsodonty index as pointed out by SHER (1971). The parameters of this elephant correspond to the adaptive peak of the *M. trogontherii trogontherii* lectotype on the diagrams. Obviously, this peak, the linkage with *A. wuesti* discussed before is well seen on the European diagram (Fig. 1) and starts the sequence of the East Siberian thin-enamel forms.

On the basis of the present results, a parallel development of early mammoths in East Siberia can be assumed. These mammoths probably originated from forms which strongly diverged in the period of isolation of the Eurasian and North American populations. The role of Beringia in the formation of Holarctic fauna, the peculiarity of North-Eastern elephants and their phylogenetic links with other representatives of the Mammoth lineage, are described in detail in other papers (SHER 1971, SHER et al. 1995, etc.) The two evident depressions correspond to borders of the lineage (Fig. 1-4); the first one, between *M. intermedius* and the early form of *M. primigenius* (from VANGENGEIM 1961), the second border lies at the bottom of the adaptive peak with the parameters of *M. primigenius primigenius* nominative subspecies (Fig. 1-4). Both borders are marked by the decrease of crown width. In addition, the last one has a considerable increase of the hypsodonty index. The European phenotypes appear to be less advanced than the East and West Siberian at this stage, as well as the earlier stages of the lineage development. The mammoth stage, together with detailed characteristics of phenotypes and their interregional comparisons, was previously described by FORONOVA - ZUDIN (1986).

CONCLUSIONS

Problems of the proboscidean phylogeny and origin and extinction of mammoths, have been topical for many decades. Currently, beside the traditional comparative-morphological descriptions, genetical and statistical populational approaches have been applied.

The method of multidimensional statistical analysis of morphometric data, developed by the authors substantially increases the informativity of the traditional techniques, and allows the graphical presentation of a large amount of data (on separate species, as well as on the lineage in general) and the analysis of its populational aspect.

The reconstructed diagrams illustrate that the process of the *Archidiskodon-Mammuthus* development lineage did not follow a simple phyletic sequence, but show a wide species variability of the group (on micro- and macroevolutionary level). It is still difficult to determine precisely how the polymorphism of isochronous populations is geographically expressed. The presented evolutionary model is based on the consecutive (populational) speciation affected by selective impacts of environment in accordance with the dynamics of Quaternary climatic changes. The transcontinental occurrence of adaptive peaks (optimal phenotypes) allows their taxonomical status to be derived, and is indicative of a chiefly autochthonous speciation in the lineage. Displacement of the majority of analogous (regional) phenotypes, not extending beyond the 75 % proximity limits, can be indicative of a different reaction of the environment to global climatic changes (geographical clinal variability). This also allows the derivation of two speciation directions (European-Asian and East Siberian-European) on different stages of the *Archidiskodon-Mammuthus* lineage development. Significance of a palaeogeographical factor in the lineage development is emphasized by the special role of thin-enamel (periglacial) adaptations. Thin enamel forms can be traced throughout the lineage from the earliest *Archidiskodons*. The diagrams clearly record several stages of the enamel-thickness reduction throughout the lineage, which correspond to the depressions (taxonomical borders). It is supposed that thin-enamel forms pioneered the inhabitation of new adaptive zones and provided the progressive development of the lineage.

These adaptive peculiarities, still not completely described, conditioned a considerable taxa polymorphism which provided this group with an environmental flexibility and predominance among the North Eurasian Quaternary faunas. Undoubtedly, the actual evolutionary history of the lineage was more complex and diverse, and requires further studies.

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