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Discreteness of evolution and variability i n mammoth lineage: method for group study

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SUMMARY: Crucially new information on of mammoth lineage development was obtained. Based on large paleontological material, authors created a pioneering multidimensional model of lineage structure. It illustrates discreteness of macro- and microevolutionary processes and considerable variability implying a powerful genetic potential of the group under study that have provided it with flexibility and predominance among the Quaternary faunas of Northern Eurasia. These important results were realised while studying the main morphometrical features last molars (M3) with the help of the authors' original approach based on building and analysing of multidimensional diagrams. The method allows to demonstrate visually and to analyse vast amounts of paleontological material in the context of populational studies. The model of the structure clearly demonstrates discreteness of evolutionary processes, polytypism and polymorphism of the taxa. It allows to trace ecological adaptations in the group, to define dynamics of stations, to carry out paleozoogeographical and paleoecological reconstructions.

1. Introduction*

Elephants of Archidiskodon-Mammuthus lineage are traditionally considered to be the main group in Quaternary paleontology and biostratigraphy. Permanent improvement of dental system and ability of wide migration conditioned relatively high evolution speed and wide adaptive radiation in geographically different and frequently changing paleoclimatic conditions. The transformations in dental system, easily traced from 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 the means of dental structures such as: enamel, cement, and dentine, as well as of specific construction of a tooth as a whole. Wide spreading of elephants on the vast territories of Eurasia and North America in Pliocene and Pleistocene caused the appearance of large variety of forms. The group systematics based partly on cranial morphology features and mainly on molar structure, is complicated and often confused, and taxonmical definitions are impeded by wide range of variability of the features mentioned. The method proposed allows to solve these problems and to obtain new information on group development during the Quaternary (Foronova & Zudin 1986, 1995, 1999).

2. Material and Method

Over 2000 molars were studied. They belong to representatives of all the taxa known in the lineage originating from numerous localities of Northern Eurasia. The study was based on

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It was included in this volume as it represent a completion of the arguments discussed by Foronova in this volume.

building of two-dimensional distribution in coordinates of plate frequency on a 100 mm stretch of crown length (average plate length is marked on a parallel scale) and enamel thickness. These features are traditionally regarded as the major ones for defining of taxonomic position of mammoth-lineage elephants. Proposed method for data processing and diagram-building is applied for the first time in Quaternary palaeontology. It permitted to derive a maximal amount of information from morphological features and to analyse vast complexes of material from the whole lineage and its regional variations.

The operating sequence of the method was the following: 1) Building of punctuated diffusion diagrams. 2) Converting "point clouds" into numeric values of distribution density, and simultaneous sliding averaging (replacing of a single square-platform to the half of its side). 3) Building of distribution density isolines and normalising of distribution density values in the units of the Law of Uniform Density (division of the sample volume by the variability range square). 4) Hierarchic procedures that imply varying of the sizes of 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 did not depend on a building technique.

It was found that 30-50 specimens are enough for its stabilisation. While making samples, all types of variability except the intraspecific one were being excluded. Separate dia-

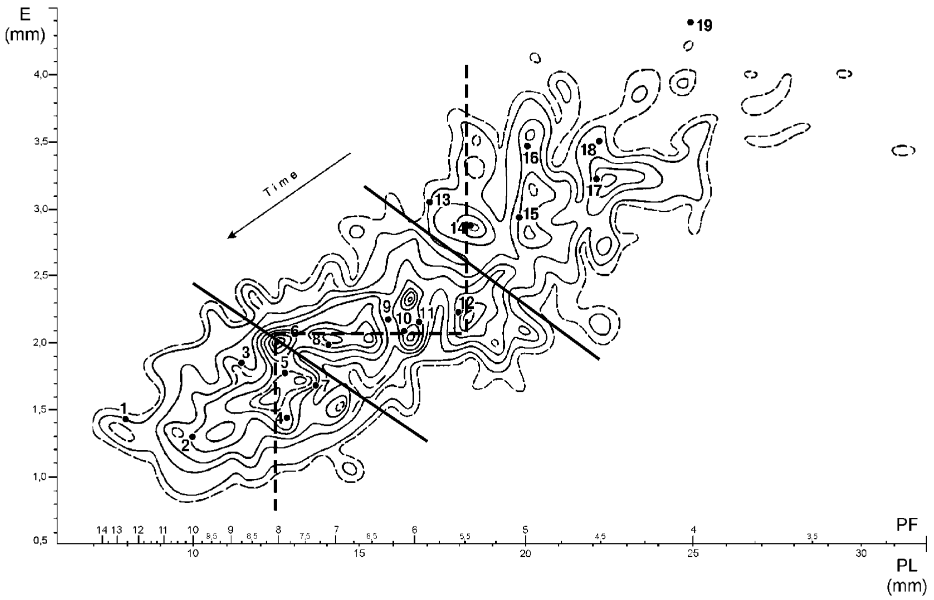

Fig.1 - Variability of the elephants of the Mammoth lineage in Europe (according to M3 parameters). Coordinate axis: E - enamel thickness; PF - plate frequency on 100 mm stretch; PL - length of one plate. Continuous isolines of distribution density are drawn through 0.5 Uniform Density Units, punctuated isolines are drawn through 0.25 Units, outer isoline corresponds to 0.25. Whole lines show the largest depressions (?taxonomical boundaries). Puncntuated lines show the assumed direction of lineage development due to selection pressure.

Points are the coordinates of typical specimens of taxa distinguished in the lineage and some peculiar forms: 1. *Mammuthus 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*, holotype; 9. *M. trogontherii chosaricus*, holotype; 10. *M. trogontherii chosaricus*, holotype (authors' measurements); 11. *M. trogontherii trogontherii*, lectotype; 12. *A. trogontherii* (Azov museum; authors' measurements) = *A. wüsti*; 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*.

grams 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.

3. Results and Discussion

Generally, the variability area (from archaic forms to the latest mammoth) reflects canalising selection in the lineage due to global natural changes of the Quaternary (Fig. 1). However, the most important and innovative result is that selection of combinations of the features under study (i.e. of levels of dental system specialisation, 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 "Wright's symbolic picture" (in terminology of Dobzhansky 1951). The peaks group into ensembles, so an hierarchy of marginal depressions can be seen. One of the large 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.

Adaptive peaks are regarded as stages of phenotype stabilisation (or as phenotypes), their definite positions in the lineage allowing to correlate them with elementary evolving structures-populations. Non-consistency of intrapopulational variability was observed both in heterochronous and isochronous populations (samples from some archaeological sites, as well as samples of contemporary African and Asian elephants). Predominance of one (sometimes two) phenotypes in these populations permits to use molars for evolution studies, but also shows the possibility of making mistakes while working with small samples or single specimens. The fact that the structure is multiconed implies populational variability in the lineage (polymorphism) and polytypism of taxa. Parameters of typical specimens of some taxa correspond to optimums of adaptive peaks.

Comparison of regional diagrams shows transcontinental penetration of the majority of phenotypes and chiefly autochthonous speciation almost within entire station. 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 adaptaion. Many facts -morphofunctional differences, accompanying fauna and flora, different stations, physical dates, and certain agreement between the sequence of these forms and the stages of oxygene-isotope Ocean scale-provide grounds to link thick-enamel and thin-enamel adaptations with interglacial and periglacial environments respectively. Different stations are serious argument in favour of paleoecological specialisation of mammoths. The station of the elephants with thin-enamel phenotypes lied in a relatively narrow transcontinental zone (approx. $^1/_3$ of *M. primigenius* sensu lato maximal station). The forms with thick-enamel and axial phenotypes were spread considerably wider. Their stations overlaped the previous one and covered the territory of former glaciers.

Apparently, thin-enamel forms, which can be traced all the way through the lineage, played a special role. It was them that could pioneer new adaptive zones, since chiefly thin-enamel phenotype was being selected during the evolution. Figure shows several moments of abrupt decrease of enamel thickness before depressions-possible taxonomical boundaries within the lineage. The first of such events can be seen before a generic border (points 13, 14, 12) on the stage of late archidiskodonts (1.0-0.8 Ma BP approx.). The second one is before a border between the "early" and "late" forms of *M. primigenius* (points 6, 5, 4), on the stage of the early one (0.16 Ma BP approx.). It is remarkable that it is these mammoths that are characterised by the maximal plate quantity in the lineage (30). These boundaries are remarkable by their outstanding paleogeographical events, which probably caused two large waves of station expansions: first, to the middle latitudes of Eurasia, and then to the extremely high ones.

References

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