History of Quaternary Proboscideans of the South of Western Siberia inferred from dental system analysis

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SUMMARY: Detailed history of mammoth lineage development — from ancient archidiskodonts to the latest mammoths — was reconstructed for the South of Western Siberia. Vast material from the Kuznetsk Basin characterizing rather detailed stratigraphic sequence of the Quaternary was studied using an original method of molar analysis of the author. Multidimensional diagrams show diversity of dental phenotypes in the framework of evolutionally directional selection during all the lineage development. Most of them compose successions in thick- and thin-enamel zones of distribution. Morphofunctional differences between these forms, as well as complex of other data, are indicative of chronological and paleoecological nature of dental system changes of proboscideans. It was found that the tendencies of group development in this region (as well as in Eurasia as a whole) were determined by adaptations to periodic changes of periglacial and interglacial environments.

1. Introduction

Paleontological material from the Kuznetsk basin occurs in sediments that make almost continuous sections from the beginning of Lower Pleistocene to Holocene (Foronova 1999). The fossils allowed to reconstruct a sequence of both glacial and periglacial faunas and to compare it with climatic-stratigraphic horizons of West-Siberian scheme. Proboscideans are represented on this territory by a majority of well-known forms, as well as by a number of first recorded ones belonging to genera *Archidiskodon* and *Mammuthus*. Collection contains crania fragments, mandibles, over 500 molars.

2. Method

Systematic identification of elephants is commonly established by morphological composition characters of last molars. Traditionally, average plate frequency on 100 mm stretch, plate length and enamel thickness are regarded as the most informative features. We do not consider number of plates as a definitive feature because of two reasons: 1) it is inconvenient for statistical procedures (complete molars are few and they substantially reduce sample); 2) it was found that there were no sequential (form by form) increase of number of plates in a crown, as it was previously thought. Maximal plate number (29-30) is typical of very large mammoths that existed in the final stage of Riss (seconds half of Zaale, about 160 ka) but not of the latest *Mammuthus primigenius*. Material was studied using authors' method for analysis of mentioned features, building and analyzing of multidimensional diagrams (Foronova & Zudin 1986; 1999; 2001) that allowed to retrieve new information on the lineage history. To finally define a taxonomical range of forms established using this information one needs to make a revision of the entire group. Currently, preliminary description of material is substantially complicated by restrictions of present nomenclature.

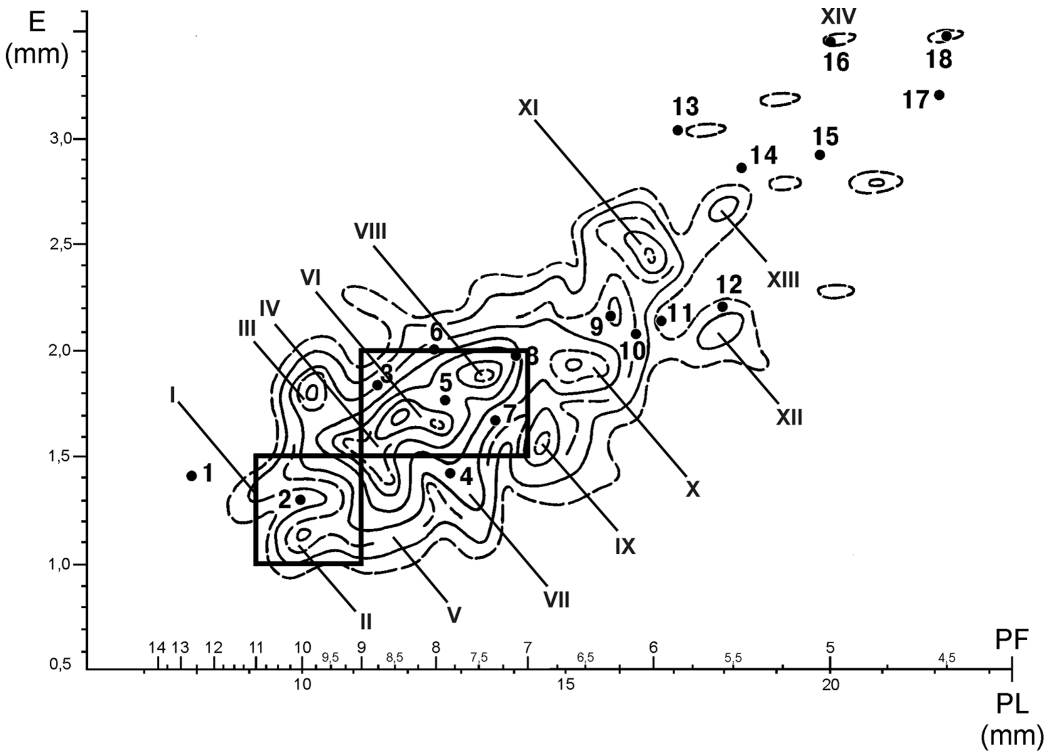

Fig.1 - Variability of elephants of the mammoth lineage, after the material from Kuznetsk Basin (Southeast of Western Siberia)

Coordinate axis: E — enamel thickness; PF — plate frequency on 100 mm; PL — plate length.

Rectangles show variability limits for features of early and late form of *Mammuthus primigenius* Blum. (according to Vangengeim E.A., 1961).

Points show coordinates of type specimens of taxa established before or assumed (see Fig. 1, Foronova & Zudin, this volume).

Adaptive peaks (forms): I, II - *Mammuthus primigenius* (late form); III, IV - *M. primigenius* (intermediate thick-enamel form); V — *M. primigenius* (intermediate thin-enamel form); VI — *M. primigenius* (early form); VII — *M. primigenius* cf. *fraasi*; VIII — *M.* cf. *intermedius*; IX — *Mammuthus* sp.; X — *M.* aff. *chosaricus*; XI — *M. trogontherii*; XII — *Archidiskodon* aff. *wusti*; XIII — *A. meridionalis* ex gr. *tamanensis*; XIV — *A.* cf. *meridionalis*.

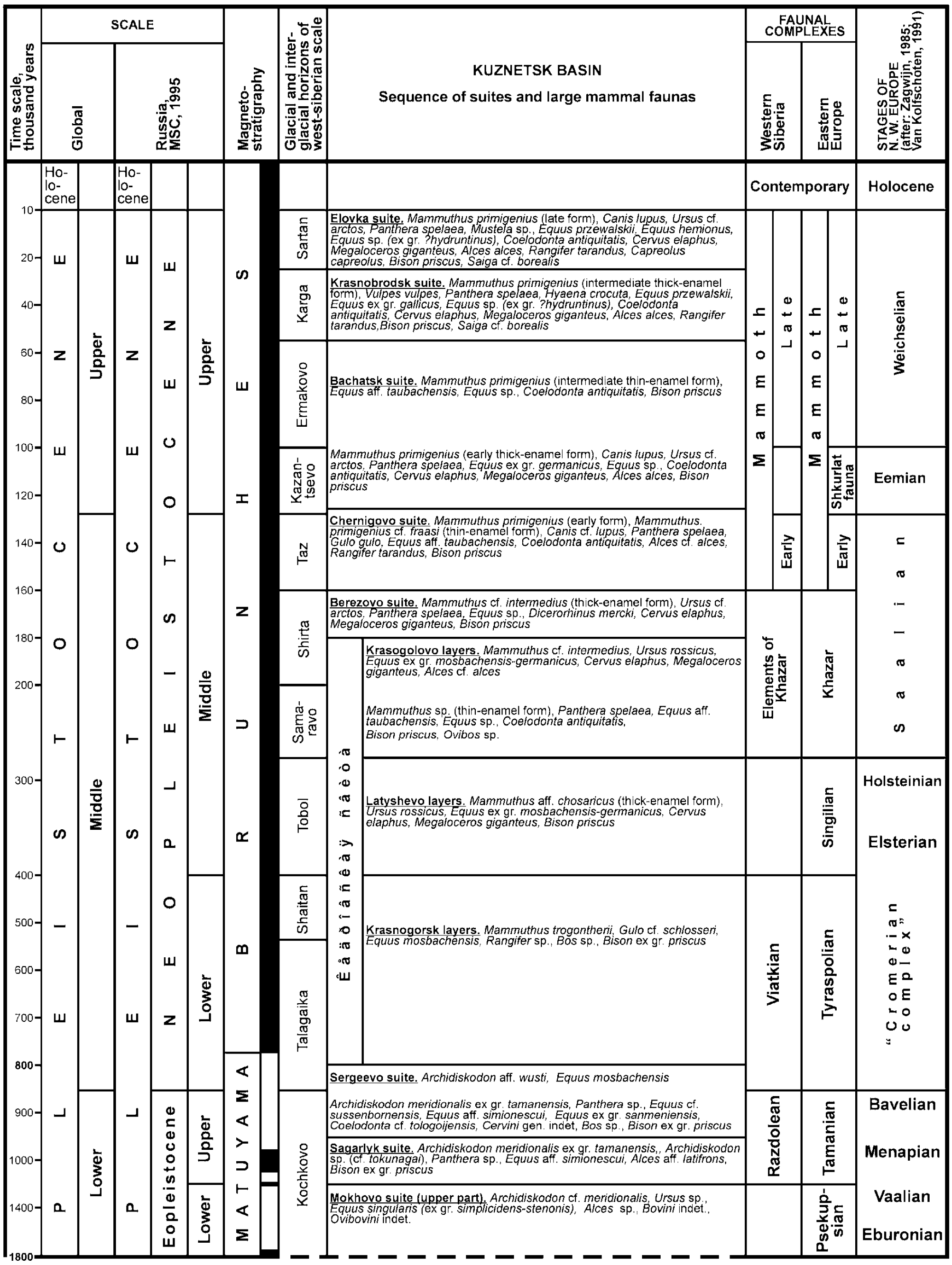

Fig.2 - Biostratigraphy of Quaternary sediments in the Kuznetsk Basin.

3. Main Results

The most ancient proboscideans on the South-East of Western Siberia were found in reverse-magnetized sediments of Lower Pleistocene (Lower Eopleistocene in the Russian Scale). In plate frequency and enamel thickness they are similar with typical *Archidiskodon meridionalis* (Nesti) (Fig. 1, adaptive peak (a.p.) XIV). These morphological characteristics, as well as information on accompanying forms, permit to correspond this fauna with Late Villafranchian fauna of Italy (Sardella *et. al.* 1998). However, Siberian *A.* cf. *A. meridionalis* has a number of peculiar features: high hypsodonty of a crown, absence of medial sinus on a plate, close positioning of plates. These differences were probably caused by climatic conditions differing from of conditions of Southern elephant's habitat in Europe. A form similar to progressive *A. meridionalis* ex gr. *tamanensis* (= *cromerensis - voigtstedtensis*) (Fig. 1, a.p. XIII) existed here in the second part of Early Pleistocene (in the beginning of Late Eopleistocene in Russia or in the end of Late Villafranchian / beginning of Galerian in Italy (Sardella *et al.* 1998).

Considerable climatic and environmental changes in the end of Early and especially in the beginning of Middle Pleistocene (Lower Eopleistocene of Russian Scale, Foronova 1998) have conditioned further development of mammoth lineage. Periodic changes of landscape and vegetation have caused an increase of plate number and frequency in a crown, and decrease of plate length and enamel thickness. Obtained diagrams show these changes to be successive stages of elephants' adaptation to periodic environmental changes. Successions (rows) of ecologically different thick- and thin-enamel forms can be distinctly traced in the lineage from the beginning of Middle Pleistocene.

Most advanced form of genus *Archidiskodon* existed in the Kuznetsk Basin in the fauna of the beginning of Early Neopleistocene (Russian scale) analogous to Early Cromerian faunas in Europe, in the end of Matuyama epoch. On the diagram it can be seen as first well-pronounced thin-enamel group (Fig. 1, a.p. XII). These elephants are similar to late *A. meridionalis* in average plate frequency, but differ from them by significantly low enamel thickness. According to our data (Foronova & Zudin 1999), it is this form, being on the boundary between two genera, that could have been a transition from archidiskodonts to mammoth and could have given a new direction for the lineage development. *Mammuthus trogontherii*, having an enamel somewhat thicker than with this form lectotype (Fig. 1, a.p. XI), was a main element in the fauna of Early Neopleistocene (analogous to Tyraspolian fauna of Southern Europe and faunas of major part of Cromerian and Elsterian of Western Europe) (Fig. 2).

Many paleontologists strove to find transitional forms in the mammoth lineage. These studies however were complicated by a serious obstacle — overlap of features of closely related forms. Our diagrams could help to partially resolveclarify this problem.

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 Middle Neopleistocene (Tobol, Samarovo, and Shirta horizons of West-Siberian Scale = Holstenian and major part of Saalian of Western Europe) *M.* aff. *chosaricus* (Fig. 1, a.p. X) with a relatively thick enamel is typical of Tobol interglacial. Very large thin-enamel *Mammuthus* sp. (Fig. 1, a.p. IX) corresponds to Samarovo glaciation item. Due to some of its features it can be established as a separate taxon. A peculiar thick-enamel *M.* cf. *intermedius* (Fig. 1, a.p. VIII) with a habitat covering entire Europe and Western Siberia could exist during Shirta (within Saalian) warming.

According to traditional concepts, further lineage development must have matched the parameter limits determined by E.A. Vangengeim (1961) for "early" and "late" forms of *M. primigenius*. It was found, however, that in the end of Middle and Late

Pleistocene there was maximal variability in the lineage (Foronova & Zudin 1989, 1999). Series of thick- and thin-enamel forms (Fig.1) going far beyond the parameter limits can be distinguished within the vast and still conventionally used species of *M. primigenius*. They are characterised by different morphofunctional adaptations caused by climatic changes.

Mammoth with thick-enamel phenotype (Fig. 1, a.p.: VI, III, IV) occurred on the South of Western Siberia in interglacial Kazantsevo (Eemian) and Karga (inside Weichselian) epochs. It is remarkable that the later form (Fig.1, a.p. III) looks more distinct on the diagram. Its correspondence with mentioned period is confirmed by a number of ^{14}C-dates: from 45220 +/-1700 to 28870 +/-60. These mammoth are known throughout the Eurasia.

Mammoth with narrow band-like plates and thin low-folded enamel (Fig. 1, a.p. VII, V) were predominant in periglacial faunas, in Tazov (Late Saalian) and Early Zyriansk (Early Weichselian) epochs. Remarkable is the form *M. primigenius* cf. *fraasi* (Fig. 1, a.p. VII) whose plate composition was the most typical for the teeth of thin-enamel phenotype and the most adjusted for functions of cutting and grating. In the final stage of lineage development corresponding to the time of Sartan glaciation mammoths had maximal number of plates and the thinnest enamel. This stage corresponds to parameters of Taimyr mammoth defined as a neotype for species *M. primigenius* Blum. Nevertheless, even on this stage the diagram shows two adaptive peaks — conventionally thick-enamel and thin-enamel ones (Fig.1, a.p.: I, II), the first being more advanced in plate frequency. No more progressive forms were not found in the Western Siberia, while one more form — the last one from the thick-enamel succession (Fig. 1, point 1) with maximal plate frequency (14 on 100 mm) — was established in Europe and Eastern Siberia (Foronova & Zudin 1986; 2001).

4. Conclusion

An assumption about autochthonous speciation in mammoth lineage within the entire station (Foronova & Zudin 1999) is confirmed on the example of stratified material from the Kuznetsk Basin — the largest stratigraphic region on the South of Western Siberia. Comparison of the diagram with analogous schemes made for different regions of Northern Eurasia shows general similarity of lineage structure and presence of the majority of adaptive peaks (forms), analogous by their position in the structure. Some mismatch in their parameters on the diagrams for Europe, Western and Eastern Siberia is indicative of geographical clinal variability caused by various response of regional environments to global climatic changes. Results obtained with the help of the method provide new information on development of Quaternary proboscideans and give an opportunity for morphofunctional diagnostics of periglacial and interglacial forms which in turn may be used in climatic stratigraphy and paleoecological reconstructions.

5. References

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