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Data on DNA give evidence for parallel development in mammoths and elephants

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The studies on DNA in mammoth in comparison with extant elephants (fragments of the loci 16S rRNA, 12S rRNA, and cytochrome b) are reviewed. Based on these data, genetic diversity of mammoth and intraspecific and interspecific genetic differentiation of *Mammuthus primigenius*, *Loxodonta africana*, *Elephas maximus*, and *Mammut americanus* are considered. Apparently, the lineages of mammoth and living elephants diverged simultaneously from a common ancestor, the greater morphological similarity between the Asian elephant and mammoth is a result of parallel evolution. Significance of genetic data for phylogenetic reconstruction is considered.

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INTRODUCTION

During the last decades, methods for amplification and sequencing of DNA fragments were applied to fossil remains and provided a means for comparative genetic studies on extinct and related living forms. DNA of an extinct animal (a quagga) was first studied in 1984 (cited from Pääbo *et al*. 1992). DNA was cloned from a 4400 year old Egyptian mummy (Pääbo 1985), 7000 year old human brain (Pääbo *et al.* 1988), and a number of fossil animals and birds.

As regards the Elephantidae, successful PCR amplification and sequencing was performed for the following mitochondrial genes of mammoths aged by radiocarbon method > 50,000 to 9,700 BP (Table 1): 93 base pair (bp) fragment of the 16S ribosomal RNA gene (Hoss *et al.* 1994), 961 bp (complete sequence) of the 12S rRNA gene (Noro *et al.* 1998), and fragments of the cytochrome b gene of 242 bp, 277 bp (Hagelberg *et al*. 1994), 228 bp (Yang *et al*. 1996), 1005 bp (Ozawa *et al*. 1997), and a complete sequence of 1137 bp (Noro *et al.* 1998). These data were compared with the sequences for living Asian and African elephants. In addition, Yang *et al.* (1996) extracted and analysed a 228 bp fragment of the cytochrome b gene of American mastodon (*Mammut americanus*). The purpose of this paper is a brief review of the data on mammoth DNA and consideration of possible phylogenetic interpretations of these data. To gain a pictorial rendition of relationships between considered individuals, we applied the method of multidimensional scaling to the matrix of pairwise genetic distances (Kruskal 1964). The latter were computed as the percentage of substitutions distinguishing two individuals from each other corrected by Kimura's two-parameter model.

RESULTS

In each study including material on several mammoths, they were polymorphic and differed from each other by a greater or lesser number of substitutions. The study on the 16S rRNA (Hoss *et al.* 1994) is noteworthy in this respect, notwithstanding the fact that this was the shortest sequence examined. Four mammoths of different geological age were studied and appeared divided into two pairs, in each of which DNA sequence was identical, and the pairs differed from each other by five substitutions (5.4%). A comparison of this sequence in mammoths and one individual Asian elephant revealed four and three substitutions (for the first and second mammoth pairs), the African elephant differed from mammoths by four and five substitutions, respectively, and from the Asian elephant by only two (unfortunately, only one individual of each extant species was examined; it should furthermore be noted that, in this case, two, three, four or five substitutions differ from each other nonsignificantly). Figure 1 shows differentiation of living elephants and mammoths in the space of two first co-ordinates of multidimensional scaling. The differences between the mammoth pairs are relatively great in comparison with intergeneric differences between *Loxodonta, Elephas*, and Mammuthus (only *M. primigenius* represents the genus *Mammuthus*). This is attributable to either a high individual genetic diversity of *M. primigenius* or to belonging of the examined mammoths to different geographical or (and) temporal forms. In this connection, it is expedient to consider the data on geological age of examined animals.

The mammoths of the first pair were ^{14}C dated as approximately 42,000 BP (mammoth from Shandrin) and 53,000 BP (Khatanga), respectively; this was corroborated by independent biostratigraphic studies. Of the second pair, the Yuribei mammoth was reliably dated to the end of the Pleistocene or the onset of the Holocene by the in situ burial position in fluvial deposits of the first terrace of the River Yuribei; this was in agreement with ^{14}C dating of 9,730 ± 100 BP for soft tis-

Table 1 Localities and geological age of Mammoths (M1-M8) and Mastodon (MAS) examined with reference to DNA.

Indivi -duals	Locus (number of base pairs)	Source*	Locality	Age, years old	Source*
M1	16S rRNA (93) cytochrome *b* (242)	(1) (2)	Taimyr Peninsula, Khatanga	> 53170	(6)
M2	16S rRNA (93)	(1)	Yakutia, Shandrin	41750±1290	(6)
M3	16S rRNA (93) cytochrome *b* (1005)	(1) (5)	Magadan Region, Stream Kirgilyakh	26000± 1200 43800±4200	(7) (8)
M4	16S rRNA (93)	(1)	Gydan Peninsula, River Yuribei	9730±100	(9)
M5	cytochrome *b* (1137) 12S rRNA (961)	(3) (3)	Taimyr Peninsula, Pyasina	25100±550	(10)
M6	cytochrome *b* (277)	(2)	Yakutia, River Alaikha	46100±1000	(11)
M7	cytochrome *b* (228)	(4)	Bolshoi Lyakhovskii Peninsula	>46000	(4)
M8	cytochrome *b* (228)	(4)	Alaska, Firebank	≈ 20000 (?)	(4)
MAS	cytochrome *b* (228)	(4)	Southern Michigan, Oakland County	10200±170	(4)

(1) Hoss *et al.* 1994; (2) Hagelberg *et al.* 1994; (3) Noro *et al.* 1998; (4) Yang *et al.* 1996; (5) Ozawa *et al.* 1997; (6) Arslanov *et al.* 1980; (7) Bennett *et al.* 1978; (8) Shilo & Lozhkin 1981; (9) Evseev *et al.* 1982; (10) Zubakov & Kind 1974; (11) Sulerzhitskii & Lavrov 1992.

sues and 9,600 ± 300 BP for food from the stomach (Evseev *et al.* 1982). As regards the geological age of the baby mammoth from the Kirgilyakh Stream (Dima), opinions differ. In 1977, the burial place was studied by the researchers from Magadan, Moscow, and Leningrad (St. Petersburg), and the death of the baby mammoth was dated on the basis of geological and geomorphologic data as 10,000-13,000 yBP, i.e., the end of the Sartanian phase of the Late Pleistocene (Shilo et al. 1977). A complex investigation of Quaternary geology of the Kirgilyakh Stream valley undertaken in 1978 corroborated the Late Sartanian age of the burial (Dubrovo 1981a).

Subsequently, ^{14}C dating of soft tissues of the baby mammoth were performed in Magadan and Leningrad and showed the dates 40,600 ± 700 to 43,800 ± 4200 BP (Shilo & Lozhkin 1981) and 38,590 ± 850 to 39,570 ± 870 BP (Arslanov et al.1981). This made some researchers change original conception concerning geological age of the baby mammoth from the Sartanian to Zyryanian Time (Shilo & Titov 1981) and, subsequently, to the Karginian (Shilo *et al*. 1983). When considering a Zyryanian age (more than 45,000 yBP) for the baby mammoth, Shilo & Titov (1981) proposed a possibility of "a later, Holocene, reburial of the baby mammoth corpse as a result of catastrophic reorganisation of the relief of this site". However, they indicated in the same paper that neither a deep cutting nor great deposition occurred from the moment of death and burial of the mammoth (Shilo & Titov 1981: 23). A trace of Late Pleistocene tectonic or volcanic (i.e., catastrophic) processes was not revealed in this area. Paleoclimatical, paleobotanical, and taphonomical data contradict the conclusion by Shilo *et al*. (1983) concerning dating the baby mammoth's death to the Karginian interval (about 40,000 yBP) and subsequent displacement of the lens containing the corpse down the valley slope and reburial in the later strata of the Late Pleistocene. Actually, (1) 38,000-36,000 years ago, there was a considerable climatic warming accompanied by thawing

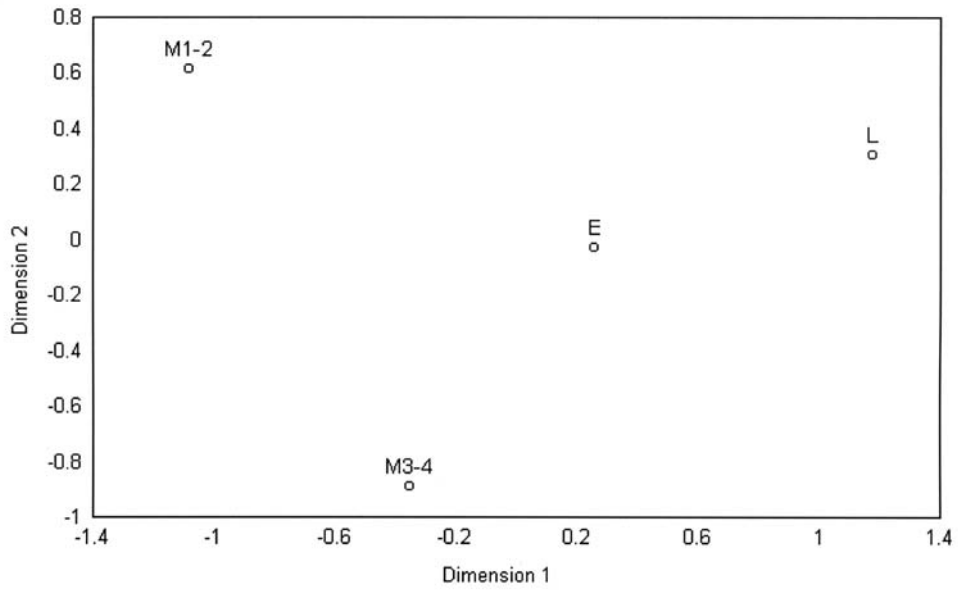

Figure 1 The positions of (M1-M4) four mammoths, (**L**) African and (**E**) Asian elephants in the space of two first coordinate axes of multidimensional scaling of genetic distances based on a 93-bp fragment of the 16S a rRNA gene; (**M1-2**) mammoths from Khatanga and Shandrin, (**M3-4**) Yuribei and Kirgilyakh mammoths, using the data from Hoss *et al.* (1994).

the previously formed ice-sedimentary complex; within 30,000-28,000 yBP, the second Karginian warming occurred (Shilo *et al*. 1983); (2) over the Karginian interval, forest vegetation predominated in the area under consideration; and (3) the lens containing the baby mammoth was enclosed in solifluction-deluvial loam developed on the alluvium of the second terrace of the Kirgilyakh River and appeared in the centre of a cryogenic polygon (Dubrovo *et al.* 1980; Dubrovo 1981a). There is no reason for any doubt concerning the position of the lens with the corpse *in situ*. The fact that "dating the baby mammoth muscular tissue to 39 and 41 thousand years ago is in a rather poor agreement with geomorphologic data" was also indicated by Vereshchagin (1981: 278). The data on insect faunas suggest that the baby mammoth burial should be dated to 11,000-15,000 yBP (Kuz'mina & Ponomarenko 2001).

A burial of a well-preserved mummified corpse could occur only under the conditions of relatively cold periglacial climate. This is corroborated by paleobotanic data indicating that, during the baby mammoth's lifetime, this area was occupied by cold steppe or tundra with bush and forest vegetation developed only within the river valleys (Ukraintseva 1981). Radiocarbon analysis of wood from diluvial-solifluction ice layer at the level of the burial and at the level just above it revealed 9,390 ± 40 and 9,860 ± 80 BP (Dubrovo 1981b). Thus, all geological and paleogeographic data, as well as some taphonomical and radiocarbon data corroborated the Sartanian age of the Kirgilyakh baby mammoth.

All researchers agree (on taphonomic and paleobotanic data) that the baby mammoth died during some glacial phase of the Late Pleistocene, i.e., during the Zyryanian or Sartanian intervals. However, it is impossible to adopt a Zyryanian age (45,000-70,000 y) for the Kirgilyakh baby mammoth, as it was buried *in situ* in the deposits overlaying the Karginian strata aged 25,000-45,000 y. It is noteworthy that Bennett *et al.* (1978) ^{14}C dated soft tissues of Dima to 26,000 ±1,200 BP (i.e., the onset of the Sartanian phase). Thus, we believe that a Sartanian age of the Kirgilyakh mammoth is most probable; and this is comparable to the age of Yuribei mammoth. If this is the case, the above-mentioned mammoth pairs distinguished from each other by the fragment of the 16S rRNA gene differ in geological age as well. It may well be that these differences reflect belonging to different temporal forms of *Mammuthus*. This poses the question for further thorough morphological studies as to what is similar in the individuals within each pair and what distinguishes the pairs from each other.

Thus, the data on the 16S rRNA gene (Hoss *et al.* 1994) enable one to conclude that (1) in *M. primigenius*, this gene showed a high diversity comparable to or higher than the differences between three considered genera of elephantids; (2) the differences within mammoths are possibly associated with geological age; and (3) genetic distance between *Mammuthus* and *Elephas* differs non-significantly from the genetic distance between *Mammuthus* and *Loxodonta*.

As mentioned above, the studies on the other loci considered longer DNA fragments of one or two mammoths and living elephants. Small sample sizes gave no way of considering intraspecific variation and attention was paid to the triangle *Mammuthus-Loxodonta-Elephas*. The necessity of studying sequencing data from additional informative DNA regions and a larger number of both mammoths and extant elephants was repeatedly indicated. On the basis of available data, the researchers concluded that "our results are unable to resolve this trichotomy conclusively" (Hagelberg *et al*. 1994) or reported that they resolved the trichotomy in favour of closer relations between mammoths and the Asian elephants (Yang *et al.*1996; Ozawa *et al.*1997), or between mammoths and the African elephants (Noro *et al.* 1998).

The question about which of the living elephants is more closely related to the mammoth is considered as the main or the only

problem of these papers. This is appreciably influenced by currently accepted computer methods for the analysis of DNA sequences. As a result of such data processing, computer creates 'an objective phylogenetic tree' consisting of successively branching clusters and similar in appearance to phylogenetic schemes obtained in classical evolutionary studies. Thus, all that remains for researchers is to describe such trees and indicate the features that are in common with, or distinguished from, the trees obtained on the basis of other characters. At the same time, we believe that the entire set of data on the DNA sequences in mammoth enables not only to resolve the trichotomy but to consider the general questions concerning the relations between evolutionary events at morphological and genetic levels of life organisation, the role of genetic data in resolving phylogenetic problems, and the rate of evolutionary transformations. Significance of the data on DNA in mammoths and elephants is substantially greater than the questions of special genetics of three proboscidean genera.

To illustrate the above, let us consider the data on complete sequence (961 bp) of the 12S rRNA gene in mammoth and living elephants (Noro *et al.* 1998). Figure 2 shows the position of these forms in the space of two first coordinate axes of multidimensional scaling based on genetic distances calculated using the data on this gene. Mammoth is approximately equidistant from each living elephant; moreover, random error is substantially greater than the differences between the distances *Mammuthus-Loxodonta, Mammuthus-Elephas*, and *Loxodonta-Elephas* (the distances between individuals within each elephant species are substantially lower than interspecific distances). Thus, the elephantid genera under consideration show approximately equal genetic distances between each other. At the same time, cluster analysis of the same distances reveals nothing but a series of bifurcations. Moreover, the sequence

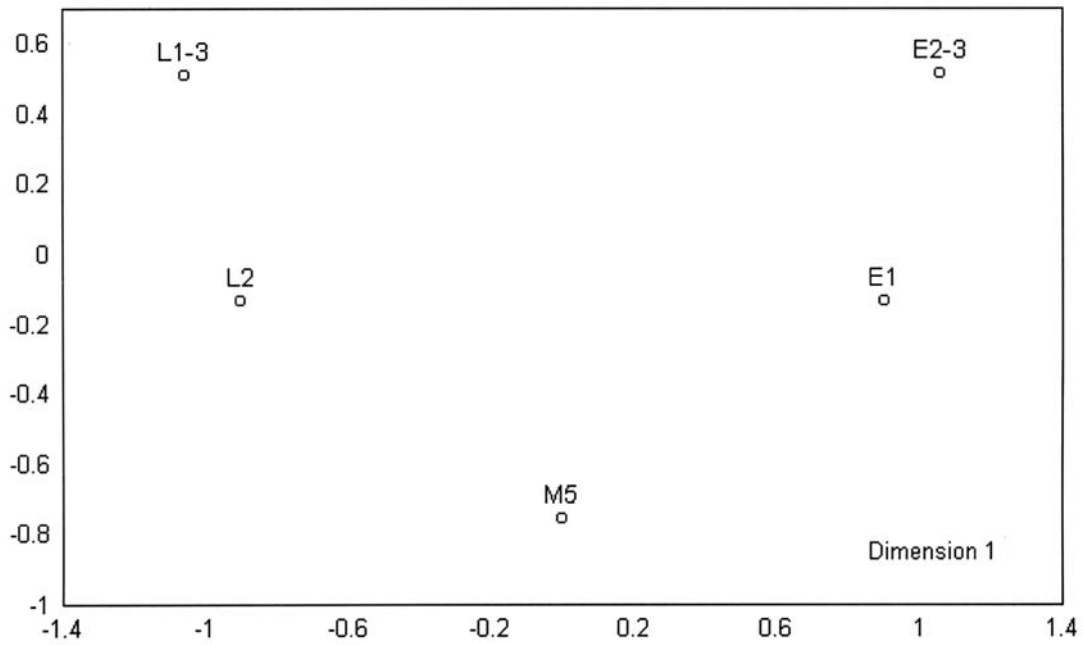

Figure 2 The positions of (**M5**) mammoth, (**L1-3**) three African and (**E1-3**) three Asian elephants in the space of two first coordinate axes of multidimensional scaling of distances based on a complete 961-bp sequence of the 12S rRNA gene, using the data from Noro *et al.* (1998).

of branching depends on the cluster method applied (Fig. 3). The authors of original genetic data (Noro *et al.*, 1998) used the neighbour-joining and maximum parsimony methods, obtained 'phylogenetic trees' in which the first division isolated the cluster of the Asian elephants from the cluster including the African elephant and mammoth, and the second division isolated mammoth from the African elephant (as in Fig. 3a), and concluded that "*Mammuthus* and *Loxodonta* are more closely related to each other than to Elephas". In our opinion, this material does not allow such interpretation, and it should be concluded that, within the limits of random error for distance estimates, the three genera are equidistant from each other (in this case and below, we estimated random errors and

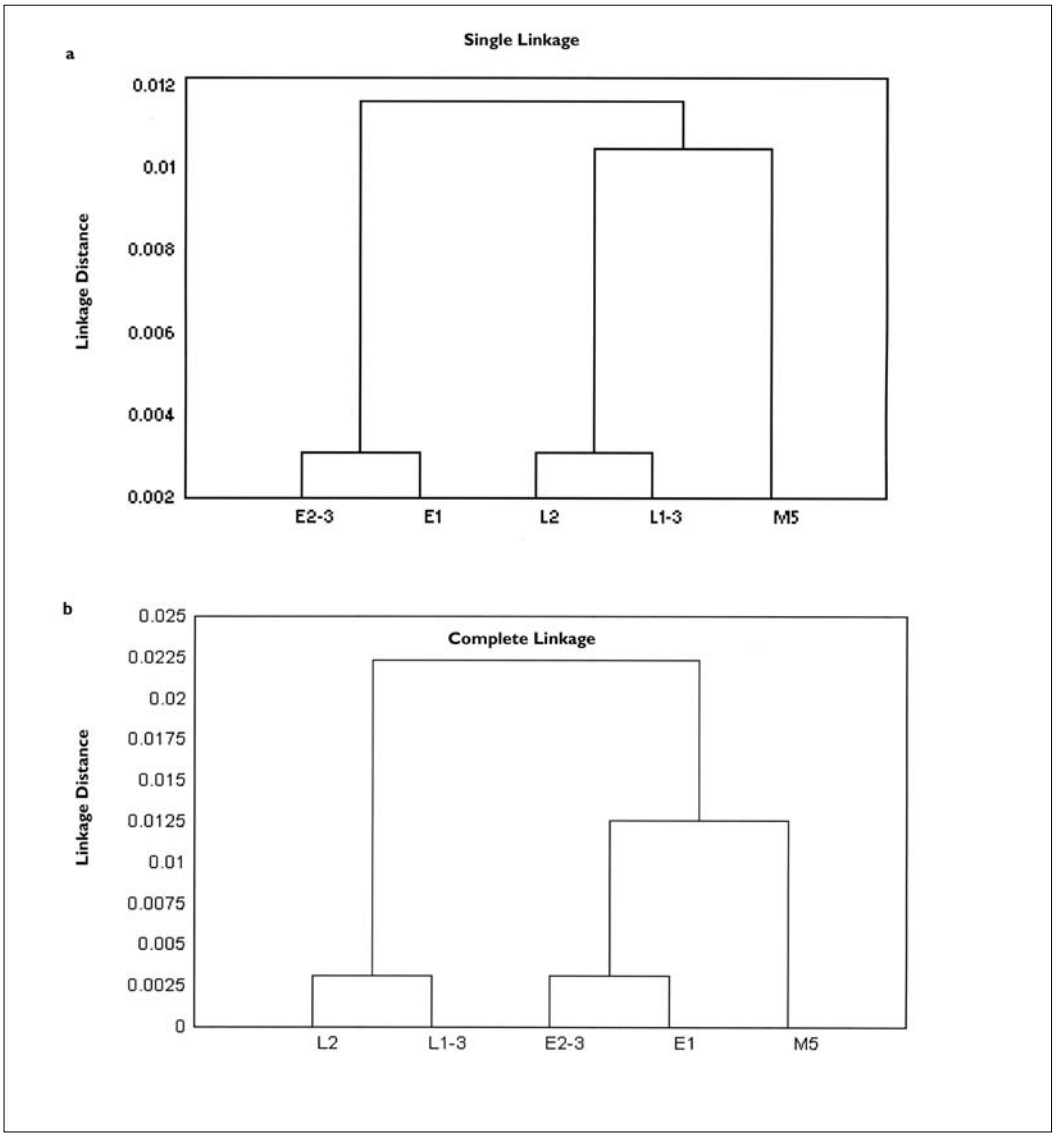

Figure 3 Results of cluster analysis of genetic distances based on the 12S rRNA gene (the same data as in Figure 2), according to the method of (**a**) single linkage and (**b**) complete linkage.

significance of differences between the distances on the basis of the data from original studies).

More extensive material was obtained for the fragments of the cytochrome b gene, examined independently by several research groups from different individuals of mammoths, elephants, and one American mastodon, *Mammut americanus* (Hagelberg *et al.* 1994, Yang *et al.* 1996, Ozawa *et al.* 1997, Noro *et al.* 1998). We analysed genetic distances computed on the basis of 222 bp fragments examined in all elephantids considered in these studies (Figs 4, 5). Figures 4a and 5 show distinct isolation of *Mammut americanus* from the other forms revealed by both

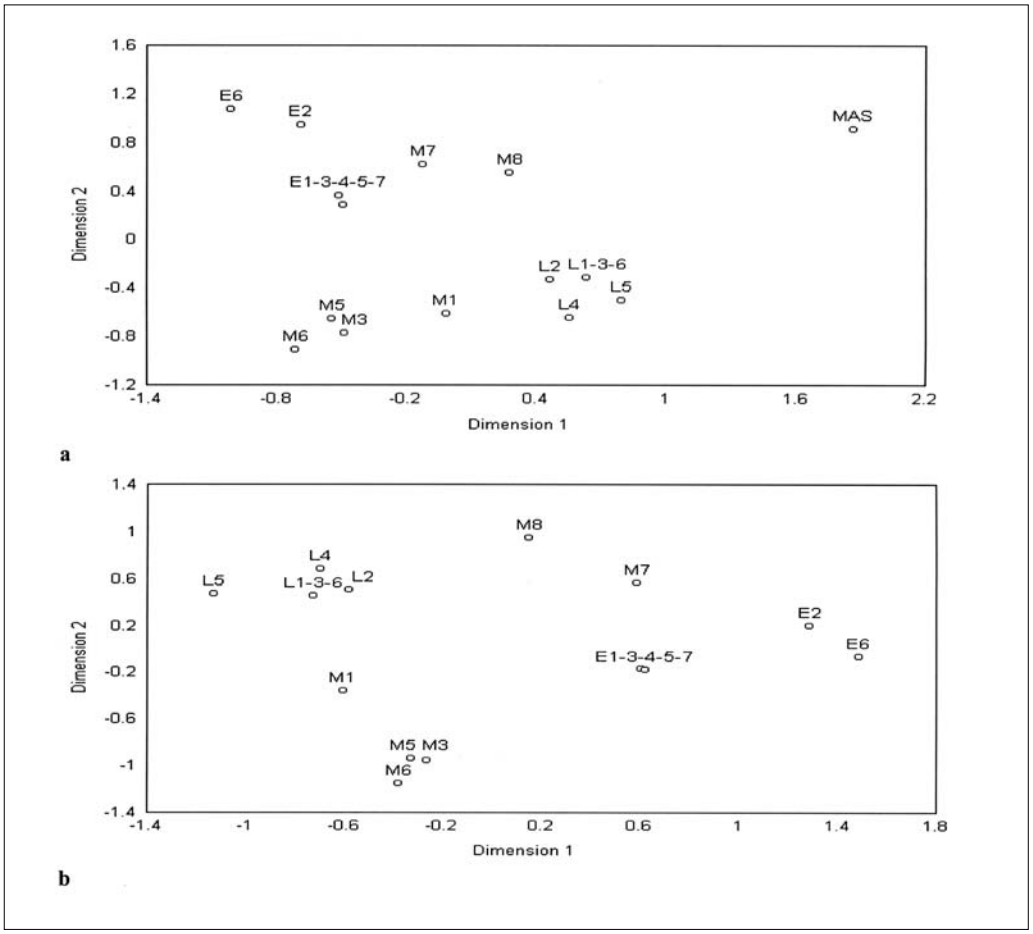

Figure 4 The positions of mammoths, African and Asian elephants, and American mastodon in the space of two first coordinate axes of multidimensional scaling of genetic distances based on a 222-bp fragment of the cytochrome b gene: (M1, M3, M5-M8) mammoths: **M1** and **M6** (after Hagelberg *et al.* 1994), **M3** (after Ozawa *et al.* 1997); **M5** (after Noro *et al.* 1998), **M7** and **M8** (after Yang *et al.* 1996), (L1-L6) the African elephants: **L1-L4** (after Noro *et al.* 1998), **L5** (after Irwin *et al.* 1991), **L6** (after Yang *et al.* 1996); (E1-E7) Asian elephants: **E1-E4** (after Noro *et al.* 1998), **E5** (after Hagelberg *et al.* 1994), **E6** (after Yang *et al.* 1996), **E7** (after Ozawa *et al.* 1997); and (**MAS**) mastodon (after Yang *et al.* 1996): (**a**) including mastodon and (**b**) excluding mastodon. Here we intended to analyse the greatest possible number of animals and compared the sequences presented in all cited studies, namely, (228 - 6) = 222 bp, as Yang *et al.* (1996) reported the data on the shortest fragment (228-bp), but the paper by Hagelberg *et al.* (1994) contained an apparent typographical error, which deleted six bases; therefore, we excluded this 6-bp fragment from the consideration.

multidimensional scaling and cluster analysis. The mean distances from mastodon to *Mammuthus*, *Loxodonta*, and *Elephas* are approximately equal to each other (differ within the limits of random error). They are 0.063, 0.056, and 0.057, respectively, and significantly differ from mean distances between the pairs *Mammuthus-Elephas, Mammuthus-Loxodonta* and *Loxodonta-Elephas* making 0.032, 0.033, and 0.042, respectively. At the same time, the differences between the latter three estimates are non-significant and lower than intraspecific distances those are 0.031, 0.010, and 0.011 in *Mammuthus*, *Elephas*, and *Loxodonta*, respectively. Thus, as in two previous cases, the data on the cytochrome b gene fragment suggest that *Mammuthus*, *Elephas*, and *Loxodonta* are approximately equidistant from each other (within the limits of random error). At the same time, in mammoths, this sequence is distinctly more diverse than in living elephants. The authors of original data did not reveal this, since they did not analyse combined primary data but only compared their results with the conclusions of the earlier studies. To illustrate clearly the relationships between mammoths and living elephants, we applied multidimensional scaling, excluding mastodon from the analysis (Fig. 4b). The individuals of each living elephant form a relatively dense group, whereas mammoths are divided into two groups (M1-M3-M5-M6 and M7-M8), the mean distance between which is 0.045, i.e., approximately the same as between different elephant genera. This was the reason for a relatively high mean distance within mammoths. At the same time, differentiation in either mammoth group is comparable to that in each elephant species, namely, the distance M7-M8 is 0.022 and the mean distance within M1-M3-M5-M6 is 0.013.

As in the case of the 16S rRNA gene, high

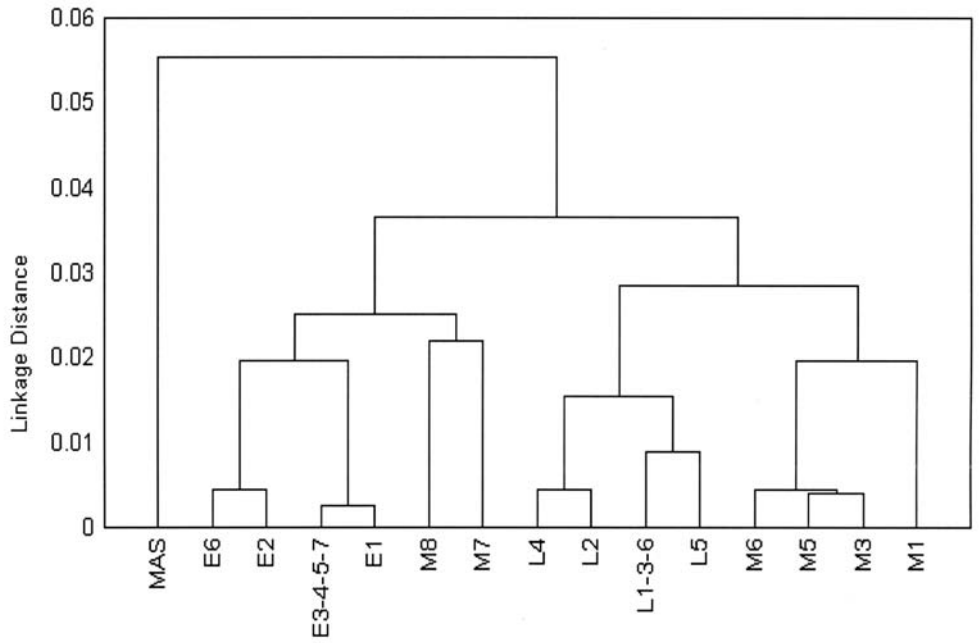

Figure 5 The results of cluster analysis of genetic distances based on a 222-bp fragment of the cytochrome b gene (the same data as in Figure 4).

differences between the mammoth groups could be explained by an extremely high individual genetic diversity of *M. primigenius* or by belonging to different geographical or (and) temporal forms. The first possibility appears less probable, as it implies that mammoths were characterised by a substantially higher diversity than living elephants. However, available data do not allow us to reveal a correlation between belonging to the groups distinguished on the basis of the cytochrome b gene and geological age or geographic position (Table 1).

Thus, the general result of comparative studies on mammoth DNA (fragments of three loci) is as follows: (1) Genetic differentiation within mammoths is high, they can be divided into two groups substantially distinguished from each other (based on two genes of three, excluding the 12S rRNA gene examined in only one individual). (2) The question of association between mammoth groups and geological or geographical occurrence necessitates further investigation, as available data do not allow to substantiate this correlation. (3) The trichotomy *Mammuthus-Loxodonta-Elephas* is resolved in favour of approximately equal genetic distances (non-significantly distinguished from each other) between each pair of these forms; moreover, approximately the same distance describes the differences between two groups revealed within mammoths. The latter enables us to propose that *M. primigenius* is probably represented by at least two forms (apparent species) isolated from each other for a long time. This question necessitates a thorough morphological examination of common and distinctive features within and between these groups. In other words, available data allow us to consider not only the trichotomy but also the tetrachotomy of genetically equidistant forms. (4) The data on mastodon (*Mammut americanus*) examined in only one individual with reference to a fragment of only one gene (cytochrome b) indicate that three levels of genetic differentiation can be distinguished within the currently studied group of proboscideans: (a) individual variation within each form of elephants and mammoths; (b) divergence of these four forms; and (c) an earlier divergence of the elephant lineage from mastodons (Fig. 4a, 5).

DISCUSSION AND CONCLUSION

What is the biological significance of results obtained by comparative analysis of DNA sequences in living and extinct proboscideans? And how can these results be incorporated in phylogenetic reconstruction and compared with the results of morphological studies? It should be noted that a peculiar feature of genetic traits is the fact that they undergo only indirect influence of natural selection and, consequently, their evolution is basically independent from morphological evolution. Among other things, this led to the development of the neutral theory of molecular evolution proceeding from the assumption of an approximately constant rate of molecular substitutions (named the 'molecular clock'; Zuckerkandl & Pauling 1965; Kimura 1983). In some cases, researchers indicate that the clock may be fast or slow; however, a number of genetic phenomena agree satisfactorily with this theory. Molecular characteristics follow morphological and ecological divergence of forms only to a limited extent. However, within the limits of validity of the molecular clock concept, one can obtain data on relative isolation time of certain phylogenetic lineages. On the contrary, the rate of morphological and ecological divergence vary extremely widely (Simpson 1953) and evolutionary transformations cannot be generally reduced to a simple function of time that passed from a moment of isolation of daughter lineages from a common ancestor. This essential difference between genetic and morphological material follows from the fact that organisms are substantially more stable than the molecular elements they are composed of (Schmalhausen 1968); this results from dissipative nature of organisms provided with a well developed system of regulatory mechanisms supporting homeostasis, as

against equilibrium molecules. This is evidenced in particular by the existence of so-called living fossils and certain groups persisting for a rather long time (even on a geological time scale) at any moment of the geological history. In other words, the organismal level of organisation is characterised by a potential (not necessarily realised) capability for self-preservation over any time intervals. On the contrary, various molecular structures are in permanent drift, although the rate of this drift may change. Therefore, one may use the principle of a molecular clock, notwithstanding a greater or lesser variation in the rate of molecular substitutions.

Thus, comparisons between evolutionary transformations of genetic and morphological parameters (i.e., genetic distances and evolutionary paths passed by diverging groups and fixed in morphological characters) are analogous to comparisons between time and distance passed along a certain route (where genetic distances are an analogue of time and morphological transformations are an analogue of traversed path). Actually, the greater the distance, the longer it takes to overpass; however, one can remain on the spot or move in parallel. In these cases, morphological results are different, whereas the molecular clock continues running (even if occasionally somewhat fast or slow). Therefore, morphological and genetic parameters reflect different aspects of the evolutionary process. Nevertheless, genetic differentiation in the form of molecular phylogenetic trees are commonly compared with the results of phylogenetic reconstruction based on morphological data to conclude that the latter corroborate or contradict the trees based on genetic characteristics. Moreover, molecular phylogenetic trees are commonly constructed without adequate consideration of random errors. We believe that each case of non-significant difference between compared genetic distances should be indicated, as this may well be a result of simultaneous divergence of several forms and available data do not allow to reveal the sequence of branching. Therefore, the trees constructed on the basis of such genetic distances are not only useless but even injurious to phylogenetic reconstruction, as they create a false impression of resolution. Molecular phylogenetic trees are unsuitable for describing simultaneous divergence of several branches from the same point (adaptive radiation), as a probability of two or more exactly equal distances is extremely low because of random errors and the branching pattern always appears as a series of successive bifurcations attributed to different moments.

The above can be illustrated by the results of studying the cytochrome b gene in mammoths and elephants. Only in the first study, the authors indicated that their results were unable to resolve the trichotomy *Mammuthus-Loxodonta-Elephas* (Hagelberg *et al*. 1994). In subsequent papers, mammoth was definitely considered to be more closely related to one of the living elephants (Yang *et al*. 1996; Ozawa *et al*. 1997; Noro *et al*. 1998). At the same time, these conclusions are baseless, as genetic distances between each pair of three considered species non-significantly differed from each other.

In our opinion, the entire set of molecular data on three examined loci give evidence for equal genetic distances between three species (within the limits of random error) and, consequently, simultaneous divergence of phylogenetic lineages leading to *Elephas*, *Loxodonta*, and *Mammuthus* (the latter of which was probably represented by two forms). This conclusion agrees with the results of immunological studies (Lowenstein 1985) and comparisons of hair structure (Valente 1983); in these parameters, three elephantid genera appeared equidistant.

Simultaneous divergence?

Most zoologists and paleontologists agree with almost simultaneous (on geological time scale) divergence of three elephantid lineages leading to *L. africana*, *M. primigenius*, and *E. maximus* dated approximately 5-6 My ago (Maglio 1973; Lister & Bahn 1994; Dubrovo 1997). A closer morphological affinity of

Mammuthus to Elephas than to *Loxodonta* (Maglio 1973) combined with approximately equal genetic distances between these genera suggests that similar features of the Asian elephant and mammoth appeared as a result of parallel evolutionary development. Moreover, if the data on the existence of two genetic groups within mammoths are correct, the same is true with reference to these groups, i.e., they diverged approximately simultaneously to the other elephantid lineages and developed parallel to each other, so that they did not achieve essential morphological distinctions and were not described as separate species (possibly, this will appear necessary in the future). The lineages of mammoth and Asian elephant developed in parallel, but achieved generic differences. The latter is probably associated with the adaptation of mammoths to newly arisen landscapes of the glacial epoch. The lineage of the African elephant appeared morphologically detached from three mentioned forms, partially because of retaining a number of primitive characters. Phylogenetic transformations of morphological characters, such as the structure and proportions of skeleton, skull, and teeth may be interpreted from the viewpoint of adaptation, as they are associated with the environmental conditions and feeding pattern. From the moment of isolation up to the Recent, the genus *Loxodonta* existed under relatively constant conditions which provided affinity to Primelephas (the form considered to occupy the position at the base of the Elephantinae) in a number of key taxonomic characters, such as a small number and low frequency of tooth plates, thick enamel, etc. (Maglio 1973; Dubrovo 1997). On the contrary, *E. maximus* and *M. primigenius* are similar in advanced characters, increased height of the tooth crown, a large number and high frequency of plates, reduction of enamel thickness, etc. Based on the above, one can propose an evolutionary scheme reflecting the time of divergence within elephantids and the extent of morphological advantage (Fig. 6).

Genetic equidistancy of these forms reflects

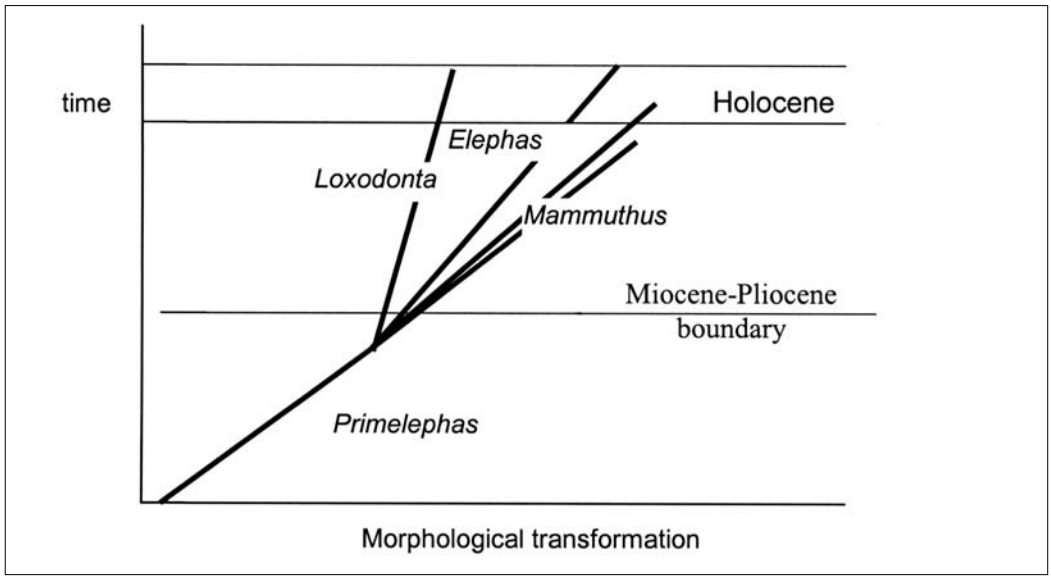

Figure 6 Scheme of phylogenetic relationships among genetically studied Elephantinae. Relatively primitive morphological characters of *Loxodonta* are shown by its closer position to the common ancestor, and similarity between *Elephas* and *Mammuthus* (represented by two lineages) in advanced features are shown by their close position to each other and deviation from the ancestor. At the same time, all these forms radiated simultaneously, most probably at the boundary between the Miocene and Pliocene.

the temporal aspect of their divergence and is only indirectly associated with adaptive evolution of elephantids. Thus, genetic (molecular) data are interesting not only as a source of information on new parameters and can be used not only for estimation of the extent to which they follow evolutionary transformations at the morphological level; the main significance of these data is the fact that they enable one to estimate available morphological information from a new position. In the case of elephantids, they provide substantiation for parallel development of certain key characters.

Extensive data on parallel development in various plant and animal groups accumulated during almost 150 years of evolutionary biology, and currently parallelisms appear as natural and inevitable evolutionary phenomena, rather than rare and isolated events (Rautian 1988). The most amazing and well-grounded examples are parallel reptilisation (Olson 1965; Tatarinov 1976), mammalisation (Tatarinov 1959; Crompton 1963), microtisation (Agadjanian 1992), angiospermisation (Meyen 1987; Krassilov 1989), etc. Now, we can supplement this list with parallel elephantisation in the lineages of the Asian elephant and mammoth and even parallel mammothisation in two branches of mammoths. It is noteworthy that the list is enlarged in the scarcest part, namely, in the field of low rank taxa. The latter is particularly important, as this shows essential uniformity of laws and patterns of macro-evolution at different taxonomic levels.

The recognition of wide occurrence of parallel evolutionary development essentially changes the conception of the patterns of phylogenesis. With reference to the data on elephantids this means that: (1) by the moment of divergence, the common ancestor of *Loxodonta*, *Elephas*, and *Mammuthus* was more similar to the African elephant than to the Asian elephant and mammoth in many plesiomorphic characters; consequently, (2) the common ancestor of two mammoth branches (possibly, twin species) should resemble the African elephant to a greater extent than the Asian elephant; (3) the synapomorphies of the Asian elephant and each mammoth branch arose independently in each lineage and were absent in the common ancestor (the latter possessed only the potentiality for developing these characters); hence, (4) the common ancestor of the Asian elephant and mammoths should be beyond the taxon uniting them, in the depth of the ancestral taxon. In this case, as in other similar situations, there is no reason for doubt about the origin from a common ancestor, but it is reasonable to believe that the taxa developing in parallel to each other are not monophiletic (i.e., common ancestor and derivative taxa are not members of the same taxon).

In addition, combined consideration of evolutionary transformations at morphological and genetic levels of organisation can be used as a new method for revealing the phylogenetic lineages, which were isolated from each other as a result of one and the same phase of adaptive radiation. The principle of adaptive radiation (irradiation) was formulated in 1873 (Kowalewsky 1948) to designate simultaneous (on the geological time scale) divergence of a number of forms from a common ancestor as a result of gaining certain adaptations of rather wide adaptive significance, so that they could provide a base for developing various ecological niches. This results in relatively fast divergence of forms mastering available niches and adaptive zones. Within the intervals between the phases of adaptive radiation the taxa continue evolution towards adaptation to their niches, but this is not accompanied by initiation of new taxa of the same rank. This implies that the cases of simultaneous divergence of three or more taxa should be a common event occurring widely in the phylogenesis of various groups. Let us pay attention once again that commonly accepted methods for the analysis of genetic data are not adapted for discovering such situations. Thus, for example, figure 5 shows a tree for genetically examined proboscideans, in which one mammoth group forms a

common cluster of second order with the Asian elephants and the second group is united with the African elephants. Actually, genetic distances between these four forms can be taken as approximately equal (see above), which suggests simultaneous divergence of the four forms, i.e., realisation of the principle of adaptive radiation (Fig. 6). In this respect, data processing by the method of multidimensional scaling is undoubtedly favoured, as it shows the extent of differentiation (or similarity) between the forms and does not impose the pattern of branching. We propose that thorough analysis of genetic data on other groups will reveal a number of cases exemplifying the principle of adaptive radiation.

Thus, combined consideration of genetic and morphological data promises more reliable substantiation of such phenomena as parallel development and adaptive radiation; the data on proboscideans considered in this study provide an illustration of this.

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