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Approaches to the Resolution of Contradictions between Phylogenetic Reconstructions Based on Morphofunctional and Genetic Data

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Abstract—Essential differences between genetic and morphofunctional characteristics as sources of information about evolutionary development are discussed using examples of mammal taxa. The approaches to combined analysis of data characterizing different levels of biological organization in phylogenetic reconstructions are considered using examples of certain mammalian taxa.

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INTRODUCTION

With the development of phylogenetic studies based on genetic and morphophysiological data, the number of contradictions between final phylogenetic reconstructions grows constantly. It is reasonable to suppose that, as they are resolved, these contradictions will provide fruitful new insights into the patterns of evolution and the correlation of evolutionary changes at different levels of biological organization. An important obstacle to this is the profound differences in generally accepted methods in different fields of biology, and their mostly independent development. An alarming sign of this discordance is the recently emerging practice to introduce new taxonomic names based on the results of molecular studies, regardless of the absence of any analogues in taxonomic systems based on classical approaches. Running its natural course, this situation will result in the development of two independent phylogenetic reconstructions and the loss of the constructive connection between studies at molecular and morphophysiological levels. Taking into account the fact that molecular studies mostly involve similarities and dissimilarities of uncertain biological significance, such newly created molecular taxa cannot be diagnosed in a biologically meaningful way. Reasonable diagnoses are presently possible only at the morphophysiological level, although even in this case the degree of biological understanding is still a long way from perfect. In other words, a taxonomic group recognized based on molecular traits should necessarily be comprehended in terms of the morphophysiological properties of organisms. For the moment, molecular taxa remain “a thing to themselves.” They add little to the understanding of the nature of organisms, or to ordering our knowledge of biodiversity and, hence, cannot provide the basis for further biological studies. In particular, it is only possible to test molecular phylogenies by increasing the quantity and quality of molecular data. Over the last 40 years or more, this trend in the development of genetic phylogenies showed only a slight tendency to approach the results in the context of traditional phylogenetic reconstructions, but they have remained quite different in essence. However, the search for a constructive dialogue aimed to reveal and overcome the contradictions between phylogenetic reconstructions at molecular and morphophysiological levels is the most topical problem of modern phylogenetics.

For the synthesis of phylogenetic studies at different levels of organization, the basic, essential distinctions between evolutionary transformations at the molecular–genetic and higher (primarily organismal) levels of biological organization should be outlined. The major distinctive feature of phenotypic evolution is the fact that it is directly controlled by natural selection, whereas the dependence of genetic characteristics on selective pressure is always indirect, and is determined by the extent to which they have a selectively significant phenotypic manifestation.

As early as 1938, Schmalhausen (1938, 1949) formulated that phenotypic characters are potentially much more stable than the genetic traits providing the basis for their development. This concept agrees with the empirical generalization that Timofeev-Resovsky (1958) named Chetverikov’s principle (Chetverikov, 1926, 1983). It states that uniform phenotypes of the *wild type* (Schmalhausen named it the *adaptive norm*) are underlain by a vast genetic diversity, which can be discovered in laboratory conditions through inbreeding, but usually has no phenotypic manifestation in nature.

The adaptive norm is defined as an ensemble of individual ontogenies (life cycles) or their stages arising as a historically (phylogenetically) use-proven, stable (adaptive) response, reproduced in a descending line of generations (hereditary) to historically typical (adjusted in the course of preceding phylogeny) factors of external and internal (including genotypic) environments (Rautian, 1988). In cases with more or less pronounced polymorphism of the natural population, it is possible to recognize several adaptive norms within the general adaptive norm of a species or a population (Schmalhausen, 1949). Gershenzon (1941) and Schmalhausen (1949) named the genetic diversity buried under the cover of the adaptive norm the *mobilization reserve of intraspecific variability*, while Muller (1950) named it the *genetic load.* In rare cases, when the hidden hereditary traits manifest themselves in the phenotype as abnormalities, this manifestation is usually not inherited in natural conditions (i.e., absent in descendants), as was understood rather early (Semenov-Tyan-Shanskii, 1910). As Chetverikov indicated, in the nearest generations, the population "absorbs like sponge" such accidentally manifested mutations. In other words, according to Schmalhausen, the stability of the adaptive norm (= wild type) is maintained in spite of genotypic diversity rather than due to genotypic uniformity.

Stabilizing (canalizing) selection, which functions in all evolutionary phases, produces and constantly maintains structural variants that are capable of persisting over potentially infinite periods of geological history (irrespective of the accumulation of genetic change). Therefore, the rates of morphological evolution not only vary within a very wide range but, more importantly, can be extremely low, supporting successful variants of organization. This is corroborated, in particular, by the existence of living fossils and long-lived groups at any time in the geological history of Earth. Thus, the organismal level of biological organization has the potential (not necessarily realized) for self-preservation over an arbitrarily long time period.

The periods when stabilizing selection favoring the old adaptive norm ceases to be the major developmental factor are short and rare because they result in unstable conditions of organization and are fraught with extinction. However, they necessarily precede such phenomena as a change of specialization, penetration into new adaptive zones, the emergence of new taxa (particularly those of high order), and adaptive radiation. These phases are characterized by a set of regular changes in evolving systems, which were recognized and generalized by researchers in the field of macroevolution in the form of patterns, modes, and restrictions of phylogenetic development. Figure 1 shows general relationships between key evolutionary characteristics, such as specialization, continuity of development, differentiation, etc. in time, and indicates the researchers who introduced special terms to designate particular phases of the phylogenetic cycle. This topic was considered by Rautian (1988), while a detailed discussion on these questions is beyond the scope of the present study. Here, it is important to emphasize that (1) during the phases of stabilization and destabilization, an evolving system undergoes definite changes in its essential characteristics; (2) the phase of stabilization is the basic phase and lasts for a geologically long time, while the phase of destabilization may be absent over an arbitrary long period of the existence of a group; and (3) adaptive radiation giving rise to taxa of the first order usually immediately follows a phase of destabilization; in the course of subsequent stabilization, adaptive radiations produce taxa of lower ranks. A repeated increase in the rank of taxa emerging through an adaptive radiation occurs only as a result of a new, rather deep destabilization. Certainly, low-rank taxa may appear simultaneously with high-rank taxa, the degree of destabilization restricts only the highest possible rank of taxa produced by an adaptive radiation event.

Molecular–genetic characteristics are only indirectly influenced by natural selection; in particular, they are only indirectly subjected to stabilization. Therefore, in contrast to morphofunctional characteristics, they are incapable of remaining constant over arbitrary long periods and **inevitably change** in the course of evolution. In particular, even under conditions of long stabilizing selection of the phenotypes (for example, in living fossils), more or less neutral genetic changes are constantly accumulated. These features gave rise to the neutral theory of molecular evolution and the concept of the molecular clock, implying an approximately constant rate of molecular substitutions (Zuckerkandl and Pauling, 1965; Kimura, 1983). It is often marked that the clock may be fast or slow; however, many genetic phenomena agree satisfactorily with this theory and allow for the quantitative estimation of divergence between phylogenetic branches. This is impossible in the case of morphological characteristics, because their rate of change varies over an extremely wide range (Simpson, 1953), and, in general, evolutionary transformations cannot be reduced to a simple function of time passed from the moment of isolation of daughter lineages from a common ancestor.

The more neutral genetic change that occur in a certain group, the more reliable is information on the sequence of branching and the time of divergence they provide, but the less they are suitable for the recognition of boundaries between taxa (both species and higher rank taxa), because they cannot provide a measure of the biological significance of changes. Thus, the tasks of splitting phylogenetic branches into particular taxa and the creation of hierarchical phylogenetic classification are still solvable only on the basis of morphofunctional characteristics. In other words, genetic and morphological approaches mostly supplement each other rather than impose rigid restrictions on the interpretation of results.

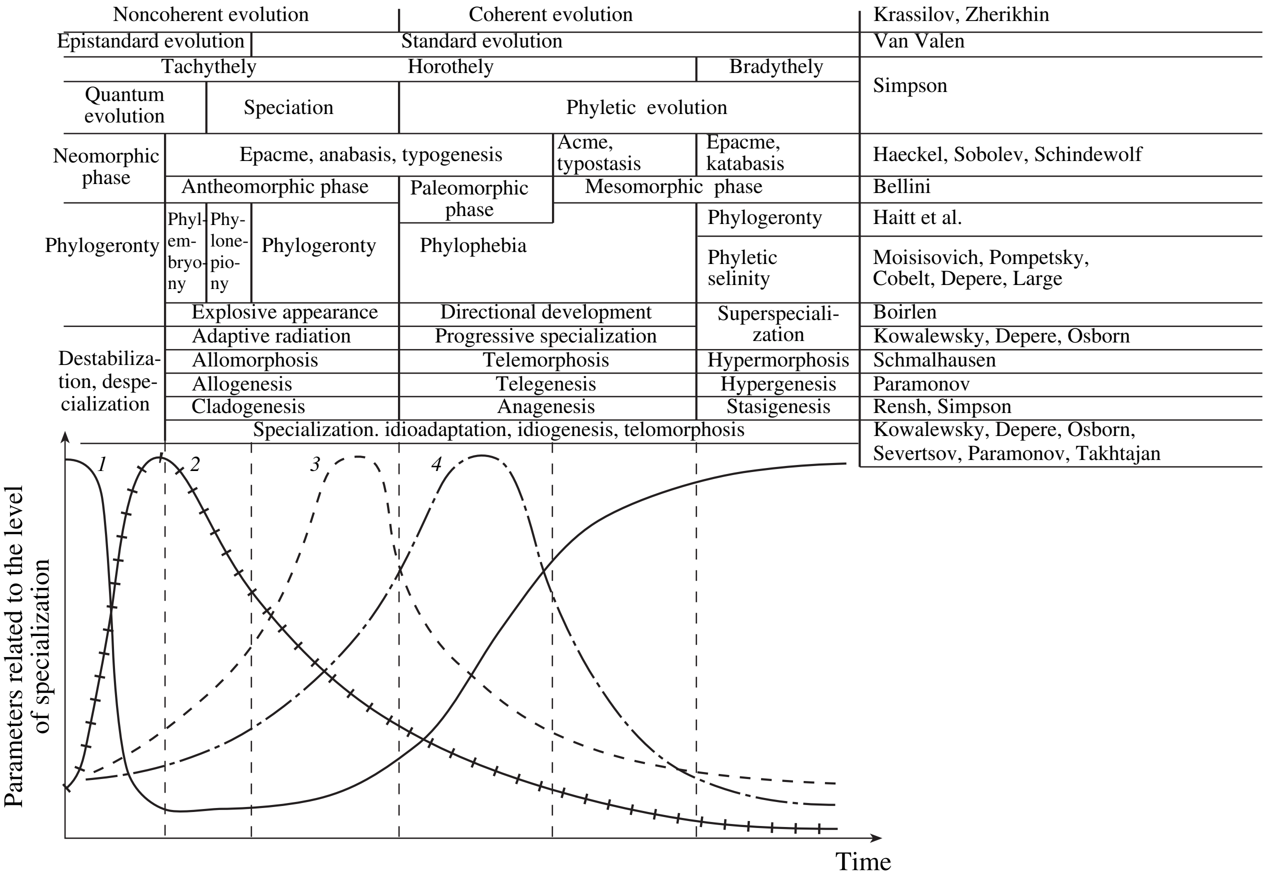

Fig. 1. The major phases of a complete phylogenetic cycle (typical sequence of adaptation modes), their properties and classifications proposed by experts in macroevolutionary patterns: (*1*) extent of specialization, resistance, stability, continuity, adaptation of states of the developing system, and directedness of its development; decrease in freedom of choice (in variability) and in creativity; (*2*) rate and level of emanation (destabilization, extinction), decrease in specialization, resistance, stability, continuity, adaptation of states of developing system, and directedness of its development; (*3*) rate of diversification: divergent evolution, adaptive radiation; and (*4*) rate of specialization (phyletic evolution) and increase in integrity (after Rautian, 1988).

RESULTS AND DISCUSSION

It is possible to illustrate the above statements using examples of combined consideration of data on genetic and morphological differentiation of certain mammalian taxa.

Mammuthus–Loxodonta–Elephas Trichotomy

A number of recent studies were devoted to the analysis of nucleotide sequences of mammoths (*Mammuthus primigenius*) and comparisons with extant elephants (Hagelberg et al., 1994; Höss et al., 1994; Hauf et al., 1995, 1999, 2000; Yang et al., 1996; Derenko et al., 1997; Ozawa et al., 1997; Noro et al., 1998; Barriel et al., 1999; Dubrovo and Rautian, 1999; Rautian and Dubrovo, 1999, 2001, 2003; Thomas et al., 2000; Poulakakis et al., 2002; Debruyne et al., 2003; Joger et al., 2003; Krause et al., 2005; etc.). These studies are of special interest because they allow not only a consideration of relationships between some elephantids, but also a better understanding of general questions of phylogenetic reconstruction based on genetic and morphofunctional characters.

In each study including material of more than one specimen, mammoths are polymorphic and differ from each other in a greater or lesser number of substitutions. The study of 16S rRNA (Höss et al., 1994) is noteworthy in this respect, although this was the shortest sequence examined. Four mammoths of different geological age were studied and split into two pairs, in each of which the DNA sequence was identical, while the pairs differed by five substitutions (5.4%). A comparison of this sequence in mammoths and one Asian elephant revealed four and three substitutions (for the first and second mammoth pairs, respectively). The African elephant differed from mammoths by four and five substitutions, respectively, and from the Asian elephant by only two[1] (unfortunately, only one individual of each

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[1] It should be noted that, in this case, two, three, four, or five substitutions differ from each other nonsignificantly because of the very short sequence examined.

Table 1. Pairwise sequence divergence estimates (above diagonal) and numbers of nucleotide substitutions (below diagonal) based on the complete 12S rRNA gene sequences (after Noro et al., 1998)

	MP	L1	L2	L3	E1	E2	E3	DDU	TMA
MP		1.37	1.05	1.37	1.16	1.26	1.27	22.1	28.8
L1	13/0		0.31	0	1.91	2.23	2.24	21.0	28.9
L2	10/0	3/0		0.31	1.58	1.91	1.91	20.8	28.8
L3	13/0	0/0	3/0		1.91	2.23	2.24	21.0	28.9
E1	10/2	17/1	14/1	17/1		0.31	0.31	20.7	28.9
E2	10/2	19/2	16/2	19/2	2/1		0	21.1	29.2
E3	10/2	19/2	16/2	19/2	2/1	0/0		20.9	29.2
DDU	125/49	120/49	119/49	120/49	119/48	121/49	119/49		22.0
TMA	137/78	138/80	137/80	138/80	138/80	139/81	137/81	110/64	

* The upper right matrix shows Kimura two-parameter distances. The lower left matrix shows the number of transitions/number of transversions. (MP) mammoth, (L1–L3) three African elephants, (E1–E3) three Asian elephants, (DDU) *Dugong dugong*, and (TMA) *Trichechus manatus*.

extant elephant species was examined with reference to 16S rRNA).

The studies devoted to other loci used longer DNA fragments (or even the complete mitochondrial genome) of one or several mammoths in comparison with those of living elephants. Attention was mostly paid to the relative order of deviation of the *Mammuthus, Loxodonta*, and *Elephas* lineages from the ancestral stem. Even when the same genes were sequenced, the phylogenetic trees reconstructed were strikingly different: researchers concluded that available data suggest a closer affinity between mammoths and Asian elephants (Yang et al., 1996; Ozawa et al., 1997; Hauf et al., 1999), mammoths and African elephants (Hauf et al., 1995; Noro et al., 1998; Barriel et al., 1999; Thomas et al., 2000; Debruyne et al., 2003), African and Asian elephants (Hauf et al., 2000), or simultaneous (on geological time scale) divergence of branches leading to the three elephantid genera (Dubrovo and Rautian, 1999; Rautian and Dubrovo, 1999, 2001, 2003). Thus, all logically conceivable variants of relationships between the three genera have been proposed. Moreover, most of the working teams reported good bootstrap support for their results; this indicates once again that the bootstrap support tests only statistical correspondence of results to the computer model used, and indirectly shows that these models do not describe biological aspects of evolutionary change. Thus, the conflicting results are probably attributable to rather small differences between the pairwise genetic distances (*Mammuthus–Loxodonta, Mammuthus–Elephas*, and *Loxodonta–Elephas*), the short DNA fragments analyzed in the majority of studies, small sample size, and inadequate, simplified models of genetic change, which are used in the course of computer data processing.

These statements are evident from the comparison of the complete sequence (961 bp) of the 12S rRNA gene in one mammoth and several living elephants (Noro et al., 1998). Table 1 shows pairwise genetic distances between the individuals investigated. The distances from the mammoth to extant elephants are approximately equal, i.e., the random error is greater than the difference between the *Mammuthus–Loxodonta* and *Mammuthus–Elephas* distances. Moreover, this difference is less than the distances between specimens of the same species. To gain a better appreciation of genetic relationships, Rautian and Dubrovo (1999, 2001, 2003) applied the method of multidimensional scaling (MDS, see Kruskal, 1964). This method supplements the picture of molecular phylogenetic trees, which depend on the model used by researchers and, in our opinion, show only a formal, superficial resemblance to natural phylogenetic schemes. Taking such trees as analogues of phylogenetic reconstructions, the pictures produced by MDS can be taken for analogues of the horizontal section of phylogenetic schemes. Thus, they provide additional information concerning relationships between objects involved in comparison. An advantage of multidimensional scaling is the fact that it gives a two-dimensional (actually, n-dimensional) picture and, consequently, is more heuristic and provides a better insight into true relationships.

Figure 2 shows the positions of the mammoth and living elephants in the space of the first two coordinate axes of MDS of genetic distances based on this sequence. The mammoth is approximately equidistant from each living elephant genus; moreover, the individual variation in each living elephant is substantially greater than the differences between the distances *Mammuthus–Loxodonta* and *Mammuthus–Elephas.*

As the same genetic distances are analyzed by one or another tree-building method, nothing but a system of dichotomizing branches is obtained. The tree topology (sequence of branching) depends on the methods of clustering used (Rautian and Dubrovo, 2001, 2003).

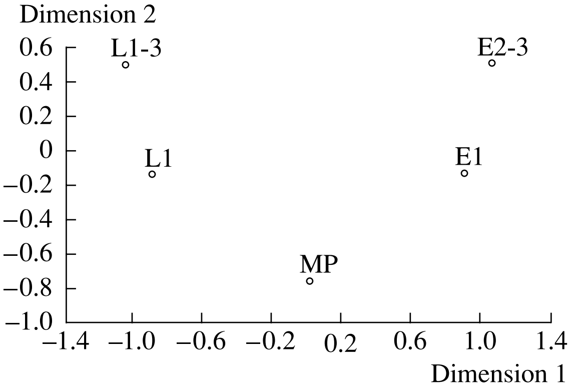

Fig. 2. Positions of (MP) mammoth, (L1–L3) three African and (E1–E3) of three Asian elephants in the space of two first axes of multidimensional scaling of genetic distances based on the complete 961-bp sequences of the 12S rRNA gene (after Rautian and Dubrovo, 2001, 2003, using data from Noro et al., 1998).

The authors of primary genetic data obtained phylogenetic trees where the lineage of Asian elephants deviates first, while the African elephants composed a sister group of the wooly mammoth (Fig. 3). The bootstrap support of most of the nodes in the trees was rather high, so, the authors drew an unequivocal conclusion that the woolly mammoth is more closely related to the African elephant than to the Asian elephant (Noro et al., 1998, p. 314).

In our opinion, these data do not allow such an interpretation (and nor do the data from all other studies where the woolly mammoth is placed closer to one or another living elephant). A more accurate conclusion is that the three elephantids are equidistant to within the error of estimation of interspecific distances, and probably emerged as a result of the same event of adaptive radiation. Here it should be noted that the elementary unit of evolution is not an individual (or a DNA fragment), but a population. Therefore, a correctly posed question of genetic change in the course of evolution means the estimation of **transformations of the gene pool of the ancestral population into the pool of descendent species** rather than changes in individual genotypes. Hence, it should involve adequate analysis of intraspecific genetic diversity of the species under study. The solution of this question faces certain technical difficulties, such as a small sample size of each species. However, this circumstance should be taken into account at least at the interpretation of results. Otherwise, genetic trees would reflect only changes of particular characters (nucleotide sequences) instead of evolution of population and taxa. In fact, all studies devoted to the genetics of mammoths and related elephantids considered changes in genes, while conclusions concerned the phylogeny of certain lineages. At present, it is impossible to enlarge substantially the material of each species (to get representative population samples); therefore, intraspecific diversity should be estimated indirectly and compared with the differentiation of taxa.

In a number of studies, the nucleotide sequences of the cytochrome *b* gene in several woolly mammoths, African and Asian elephants, and one American mast-

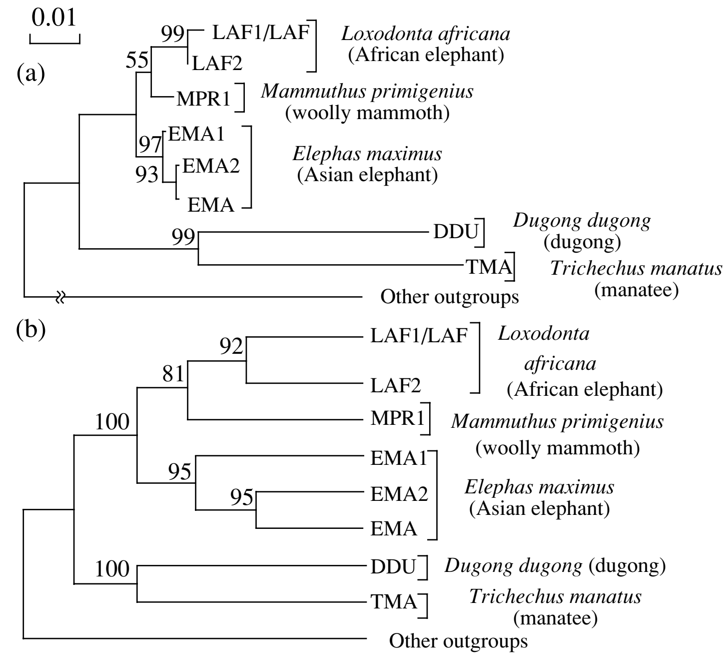

Fig. 3. Phylogenetic tree of the 12S rRNA sequences constructed by (a) neighbor-joining and (b) maximum parsimony methods; numbers on internal branches are bootstrap values derived from (a) 1000 and (b) 100 replications; scale bar, substitutions per site, estimated by Kimura's two-parameter method (after Noro et al., 1998).

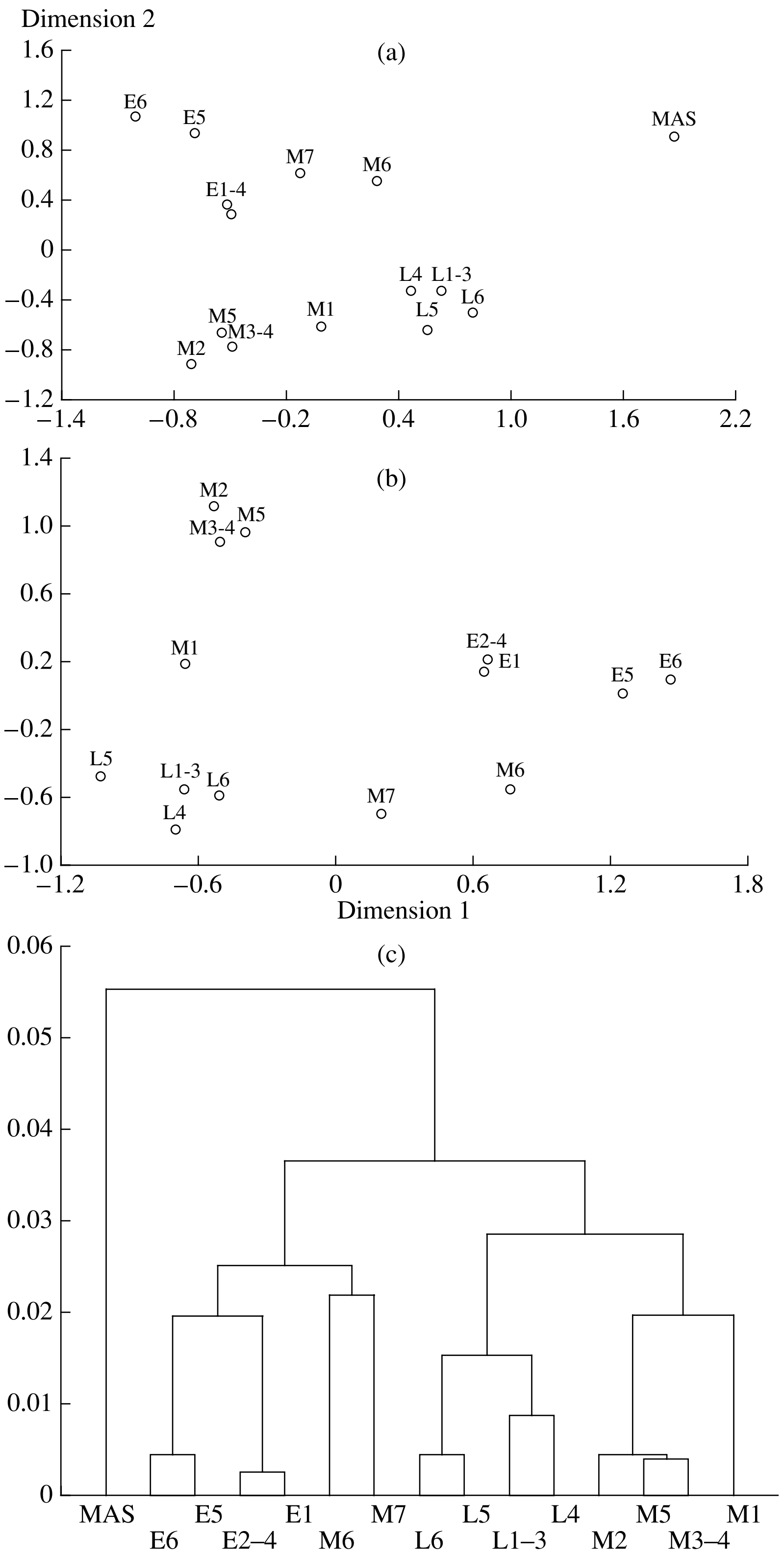

Fig. 4. Positions of mammoths, African and Asian elephants, and American mastodon (*Mammut americanum*) based on a 222-bp fragment of the cytochrome *b* gene: (M1–M7) mammoths: M1 and M6 (after Hagelberg et al., 1994), M3 (after Ozawa et al., 1997); M4 (after Derenko et al., 1997), M5 (after Noro et al., 1998), M6 and M7 (after Yang et al., 1996); (L1–L6) African elephants (E1–E6) Asian elephants; and (MAS) mastodon (after Yang et al., 1996): (a, b) in the space of two first coordinate axes of multidimensional scaling of genetic distances, (a) including mastodon, (b) excluding mastodon; and (c) phylogenetic tree constructed by the neighbor-joining method (after Rautian and Dubrovo, 2001, 2003, modified).

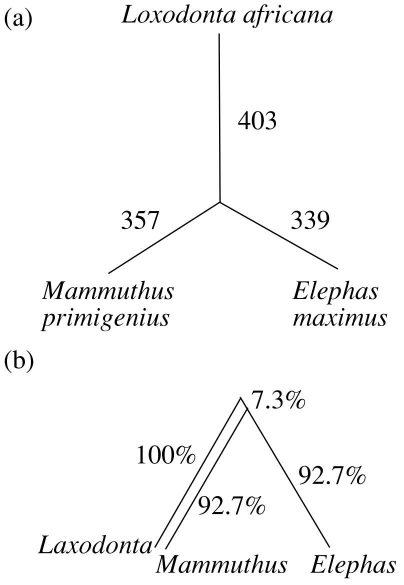

Fig. 5. Relationships between three elephantid genera based on complete mitochondrial DNA sequences: (a) absolute number of phylogenetically informative positions on which the three-species test is based and (b) relative length of the internal branch for clock-like phylogenetic tree, using the substitution data from (a) and rooted by midpoint rooting (after Krause et al., 2005).

odon (*Mammut americanus*) were reported (Hagelberg et al., 1994; Hauf et al., 1995, 1999; Yang et al., 1996; Derenko et al., 1997; Ozawa et al., 1997; Noro et al., 1998; Thomas et al., 2000; Debruyne et al., 2003; Joger et al., 2003). We combined the data from different works in which the same fragment (222 bp) was examined in different specimens, and analyzed genetic distances between them (Fig. 4). Figures 4a and 4c show distinct isolation of *Mammut americanus* from the other taxa, which is revealed by both multidimensional scaling and cluster analysis.

The mean distances from mastodon to *Mammuthus, Loxodonta*, and *Elephas* are approximately equal to each other (differ within random error). They are 0.063, 0.056, and 0.057, respectively, and significantly differ from the mean distances between the pairs *Mammuthus–Elephas, Mammuthus–Loxodonta*, and *Loxodonta–Elephas*, which are 0.032, 0.033, and 0.042. At the same time, the differences between the last three estimates are nonsignificant and lower than the mean intraspecific distances, which are 0.031, 0.010, and 0.011 in *Mammuthus, Elephas*, and *Loxodonta*, respectively. In *Mammuthus*, the mean intraspecific distance is significantly greater than in living elephants. This could have resulted from incorrect determination of some mammoth nucleotide sequences (as was suggested by Thomas et al., 2000) or from the existence of two species of woolly mammoth, the morphological distinctions between which were not revealed (as was proposed by Rautian and Dubrovo, 2001, 2003; see Figs. 4a–4c, mammoths are divided into two groups, M1–M5 and M6–M7). Therefore, it is probable that the mean genetic distance between mammoths does not reflect intraspecific variation. However, even if the data on individual variation of mammoths are excluded from consideration, the intraspecific variations of extant elephants are too high to be neglected when phylogenetic trees are constructed.

Thus, the data on the cytochrome *b* sequence suggest approximately equal genetic distances between the three elephantid genera, as in the case with the 12S rRNA gene; this supports the conclusion that they could have diverged as a result of the same adaptive radiation event.

Recently, Krause et al. (2005) determined a complete (16770 bp) mitochondrial DNA sequence of a mammoth from Berelekh and compared it with that of the African and Asian elephants. The researchers concluded that the mammoth is more closely related to the Asian elephant than to the African elephant. However, the length of the internal branch leading from the point of divergence between the African elephant and the common ancestor of the Asian elephant and woolly mammoth to the point of divergence between the mammoth and Asian elephant is only about 7.3% of the total length of the phylogenetic tree for the three evolutionary lineages (Fig. 5). On the basis that a divergence of Asian and African elephants and mammoths occurred about six million years ago, Krause et al. (2005) calculated that the divergence between the mammoth and Asian elephant took place only 440000 years after the divergence of the African elephant. At the same time, the study considered the mitochondrial DNA of only one mammoth, one Asian and one African elephant. Thus, as in earlier studies, intraspecific (population) variation was not taken into consideration; consequently, these estimates concerned differences between individual mitochondrial sequences rather than changes in the population gene pool in the course of evolution.

It is possible to bridge this gap in part, using the results of studies of intraspecific genetic variation of extant elephants. Roca et al. (2001) examined the DNA sequence variation in four nuclear genes (1732 base pairs) in 195 free-ranging African elephants from 21 populations of two subspecies *Loxodonta africana africana* Blumenbach, 1797 (African savannah elephant) and *L. africana cyclotis* Matschie, 1900 (African forest elephant).[2] The researchers revealed high interpopulation genetic differences and on this basis estimated the time of divergence between the forest and savannah elephant subspecies as 2.63 ± 0.94 Ma (i.e.,

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[2] Genetic differences between forest and savannah elephant populations were 58% of the difference in the same genes between the elephant genera *Loxodonta* and *Elephas.* Based on this and differences in the multiple genetically fixed nucleotide sites, morphological and habitat features, Roca et al. (2001) proposed that the forest and savannah elephants should be regarded as two species, *Loxodonta africana* and *Loxodonta cyclotis.* However, the presence of clear gene flow between these forms corroborates their subspecies rank (Debruyne, 2001).

much more than 440000 years, the time interval between the deviation of the African elephant lineage and the divergence of the Asian elephant and mammoth as estimated by Krause et al., 2005). Thus, the intersubspecific differences in the African elephant are much greater than the differences between the distances *Mammuthus–Elephas* and *Mammuthus–Loxodonta*. Moreover, using the same method and data from Roca et al. (2001), we estimated the time that would have been required for the divergence of forms the difference between which is the same as the mean distance between individuals of the forest elephant *L. a. cyclotis* as 510000 years. Thus, the intraspecific variation of elephants is high enough to regard the distances *Mammuthus–Elephas, Mammuthus–Loxodonta*, and *Loxodonta–Elephas* as equal (from the population genetic point of view, they differ from each other nonsignificantly, even in the case of the complete mitochondrial genome).

The conclusion that *Mammuthus, Elephas*, and *Loxodonta* are genetically equidistant agrees with the results of immunological studies (Lowenstein, 1985) and comparisons of hair structure (Valente, 1983); in these parameters, the distances between the three elephantid genera are also approximately equal to each other. Thus, on the assumption of approximately constant rate of genetic substitutions, the emergence of the phylogenetic lineages leading to *Elephas, Mammuthus*, and *Loxodonta* should be regarded as a simultaneous event (on geological time scale). It is possible to explain certain differences between these distances by the origin of the three lineages from different populations of the same ancestral species; these populations were probably rather similar genetically and could have been indistinguishable morphologically.

At the same time, in a number of advanced morphological characters, such as the increased height of the tooth crown, the large number and high frequency of plates, thin enamel, etc., *Mammuthus* is much closer to *Elephas* than to *Loxodonta* (Maglio, 1973; Dubrovo, 1997). This clearly shows essential differences in the rates of molecular–genetic and functional–morphological evolution and the parallel development of advanced morphological characters in mammoth and Asian elephant. The latter conclusion follows from the fact that their common ancestor was also the ancestor of the African elephant and, hence, its characters could not be in a more advanced condition than in *Loxodonta* (Dubrovo and Rautian, 1999; Rautian and Dubrovo, 1999, 2001, 2003).

The genetic equidistancy of the three genera reflects the temporal aspect of their divergence and is only indirectly associated with adaptive evolution of elephantids. Thus, molecular–genetic 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 allow available morphological information to be examined from a new point of view. In particular, in the case of elephantids, they support the parallel development of certain key characters.

Over the almost 150 years of the evolutionary era in biology, extensive data on parallel development in various plant and animal groups have been accumulated. Parallelisms have proved to be frequent and inevitable evolutionary phenomena, rather than rare and isolated events (Rautian, 1988). The most amazing and well-grounded examples are parallel reptilization (Olson, 1965; Tatarinov, 1976), mammalization (Tatarinov, 1959; Crompton, 1963), microtization (Agadjanian, 1992), angiospermization (Meyen, 1987; Krassilov, 1989), etc. Now, we can supplement this list with parallel elephantization in the lineages of the Asian elephant and mammoth. It is noteworthy that the list is enlarged in the most scarce part, namely, in the field of low-rank taxa. The latter is particularly important, because this shows the essential uniformity of laws and patterns of macroevolution at different taxonomic levels.

The fact that our interpretation of genetic data on elephantids agrees with the general rule of parallel evolutionary development indirectly supports the trustworthiness of this interpretation and encourages us to look for other cases where genetic data can help in the substantiation of parallel development of certain morphophysiological characters.

Differentiation of Vespertilionid Bats

Another interesting example of tentatively simultaneous differentiation (adaptive radiation) of a series of taxa is considered using the example of vespertilionid bats.

We analyzed the data on the nucleotide sequence of the cytochrome *b* gene (1140 bp) reported by Stadelmann et al. (2004) for representatives of four subfamilies of the family Vespertilionidae. Sequences were aligned using MegAlign (DNASTAR. Inc.) with default parameters and subsequently modified by eye. A phylogenetic tree (Fig. 6) was constructed using the package PAUP*4.0b10 (UPGMA, with HKY85 distances) (Swofford, 2002). Statistical support for the nodes was assessed using bootstrap analysis, with 1000 replicates (Felsenstein, 1985). Figure 6a shows a weak bootstrap support of many nodes; therefore, we removed all nodes with support less than 60% (Fig. 6b). For a better understanding of relationships among the bats considered we also applied the MDS method to the genetic distances (Fig. 7).

Figures 6b and 7 show that most of the bats considered form a large cluster (with bootstrap support of 90%) that comprises taxa of different rank, i.e., the subfamilies Murininae (including the genera *Harpiocephalus* Gray, 1842 and *Murina* Gray, 1842) and Kerivoulinae (*Kerivoula* Gray, 1842) and a series of species of the genus *Myotis* Kaup, 1829, including *M. muricola* (Gray, 1846), *M. evotis* (H. Allen, 1864), *M. alcathoe*

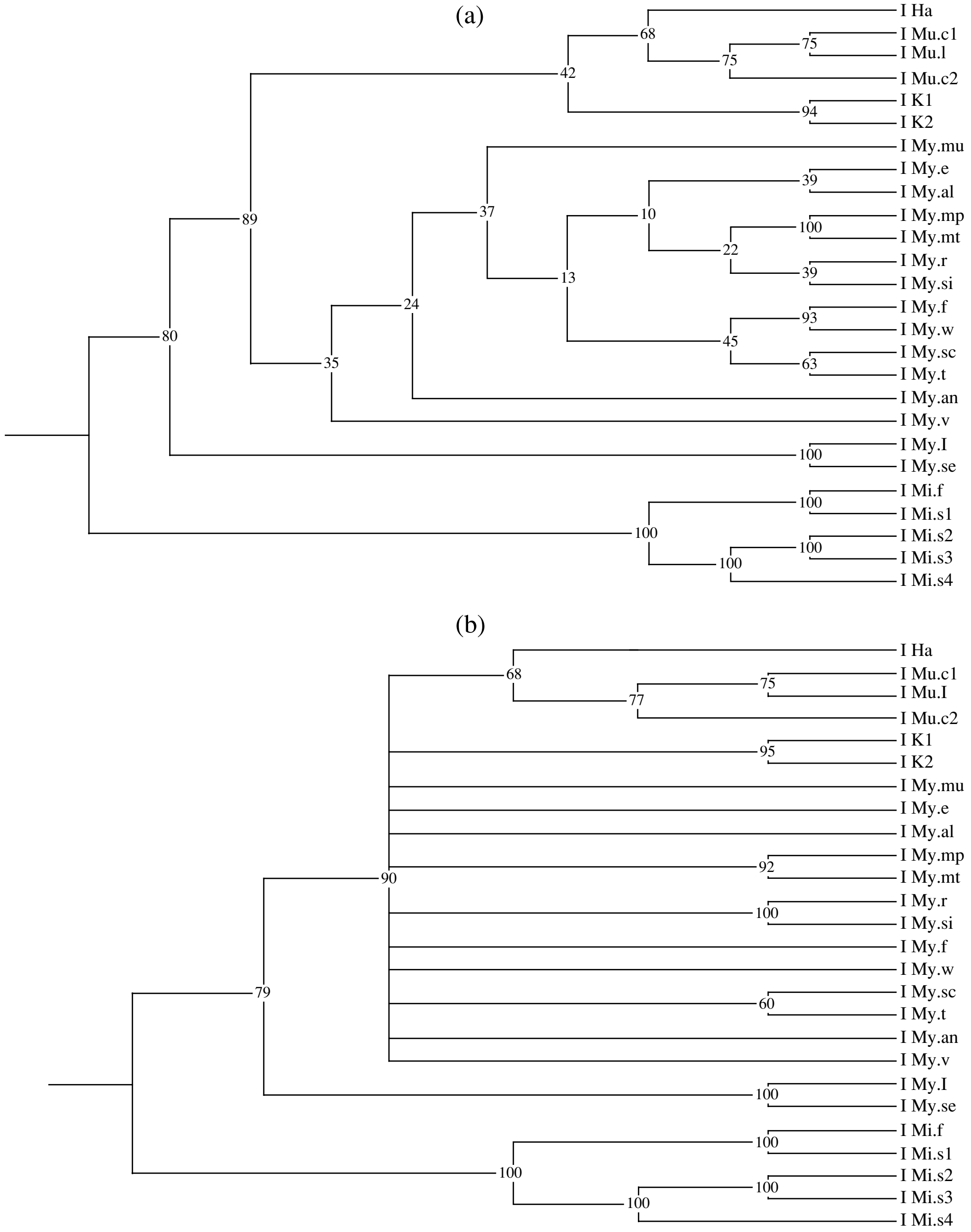

Fig. 6. Phylogenetic trees for vespertilionid bats based on the complete cytochrome *b* gene sequence; numbers on internal branches are bootstrap values derived from 1000 replications, %: (a) all nodes are shown and (b) only nodes with more than 60%-bootstrap support are retained. Designations: (Ha) *Harpiocephalus mordax*, (Mu.c1) and (Mu.c2) *Murina* cf. *cyclotis*, (Mu.l) *Murina leucogaster*, (K1) and (K2) *Kerivoula* cf. *papillosa*, (Mi.f) *Miniopterus fraterculus*, (Mi.s1–Mi.s3) *Miniopterus schreibersii*, (My.mu) *Myotis muricola*, (My.an) *Myotis annectans*, (My.e) *Myotis evotis*, (My.f) *Myotis formosus*, (My.l) *Myotis lesueuri*, (My.mp) *Myotis macropus*, (My.mt) *Myotis macrotarsus*, (My.al) *Myotis alcathoe*, (My.r) *Myotis ricketti*, (My.sc) *Myotis scotti*, (My.se) *Myotis seabrai*, (My.si) *Myotis sicarius*, (My.t) *Myotis tricolor*, (My.v) *Myotis vivesi*, and (My.w) *Myotis welwitschii.*

Helversen et Heller, 2001, *M. macropus* Gould, 1855, *M. macrotarsus* (Waterhouse, 1845), *M. ricketti* (Thomas, 1894), *M. sicarius* Thomas, 1915, *M. formosus* Hodgson, 1835, *M. welwitschii* Gray, 1866, *M. scotti* Thomas, 1927, *M. tricolor* Temminck, 1832, *M. annectans* (Dobson 1871), and *M. vivesi* Menegaux, 1901, while *Myotis lesueuri* along with *M. seabrai* as well as the subfamily Miniopterinae (*Miniopterus* Bonaparte, 1837) form separate clusters. Thus, a number of bat taxa are almost equidistant genetically. In addition, it is possible to disregard certain differences between genetic distances because of rather high intraspecific variation (as in the case of elephantids).

On the assumption that genetic substitutions occurred at approximately the same rate, it is possible to propose simultaneous (on geological time scale) differentiation of the large cluster of equidistant taxa as a result of the same radiation event. This raises the question as to whether this radiation event produced sister taxa of different ranks, or their rank should be revised (giving all of them, or some of them the same taxonomic rank).

Theoretically, it is not impossible for lineages to differentiate simultaneously to produce taxa of different ranks. This question was considered in detail by Schwatz (1980), using the example of voles. Therefore, genetically equidistant taxa are not necessarily of the same rank. A prominent example is provided by the genera *Homo, Pan*, and *Gorilla.* Many genetic (including cytogenetic, biochemical, and molecular) studies show that these three genera are approximately equidistant genetically, or, more precisely, humans and chimpanzees are more similar to one another than to gorillas (Chen and Li, 2001). However, it is generally accepted that chimpanzee and gorilla belong to the family Pongidae, while humans are placed in the family Hominidae along with their extinct relatives. This is caused by the fact that, notwithstanding relatively small genetic changes, hominids transformed significantly morphologically, mastered an essentially new adaptive zone, and created a new form of relationship with the environment (see, for example, King and Wilson, 1975).

A similar situation of different taxonomic rank in genetically equidistant taxa may well occur in the bats considered. Actually, genetic traits do not provide criteria for the establishment of taxonomic rank. Similarly, there is no way to recognize biologically advanced features based on the extent to which taxa differ in genetic traits. At the same time, evolutionary systematics, with its hierarchical structure, is based on the principles of progressive development, recognition of advanced characters that allow the penetration into new adaptive zones, along with adaptive radiation in these zones. This task is only realizable within the framework of the morphophysiological approach.

Thus, we face the necessity of a division of labor between the molecular–genetic and morphofunctional approaches with reference to phylogenetic and taxonomic conclusions: the first gives much for the reconstruction and understanding of particular lineages, their continuity, genetic relationships, etc., while the second enables the recognition of advanced and other derived characters and reconstruction of natural evolutionary relationships and, hence, evolutionary systematics. At the present stage of the development of molecular phylogenetics, it is frequently overlooked that the foundation for its reconstructions is primarily provided by studies at the morphophysiological level, first of all, those using paleontological material. The rapid development of molecular phylogenetic studies combined with the evident decrease in the intensity of phylogenetic studies at all other levels of organization is fraught with the situation that the data forming the basis for molecular reconstructions would appear to be the weak point.

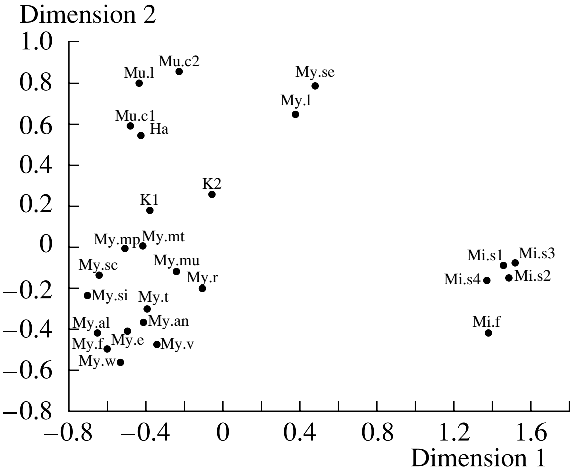

Fig. 7. Positions of vespertilionid bats in the space of two first coordinate axes of multidimensional scaling of genetic distances based on the complete 1140-bp sequences of the cytochrome *b* gene (for designations, see Fig. 6).

Thus, in order to support (or change) the taxonomic structure of the bats under consideration, it is necessary to consider their taxonomically important characters.

Myotis is the most numerous and most widespread genus of the entire order Chiroptera. Within the family Vespertilionidae, the genus *Myotis* is conspicuous for the retention of the most primitive dental formula, lacking only one upper incisor, one upper premolar, and one lower premolar of the complete eutherian armature, and for the absence of specialized features of cranial structure and individual tooth form, which characterize many of the bat genera with limited range (Miller and Allen, 1928). The majority of species of *Myotis* display the following primitive dental characters (Rossina, 2002): three upper and lower premolars; a vertical outgrowth of the cingulum on the anterolingual side of P^4; the presence of conules (paraconule) and lophs (paraloph and metaloph) on M^1–M^3. In addition, members of the genus *Myotis* share primitive structural features of the sternum and, probably, of the basisphenoid. The basisphenoid fossae are poorly developed, the basisphenoid is somewhat recessed relative to adjacent bones (in the dorsal view of the choanal region). A more primitive structure of the basisphenoid region is only observed in the African genus *Cistugo* Thomas, 1912.

Myotis is usually regarded as a primitive genus, because it is similar in tooth row morphology to the presumably ancestral form of Kerivoulinae (Miocene) and to *Stehlinia* (Eocene) (Slaughter, 1970; Horacek, 1986).

Kerivoula is characterized by the same dental formula and myotodont lower molars as *Myotis* and differs in certain other dental characters. Its P_3 is only slightly smaller than P_2, while in *Myotis* it is the smallest of the upper premolars. P_3 of *Kerivoula* is equal to, or somewhat larger than P_2 and is similar in size to P_4, which is atypical for *Myotis* (Miller, 1907). In addition to the dental structure, *Kerivoula* differs from all other species of the family Vespertilionidae in the sternal structure and certain exterior characters, such as a long tail (Miller, 1907).

The subfamily Murininae (including *Murina* and *Harpiocephalus*) is clearly distinguished from other Vespertilionidae by both the exterior features (narial structure, pattern of hair distribution, etc.) and a number of dental characters, including the extreme development of a circular cingulum in all teeth. The teeth are massive, robust and usually have blunt apices. P^3 is completely reduced, while P^2 is extremely massive and has a well-pronounced anterolingual projection of the cingulum and a well-developed heel on the dorsolingual side. The enamel on the buccal side of the massive, irregularly quadrangular P^4 has a unique additional vertical crest deviating from the central cusp.

Unlike other Palearctic chiropters, the upper molars of the tube-nosed bat have a well-developed stylar shelf bordered by the cingular crest. The parastyle of each upper molar in projection on the tooth crown is higher than the mesostyle, which is atypical of the majority of the Vespertilionidae. A genus-specific character of *Murina* is the murinodont structure of the lower molars, which is distinct from the nictalodont and myotodont structural patterns of the lower molars of chiropters (Rossina, 2003).

Miniopterus markedly differs from all other vespertilionid bats in many characters, including the structure of hair (Miller, 1907), tongue, and bulbourethral glands (Tiunov, 1997), embryonic (Gopalakrishna and Karim, 1980; Gopalakrishna and Chari, 1983), and immunological (Pierson, 1986) characters; the absence of a baculum (Matthews, 1942); the presence of a tendon locking mechanism (Simmons, 1998), supplementary vestigial tooth between the upper canine and the first premolar (Mein and Tupinier, 1977); and the second phalanx of the third digit being three times as long as the first phalanx (Miller, 1907). Because of these distinctions, it has been repeatedly proposed to place *Miniopterus* in a separate family, the Miniopteridae.

Thus, the results of genetic and morphological comparisons agree in respect to the early isolation and most significant deviation of *Miniopterus* from the other bats discussed; genetic data provide new evidence for familial rank of this taxon. At the same time, there is no reason to give identical taxonomic ranks to Murininae, Kerivoulinae, and certain species of *Myotis* (i.e., to rise the species included in the above "large cluster" to generic or subfamilial rank or to include members of Murininae and Kerivoulinae in the genus *Myotis*). This is because species of *Myotis* are uniform morphologically, while the relatively large genetic distances between them are attributable to a long period of independent development, which did not result in the appearance of advanced morphological characteristics (the development was relatively slow with reference to morphofunctional features).

In contrast to *Myotis*, approximately the same time interval was enough for the lineages of Murininae and Kerivoulinae to deviate significantly from the ancestral taxon; i.e., they evolved morphologically at a higher rate and acquired considerable distinctions deserving subfamilial rank.

The positions of *Myotis lesueuri* and *Myotis seabrai* are of special interest. They are at a relatively great genetic distance from the other species of this genus and are separated from them by a clear hiatus in the space of multidimensional scaling (Fig. 7). This is a situation where genetic data provoke a question as to whether or not these two species possess taxonomically significant characters that merit their removal from the genus *Myotis* to a separate genus or taxon of a higher rank. The extent of genetic distinctions alone does not allow the resolution of such questions.

The conclusion about approximately equal genetic distances between the above chiropteran taxa is tentative; as genetic data are enlarged, the support of certain nodes of the initial tree (Fig. 6a) would probably increase, and the branching structure would become more complex than is shown in Fig. 6b. Nevertheless, we believe that it is expedient to consider this example in order to outline an important field that virtually escapes the attention of researchers. The idea that the same radiation event can lead to the development of different-ranked taxa has usually been neglected in recent interpretations of genetic data; this results in numerous attempts to raise the rank of taxa to the highest rank of sister taxa.

It should be noted that the functions of classical systematics and phylogenetics were quite different. A taxonomist distinguished taxa based primarily on hiatuses and combined them in a hierarchical system. Subsequently, a phylogeneticist (who was frequently, although not always, the same researcher) provided the system with a phylogenetic interpretation (reconstruction). The same system could have been provided with several alternative phylogenetic reconstructions.

The phylogeneticist often improved the initial system based on his phylogenetic reconstruction. Such a modified system that underwent additional testing in the course of phylogenetic reconstruction was named a phylogenetic system.

In the case that a system is only intended for the visualization of phylogeny, which frequently implies only a sequence of branching lineages, it can hardly be taken as a natural system of organisms, because it does not necessarily reflect essential properties of organisms. S.V. Meyen (personal communication) used to say that such a system is artificial, whereas any artificial system, as it is constructed on the basis of properties of real organisms, is natural.

A taxonomic system based on the order of branching received from molecular data may be particularly

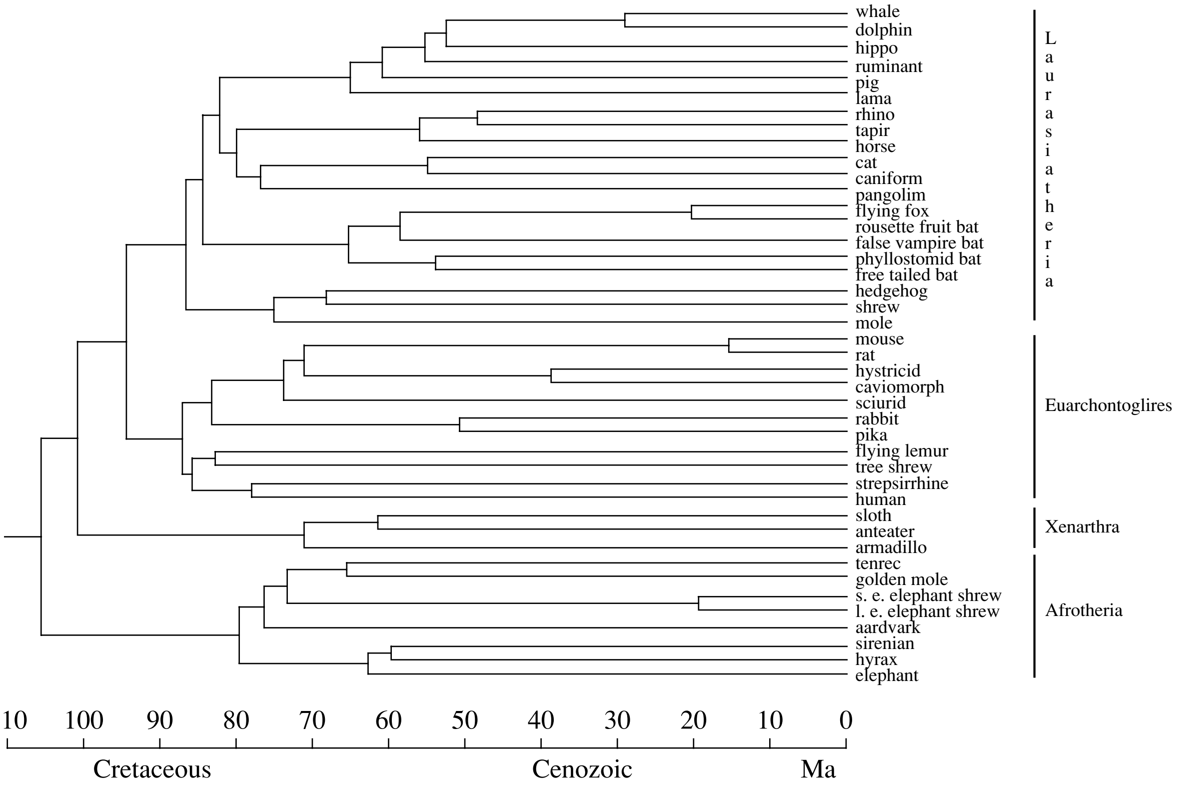

Fig. 8. Molecular phylogenetic tree for placental mammals based on the 16 397-bp data set, maximum likelihood method (after Murphy et al., 2003, modified); The names of particular clusters (at the left of the figure) are frequently used as taxonomic names.

surprising, because its taxa may include organisms that differ strongly in morphophysiological characteristics, while morphologically similar organisms may fall into remote taxa.

These statements are illustrated with examples of some higher taxa of placental mammals.

The progressive accumulation of DNA sequence data during recent years has provided new important data on the phylogenetic relationships of various taxa. In particular, a number of studies was devoted to the reconstruction of phylogenetic trees for eutherian mammals on the basis of mitochondrial and nuclear sequences (Madsen et al., 2001; Murphy et al., 2001a, 2001b; etc.). Extant placentals were divided into three or four primary clades, which were regarded as superordinal taxa: (I) Afrotheria (including elephants, manatees, hyraxes, tenrecs, golden moles, aardvark, and elephant shrews); (II) Xenarthra (sloths, anteaters, and armadillos); (III) Euarchontoglires (rodents, lagomorphs, primates, flying lemurs, and tree shrews); and (IV) Laurasiatheria (cetaceans, artiodactyls, perissodactyls, carnivores, pangolins, bats, hedgehogs, moles, and shrews) (Fig. 8). These phylogenetic reconstructions are partly consistent and partly markedly discrepant with those generated from morphological studies (Novacek, 2001).

Relationships of the taxa included in the group Afrotheria are of special interest, because this group is clearly defined and separated from other eutherian groups in a large number of genetic studies. However, the establishment of the superorder Afrotheria is incompatible with the evolutionary morphological system, because, among other things, its members do not share any apomorphies. Morphological studies support the grouping of elephants, hyraxes, and sirenians (which are combined in the subcohort Paenungulata Simpson, 1945). However, in addition to Paeunungulata, Afrotheria comprises tenrecs, golden moles, elephant shrews, and aardvarks, the morphophysiological characters of which disagree with their close positions in the taxonomic system. Elephant shrews and aardvarks are presently assigned to separate orders, while tenrecs and golden moles are generally referred to insectivores (order Lipotyphla), along with shrews, moles, and hedgehogs. Thus, acceptance of such group as Afrotheria would suggest a radical shakeout of the placental tree in ways not anticipated by morphological work (Novacek, 2001, p. 573).

In our opinion, this disagreement is resolvable using the same approach as in the case of vespertilionid bats. Since genetic and morphophysiological characteristics reflect different aspects of evolution, such that genetic data allow one to trace genetic affinity of taxa, but play a minor role in the establishment of taxa, their ranks, and boundaries between them, these tasks remain within the grasp of the morphophysiological approach.

Thus, it is possible to propose the following interpretation. The phylogenetic lineages that lead to shrews, moles, hedgehogs, tenrecs, and golden moles (which are assigned to the order Lipotyphla) deviated early from the ancestral eutherian stem. During their long subsequent evolution, they accumulated considerable genetic changes, which resulted in the remote positions of these groups in molecular phylogenetic trees. However, the rates of morphological evolution were relatively low, so that these animals retained many primitive characters up to the present time. Their morphological pattern was restricted to relatively small invertebrate-eating mammals and was possibly established as early as the Late Jurassic under the condition that the dominant block of the community was composed of dinosaurs (Agadjanian, 2003a, 2003b). Morphological studies of extant and extinct insectivores strongly suggest that all of them should be assigned to the same order (for a recent review, see Lopatin, 2005).

The other groups of Afrotheria (orders Macroscelidea, Tubulidentata, Hyracoidea, Proboscidea, and Sirenia) differentiated later and evolved from a taxon genetically similar to the ancestors of Tenrecomorpha and Chrysochloridea, but showed higher rates of morphological evolution, so that their distinctions reached the ordinal rank or, in the case of Paenungulata, the subcohort rank. On the contrary, Tenrecidae, Chrysochloridae, Soricidae, Talpidae, and Erinaceidae retained essentially the same morphological pattern as in the time of their emergence, even when they adapted to a subterranean mode of life (Chrysochloridae and Talpidae). Consequently, they do not merit splitting into several orders, although they differentiated considerably genetically. Thus, it is possible to solve the contradictoriness of Afrotheria by the removal of its taxonomic (superordinal) status, i.e., taking this cluster as a group comprising genetically related orders and subordinal taxa derived from the ancestral taxon (which comprises extinct and extant Lipotyphla).

A similar situation is observed in the case of the order Cetacea, which is a sister group of the family Hippopotamidae within the molecular phylogenetic tree (Fig. 8). It would have been inexpedient to give Hippopotamidae an ordinal rank and consider Hippopotamidae + Cetacea to be a superorder (which would have been opposed to other Artiodactyla). The positions of Hippopotamidae and Cetacea can be explained by an almost simultaneous deviation of the lineages leading to these groups from a common ancestor, followed by morphological evolution at substantially different rates. As a result, the Hippopotamidae mostly preserve ancestral morphological pattern and, hence, should be retained in the order Artiodactyla, while cetaceans underwent considerable morphological changes and deserve the assignment to a separate order.

The examples of Afrotheria and Cetacea are very important, because similar contradictions between phylogenetic reconstructions based on genetic and morphological data have repeatedly arisen in many studies and will arise in the future.

CONCLUSIONS

Phylogenetic reconstructions based on genetic and morphophysiological data often come into conflict, the basic reason for which is different patterns of evolutionary change at different levels of biological organization. An important obstacle to the synthesis of results obtained by different approaches is a profound differentiation of methods generally accepted in different fields of biology and their mostly independent development. Thus, combined consideration of genetic and morphological data in phylogenetic reconstructions promises great advantages in the understanding of evolution and its particular phenomena (such as parallel development, adaptive radiation, and many others). We believe that the theoretical basis for the synthesis of results obtained by the studies at different levels is provided by the theory of stabilizing (canalizing) selection (Schmalhausen, 1949), which put in order many biological phenomena.

The rates of evolution at the genetic and morphological levels may not only differ considerably, but are controlled by different factors. Newly obtained genetic data support Schmalhausen’s idea that phenotypic characteristics are potentially more stable than the genetic traits providing the basis for their development. The general rule is that morphofunctional (phenotypic) characteristics are capable of persisting over potentially infinite periods of geological history, while genetic characteristics inevitably change in the course of evolution. The molecular clock may be fast or slow; however, many genetic phenomena agree satisfactorily with this theory and allow estimation of the temporal aspect of evolution.

As a result of different patterns and rates of evolution at genetic and morphological levels, the two approaches supplement each other rather than lead to unsolvable conflicts. The first gives much to the reconstruction and understanding of particular lineages, their continuity, etc., while the second enables the recognition of advanced and other derived characters and the reconstruction of natural evolutionary relationships and, hence, the development of evolutionary systematics.

Sister taxa in molecular phylogenetic trees may differ in rank. Moreover, it is possible to propose that taxa combining a relatively low taxonomic rank with high genetic differences between its members most likely possess primitive (ancestral) morphophysiological characteristics. This follows from early differentiation and, hence, accumulation of genetic substitutions, but a low rate of morphological change and, hence, retention of ancestral characteristics and low rank of such taxa (an example is provided by the genus *Myotis* in comparison with other vespertilionid bats).

Thus, adequate synthesis of data obtained in different fields of biology will provide a new insight into the patterns of evolution and promote the development of the theory of phylogeny and systematics and result in the reconstruction of noncontradictory evolutionary systematics.

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