Hystrix, (n.s.) *11 (2)* (2000): 5-15

CHROMOSOMAL EVOLUTION IN SMALL MAMMALS (INSECTIVORA, CHIROPTERA, RODENTIA)

JAN **ZIMA**

Department of Zoology, Faculty of Science, Charles University, Viniěná 7, CZ-12844 Praha, and Institute of Vertebrate Biology, Academy of Sciences, Květná 8, CZ-60365 Brno, Czech Republic

ABSTRACT - Extensive descriptive, comparative, and experimental research on the chromosomes of natural populations of small mammals has been conducted in the last 50 years. These studies have revealed a surprisingly large amount of karyotypic variation within and between individuals, populations, species, and higher taxa. In the Palaearctic region, the karyotypes of 80 to 90% of the species of insectivores, bats and rodents have already been described, and almost all European species belonging to these orders have been examined. More than 40 cryptic species of small mammals with a unique karyotype have been described in the Palaearctic region, including 24 species in Europe. A polymorphic or polytypic karyotype was found in 118 Palaearctic and 42 European species. This high degree of intraspecific karyotypic variation has resulted in problems in the naming of various chromosomal races, since the subspecies is clearly not the appropriate category for this purpose. The driving forces of karyotypic evolution may be found either in selection or drift acting at the organismal level, or in the internal processes occurring within the cell. The forces acting at the organismal level are based on either negative heterosis of chromosomal rearrangements or on the altered pattern of gene expression resulting from karyotypic repatterning. Little evidence for the direct adaptive nature of chromosomal alterations has been presented up to now and the significance of this factor remains unclear. Chromosomal change is, however, obviously correlated with speciation and divergent evolution, even if karyotypic alterations in certain lineages need not be directly related to the formation of a reproductive barrier. Chromosomal studies are still an important tool to record and describe biological diversity, and often represent a simple and indispensable method for identification of various taxa.

Key words: karyotype, evolutionary alterations, insectivores, bats, rodents.

INTRODUCTION

The evolution of the number and morphology of chromosomes is one of the traditional enigmas of biological research. Despite long-term and intensive research on various groups of organisms, the basic causes and consequences of karyotypic evolution remain unclear. There is immense variation in chromosome number among natural populations and species; differences in karyotype are frequently observed even between morphological sibling species and/or between different populations of a single species. The biological meaning of this variation is obviously significant for our understanding of the fundamental relationships between organisms and their habitats.

From a broad array of possible interpretations, it is possible to point to two extreme and contradictory answers to this question. The first interpretation adheres to the idea that the forces driving chromosomal evolution are the same as those acting at the or-

ganismal level, and that the selection of chromosomal changes is mediated, either directly or indirectly, through the'phenotype. The other concept rejects the immediate selective influence of the environment on the karyotype and presumes that evolutionary chromosomal alterations simply reflect autonomous processes taking place in the internal nuclear environment.

CHROMOSOMAL CHANGE AND THE PHENOTYPE

To evaluate the validity of both these interpretations, we should first consider the possible adaptive consequences of karyotypic change. Our considerations are limited to organisms with regular and stable sexual reproduction, mammals in particular. In such groups, quantitative changes of the whole genome via polyploidisation are practically unknown, and we shall ignore this mechanism hereafter. Two basic types of chromosomal mutation occur which differ in their effect on genome size. The rearrangements that cause a quantitative change, i.e. deletion or addition of hereditary material, are called 'unbalanced mutations'. Such changes are usually not tolerated, and their carriers are subject to strong negative selection. In this sense, most new chromosomal rearrangements confer an unfavourable genetic load. It is believed that a considerable proportion of zygotes and embryos die in early development because of the appearance of unbalanced chromosomal rearrangements (Gardner and Sutherland, 1989). This is why the incidence of animals with an unbalanced karyotype is extremely low in natural populations. The negative selection pressure can be less intense in the case of changes in heterochromatic regions and/or in segments containing only a few structural genes, e.g. the sex chromosomes (Zima *et al.*, 1992).

The other type of chromosomal mutation results in structural changes in the chromatin arrangement or in changes in the chromosome number. Such alterations do not have any quantitative effect on genome size, particularly with respect to the euchromatic regions. What are the consequences of such mutations on the adaptive abilities of an organism? We can consider two possible outcomes: first, the structural heterozygosity of the set of chromosomes affects the course of meiosis, and the rate of non-disjunction increases in relation to the particular type of rearrangement. As a result, a reduction in fertility is expected in the heterozygote carrying a new mutation, as well as in a hybrid between parents with different karyotypes. The negative effect of heterozygosity may also result from alterations of the internal topography of chromosomes in the interphase nucleus (Capanna and Redi, 1994). The expected negative heterosis manifested in the carrier of a new chromosomal mutation represents the basic paradox of the theories of karyotypic evolution. **A** rearrangement can overcome the disadvantageous heterozygous state and spread only with the help of certain facilitating mechanisms (Wright, 1941); such mechanisms are often assumed to be either random genetic drift or deterministic selection. On the other hand, the lowering of the fitness in hybrids results in the limitation of gene flow between populations with different karyotypes; this may represent the beginning of the formation of a reproductive barrier. In this sense, karyotypic changes should be relevant to speciation and, consequently, to cladogenesis or divergent evolution.

Second, evolutionary rearrangements of the karyotype also potentially have various genetic consequences. For example, a new rearrangement of the genome, resulting from chromosomal alterations, may cause various positional effects; thus it may be related to gene expression and perhaps also to its regulation. Such changes may be directly manifested in various phenotypic adaptations or may be related to the maintenance of viability. These effects also relate karyotypic changes to anagenesis or phyletic evolution.

ADAPTIVE NATURE OF CHROMOSOMAL EVOLUTION

The direct adaptive character of karyotypic evolution has been advocated in several concepts, often elaborated in concrete models and hypotheses. An important concept was proposed by A.C. Wilson and his collaborators (Bush *et al.*, 1977; Larsson *et al.*, 1984; Wilson *et al.*, 1974, 1975). The model was originally based on the comparison of certain biological features between anuran amphibians and mammals. These two lineages have had a relatively long phylogenetic history. The number of extant species is approximately the same in both groups. However, the number of recognised orders is considerably higher in mammals. The difference in the extent of phenotypic diversity between frogs and mammals is obvious and can be explained by a different rate of morphological evolution. Similar differences in karyotypic variation have also been found between the two groups. The karyotypes within frog genera are largely uniform, whereas rich variation and diversification are observed in mammals. Thus, the rate of karyotypic evolution is considerably higher in the latter group, while the divergence rate of structural genes, measured by distances derived from protein divergence, seems very similar in both lineages. Therefore, it has been suggested that chromosomal rearrangements could effect regulatory mechanisms of gene expression and that the increased rate of regulatory changes could accelerate phenotypic evolution. The higher rate of chromosomal evolution in mammals than in frogs can be explained by the complex social structuring of mammalian populations which may enhance the effects of random genetic drift.

Another important hypothesis concerning the adaptive character of chromosomal changes is even more straightforward. The concept was published by Bickham and Baker (1979) as the 'canalisation model' of chromosomal evolution. This hypothesis proposes a direct adaptive significance of the chromosomal complement and a direct influence of karyotypic rearrangements on fitness. The hypothesis predicts that karyotypic evolution occurs in three successive stages. Each cycle starts immediately after penetration of a lineage to a new adaptive zone. In this initial stage, the rate of karyotypic divergence is highest, owing to intense selection exerted on newly emerging karyotypic variants. In the subsequent stage, the rate of divergence diminishes and, finally, the lineage enters the stasis stage with no or minimal changes.

Imai *et al.* (1986) suggested that selection for reduced opportunity of spontaneous, negatively heterotic chromosomal rearrangements could be a possible adaptive advantage of chromosomal change. This concept envisages meiosis and the interactions between non homologous chromosomes as the selective milieu governing karyotypic evolution. The adaptive significance of chromosomal change is then mediated by fertility problems of the heterozygous carriers of negatively heterotic rearrangements, particularly the reciprocal translocations.

The last important group of hypotheses advocating the adaptive character of chromosomal change is related to the effect of karyotypic rearrangements on genetic recombination. A comprehensive concept of this kind was proposed by Qumsiyeh (1994). The influence of the number of chromosomes on the potential variability in offspring is obvious. Considering the other possible cytogenetic effects of recombination, one may expect that the higher the chromosome number, the higher the recombination level and genetic variation in offspring. The high number of chromosomes should thus facilitate the exploitation of a wide ecological niche and the dispersal over a large geographical range. On the other hand, rearrangements resulting in a decrease in the chromosome number and the recombination level ought to be selected in organ-

isms living in stable environments and occupying a narrow ecological niche and small geographical range.

These hypotheses have attracted much attention, but the prevailing opinion about them has been largely negative (Chambers, 1987; King, 1985, 1993; Patton and Sherwood, 1983; Sites and Moritz, 1987; Sites and Reed, 1994). In general, the hypotheses have been criticised because of difficulties in testing the respective predictions. The models have often been changed in a series of successive papers and various ad hoc hypotheses have been added. The argumentation for the models has frequently been based on carefully documented correlations. Nevertheless, no evidence of causal relationships between the correlated variables has been provided. Wilson's model has been particularly criticised for insufficiently representative original data sets. Many observations do not meet the predictions of the models; for example, extensive karyotypic alterations are not usually accompanied by obvious phenotypic changes, and the geographical distribution of intraspecific chromosomal races has no habitat-specific pattern. In addition, the dynamics of intra-population polymorphism is usually not correlated with changes in environmental conditions.

Thus, there is no definitive answer to the question of the adaptive significance of chromosomal evolution. In my view, karyotypic evolution should not be perceived as a pure and simple genomic game within the cell. This may be valid in some segments containing sequences of selfish or parasitic DNA, perhaps in supernumerary chromosomes. It is more probable that karyotypic rearrangements have their important consequences at the organismal level, but not by means of direct adaptive effects. The most important feature of the process of chromosomal evolution should be searched for in disturbances of the meiosis of heterozygous individuals. Speciation initiated by random chromosomal rearrangements may be considered an adaptive response to the postmating reproductive problems resulting from hybridisation between populations and races with different karyotypes. Random drift, mediated by an appropriate population structure and changes in population numbers, is undoubtedly an important factor of the process of karyotypic change. Chromosomal evolution thus appears to be an important component of the divergent evolutionary process. However, the forces affecting evolutionary divergence of the karyotype, and speciation events in general, may be largely the same or overlapping. That is why the causal relationship between chromosomal evolution and speciation may be occasionally missing, since both processes can also run in parallel. In particular, such a situation can evolve if negative heterosis of chromosomal rearrangement is weak or absent (Baker ***et*** *al.*, 1987; King, 1987).

KARYOTYPIC VARIATION IN SMALL MAMMALS

Small mammals are often defined as mammals weighing less than 1 kg, and usually include insectivores, bats, and rodents (Searle, 1996). These mammalian groups are exceptionally convenient for the study of general problems of speciation and evolution. I will focus further on the Palaearctic or European small mammal fauna which is relatively rich in species; the biology of most of the species is relatively well-known and knowledge about their karyotypes is almost complete (Table 1). Cytogenetic studies have been performed on about 80% of the species inhabiting the Palaearctic region and in almost all the species with a European distribution.

Chromosomal studies are extremely useful for the identification of sibling species with a similar morphology. The discovery of karyotypic differentiation within a nominal species has frequently initiated studies of other characters, resulting in discoveries of new cryptic species. At present, more than 40 such species are known in the Palaearctic and 24 in Europe (Table 2).

Table 1 - Karyotypically studied species (n) in the Palaearctic region and Europe. The considered orders are specified. In part from Zima (1993). The species number adapted after Wilson and Reeder (1993).

	Palaearctic region		Europe	
	total species	studied species	total species	studied species
Insectivora	81	72 (88.9%)	39	38 (97.4%)
Chiroptera	73	57 (78.1%)	37	36 (97.3%)
Rodentia	299	240 (80.3%)	106	105 (99.1%)

Table 2 - Cryptic species (n) discovered in chromosomal studies in the Palaearctic regidn and Europe. In part from Zima (1993).

	Palaearctic region		Europe	
	total species	cryptic species	total species	cryptic species
Insectivora	81	15 (12.3%)	39	10 (25.6%)
Chiroptera	73	0	37	0
Rodentia	299	26 (8.7%)	106	14 (13.2%)

Table 3 - Palearctic and European species (n) with variable karyotype. In part from Zima (1993).

	Palaearctic region		Europe	
	studied species	variable species	studied species	variable species
Insectivora	72	15 (20.8%)	38	7 (18.4%)
Chiroptera	57	7 (12.3%)	36	1 (2.8%)
Rodentia	240	96 (40.0%)	105	34 (32.4%)

Chromosomal differentiation between populations, classified within single morphological species, is not necessarily evidence for the existence of a separate biological species. It has become obvious that intraspecific chromosomal variation is the rule rather than the exception, especially among species of small mammals. Table 3 shows the extent of intraspecific chromosomal variation in small mammals from the Palaearctic region and Europe, respectively. Some species have extreme variation in diploid number and other karyotypic characteristics. The common shrew, ***Sorex*** *araneus*, is one of the most variable mammals, with more than 50 known chromosomal races (Searle and Wójcik, 1998; Zima *et al.*, 1988, 1996). Currently, there are serious problems related to the naming of the intraspecific karyotypic forms or races. The international code of zoological nomenclature is simply not appropriate in such cases, and new special systems have been proposed and applied to the common shrew (Hausser *et al.*, 1994).

Intraspecific chromosomal variation can be manifested either as polymorphism within a single population or as polytypy between populations. Table 4 shows that there is no apparent prevalence of any particular mode

Table 4 - Mechanisms responsible for karyotypic variation in Palaearctic small mammals. After Zima (1993).

	polymorphic species (n)	polytypic species (n)	variable species (n)	studied species (%)
Rb translocation	26	22	48	10.0
pericentric inversions	26	9	35	7.3
heterocromatin	17	8	25	5.2
supernumeraries	20		20	4.2
other or unclear	10	22	32	6.7

of variation. The most frequent mechanism responsible for intraspecific chromosomal variation in the Palaearctic small mammals seems to be Robertsonian translocations (chromosomal fusions and fissions), followed by pericentric inversions, heterochromatin changes and the occurrence of supernumerary chromosomes. Because of insufficient or inconclusive data, it has not been possible to evaluate the respective mechanism in some species.

In certain model species, data have accumulated to such an extent that biogeographical conclusions can be drawn from the present pattern of distribution of individual karyotypes in populations, races, or species. Generally, the pattern of geographic distribution of sibling species or karyotypic races is not in accordance with the classical view of a species structure consisting of two or more subspecies. The subspecies is still of importance as a taxonomic unit but most described subspecies obviously lack any biological meaning.

In many species, extensive karyotypic variation originates from a single type of chromosomal rearrangement. White (1973) designated this process as 'karyotypic orthoselection', and it has been well-documented in many species of small mammals. In the species showing this kind of chromosomal divergence between populations, the question of a parallel, independent fixation of an identical chromosomal rearrangement can be evaluated. It seems probable that such events are common and that the karyotype should be treated like any other taxonomic trait or phylogenetic marker. Identical, but independent chromosomal changes in different geographical populations also support the idea of the vicariant rather than migratory origin of individual intraspecific karyotypic races (Zima *et al.*, 1997a).

The pattern of intraspecific distribution of karyotypic races also provides information about the geographical character of chromosomal evolution. In various species, this pattern demonstrates that the process of karyotypic divergence between populations was initiated in the centre of the extant species range, and not in peripheral populations. These data also provide indirect evidence that the presence of large geographical barriers is not a necessary condition for the divergence of the karyotype between populations.

In the common shrew, the ancestral karyotype evidently possessed acrocentric, unfused autosomes. Therefore, populations with a higher diploid number should be considered more primitive than populations with a lower diploid number. The all-metacentric populations, i.e. those with the most advanced karyotype, are concentrated mainly in the longitudinal centre of the species range, whereas populations with the highest diploid numbers occur on the south-western and eastern margins of the range (Searle and Wójcik, 1998; Zima *et al.*, 1996). In the pine vole, *Microtus sub-*

terraneus, two chromosomal races have been recorded, with 52 and 54 chromosomes, respectively. The 54 chromosome race was found in western Anatolia, an isolated part of the range, separated from the other populations some 10 000 years ago by the Bosporus. This is good evidence that the 54-chromosome karyotype is primitive. Again, the populations with the primitive karyotype are distributed in marginal populations at edges of the distribution range (Kryštufek *et al.*, 1994; Zima *et al.,* 1995). The garden dormouse, *Eliomys quercinus,* expanded its range in the post glacial period from the Mediterranean area to the north and east. It is quite probable that during this expansion, certain dispersing populations experienced chromosomal alterations resulting in a change in the diploid number. However, the northern most studied population, from the vicinity of Saint Petersburg in northwest Russia (Graphodatsky and Fokin, 1993), has a karyotype which is quite similar to most populations in the Mediterranean. This means that range expansion probably preceded the chromosomal changes and that these happened approximately in the centre of the current distribution (Zima *et al.,* 1997b).

The common distribution pattern of chromosomal races in the above three species is in agreement with predictions of the model of stasipatric speciation proposed by White (1978). However, this agreement could simply indicate a common mode of chromosomal divergence; it is not necessarily evidence for the causal relationship between karyotypic evolution and speciation. Further studies are needed to prove this relationship.

The extent of interspecific karyotypic differences may vary greatly. Certain lineages are actually extremely variable with respect to the diversified karyotypes of their species, whereas other lineages are rather conservative. Table 5 shows the extent of karyotypic variation between species in certain genera of Palaearctic mammals. After Bengtsson (1980), the extent of variation is expressed as the standard deviation of the mean diploid number and the number of autosomal arms. According to this characteristic, some genera can be classified as uniform (e.g., *Neomys, Myotis, Clethrionomys),* other genera as highly variable *(Sorex, Calomyscus, Myospalax, Sicista).* The same comparison performed for the families of Palaearctic small mammals (Table 6) reveals the lineages with more (Soricidae, Cricetidae, Muridae) and less variation (Erinaceidae, Rhinolophidae, Sciuridae, Dipodidae). These differences between individual taxa or lineages reflect the past history of chromosomal divergence. The lineages with less variation are assumed to have experienced a lower rate of chromosomal evolution, and vice versa. The extent of chromosomal variation can be related to the known phylogenetic age of a lineage and to the ecological and behavioural characteristics of the species included.

As an example, such considerations can be demonstrated in the differences in variation on various levels between bats and the two other orders of small mammals. Generally, the bats are less karyotypically variable (Tables 2-6) and, therefore, reveal a lower rate of chromosomal evolution than insectivores and rodents. The karyotype of temperate species of vespertilionid bats is usually uniform across various species belonging to a single genus (Volleth, 1994; Zima and Horáček, 1985). There may be several reasons for this karyotypic uniformity at the generic level. First, the extant lineages of the bat genera are phylogenetically much older than those of insectivores and rodents. The period of rapid morphological and chromosomal diversification was completed many generations ago in this lineage, which is now in a stage of karyotypic stability. This is consistent with the canalisation model of chromosomal evolution (Bickham and Baker, 1979), which was based principally on investigations of bats. Second, there is also a

Table 5 - Karyotype variability level in certain genera of Palaearctic mammals. After Zima (1993). SD: standard deviation of the mean diploid number of chromosomes (2N) or autosomal arms (AFn).

	SD^{2N}	SD^{AFn}	SD^{TOTAL}
Erinaceus	0.0	4.1	4.1
Sorex	11.1	11.0	22.0
Neomys	0.0	0.0	0.0
Crocidura	7.5	11.8	19.3
Talpa	1.4	4.3	5.6
Rhinolophus	2.0	1.8	3.8
Myotis	0.0	0.8	0.8
Pipistrellus	7.2	2.7	9.9
Nyctalus	1.1	0.0	1.1
Marmota	0.8	1.6	2.4
Spermophilus	2.5	2.9	5.4
Calomyscus	7.2	7.3	14.5
Cricetulus	2.9	1.9	4.8
Mesocricetus	2.5	4.2	6.7
Myospalax	7.9	12.4	20.3
Clethrionomys	0.0	0.0	0.0
Ellobius	7.1	0.7	7.8
Microtus	9.1	7.7	16.8
Gerbillus	11.6	9.6	21.2
Meriones	9.7	4.4	14.1
Spalax	5.3	18.0	23.3
Apodemus	0.9	3.1	4.0
Mus	6.5	0.0	6.5
Acomys	12.6	2.3	14.9
Sicista	9.7	9.2	18.9
Allactaga	0.0	1.4	1.4

distinct difference in the population dynamics and population structure of bats and the other small mammals. Reproduction and population turnover rates are usually very high in insectivores and rodents, and conspicuous annual and long-term changes in densities are usually characteristic of these orders. The social structuring of populations of small terrestrial mammals in small demes of closely related individuals often provides the conditions for inbreeding. In contrast, the r-strategic features of reproduction generally do not occur in the Palaearctic bats, particularly not in the temperate species. Their population size is usually rather stable over some years, and the reproductive strategy in seasonal roosts is probably highly promiscuous. These patterns of population structure suggest that the insectivores and rodents are more likely to be exposed to random drift and the founder or bottleneck effects: the factors potentially enhancing the probability of fixation of new chromosomal rearrangements.

The karyotypic differences between the extant vespertilionid genera are almost of the same magnitude as those between the individual geographical populations of the common shrew. It is possible to suppose then that the ancestor of the vespertilionid lin-

Table 6 - Karyotype variability level in certain families of Palaearctic mammals. After Zima (1993). For explanations see Table 5.

	SD^{2N}	SD^{AFn}	SD^{TOTAL}
Erinaceidae	0.0	4.1	4.1
Soricidae	10.2	15.7	25.9
Talpidae	1.4	4.3	5.7
Rhinolophidae	2.0	1.8	3.8
Vespertilionidae	5.2	2.0	7.2
Sciuridae	2.2	4.2	6.4
Cricetidae	9.3	16.6	25.9
Myospalacidae	7.9	12.4	20.3
Arvicolidae	9.2	7.9	17.1
Gerbillidae	11.0	7.1	18.1
Spalacidae	5.3	18.0	23.3
Muridae	9.6	12.5	22.1
Gliridae	5.2	11.6	16.8
Zapodidae	9.7	9.2	16.8
Dipodidae	2.2	2.0	4.2

eage had the same pattern of chromosomal variation as the extant species, ***Sorex*** *araneus*. We can further speculate that the population structuring of this ancestor might be quite different from that in the extant Palaearctic species, perhaps similar to certain extant species of bats occurring in the Tropics. The present pattern of chromosomal variation found in certain groups of vespertilionid bats from the Tropics also supports the possible relationships between population structuring and rate of chromosomal divergence. The bats in the Temperate Zone are represented by phylogenetically old, K-selected species, with a well-balanced distribution of ecological niches. In such a situation, continual evolution of the karyotype, as well as new speciation events are unlikely to occur.

CONCLUDING REMARKS

In conclusion, I would like to stress that the evolutionary causes and consequences of chromosomal alterations are still unclear. This research topic is still interesting for many reasons, and small mammals represent an extraordinarily suitable model to study it. It is possible that the data facilitating our understanding will be derived from recent Fluorescence *In Situ* Hybridisation techniques and/or from an area different from cytogenetics. Nevertheless, traditional chromosomal studies are still an important tool to record and describe biological diversity. Even in the times of advanced molecular methods, karyotyping is often a simple and indispensable method for the identification of various taxa. We can assume that, especially in the initial stages of speciation, the rates of evolution at the organismal (phenotypic), chromosomal (karyotypic) and molecular (genotypic) levels are independent. Knowledge about the karyotypes thus remains a significant complement to other methods in any taxonomic or phylogenetic study.

ACKNOWLEDGEMENTS

Preparation of this contribution was supported by a grant No. VS97102 from the Ministry of Education, Youth and Sport of the Czech Republic. Thanks are due to Dr. Heidi Hauffe who improved the English throughout the text.

REFERENCES

Baker, R.J., Qumsiyeh, M.B. and Hood, C.S., 1987. Role of chromosomal banding patterns in understanding mammalian evolution. In: Genoways, H.H. (ed.), Current Mammalogy, Vol. 1. Plenum Publishing Corporation, New York, pp.: 67-96.

Bengtsson, B.O., 1980. Rates of karyotype evolution in placental mammals. Hereditas, 92: 37-47.

Bickham, J.W. and Baker, R.J., 1979. Canalization model of chromosomal evolution. Bull. Carnegie Mus. Nat. Hist., 13: 70-84.

Bush, G.L., Case, S.M., Wilson, A.C. and Patton, J.L., 1977. Rapid speciation and chromosomal evolution in mammals. Proc. Natl. Acad. Sci. USA, 74: 3942-3946.

Capanna, E. and Redi, C.A., 1994. Chromosomes and microevolutionary process. Boll. Zool., 61: 285-294.

Chambers, S.M., 1987. Rates of evolutionary change in chromosome numbers in snails and vertebrates. Evolution, 41: 166-175.

Gardner, R.J. and Sutherland, G.R., 1989. Chromosome abnormalities and genetic counseling. Oxford University Press, New York.

Graphodatsky, A.S. and Fokin, I.M., 1993. Comparative cytogenetics of Gliridae (Rodentia). Zool. Zh., 79: 104-113. (in Russian, English summary).

Hausser, J., Fedyk, S., Fredga, K., Searle, J.B., Volobouev, V., Wbjcik, J.M. and Zima, J., 1994. Definition and nomenclature of the chromosome races of *Sorex araneus*. Folia Zool., 43 (Suppl. 1): 1-9.

Imai, H.T., Maruyama, T., Gojobori, T., Inoue, Y. and Crozier, R., 1986. Theoretical bases for karyotype evolution. I. The minimum-interaction hypothesis. Am. Nat., 128: 900-920.

King, M., 1985. The canalization model of chromosome evolution: A critique. Syst. Zool., 34: 69-75.

King, M., 1987. Chromosomal rearrangements, speciation and theoretical approach. Heredity, 59: 1-6.

King, M., 1993. Species evolution: The role of chromosomal change. Cambridge University Press, Cambridge.

Kryštufek, B., Filippucci, M.G., Macholán, M., Zima, J., Vujoševic, M. and Simpson, S., 1994. Does *Microtus majori* occur in Europe? Z. Saugetierkunde, 59: 349-357.

Larsson, A., Prager, E.M. and Wilson, A.C., 1984. Chromosomal evolution, speciation and morphological change in vertebrates. In: Bennett, M. D., Gropp, A. and Wolf, U. (eds.). Chromosomes today, Vol. 8. George Allen and Unwin, London, pp. 215-228.

Patton, J.L. and Sherwood, S.W., 1983. Chromosome evolution and speciation in rodents. Ann. Rev. Ecol. Syst., 14: 139-158.

Qumsiyeh, M.B., 1994. Evolution of number and morphology of mammalian chromosomes. J. Hered., 85: 455-465.

Searle, J.B., 1996. Speciation in small mammals. Symp. Zool. Soc. Lond., 69: 143-156.

Searle, J.B. and Wbjcik, J.M., 1998. Chromosomal evolution: The case of *Sorex araneus*. In: Wojcik, J.M. and Wolsan, M. (eds.), Evolution of shrews. Mammal Research Institute PAS, Bialowieza, 458 pp.

Sites, J.W.Jr. and Reed, K.M., 1994. Chromosomal evolution, speciation, and systematics: some relevant issues. Herpetologica, 50: 237-249.

Sites, J.W.Jr. and Moritz, C., 1987. Chromosomal evolution and speciation revisited. Syst. Zool., 36: 153-174.

Volleth, M., 1994. Phylogenetic relationships of vespertilionid genera (Mammalia: Chiroptera) as revealed by karyological analysis. Z. Zool. Syst. Evolut.-forsch., 32: 11-34.

White, M.J.D., 1973. Animal cytology and evolution. 3rd edition. Cambridge University Press, London.

White, M.J.D., 1978. Modes of speciation. Freeman, San Francisco.

Wilson, A.C., Bush, G.L., Case, S.M. and King, M.C., 1975. Social structuring of mammalian populations and rate of chromosomal evolution. Proc. Natl. Acad. Sci. USA, 72: 5061-5065.

Wilson, A.C., Sarich, V.M. and Maxson, L.R., 1974. The importance of gene rearrangement in evolution: Evidence from studies on rates of chromosomal, protein, and anatomical evolution. Proc. Natl. Acad. Sci. USA, 71: 3028-3030.

Wilson, D.E. and Reeder, D.M. (eds.), 1993. Mammal species of the world: A taxonomic and geographic reference. 2nd edition. Smithsonian Institution Press, Washington and London.

Wright, S., 1941. On the probability of **fix**ation of reciprocal translocations. Am. Nat., 75: 513-522.

Zima, J., 1993. Comparative cytogenetics of Palaearctic mammals. Folia Zool., 42: 97-104.

Zima, J., Fedyk, S., Fredga, K., Hausser, J., Mishta, **A.,** Searle, J.B., Volobouev, V.T. and Wójcik, J.M., 1996. The list of the chromosome races of the common shrew *(Sorex araneus)*. Hereditas, 125: 97-107.

Zima, J. and Horáček, I., 1985. **A** synopsis of karyotypes of the vespertilionid bats. Acta Univ. Carol. - Biologica, 1981: 311-329.

Zima, J., Filippucci, M.G., Kryštufek, B. and Macholán, M., 1995. The systematics and distribution of the *Microtus subterraneus/majori* group. In: Gurnell, J. (ed.), 2nd European Congress of Mammalogy, Southampton University, England. Abstracts of oral and poster papers, p. 159.

Zima, J., Macholán, M., Anděra, M. and Červeny, J., 1997b. Karyotypic relationships of the garden dormouse *(Eliomys quercinus)* from central Europe. Folia Zool., 46: 105-108.

Zima, J., Macholán, M., Míšek, I. and Štìrba, O., 1992. Sex chromosome abnormalities in natural populations of the common vole *(Microtus arvalis)*. Hereditas, 117: 203-207.

Zima, J., Slivková, L., Andreas, M., Benda, P. and Reiter, A., 1997a. Karyotypic status of shrews ***(Sorex)*** from Thrace, European Turkey. Z. Saugetierkunde, 62: 315-317.

Zima, J., Wbjcik, J. M. and Horáková, M., 1988. The number of karyotypic variants in the common shrew ***(Sorex araneus)***. Acta Theriol., 33: 467-475.