Hystrix, (n.s.) 6 (1-2) (1994): **63** - 76 (1995) Proc. II Conf. on Dormice

CHROMOSOMAL VARIATION AND SYSTEMATICS OF MYOXIDS

JAN ZIMA (*), MILOŠ MACHOLAN (*) & MARIA GRAZIA FILIPPUCCI (**)

(*) *Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, Veveří 97, CZ-602 00 Brno, Czech Republic*

(**) Dipartimento di Biologia, Università di Roma "Tor Vergata", Via della Ricerca Scientifica, I-00133 Roma, Italy

ABSTRACT – A synopsis of cytogenetic studies performed on various species and populations of myoxids is presented. Interspecific phylogenetic relationships derived from chromosomal data are evaluated and the evolutionary importance of intraspecific karyotypic variation is discussed. New data on the karyotypes of *Dryomys nitedula* from Asia and *Muscardinus avellanarius* from Europe are presented and discussed with special emphasis on the contrasting pattern of chromosomal differentiation in *Eliomys* vs. *Dryomys* and other myoxids. **A** bibliography of myoxid cytogenetics and karyology is compiled.

Key words: Karyotype, Chromosomal variation, Systematics, Evolution, Myoxidae

RIASSUNTO – *Variazione cromosomica e sistematica dei Mioxidi* – Viene presentata una sinossi degli studi citogenetici effettuati su varie specie e popolazioni di Mioxidi. Vengono valutate le relazioni filogenetiche interspecifiche derivate da dati cromosomici e viene discussa l'importanza evolutiva della variazione cariotipica intraspecifica. Vengono presentati nuovi dati sui cariotipi di *Dryomys nitedula* asiatico e di *Muscardinus avellanarius* europeo e discussi con particolare enfasi sul contrastante pattern di differenziamento cromosomico di *Eliomys* rispetto a *Dryomys* ed altri Mioxidi. Viene compilata una bibliografia su citogenetica e cariologia dei Mioxidi.

Parole chiave: Cariotipo, Variazione cromosomica, Sistematica, Evoluzione, Myoxidae.

INTRODUCTION

The Old World family Myoxidae Thomas, 1897 is represented by seven extant genera and about 16 extant species (Honacki et al., 1982). Several interpretations of the evolutionary history and phylogeny of this mammalian group have been suggested, based on paleontological or neontological evidence (Thenius, 1969; Kratochvil, 1973; Storch, 1995). In spite of certain differences in the detailed taxonomic structure of the family, there is common agreement in treating the extant myoxid species as relics of old lineages experiencing a recent evolutionary retreat.

The first studies describing the morphology of myoxid karyotypes were published as early as the 1930s (Matthey & Renaud, 1937; Renaud, 1938) but most of the karyological and cytogenetic data has originated in the past two or three decades. The present contribution attempts to summarize the evidence available, to evaluate the importance of karyotypic data for systematic studies, and to indicate possible perspectives for further research.

MATERIAL AND METHODS

Seven individuals of *Muscardinus avellanarius* and six individuals of *Dryomys nitedula* were examined and used in this study. These animals were collected from natural populations in the following localities:

Muscardinus avellanarius
1 F; Rila Mts.. Bulgaria, 1980 (leg. V. Vohralik)
2 F, 4 M; Chernobyl District, Ukraine, 1989 (leg. V. A. Gaichenko)
Dryomys nitedula
1 F; Pelister, Baba Mts., Macedonia, 1990 (leg. B. Kryštufek)
1 M; Ankavan, Little Caucasus, Armenia, 1990 (leg. D. Frynta)
1 M; Kara Elcha, Kopet Dag, Turkmenistan, 1989 (leg. **A.** Zykin)
1 F; Sultan Mazar, Pamir, Tajikistan, 1981 (leg. B. Král)
1 M; Kalek, Batken District, Kyrghyzstan, 1988 (leg. J. Červený, I. Horáček)
1 F; Kanigut Cave, Batken District, Kyrghyzstan, 1990 (leg. J. Červený, I. Horáček)

The karyotype analysis was carried out directly from the bone marrow through the usual procedure (Ford & Hamerton, 1956). The chromosome slides were stained by Giemsa, and G-banding was attained in certain specimens by digestion with trypsin following Seabright (1971).

The individuals examined are preserved as skulls and skins in the collections of the Institute of Landscape Ecology AS CR (Brno), the Institute of Zoology. Charles University (Prague), the Institute of Zoology, Academy of Sciences (Kiev), and the Slovene Museum of Natural History (Ljubljana).

KARYOTYPES OF MYOXIDS

Karyotypes of nine myoxid species have been examined and described, with the diploid numbers of chromosomes ranging from 40 to 70 (Table 1). The African species of the genus *Graphiurus* and the Asian species of *Myomimus* are poorly known karyologically, in contrast to most of the European species, the karyotypes of which have been studied in detail in many localities (Table 2). The karyotypes of dormice are characterized by the prevalence of biarmed autosomes including usually one or two pairs carrying a prominent secondary constriction. Nucleolar organizers were demonstrated in these chromosomal regions in certain species (Arroyo Nombela et al., 1982; Filippucci et al., 1985; Filippucci et al., 1988 a; Sanchez et al., 1989; Vujošević et al., 1993). The X chromosome is of the standard mammalian size, and the Y chromosome is among the smallest elements of the set in the myoxid species examined. The C-heterochromatin is represented by faint positive bands situated in the centromeric regions of several autosomal pairs in *Eliomys* and *Dryomys* karyotypes. Distinct C-positive bands were found in both sex chromosomes of *Dryomys nitedula*, and a large C-positive block was observed in the first autosome of *Eliomys*. No other intercalary or telomeric C-bands have been observed in *Dryomys* and *Eliomys* karyotypes (Arroyo Nombela et al., 1982; Filippucci et al., 1985, 1988 a; Murariu et al., 1985). Up to the present, karyotype banding studies in dormice have been rather exceptional and limited mainly to *Dryomys* and *Eliomys* species (Faust & Vogel, 1974; Diaz de la Guardia & Ruiz

Girela, 1979; Dutrillaux et al., 1979; Arroyo Nombela et al., 1982; Filippucci et al., 1985, 1988 a, 1990; Sanchez et al., 1989, 1991; Jimenez et al., 1988; Vujošević et al., 1993; Civitelli et al., 1995). In addition, Zima (1987) reported on the G-banded karyotype of *Muscardinus avellanarius*.

Tab. 1 – Recent myoxid species of the world and chromosome diploid numbers (2n) in the species studied. List of species after Honacki et al. (1982).

SPECIES	2N	REFERENCES
Dryomys laniger		
Dryomys nitedula	48	Tab. 2
Eliomys quercinus	48-54	Tab. 2
Eliomys melanurus	46-48	Tab. 2
Glirulus japonicus	46	Tsuchiya (1979)
Graphiurus crassicaudatus		
Graphiurus hueti	40	Tranier & Dosso (1979)
Graphiurus murinus	70	Tranier & Gautun (1979)
Graphiurus ocularis	-	
Graphiurus parvus		
Graphiurus platyops		
Muscardinus avellanarius	46	Tab 2
Myomimus personatus	44	Craphodatsky & Fokin, 1993
Myomimus roachi	44	Civitelli et al (1995)
Myomimus setzeri		
Myoxus glis	62	Tab. 2

INTERSPECIFIC KARYOTYPE VARIATION

Myoxids represent a karyotypically well-differentiated group, and each genus and species examined possessed a distinct karyotype. Nevertheless, the karyotypes of different species share various common features, such as the large number of biarmed autosomes or pronounced secondary constrictions. In spite of this similarity, a comparative banding study of *Dryomys* and *Eliomys* revealed few apparent homologies, especially between the autosomal pairs of both species (Filippucci et al., 1985). If we accept the scheme of the phylogenetic divergence of dormice, as suggested by Kratochvíl (1973) and shown in Fig. 1, the plesiomorphic features of the myoxid karyotype should include the low diploid number, a large autosomal pair shared by *Muscardinus* and *Dryomys*, the metacentric X chromosome, and a single secondary constriction. The apomorphic features include the high diploid number (found in *Myoxus*), the increasing proportion of acrocentric autosomes, the submetacentric X chromosome, and a duplicated secondary constriction.

Tab. 2 – Karyotypic data in *Dryomys, Eliomys, Muscardinus,* and *Myoxus* **species.**

SAMPLE LOCALITIES	2N	REFERENCES
Dryomys nitedula		
Alps; Switzerland	48	Renaud (1938)
Carpathian Mts.: Romania	48	Raicu et al. (1972)
Caucasus; Daghestan	48	Dzuev & Tcntbotova (1980)
Azerbaijan	48	Kuliev (1984)
Pollino Massif; Italy	48	Filippucci et al (1985)
Czechoslovakia	48	Zima (1987)
Trabzon: Turkey	48	Dograrnaci & Kefelioglu (1990)
Edirne; Turkey	48	Civitelli et al. (1995)
Tarvisio; Italy	48	Civitclli et al. (1995)
Upper Galilee; Israel	48	Civitelli et al. (1995)
Baba Mts : Macedonia	48	this paper
Little Caucasus: Armenia	48	this paper
Kopet Dag; Turkmenistan	48	this paper
Pamir; Tajikistan	48	this paper
Tien Shan: Kyrghyzstan	48	this paper
Eliomys quercinus		
Apennines, Sicily; Italy	48	Cristaldi & Canipari (1976)
Adriatic Coast: Croatia	48	Dulić (1978)
Lipari, Aeolian Islands: Italy	48	Godena et al. (1978)
South of Iberian Peninsula: Spain	48	Diaz de la Guardia & Kuiz Gircla (1979)
North of Iberian Peninsula: Spain	48	Diaz de la Guardia & Kuiz Gircla (1979)
Pyrenees. Cantabrian Mts , Iberian Mts.: Spain	48	Arroyo Nombela et al (1982)
Dolj; Romania	48	Murariu et al. (1985)
Corsica; France	48	Orsini (1987)
Pollino Massif Italy	48	Filippucci et al. (1988 a)
Granada; Spain	48	Sanchez et al. (1989, 1991)
Belgium	50	Leonard et al. (1970)
Sardinia. Italy	50	Cristaldi & Canipari (1976)
France	50	Dutrillaux et al. (1979)
Lyon; France	50	Arroyo Nombela et al. (1982)
Vorarlberg; Austria	50	Filippucci et al. (1988 a)
Jura Mts.: France and Switzerland	50	Filippucci et al. (1990)
Southern Germany	50	Winking in Filippucci et al (1990)

Tab. 2 - continued.

SAMPLE LOCALITIES	2N	REFERENCES
Eliomys quercinus		
Switzerland	52	Matthey & Renaud (1937), Renaud (1938)
Gran Paradiso; Italy	52	Cristaldi & Canipari (1976)
Central and Eastern Alps: Italy	52	Filippucci et al. (1988 a)
Gran Paradiso; Italy	54	Cristaldi & Canipari (1976)
Western Alps; Italy	54	Filippucci et al. (1988 a)
Valais; Switzerland	54	Filippucci et al. (1990)
Eliomys melanurus		
Cap Bon Tunisia	46	Tranier & Petter (1978)
Middle Atlas , Morocco	46	Delibes et al. (1980)
Cap Spartel and Ouezzane; Morocco	46	Filippucci et al. (1988 a)
Negev Desert, Israel	48	Filippucci et al. (1988 b, 1990)
Muscardinus avellanarius		
Alps: Switzerland	48	Renaud (1938)
Frushka Gora; Serbia	46	Savic & Soldatović (1972)
Czechoslovakia	46	Zima (1987)
Pirin Mts ; Bulgaria	46	Belcheva et al. (1988)
Rila Mts , Bulgaria	46	this paper
Chernobyl District; Ukraine	46	this paper
Myoxus glis		
S-W Serbia; Adriatic Coast, Croatia	62	Dulić et al. (1971)
Carpathian Mts ; Romania	62	Raicu et al. (1972)
Samarskaya Luka; Russia	62	Belyanin et al. (1976)
Spain	62	Diaz de la Guardia et al. (1980)
Salina Island; Italy	62	Cristaldi & Amori (1982)
Czechoslovakia	62	Zima (1987)
Balkan Mts.; Bulgaria	62	Belcheva et al. (1988)
Tarvisio; Italy	62	Civitelli et al. (1995)
Pollino Massif, Sila, Aspromonte Mts.; Italy	62	Civitelli et al. (1995)
Istranca Mts.: Turkey	62	Civitelli et al. (1995)

INTRASPECIFIC KARYOTYPE VARIATION

The only Myoxid species known to possess a distinctly polytypic karyotype are those of the genus *Eliomys*. In *Eliomys quercinus*, Filippucci et al. (1988 a) concluded that the Chromosomal variation originated basically by Robertsonian rearrangements, supplemented by presumed pericentric inversions and translocations. The pattern of geographical distribution of the diploid numbers in the populations examined is shown in Fig. 2. The direction of the Robertsonian process (chromosome fusions vs. fissions) is important for distinguishing ancestral and advanced karyotypes in *E. quercinus*. Filippucci et al. (1988 a, 1990) suggested fissions as the prevailing mode of karyotype divergence in the species. If this assumption is right, the 48-chromosome complement should be the primitive one and the basic structure of the karyotype (i.e. the autosomal arms composition) should be the same in all populations studied. The presumed primitiveness of the Mediterranean 48-chromosome populations and the derived character of the populations in the Alps, western, central, and eastern Europe seems to be well confirmed by paleontological data suggesting recent dispersal from Mediterranean refugia to the north in the Holocene (Horáček, 1986).

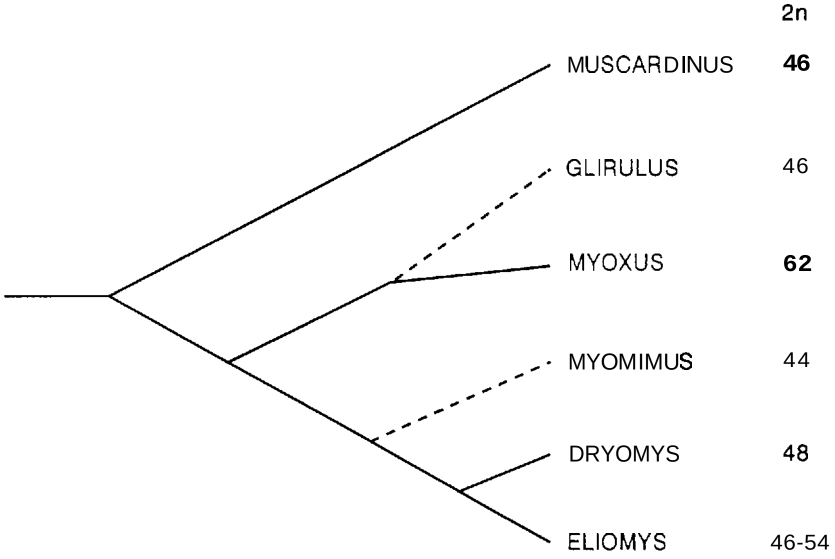

Fig. 1 – Phylogenetic and diploid chromosome number divergence in myoxids. Phylogenetic tree after Kratochvíl (1973).

However, the 48-chromosome karyotypes are apparently not identical in all regions examined. The 48-chromosome karyotype described from Romania (Murariu et al., 1985) differs substantially from the 48-chromosome complements found in Mediterranean populations. Strikingly, the Romanian karyotype closely resembles that of *Dryomys nitedula*. Furthermore, Vujošević et al. (1993) showed that 48-chromosome karyotypes from Dalmatia and Italy (*E. q. pallidus, E. q. liparensis, E. q. dalmaticus*) differ in two pairs of autosomes from *E. q. lusitanicus* described from Spain. In the latter subspecies, only one pair of acrocentric autosomes was present (Diaz de la Guardia & Ruiz Girela, 1979) whereas there were three pairs in other populations and subspecies. Similarly, variations in the number of acrocentric autosomes appear to occur also in the 50-chromosome karyotypes. In Belgium, France, Switzerland and Austria, three acrocentric autosomal pairs were described, but five pairs were observed in animals from Sardinia (see Tab. 2 for references).

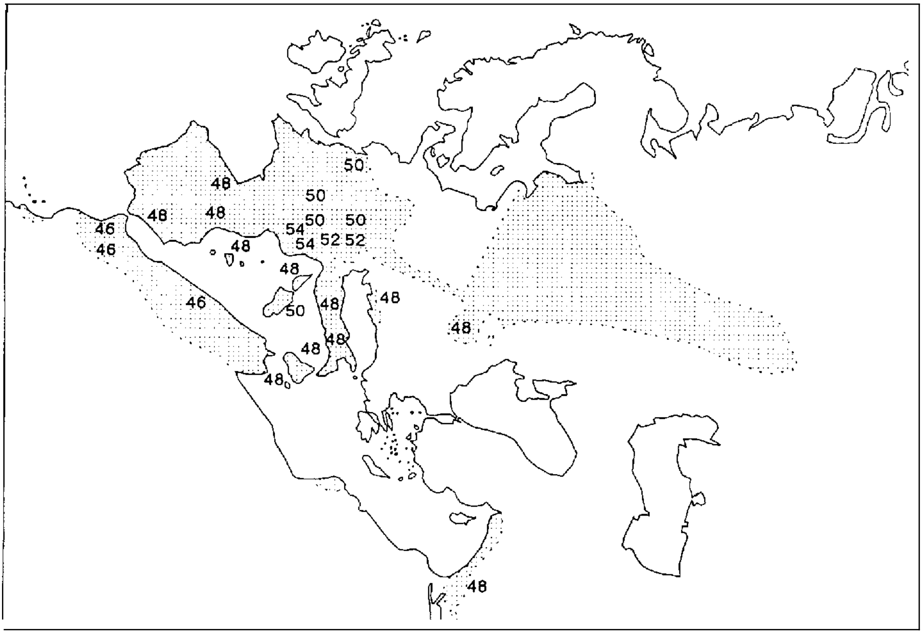

Fig. 2 – Karyotypic (2n) divergence in *Elionzys*. Sketch of the distribution range adopted after Corbct (1978).

The phyletic implications of these variations remains open for the present, especially with respect to the unknown karyotypic status of many central and eastern European populations. New chromosomal data and detailed chromosome banding studies are necessary to re-evaluate the evolutionary role of karyotype rearrangements in the evolution of *Eliomys quercinus*. *Eliomys melanurus* is another dormouse species containing at least two karyotype races. The difference between the karyotype of African and Asian populations is of non-Robertsonian nature. Two populations of *E. melanurus* from Israel differed in the G-banding pattern observed in the first autosomal pair. This difference resulted probably from a pericentric inversion (Filippucci et al., 1988 a, 1990).

By contrast, little intraspecific variation in the karyotype structure was found in other Myoxid species. We found a pericentric inversion in an individual of *Dryomys nitedula* from the Little Caucasus, and a decreased diploid chromosome number in some somatic cells resulting in a somatic mosaic of 46- and 48-chromosome cells in the bone marrow of an individual from Tajikistan (Figs. 3, 4). Both these cases probably could be characterized as polymorphic or aberrant chromosomal variants, and the karyotype of *Dryomys nitedula* is apparently rather stable throughout the geographical range of the species (Fig. 5).

Fig. 3 – Karyotypes of *Dryomys nitedula* from certain populations in Asia. a) Kalek, Kyrghyzstan; b) Kopet-Dag, Turkmenistan; c) Sultan Mazar, Tajikistan, 2n=46; d) Sultan Mazar, Tajikistan, 2n=48.

Morphological variations have been described in the sex chromosomes of *Myoxus glis*. The X chromosome was submetacentric in individuals from Spain (Diaz de la Guardia et al., 1980) but it was described as metacentric in other European populations. The dot-like Y chromosome was evaluated as either acrocentric or biarined in various *Myoxus glis* populations. Yet some of the differences between descriptions of myoxid karyotypes may result from the subjective arrangement of chromosomes in the karyotype.

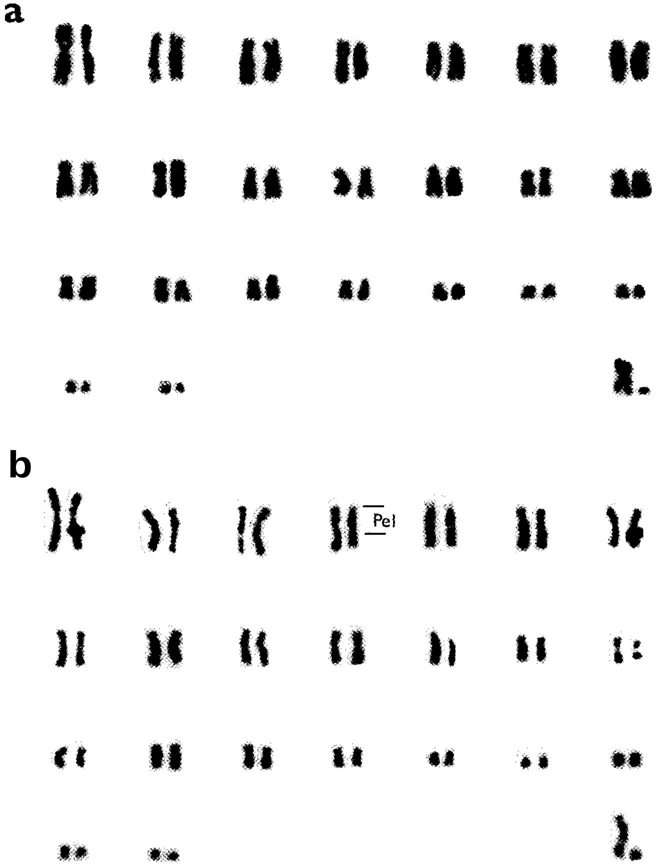

Fig. 4 – Karyotype of *Dryomys nitedula* from Ankavan, the Little Caucasus. PeI = pericentric inversion. a) conventional staining; b) G-banding.

SYSTEMATIC AND EVOLUTIONARY IMPLICATIONS

Inferences of interspecific systematic relationships of dormice based on karyotypic data are complicated by the absence of studies in many species (namely *Graphiurus* and *Myomimus* spp.), and by the scarcity of information on the fine banding pattern of myoxid chromosomes enabling detailed comparisons between species. The karyotype of most myoxids should be considered an old character, which probably persisted without considerable changes during a long geological period. This fact further diminishes the use of a purely phenetic approach in karyotype comparisons within the family.

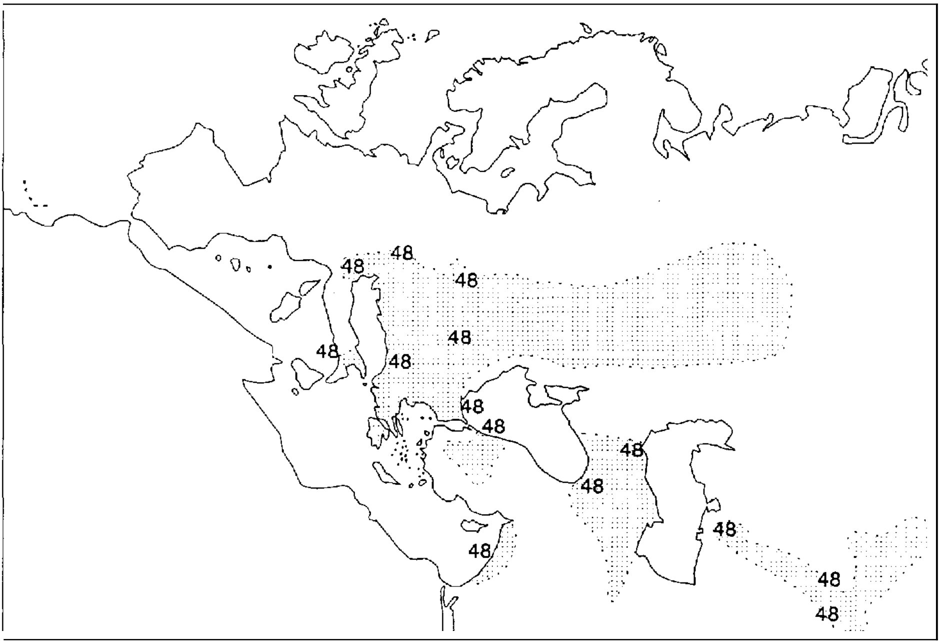

Fig. 5 – Diploid chromosome number found in different regions of the *Dryomys nitedula* range. Sketch of the distribution range adopted after Corbet (1978).

By contrast, the fascinating pattern of karyotypic divergence found in *Eliomys* spp. provides a useful tool for examining the phylogenetic relationships of various populations within a species. Karyotype races originating from a series of Robertsonian rearrangements are usually considered to be the result of quite recent evolutionary processes as, for instance, in *Sorex* and *Mus*. It is surprising to find a similar situation in the species assumed to be a relic lineage persisting without major morphological changes ever since the Lower Pleistocene. The rate of karyotype evolution can be influenced by various systematic or stochastic factors. The stochastic or random factors inherent in the effects of genetic drift, and are mediated by particular features of reproductive biology or population structure and dynamics. The systematic, non-random factors are products of the selection pressure manifest at the gametic (meiotic drive) or organismal level. Organismal selection models suppose an adaptive significance of the karyotype structure, and predict an increase in the rate of karyotype change in periods of occupying new adaptive zones (Bickham & Baker, 1980).

A contrasting pattern of karyotype divergence has been demonstrated between recent species of *Eliomys* and *Dryomys*. Comparisons of factors and characteristics capable of influencing the rate of karyotypic divergence between recent *Eliomys* and *Dryonzys* might provide an explanation of the exceptional chromosomal divergence in *Eliomys.* The postglacial dispersal of *Eliomys* in Europe is well documented in paleontological records (Storch, 1978; HoraCek , 1986). This expansion was probably enabled by specific conditions of the Holocene, different from those in earlier mid-Pleistocene interglacials (Horáček , 1986, 1987), and it was further facilitated by the growth of human civilization and deforestation accompanying evolving agriculture. Therefore, the range expansion of *Eliomys quercinus* in central Europe has occurred particularly since the Neolithic period. This process could create a new selection challenge to populations migrating to previously unoccupied areas. If so, the adaptive character of karyotype evolution should be predictable. Furthermore, the karyotype divergence could be supported by fragmentation of the range and occurrence of small isolated populations, presenting a suitable object for drift effects. However, we have found no substantial differences in various population and/or reproduction characteristics between *Eliomys* and *Dryomys* (cf. Storch, 1978). The stochastic processes of genetic drift are therefore more likely to have exerted a major impact on the karyotypic divergence of *Eliomys quercinus.*

The rate of karyotypic divergence is supposed to be correlated with taxonomic diversity of a lineage (Bengtsson, 1980). However, comparison of this characteristic between *Eliomys* and *Dryonzys* revealed the number of nominal subspecies being 10 in *Elionzys quercinus,* and 19 in *Dryonzys nitedulu* according to the list of Ellermann & Morrison-Scott (1951). The level of the karyotypic divergence in both species thus does not appear to be correlated with taxonomic diversity. On the contrary, the extent of colour variation and the variability of body dimensions seems to be greater in *Eliomys* than in *Dryomys.* The minimum:maximum body length ratio is 0.55 in *Eliomys quercinus* and 0.71 in *Dryonzys nitedula.* The same ratio computed for the condylobasal length is 0.69 in *E. quercinus* and 0.83 in *D. nitedulu* (data according to Storch, 1978). This internal tendency towards divergence within a lineage could exert additional selective pressure on karyotype evolution.

It can be concluded that systematic selection forces could play an important role in recent karyotypic divergence in *Eliomys,* but an accompanying effect of genetic drift and possible gametic selection should also be taken into consideration.

PERSPECTIVES

Due to the antiquity of myoxid species and genera and, hence, large number of chromosomal rearrangements and possible homoplasies accumulated during karyotype evolution of the family, it is difficult to trace the evolutionary history and phylogenetic relationships of dormice. Therefore, other genetic methods, including molecular studies, appear more apposite in further systematic research on myoxids. Nevertheless, karyotype data on other species within the family (namely *Myomimus*, *Glirulus*, *Graphiurus*, and *Dryonzys laniger*) and accompanied by detailed chromosome banding studies could also shed light on intra- and interspecific relationships as well. Similarly, new data on karyotypes of

Eliomys quercinus from populations in central and eastern Europe are highly desirable.

ACKNOWLEDGEMENTS – We are grateful to J. Červcný, D. Frynta, I. Horáček, B. Kral, V. Vohralik (Prague), B. Kryštufek (Ljubljana), V. Gaichenko, A. Zykin and I. Zagorodnyuk (Kiev) for their kind help in obtaining the material used in this study.

NOTE ADDED IN PROOFS – An important paper by Graphodatsky & Fokin (1993) has appeared since this manuscript was sent to the editors. The paper deals with the comparative cytogenetics of Myoxidae, and reports G-, C-, and AgNOR banded karyotypes of *Myoxus glis, Dryomys nitedula, Eliomys quercinus, Muscardinus avellanarius*, and *Myomimus personatus* (2n=44) from the former USSR. Comparative analysis of the G-banding pattern showed low degree of homology between chromosomes of the myoxids, and a scheme of phylogenetic relationships was proposed beween the five studied genera.

REFERENCES

ARROYO NOMBELA, J. J., RODRIGUEZ MURCIA C., DELIBES, M. & HIRALDO, F. 1982. Comparative karyotype studies between Spanish and French populations of *Eliomys quercinus* L. Genetica, 59: 161-166.

BELYANIN, A. N., BELYANIN, V. N. & NESTEROV, A. Yu. 1976. Karyotypes of certain rodents from Samarskaya Luka. Fisiol. Popul. Ekol. Zhivot., University of Saratov: 53-57 (in Russian).

BELCHEVA, R. G., TOPASCHKA-ANCHEVA, M. N. & ATANASSOV, N. I. 1988. Karyological studies of five species of mammals from Bulgaria's fauna. Compt. rend. Bulg. Acad. Sci., 42: 125-130.

BENGTSSON, B. O. 1980. Rates ofkaryotype evolution in placental mammals. Hereditas, 92: 37-47.

BICKHAM, J. W. & BAKER, R. J. 1979. Canalization model of chromosomal evolution. In Models and Methodology in Evolutionary Theory (J. H. Schwartz and H. B. Rollins, eds.), Bull. Carnegie Mus. Nat. Hist., 13: 70-84.

CIVITELLI, M. V., FILIPPUCCI, M. G., KURTONUR, C. & ÖZKAN, B. 1995. Chromosome analysis of three species of Myoxidae. In: Filippucci M.G. (ed.). Proc. II Conf. on Dormice. Hystrix (n.s.) 6 (1-2) (1994): 117-126.

CORBET, G. B. 1978. The mammals of the Palaearctic region. A taxonomic review. British Museum (Natural History), Cornell University Press, London and Ithaca.

CKISTALDI, M. & AMORI, G. 1982. Observations sur les rongeurs de l'Ile Salina (Iles Lipari, prov. de Messine, Italia). Mammalia, 46: 405-407.

CRISTALDI, M. & CANIPARI, R. 1976. A propos de la caryologie du lerot (*Eliomys quercinus).* Mammalia, 40: 475-488.

DELIBES, M., HIRALDO, F., ARROYO NOMBELA J.J. & RODRIGUEZ-MURCIA, C. 1980. Disagreement between morphotypes and karyotypes in *Eliomys* (Rodentia, Gliridae): The chromosomes of the central Morocco garden dormouse. Saugetierk. Mitt., 28: 289-292.

DIAZ DE LA GUARDIA, R. & RUIZ GIRELA, M. 1979. The chromosomes of the three Spanish subspecies of *Eliomys quercinus* (Linnaeus). Genetica, 51: 107-109.

DIAZ DE LA GUARDIA, R. & RUIZ GIRELA, M., M. & LADRÓN DE GUEVAKA, R. G. 1980. Los cromosomas del *Glis glis* pyrenaicus. Bol. R. Soc. Espanola Hist. Nat. (Biol.), 78: 165-168.

DOGRAMACI, S. & KEFELIOGLU, H. 1990. The karyotype of *Dryomys nitedula* (Mammalia:

Rodentia) from Turkey. Doga Turk Zooloji, Derrgisi, 14: 316-322 (in Turkish, English summary).

DULIĆ, B. 1978. Chromosomes of small mammals from the southwestern karstic regions of Yugoslavia. Abstracts 2nd ITC, Brno: 133.

DULIĆ, B., SAVIĆ, I., SOLDATOVIĆ, B. 1971. The chromosomes of two rodent species, *Dolomys bogdanovi* (V. and E. Martino, 1922) and *Glis glis* (Linnaeus, 1766) (Mammalia, Rodentia). Caryologia, 24: 299-305.

DUTRILLAUX, B., AURIAS, **A.** & LOMBARD, M. 1979. Presence de chromosomes communs chez un rongeur *(Eliomys quercinus)* (Ierot) et chez les primates. Ann. Genet., 22: 21-24.

DZUEV, R. I. & TEMBOTOVA, F. A. 1980. New data on karyotypes of the Caucasian rodents. Gryzuny, Moscow, 5: 15-16 (in Russian).

FAUST. J. & VOGEL, W. 1974. Are "N bands" selective staining of specific heterochromatin? Nature, 249: 352-353.

FILIPPUCCI, M. G., CATZEFLIS, **F.** & CAPANNA, **E.** 1990. Evolutionary genetics and systematics of the garden dormouse, *Eliomys* Wagner, 1840 (Gliridae, Mammalia): 3. Further karyological data. Boll. Zool., 57: 149-152.

FILIPPUCCI, M. G., CIVITELLI, M. V. & CAPANNA, E. 1985. Le caryotype du Ierotin, *Dryomys nitedula* (Pallas) (Rodentia, Gliridae). Mammalia, 19: 365-368.

FILIPPUCCI, M. G., CIVITELLI, M. V., CAPANNA, E. 1988 a. Evolutionary genetics of the garden dormouse, *Eliomys quercinus* Wagner, 1840. 1. Karyotype divergence. Boll. Zool., 55: 35-45.

FILIPPUCCI, M. G., SIMSON, S., NEVO, E. & CAPANNA, E. 1988 b. The chromosomes of the Israeli garden dormouse, *Eliomys melanurus* Wagner, 1840 (Rodentia, Gliridae). Boll. Zool., 55: 31-33.

FORD, C. E. & HAMERTON, J. L. 1956. A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. Stain technol., 31: 299-305.

GODENA, G., D'ALONZO, **F.,** CRISTALDI, M. 1978. Correlations entre caryotypes et biotypes chez le lerot *(Eliomys quercinus)* et les autres rongeurs de l'Ile Lipari. Mammalia, 42: 382-384.

GRAPHODATSKY, A.S. & FOKIN, I.M. 1993. Comparative cytogenetics of Gliridae (Rodentia). Zool. zh., 72: 104-113 (in Russian, English summary).

HONACKI, J. H., KINMAN, K. E. & KOEPPL, J. W. (eds.), 1982. Mammal species of the world. Lawrence, Kansas.

HORÁČEK, I. 1986. Fossil records and chorological status of dormice in Czechoslovakia. I. *Glis glis, Eliomys quercinus.* Folia Mus. rer. Natur. Bohem. Occid., **Plzen,** Zoologica, 24: 49-59.

HORÁČEK, I. 1987. Fossil records and chorological status of dormice in Czechoslovakia. II. *Dryomys* and *Muscardinus.* Folia Mus. rer. Natur. Bohem. Occid., Plzeň, Zoologica, 26: 79-96.

JIMÉNEZ, R., BURGOS, M. & DIAZ DE LA GUARDIA, R. 1988. **A** study of the Ag-staining significance in mitotic NOR's. Heredity, 60: 125-127.

KRATOCHVÍL, J. 1973. Mannliche Sexualorgane und System der Gliridae (Rodentia). Acta Sc. Nat. Brno, 7(12): 1-52.

KULIEV, G. N. 1984. Karyotypes of certain rodent species from Azerbaijan. Gryzuny, Leningrad, 6: 122-123.

LÉONARD, A., DEKNUDT, G. & MERGEAY, M. 1970. Les chromosomes du lerot *(Eliomys quercinus* L.). Acta Zool. Pathol. Antverpiensia, 50: 55-60.

MATTHEY, R. & RENAUD, P. 1937. Les chromosomes du lerot. Bull. Soc. vaud. Sc. Nat.: 59.

MURARIU, D., LUNGEANU, **A.,** GAVRILA, **K.** & STEPAN, C. 1985. Preliminary data concerning the study of the karyotype of *Eliomys quercinus* (Linnaeus, 1766) (Mammalia, Gliridae). Trav. Mus. Hist. nat. "Grigore Antipa", 27: 325-327.

ORSINI, P. 1987. Le Lerot. In: Les mammiferes en Corse. Parc Naturel Regional de Corse, Ajaccio. Gallia Prehistoire, 26 (Suppl.): 99-101.

RAICU, P., DUMA, D., KIRILLOVA, M., HAMAR, M. & POPESCU A. 1972. The karyotypes of certain species of rodents from Romania. Soc. de St. Biologica R.S.R., Genetica, 1972: 87-97 (in Romanian).

RENAUD, P. 1938. La formule chromosomiale chez sept especes de Muscardinidae et de Microtinae. Rev. suisse Zool., 45: 349-385.

SÁNCHEZ, A., BURGOS, M., JIMÉNEZ, R., CHAMORRO, S. & DIAZ DE LA GUARDIA. R. 1991. Evolution of the *Eliomys* karyotypes in western Mediterranean regions. Cytobios, 66: 25-33.

SÁNCHEZ, A., BURGOS, M., JIMÉNEZ, R., & DIAZ DE LA GUARDIA, R. 1989. Quantitative analysis of silver staining of the nucleolar organizing region in *Eliomys quercinus*. Genome, 32: 978-982.

SAVIC, I. & SOLDATOVIC, B. 1972. On the karyotype of *Muscardinus avellanarius* Linnaeus, 1758 (Rodentia, Gliridae). Arh. biol. nauka (Beograd), 24: 7P-8P.

SEABRIGHT, M. 1971. **A** rapid banding technique for human chromosomes. Lancet, I: 971-972.

STORCH, G. 1978. Familie Gliridae Thomas, 1897 - Schlafer. Handbuch der Saugetiere Europas (J. Niethaminer and F. Krapp, eds.), Band 1, Rodentia I: 201-280. Akademische Verlagsgesellschaft, Wiesbaden.

STORCH, G. 1995. Affinities among living dormouse genera. In: Filippucci M.G. (ed.). Proc. II Conf. on Dormice. Hystrix (n.s.) 6 (1-2) (1994): 51-62.

THENIUS, E. 1969. Phylogenic der Mammalia. Handbuch der Zoologie, 8(2): 290-722.

TRANIER, M & DOSSO, H. 1979. Recherches caryotypiques sur les rongeurs de Cote d'lvoire: résultats préliminaires pour les milieux fermes. Mammalia, 43: 254-256.

TRANIER, M. & GAUTUN, J. C. 1979. Recherches caryotypiques sur les rongeurs de Cote d'lvoire: resultats préliminaires pour les milieux ouverts. Mammalia, 43: 252-254.

TRANIER, M. & PETTER, F. 1978. Les relations d'Eliomys tunetae et de quelques autres formes de lerots de la region tnediterraneenne (Rongeurs, Muscardinides). Mammalia, 42: 349-353.

TSUCHIYA, K. 1979. A contribution to the chromosome study in Japanese mammals. Proc. Japan. Acad.. Ser. B, 55: 191-195.

VUJOŠEVIĆ, M., FILIPPUCCI, M. G., BLAGOJEVIĆ, J. & KRYŠTUFEK, B. 1993. Evolutionary genetics and systematics of the garden dormouse, *Eliomys* Wagner, 1840. 4 - Karyotypc and allozyme analyses of *E. quercinus dalmaticus* from Yugoslavia. Boll. Zool., 60: 47-51.

ZIMA, J. 1987. Karyotypes of certain rodents from Czechoslovakia (Sciuridae, Gliridae, Cricetidae). Folia Zool., 36: 337-343.