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B chromosomes in the wood mice (genus *Apodemus*)

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Spatial and temporal distribution of supernumerary or B chromosomes were studied in natural populations of wood mice. A total of 859 individuals belonging to several species from Eurasia were examined. A very high percentage of individuals possessing B chromosomes was found in *Apodemus peninsulae* (97.9%, *n* = 47), a high percentage in *A. flavicollis* (42.5%, *n* = 362), and a low one in *A. sylvaticus* (2.4%, *n* = 210). No B chromosomes were observed in *A. uralensis* (*n* = 10), *A. fulvipectus* (*n* = 19), *A. hermonensis* (*n* = 1), *A. agrarius* (*n* = 58), *A. mystacinus* (*n* = 7), and in *Apodemus* species collected in Turkey (*n* = 74), Israel (*n* = 1), Azerbaijan (*n* = 2), Tadjikistan (*n* = 24), and Kyrghyzstan (*n* = 44). A modest to high frequency of B chromosomes was thus observed particularly in the species confined to a forest environment, whereas no B's were found in the species dwelling in open, steppe-like or rocky habitats. Both in *A. peninsulae* and *A. flavicollis* the frequency of B chromosomes varied among local populations. Follow-up studies revealed stability in the respective proportions of B chromosomes during subsequent years. However, no unambiguous interrelationship could be found between the frequency of B chromosomes and various biological and/or ecological variables. Therefore it seems that the incidence of B chromosomes is mainly determined by stochastic effects operating within the specific genetic background of a population.

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Introduction

The evolutionary significance of certain components in the genome, particularly the regions containing highly repetitive (satellite) DNA, is still poorly understood. Different functions have been ascribed to these sequences and their adaptive role is a controversial issue. Is repetitive DNA present because it is related to the fitness of an organism or is it in fact parasitic, as suggested by Doolittle and Sapienza (1980) or by Orgel and Crick (1980)? Highly repetitive DNA tends to be associated with constitutive heterochromatin and is often concentrated in tandemly arranged blocks, located in particular chromosomal regions. Supernumerary or B chromosomes are one of many kinds of structural and numerical chromosome polymorphism supposed to be related to heterochromatin variation. B chromosomes are distinguishable from normal (A) chromosomes by their structure, genetic constitution, numerical variability, and meiotic and mitotic behaviour (Jones and Rees 1982). They do not pair with any of the A chromosomes in meiosis, and do not pair as regularly among themselves as it is the case in A chromosomes. B chromosomes are largely heterochromatic, although the amount and kind of heterochromatin may vary considerably among species. The role of B chromosomes in the genome and their influence on the organism are not well understood. Apparently, their presence within the chromosome complement is unnecessary for the normal process of growth, development and reproduction.

The Palaearctic genus *Apodemus* Kaup, 1829 comprises 21 species (Musser and Carleton 1993). Karyotypes of the *Apodemus* species examined so far seem to be rather uniform with respect to the prevailing diploid number of 48, largely acrocentric chromosomes. B chromosomes have been reported to occur in *A. peninsulae* (including *A. giliacus;* Hayata 1973, Vorontsov *et al.* 1977, Bekasova *et al.* 1980), in *A. flavicollis* (Soldatovic *et al.* 1972, Wolf *et al.* 1972, Giagia *et al.* 1985, Vujoševic *et al.* 1991), in *A. sylvaticus* (Vujoševic and Živkovic 1987), in *A. mystacinus* (Belcheva *et al.* 1988) and in *A. agrarius* (Kartavtseva 1994). B chromosomes in *Apodemus* are usually small elements with a variable position of the centromere. Remarkable differences in the distribution of B chromosomes were observed among various Asiatic populations of *A. peninsulae* (Volobouev 1979, Borisov 1990a, b, c, Borisov and Malygin 1991) and among various European populations of *A. flavicollis* (Giagia *et al.* 1985, Vujoševic and Živkovic 1987, Vujoševic *et al.* 1991). In a population of *A. flavicollis* the frequency of B chromosome stayed rather constant over several generations (Vujoševic 1992). Studies addressing the possibility of a preferential segregation of B chromosomes during meiosis yielded ambiguous results (Kolomiets *et al.* 1988, Vujoševic *et al.* 1989). In *A. peninsulae* transcriptional activity during the pachytene was shown to be lacking in B chromosomes (Ishak *et al.* 1991).

The present paper aims at contributing to the issue of adaptive vs stochastic causes being responsible for the accumulation of B chromosomes. Dependence of the temporal and spatial distribution of B chromosomes in natural populations of wood mice upon various biological and ecological variables is discussed.

Material and methods

A total of 859 wood mice collected from 110 localities in Europe and Asia were karyotyped between 1973 and 1994. Direct flame-dried chromosome preparations were made from bone marrow according to Ford and Hamerton (1956). In each individual, 30 mitotic plates were checked. In particular males, meiotic chromosomes were prepared from testicular tissue. Part of the preparations was differentially stained using G-banding (Seabright 1971), C-banding (Sumner 1972), and Ag-NOR (Howell and Black 1980) techniques. *G*- and *t*-tests (Sokal and Rohlf 1981) were used for examining differences in the incidence of B chromosomes among samples.

Species identification in European wood mice followed standard morphological and cranial criteria (eg Ruprecht 1979, Demeter and Lázár 1984, Mezhzherin 1991). The validity of species status of the various Asiatic members of the genus, and particularly of those belonging to the subgenus *Sylvaemus*, is still under discussion. Therefore, we decided to designate the wood mice collected in Asia Minor, the Caucasus and in central Asia as *Apodemus* spp., without attempting to determine their species membership explicitly. A detailed list of the material examined is given in the Appendix.

Results and discussion

Interspecific differences in B chromosome distribution

The pattern of B chromosome distribution in the species examined is shown in Table 1.

Table 1. Frequency of B chromosomes in samples of *Apodemus* species. n – sample size, n_B – number of individuals with B chromosomes. $\%_B$ – percentage of individuals with B chromosomes. x_B – mean number of B chromosomes per individual.

Species	Chromosome number								n	n_B	$\%_B$	x_B
	48	49	50	51	52	53	54	55				
A. peninsulae	1	7	15	14	4	2	2	2	47	46	97.9	2.79
A. flavicollis	208	86	45	18	3	1	1	–	362	154	42.5	0.70
A. sylvaticus	205	3	1	1	–	–	–	–	210	5	2.4	0.04
A. hermonensis	1	–	–	–	–	–	–	–	1	0	0.0	0.00
A. fulvipectus	19	–	–	–	–	–	–	–	19	0	0.0	0.00
A. uralensis	10	–	–	–	–	–	–	–	10	0	0.0	0.00
Apodemus spp.	145	–	–	–	–	–	–	–	145	0	0.0	0.00
A. mystacinus	7	–	–	–	–	–	–	–	7	0	0.0	0.00
A. agrarius	58	–	–	–	–	–	–	–	58	0	0.0	0.00

The incidence of B chromosomes in the samples studied generally agrees with previous findings in the various species (op. cit.). A very high proportion of individuals possessing B chromosomes was found in *A. peninsulae* (97.9%), a medium proportion in *A. flavicollis* (42.5%), and a low proportion in *A. sylvaticus* (2.4%). No supernumerary chromosomes were observed in the cells of all other species studied. *A. peninsulae* is currently assigned to the subgenus *Alsomys*, whereas *A. flavicollis* and *A. sylvaticus* belong to the subgenus *Sylvaemus* (Musser and Carleton 1993). The occurrence of B chromosomes is thus not confined to a particular subgenus. There is apparently no relation between the incidence of B chromosomes and the pattern of phylogenetic divergence as revealed by allozyme studies (Filippucci 1992). Furthermore, the extent of B chromosome variation does not seem to be associated with electrophoretic heterozygosity (eg Benmehdi *et al.* 1980, Mezhzherin 1990, Britton-Davidian *et al.* 1991, Filippucci 1992).

Common features of the species possessing B chromosomes may be found in their geographical distribution and habitat preference. All three *Apodemus* species with B chromosomes are distributed in the northern parts of the range of the genus. *A. peninsulae* and *A. flavicollis* represent strict forest dwellers whereas *A.*

sylvaticus is confined to forest edges and bushes. On the contrary, the species of the subgenus *Sylvaemus* living in open, steppe-like habitats (*A. uralensis*, *A. fulvipectus*) have never been reported to possess B chromosomes.

Pattern of intraspecific distribution of B chromosomes

Significant differences in the distribution of B chromosomes were found between individual populations of *A. peninsulae* and *A. flavicollis* (Tables 2 and 3). Similar findings were reported for both species by Volobouev (1979), Borisov

Table 2. Frequency distribution of B chromosomes in samples of *A. peninsulae*. For explanations see Table 1.

Region	Chromosome number								n	n_B	$\%_B$	x_B
	48	49	50	51	52	53	54	55				
Sachalin Island	1	–	–	–	–	–	–	–	1	0	0.0	0.00
Baikal Lake	–	4	14	10	4	1	–	1	34	34	100	2.65
NE Mongolia	–	3	1	4	–	1	2	1	12	12	100	3.42
										G-values:	162.19 ($p < 0.001$)	5.02 (ns)

Table 3. Frequency distribution of B chromosomes in samples of *A. flavicollis*. N and E Bohemia – collecting localities No 2, 3, 4, 5 (see Appendix). S Moravia – No 12, 13, 14, 15, 16. Moravian Karst – No 17, 18, 19, 20. For explanations see Table 1.

Region	Chromosome number								n	n_B	$\%_B$	x_B
	48	49	50	51	52	53	54	55				
N Bohemia (Filipov)	2	7	9	10	1	1	1	1	31	29	93.5	2.26
N and E Bohemia	14	2	4	–	–	–	–	–	20	6	30.0	0.50
W and S Bohemia	9	7	3	1	–	–	–	–	20	11	55.0	0.80
S Moravia	26	11	5	1	–	–	–	–	43	17	41.5	0.56
Moravian Karst	24	14	3	–	–	–	–	–	41	17	41.5	0.49
N Moravia	14	13	4	3	2	–	–	–	36	22	61.1	1.06
N Slovakia	23	8	6	1	–	–	–	–	38	15	39.5	0.61
E Slovakia	4	–	–	–	–	–	–	–	4	0	0.0	0.00
Austria	4	–	1	1	–	–	–	–	6	2	33.3	0.83
Slovenia	7	1	–	–	–	–	–	–	8	1	12.5	0.13
Macedonia	21	12	6	–	–	–	–	–	39	18	46.2	0.62
Greece	5	2	–	–	–	–	–	–	7	2	28.6	0.29
Bulgaria	7	2	–	–	–	–	–	–	9	2	22.2	0.22
Turkey	31	5	4	1	–	–	–	–	41	10	24.4	0.39
Romania	10	–	–	–	–	–	–	–	10	0	0.0	0.00
Ukraine	7	2	–	–	–	–	–	–	9	2	22.2	0.22
										G-values:	160.53 ($p < 0.001$)	3.48 (ns)

(1990a, b, c), Borisov and Malygin (1991), and Vujoševic *et al*. (1991). It is difficult, however, to find any adaptive explanation for these interpopulational differences. In our samples of *A. flavicollis* a slight trend towards a decrease in B-chromosome frequencies from central to eastern and southeastern Europe could be observed. Except for the Mt Pelister population, the incidence of B chromosomes was thus rather low in the mountains of the Balkan Peninsula. In both *A. flavicollis* and *A. peninsulae,* the frequency of B chromosomes seemed to be higher in central than in peripheral populations. There was no relationship between the B-chromosome frequency and the altitude of the sites studied.

Giagia *et al*. (1985) and Vujoševic and Živkovic (1987) suggested that B chromosomes tend to occur more frequently in populations of *A. flavicollis* inhabiting heavily polluted areas. This assumption was not confirmed by our data. The population samples of *A. flavicollis* and *A. sylvaticus* collected in certain parts of northern Bohemia (districts of Most and Česká Lípa) originated from habitats exposed to an extreme level of industrial pollution. Nevertheless, B-chromosome frequencies were lower in these sites than in particular samples from relatively well preserved areas (eg western and southern Bohemia, district of Děčín in northern Bohemia).

Temporal changes in B-chromosome frequency

In certain study areas sampling of mice was repeated during several seasons or years. Comparisons of samples collected at the same site in different periods showed that B-chromosome frequencies and the mean number of B's per individual remain relatively stable. At two localities significant differences were observed, but these are probably due to small sizes of samples collected in the respective years (Table 4). A follow-up study of temporal changes in B-chromosome frequencies at a particular site was reported by Vujoševic (1992). Also in this case the frequency of B's remained constant from generation to generation.

Other biological correlates

In samples of *A. flavicollis*, several biological and ecological variables were tested for an association with the incidence of B chromosomes: sex ratio, number of embryos per pregnant female, average litter size, and body weight.

The sex ratio of 0.66 (females/males) found in all individuals studied did not differ significantly from a ratio of 0.58 observed only in individuals with B chromosomes ($G = 0.05$, $p > 0.05$). Hence, B chromosomes appear to occur at a similar frequency in both sexes. In the sample of *A. flavicollis* 37 pregnant females were found. Of these females, 15 possessed B chromosomes while the remaining 22 had a standard karyotype. In females with B chromosomes, 1 to 8 embryos were recorded ($\bar{x} = 5.53$, SD = 1.71), in females without B chromosomes 4 to 12 embryos ($\bar{x} = 5.59$, SD = 1.67). Average litter size was not significantly different between both groups ($t = 0.106$, df = 35, $p > 0.05$). We also compared body weight

Table 4. Frequency distribution of B chromosomes in samples of *A. peninsulae* and *A. flavicollis* collected at the same site in different years and seasons, respectively. For explanations see Table 1.

Month/year	Chromosome number								n	n_B	$\%_B$	x_B
	48	49	50	51	52	53	54	55				
Lake Baikal												
July/August 1991	–	2	11	5	3	1	–	1	23	23	100.0	2.74
June/July 1992	–	2	3	5	1	–	–	–	11	11	100.0	2.45
									G-values:		0.00 (ns)	0.032 (ns)
Filipov												
June 1979	–	1	2	2	–	–	–	–	5	5	100.0	2.20
July 1983	–	3	3	4	1	–	–	–	11	11	100.0	2.27
August 1985	1	–	1	5	–	1	1	–	9	8	88.9	3.11
									G-values:		0.86 (ns)	0.197 (ns)
Skalní Mlýn												
July 1986	5	5	1	–	–	–	–	–	11	6	54.5	0.64
September 1986	1	3	–	–	–	–	–	–	4	3	75.0	0.75
September 1987	5	3	1	–	–	–	–	–	9	4	44.4	0.56
									G-values:		8.24 ($p < 0.05$)	0.028 (ns)
Belianske Tatry Mts												
May 1979	2	1	2	–	–	–	–	–	5	3	60.0	1.00
July 1981	8	3	1	1	–	–	–	–	13	5	38.5	0.62
August 1983	13	4	2	1	–	–	–	–	20	7	35.0	0.55
									G-values:		7.90 ($p < 0.05$)	0.155 (ns)
Mt Pelister												
September 1990	7	3	–	–	–	–	–	–	10	3	30.0	0.30
June 1991	14	9	5	–	–	–	–	–	28	14	50.0	0.68
									G-values:		2.53 (ns)	0.151 (ns)
Istranca Mts												
October 1993	6	2	–	–	–	–	–	–	8	2	25.0	0.25
June 1994	19	3	4	1	–	–	–	–	27	8	29.6	0.52
									G-values:		0.39 (ns)	0.097 (ns)

between samples of individuals differing as to the number of B chromosomes. Only adult animals, collected from May to September, were considered in this comparison. The average weights in samples of individuals with different diploid chromosome numbers are shown in Table 5. There seemed to be an increase of body weight along with an increasing diploid chromosome number, but pairwise differences among 2n-groups were not statistically significant. However, if just two categories [2n = 48 (B–) vs 2n > 48 (B+)] were compared, mean weights

Table 5. Weight distribution in samples of *A. flavicollis* differing in diploid number of chromosomes (2n). *n* – sample size; min, max, $\bar{x}$ – minimum, maximum, and mean value of weight in grams. SD – standard deviation.

2n	*n*	min	max	$\bar{x}$	SD
48	131	18	42	26.4	5.05
49	58	17	45	27.2	5.90
50	27	23	40	28.4	4.11
51	10	20	51	31.2	8.07
52	3	29	32	30.7	1.25
Σ (> 48)	98	17	51	28.1	5.71

between these groups were found to be significantly different ($t = 2.39$, df = 228, $p < 0.05$).

Concluding remarks

B chromosomes can vary in number among species, populations, individuals, tissues and cells. Previous sudies revealed a non-random pattern of B-chromosome distribution (Nur 1969, Thomson 1984), and various biological reasons for this have been taken into account. Due to intraspecific variation in their presence and frequency among populations dwelling in different habitats, it has been frequently stated that B chromosomes have an adaptive significance (Darlington 1963, Gibson and Hewitt 1972, Müntzing 1974, Hutchinson 1975, Carter 1978). In the present study, a differential geographic pattern of B-chromosome frequencies was observed also in *Apodemus* species, particularly in *A. flavicollis* and *A. peninsulae*, and the population specific frequencies seemed to be stable over seasons and years. However, no unambiguous relationship between B-chromosome distribution and various biological variables could be found. An alternative explanation would be that B chromosomes are parasitic and are maintained or lost independently of any adaptive benefit or handicap they provide for individuals, populations or species (Fröst 1969, Nur 1969, Patton 1972, Lucov and Nur 1973, Bougourd and Parker 1975, 1979, Thomson 1984, McQuade 1985). According to our results it seems that the incidence of B chromosomes in certain *Apodemus* species is mainly determined by stochastic effects operating within a specific genetic background of a population or species.

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References

Bekasova T. S., Vorontsov N. N., Korobitsyna K. V. and Korablev V. P. 1980. B-chromosomes and comparative karyology of the mice of the genus *Apodemus*. Genetica 52/53: 33–43.

Belcheva R. G., Topashka-Ancheva M. N. and Atanassov N. 1988. Karyological studies of five species of mammals from Bulgarian fauna. Comptes rendus de l'Académie bulgare des Sciences 42: 125–128.

Benmehdi F., Britton-Davidian J. and Thaler L. 1980. Premier report de la génétique biochimique des population a la systématique des Mulots de France continentale et de Corse. Biochemical Systematics and Ecology 8: 309–315.

Borisov Yu. M. 1990a. Cytogenetic structure of *Apodemus peninsulae* (Rodentia, Muridae) population on the coast of Teletskoye Lake (Altai). Genetika 26: 1220–1225. [In Russian with English summary]

Borisov Yu. M. 1990b. Variability of cytogenetic structure of *Apodemus peninsulae* (Rodentia, Muridae) population in West Sayans. Genetika 26: 1484–1491. [In Russian with English summary]

Borisov Yu. M. 1990c. The system of B-chromosomes is a marker of *Apodemus peninsulae* (Rodentia, Muridae) population in Pribaikal region. Genetika 26: 2215–2225. [In Russian with English summary]

Borisov Yu. M. and Malygin M. V. 1991. Cline variability of the B-chromosome system in *Apodemus peninsulae* (Rodentia, Muridae) from the Buryatia and Mongolia. Citologija 33: 106–111. [In Russian with English summary]

Bougourd S. M. and Parker J. S. 1975. The B-chromosome system of *Allium schoenoprasum*. I. B – distribution. Chromosoma (Berl.) 53: 273–282.

Bougourd S. M. and Parker J. S. 1979. The B-chromosome system of *Allium schoenoprasum*. II. Stability, inheritance and phenotypic effects. Chromosoma (Berl.) 75: 369–383.

Britton-Davidian J., Vahdati M., Benmehdi F., Gros P., Nancé V., Croset H., Guerassimov S. and Triantaphyllidis C. 1991. Genetic differentiation in four species of *Apodemus* from southern Europe: *A. sylvaticus, A. flavicollis, A. agrarius* and *A. mystacinus* (Muridae, Rodentia). Zeitschrift für Säugetierkunde 56: 25–33.

Carter C. R. 1978. The cytology of *Brachycome*. 8. The inheritance, frequency and distribution of B chromosomes in *B. dichromosomatica* (n = 2), formerly included in *B. lineariloba*. Chromosoma (Berl.) 67: 109–121.

Darlington C. D. 1963. Chromosome botany and the origin of cultivated plants. George Allen and Unwinn, London: 1–155.

Demeter A. and Lázár P. 1984. Morphometric analysis of field mice *Apodemus*: character selection for routine identification (Mammalia). Annale Historico-Naturales Musei Nationalis Hungarici (Budapest) 76: 297–322.

Doolittle W. P. and Sapienza C. 1980. Selfish genes, the phenotype paradigm and genome evolution. Nature 284: 601–603.

Filippucci M. G. 1992. Allozyme variation and divergence among European, Middle Eastern, and North African species of the genus *Apodemus* (Rodentia, Muridae). Israel Journal of Zoology 38: 193–218.

Ford C. E. and Hamerton J. L. 1956. A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. Stain Technology 31: 247–251.

Fröst S. 1969. The inheritance of accessory chromosomes in plants, especially in *Ranunculus acris* and *Phleum nodosum*. Hereditas 61: 317–326.

Giagia E., Soldatovic B., Savic I. and Zimonjic D. 1985. Karyotype study of the genus *Apodemus* (Kaup, 1829) populations from the Balkan peninsula. Acta Veterinaria (Beograd) 35: 289–298.

Gibson I. and Hewitt G. 1972. Interpopulation variation in the satellite DNA from grasshoppers with B-chromosomes. Chromosoma (Berl.) 38: 121–138.

Hayata I. 1973. Chromosomal polymorphism caused by supernumerary chromosomes in the field mouse, *Apodemus giliacus*. Chromosoma (Berl.) 42: 403–414.

Howell W. M. and Black D. A. 1980. Controlled silver staining of nucleolus organizer regions with protective colloidal developer: a 1-step method. Experientia 36: 1014–1015.

Hutchinson J. 1975. Selection of B-chromosomes in *Secale cereale* and *Lolium perene*. Heredity 34: 39–52.

Ishak B., Jaafar H., Maetz J. L. and Rumpler Y. 1991. Absence of transcriptional activity in the B-chromosomes of *Apodemus peninsulae* during pachytene. Chromosoma (Berl.) 100: 278–281.

Jones R. N. and Rees H. 1982. B chromosomes. Academic Press, New York: 1–254.

Kartavtseva I. V. 1994. The finding of the B chromosome in the karyotype of striped field mouse, *Apodemus agrarius*. Citologija i Genetika 28: 96–97. [In Russian with English summary]

Kolomiets O. L., Borbiev T. E., Safronova L. D., Borisov Y. M. and Bogdanov Y. F. 1988. Synaptonemal complex analysis of B-chromosome behavior in meiotic prophase I in the East-Asiatic mouse *Apodemus peninsulae* (Muridae, Rodentia). Cytogenetics and Cell Genetics 48: 183–187.

Král B., Zima J., Herzig-Straschil B. and Štěrba O. 1979. Karyotypes of certain small mammals from Austria. Folia Zoologica 28: 5–11.

Lucov Z. and Nur U. 1973. Accumulation of B-chromosomes by preferential segregation in females of the grasshopper *Melanoplus femur-rubrum*. Chromosoma (Berl.) 42: 289–306.

McQuade L. R. 1985. B-chromosome system in the greater glider (*Petauroides volans volans*) (Marsupialia: Petauridae). I. B-chromosome distribution. Australian Journal of Biological Sciences 38: 189–195.

Mezhzherin S. V. 1990. Allozyme variability and genetic divergence of long-tailed mice of subgenus *Sylvaemus* (Ognev et Vorobiev). Genetika 26: 1046–1054. [In Russian with English summary]

Mezhzherin S. V. 1991. On specific distinctness of *Apodemus* (*Sylvaemus*) *ponticus* (Rodentia, Muridae). Vestnik zoologii 1991 (6): 34–40. [In Russian with English summary]

Müntzing A. 1974. Accessory chromosomes. Annual Review of Genetics 8: 243–266.

Musser G. G. and Carleton M. D. 1993. Family Muridae. [In: Mammal species of the world. D. E. Wilson and D. M. Reeder, eds]. Smithsonian Institution Press., Washington and London: 501–755.

Nur U. 1969. Harmful B-chromosomes in a mealy bug: additional evidence. Chromosoma (Berl.) 28: 280–297.

Orgel L. E. and Crick F. H. C. 1980. Selfish DNA: the ultimate parasite. Nature 284: 604–607.

Patton J. L. 1972. A complex system of chromosomal variation in the pocket mouse, *Perognathus baileyi* Merriam. Chromosoma (Berl.) 36: 241–255.

Ruprecht A. L. 1979. Criteria for species determination in the subgenus *Sylvaemus* Ognev & Vorobiev, 1923 (Rodentia, Muridae). Przegląd Zoologiczny 23: 340–349. [In Polish with English summary]

Seabright M. 1971. A rapid banding technique for human chromosomes. Lancet 11: 971–972.

Sokal R. R. and Rohlf J. F. 1981. Biometry. W. H. Freeman & Co., New York: 1–859.

Soldatovic B., Savic I., Dulic B. Miloševic M. and Mikeš M. 1972. Study of the karyotype of the genus *Apodemus* Kaup, 1829 (Mammalia, Rodentia). Archives of Biological Sciences (Beograd) 24: 125–130.

Sumner A. T. 1972. A simple technique for demonstrating centromeric heterochromatin. Experimental Cell Research 75: 304–306.

Thomson R. L. 1984. B chromosomes in *Rattus fuscipes*. II. The transmission of B chromosomes to offspring and population studies support for the "parasitic" model. Heredity 52: 363–372.

Volobouev V. T. 1979. Karyological analysis of three Siberian populations of *Apodemus peninsulae* (Rodentia, Muridae). Doklady AN SSSR 248: 1452–1454. [In Russian with English summary]

Vorontsov N. N., Bekasova T. S., Kral B., Korobitsyna K. V. and Ivanitskaya E. Yu. 1977. On specific status of Asian wood mice of the genus *Apodemus* (Rodentia, Muridae) from Siberia and Far East. Zool. Zh. 56: 437–449. [In Russian with English summary]

Vujoševic M. 1992. B-chromosome polymorphism in *Apodemus flavicollis* (Rodentia, Mammalia) during five years. Caryologia 49: 347–352.

Vujoševic M., Blagojevic J., Radosavljevic J.and Bejakovic D. 1991. B chromosome polymorphism in populations of *Apodemus flavicollis* in Yugoslavia. Genetica 83: 167–170.

Vujoševic M., Radosavljevic J. and Živkovic S. 1989. Meiotic behavior of B chromosomes in yellow necked mouse *Apodemus flavicollis*. Archives of Biological Sciences (Beograd). 41: 39–42.

Vujoševic M. and Živkovic S. 1987. Numerical chromosome polymorphism in *Apodemus flavicollis* and *A. sylvaticus* (Mammalia: Rodentia) caused by supernumerary chromosomes. Acta Veterinaria (Beograd) 37: 81–92.

Wolf U., Voiculescu I., Zenzes M. T., Vogel W. and Engel W. 1972. Chromosome polymorphism in *Apodemus flavicollis,* possibly due to creation of a new centromere. [In: Modern aspects of cytogenetics: constitutive heterochromatin in man. A. Pfeiffer, ed]. F. K. Schattauer, Stuttgart and New York: 163–168.

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APPENDIX. A detailed list of the material examined (F – females, M – males).

Apodemus peninsulae (Thomas, 1907):

Russia. Svyatoi Nos Isthmus, north of Ust-Barguzin, Lake Baikal, Siberia; July and August 1991 (11F, 12M), June and August 1992 (5F, 6M, leg. M. Reiter and M. Lípa). Sokol, Dolinski District, Sachalin Island (1F, leg. S. Mezhzherin). Mongolia. Barch River, Batshireed sum, Hentei aimak Province; August 1988 (1M). Onon River, Binder sum, Hentei aimak Province; August 1988 (4F, 7M).

Apodemus flavicollis (Melchior, 1834):

Czech Republic. Northern Bohemia.

1. Filipov at Česká Kamenice, Děčín District; June 1979 (2F, 3M), August 1981 (1F, 1M), August 1983 (5F, 6M), July 1984 (1F, 2M), August 1985 (1F, 8M), August 1986 (1M). 2. Klíny, Krušné hory Mts., Most District; September 1981 (1F, 2M). 3. Fláje and Český Jiřetín, Krušné hory Mts., Most District; September June 1986 (1F), June 1988 (1M), October 1989 (1M), October 1990 (3F, 4M). 4. Hamr, Česká Lípa District; August 1978 (2F, 3M, leg. V. Vohralík). Eastern Bohemia. 5. Pec pod Sněžkou, Krkonoše Mts., Trutnov District; September 1988 (2M). Western Bohemia. 6. Štěpanice, Šumava Mts., Klatovy District; August 1979 (1F, 1M). 7. Železná Ruda, Šumava Mts., Klatovy District; June 1979 (1M). 8. Malá Chmelná at Sušice, Klatovy District; June 1983 (1M). 9. Srní, Šumava Mts., Klatovy District; August 1993 (4F, 4M). Southern Bohemia. 10. Třeboň, Jindřichův Hradec District; July 1981 (2F, 5M), September 1981 (2M). 11. Velký Tisý Pond at Lomnice nad Lužnicí, Jindřichův Hradec District; September 1981 (1M). Southern Moravia. 12. Mašovice, Znojmo District; July 1985 (5F, 4M). 13. Brno – Bystrc, September 1983 (4F, 5M). 14. Drnholec, Břeclav District; August and September 1981 (1F, 3M), May 1985 (2M), March 1989 (1F, 2M, leg. J. Nesvadbová). 15. Pohořelice, Břeclav District; October 1988 (2F, 2M). 16. Pálava Hills, Břeclav District; October 1989 (5F, 7M, leg. J. Nesvadbová). 17. Holštejn, Moravian Karst, Blansko District; September 1983 (2M), June 1985 (1M), October 1985 (1F, 1M). 18. Nový hrad at Adamov, Blansko District; October 1985 (2F, 2M). 19. Skalní Mlýn, Moravian Karst, Blansko District; June 1986 (6F, 5M), November 1986 (1F, 3M), February 1987 (1M), September 1987 (1F, 8M), August 1988 (1M), October 1990 (2F), June 1992 (1F, 2M). 20. Rudické propadání Cave at Jedovnice, Moravian Karst, Blansko District; July 1990 (1M). Northern Moravia. 21. Karlova Studánka, Jeseníky Mts., Bruntál District; October 1981 (18F, 13M), December 1981 (3F, 2M). Slovak Republic. Northern Slovakia. 22. Dolina Siedmich prameňov Valley, Belianské Tatry Mts.; May 1979 (2F, 3M), July 1981 (4F, 9M),

August 1983 (10F, 10M). Eastern Slovakia. 23. Hraň, Trebišov District; June 1990 (1F, 3M). Austria. For locations see Král *et al.* (1979). Slovenia. 24. Ljubljansko Barje at Ljubljana; May 1988 (1F), September 1990 (3M). 25. Ig, Kremenica; May 1988 (1F). 26. Podkoren, Karavanke Mts.; May 1988 (1F, 1M). 27. Radenci, Prekmurje, Murska Sobota; May 1988 (1F). Macedonia. 28. Mt. Pelister, Baba Mts.; September 1990 (3F, 3M), June 1991 (12F, 16M). 29. Galičica Mts.; September 1990 (1F). Greece. 30. Kalivia, Voras Mts.; June 1984 (2M, leg. V. Vohralík). 31. Lianotopi, Grammos Mts.; June 1984 (1M, leg. V. Vohralík). 32. Leivaditis, Rodopi Mts.; July 1994 (4M). Bulgaria. 33. Baldevo, Blagoevgrad District; August 1984 (4F, 5M). European Turkey. 34. Velika Bridge at Demirköy, Istranca Mts.; June 1992 (1F, 2M, leg. A. Reiter), May 1993 (3M, leg. M. G. Filippucci), October 1993 (3M), June 1994 (11F, 12M). 35. Dupnisa Magarasi at Demirköy, Istranca Mts.; October 1993 (2F, 3M). 36. Igneada, Istranca Mts.; June 1994 (4M). Romania. 37. Harghita Mts., Carpathians; July 1983 (4F, 2M). 38. Piatra Craiului Mts., Carpathians; July 1983 (2F, 2M). Ukraine. 39. Kuripchanna, South Bug River; September 1989 (3F, 4M, leg. V. Gaichenko). 40. Kiev – Teremki; October 1989 (1F, 1M).

Apodemus sylvaticus (Linnaeus, 1758):

Spain. Eugia, Navarra; September 1992 (1F, 1M, leg. M. Anděra and A. Červená). Czech Republic. Northern Bohemia. Filipov at Česká Kamenice, Děčín District; August 1983 (2F, 3M), July 1984 (1M), August 1985 (1F), August 1986 (1F). Fláje, Krušné hory Mts., Most District; June 1986 (1F), October 1990 (2F, 2M). Záluží, Most District; September 1981 (4F, 1M), September 1982 (2F), September 1984 (3F, 4M). Hamr, Česká Lípa District; August 1978 (1M, leg. V. Vohralík). Žatec, Louny District; June 1979 (1M, leg. V. Vohralík). Eastern Bohemia. Kameničky, Chrudim District; August 1988 (1F). Western Bohemia. Lipí at Manětín, Plzeň District; September 1981 (2M). Dolnice and Horní Ves, Cheb District; October 1991 (2F, 1M). Hranice and Dolní Paseky, Cheb District; May 1994 (1F, 1M). Soos – Kateřina, Cheb District; May 1993 (3F, 3M). Malá Chmelná at Sušice, Klatovy District; June 1983 (2F, 3M). Štěpanice, Šumava Mts., Klatovy District; August 1979 (3M). Železná Ruda, Šumava Mts., Klatovy District; August 1979 (4F, 9M). Southern Bohemia. Žofín, Novohradské hory Mts., Český Krumlov District; August 1973 (1F). Třeboň, Jindřichův Hradec District; July 1981 (3F, 2M), September 1981 (1F). Milevsko, Písek District; January 1985 (2M, leg. M. Homolka). Central Bohemia. Praha; July 1983 (1M), October 1983 (5F, 11M, leg. D. Frynta). Southern Moravia. Brno – Pisárky, Bystrc, Modřice; July 1979 (4M, 1F), September 1983 (2F, 2M), September 1988 (2F, 1M, leg. J. Nesvadbová), March 1989 (3F, leg. J. Nesvadbová), January 1990 (1F). Pohořelice, Břeclav District; October 1980 (8F, 4M), September 1988 (6M), October 1989 (2F). Drnholec, Břeclav District; September 1981 (3F, 1M). Býčí Skála, Moravian Karst, Blansko District; April 1983 (1F). Skalní Mlýn, Moravian Karst, Blansko District; September 1984 (1M), July 1986 (3F), September 1986 (1F, 8M), September 1987 (2M), July 1990 (2F, 5M). Holštejn, Moravian Karst, Blansko District; July 1990 (2F). Nový hrad at Adamov, Blansko District; October 1985 (2F). Ostrov u Macochy, Moravian Karst, Blansko District; January 1986 (1F). City of Blansko; February 1987 (2M). Northern Moravia. Karlova Studánka, Jeseníky Mts., Bruntál District; October 1981 (10F, 16M), December 1981 (1F, 2M). Slovenia.Podkoren, Karavanke Mts.; May 1988 (6F, 8M). Ljubljansko Barje at Ljubljana; September 1990 (1M). Italy. Cave, Rome Province; June 1993 (1M, leg. M.G. Filippucci). Penne, Rome Province; June 1993 (1M, leg. M. Cristaldi). San Polo dei Cavallieri, Rome Province; June 1993 (1F, 1M, leg. M.G. Filippucci). Hungary. Bar at Mohács; October 1979 (1M). Macedonia. Bistra planina Mts.; September 1990 (2F). Romania. Vadu, Dobrogea; August 1979 (1M, leg. J. Červený). Zarnesti, Brasov District; July 1983 (1F).

Apodemus hermonensis (Filippucci, Simson et Nevo, 1989):

Israel. Mt. Hermon, Golan Heights; May 1993 (1F, leg. M. G. Filippucci).

Apodemus fulvipectus (Ognev, 1924):

Ukraine. Stepanovskaya kosa, Azov Sea, Melitopol Province; September 1989 (4F, 1M). Askania Nova, Melitopol Province; September 1989 (4F, 8M). Chernomorski zapovednik Reserve, Cherson Province; September 1989 (1F, 1M).

Apodemus uralensis (Pallas, 1811):

Czech Republic. Žatec, Louny District; June 1979 (leg. V. Vohralík). Pohořelice, Břeclav District; October 1980 (1M). Drnholec, Břeclav District; August 1984 (1M). Slovak Republic. Hraň, Trebišov District; June 1990 (2F, 2M). Ukraine. Chernomorski zapovednik Reserve, Cherson Province; September 1989 (3M).

Apodemus spp.:

Turkey. Asia Minor. Gecidi, Cankurtaran, Hopa Province; July 1993 (3F, 3M, leg. P. Rödl and V. Vohralík). Caycuma, Zonguldak Province; October 1993 (2F). Sumela, Trabzon Province; October 1993 (6M). Suludere, Burdur Province; October 1993 (3F,2M). Egirdir, Isparta Province; May 1993 (1F, 1M, leg. M.G. Filippucci). Ulu Dag Mts., Bursa Province; May 1993 (1M, leg. M.G. Filippucci), July 1994 (5F, 7M). Lake Abant, Bolu Province; July 1994 (2F, 2M). Hanyatak, Kapiorman Daglari Mts.; July 1994 (2F, 2M). Yenice, Zonguldak Province; July 1994 (4F, 9M). Bolu Daglari Mts., Bolu Province; July 1994 (1F, 1M, leg. M.G. Filippucci and S. Simson). Safranbolu, Zonguldak Province; July 1994 (3M). Lake Eber, Afyon Province; July 1994 (1M). Cirpilar, Kaz Dagi, Balikesir Province; July 1994 (1F, 1M). Israel. Mt. Carmel, Haifa; May 1993 (1F, leg. M. G. Filippucci). Azerbaijan. September 1988 (2M, leg. D. Frynta). Tadjikistan. Sari Chosor; July 1981 (2F, 1M). Karatag; July 1981 (4M). Dagonidara, Jachsu; July 1981 (2F, 6M). Obi-Pitongu, Jachsu; July 1981 (3F, 2M). Chovaling, Sultan Mazar; July 1981 (3F, 1M, leg. B. Král). Kyrghyzstan. Ala Archa, Bishkek Province; July 1984 (1M, leg. I. Horáček and J. Červený). Tuja Mujun, Osh Province; August 1984 (1M, leg. I. Horáček and J. Červený). Mazar Saj, Osh Province; August 1984 (2M, leg. J. Červený and I. Horáček), September 1992 (2M). Chaidarkan, Goujan Valley, Osh Province; (1F, leg. J. Červený and I. Horáček). Kalek, Batken District, Osh Province; July 1988 (1F, 2M, leg. J. Červený and I. Horáček). Susamyr River, Kara Balta District; June 1989 (2F, leg. V. Hrabě and P. Koubek). Dzhangi Aryk, Osh Province; May 1989 (1F, leg. A. Červená). Ottuk, Issyk Kul Lake; August 1992 (1M). Kara Bulun, Issyk Kul Lake; August 1992 (1M). Arashan, Przewalsk Province; August 1992 (2F). August 1992 (3F, 2M). Cholpon, Kochkorka District; August 1992 (1M). Arsy, Kochkorka District; August 1992 (2F, 5M). Naryn Reserve, Naryn Province; September 1992 (1M). Kjogart, Suzak District; September 1992 (1M). Dangi Canyon, Kara Koktu, Osh Province; September 1992 (1F, 2M). Ak Tala, Osh Province; September 1992 (3F, 2M). Ak Dzhilga, Osh Province; September 1992 (4M). Kanigut Cave, Batken District, Osh Province; October 1992 (1M).

Apodemus mystacinus (Danford et Alston, 1877):

Macedonia. Galičica Mts.; September 1990 (1F). Bulgaria. Baldevo, Blagoevgrad District; July 1987 (1M, leg. D. Frynta). Turkey. Asia Minor. Caycuma, Zonguldak Province; October 1993 (1F). Ciglikara, Antalya Province; May 1993 (1M, leg. M.G. Filippucci). Safranbolu, Zonguldak Province; July 1994 (1M). Cirpilar, Kaz Dagi Mts., Balikesir Province; July 1994 (1F). Israel. Mt. Carmel, Haifa; May 1993 (1F, leg. M.G. Filippucci).

Apodemus agrarius (Pallas, 1771):

Czech Republic. Karlova Studánka, Jeseníky Mts., Bruntál District; October and December 1981 (2F). Slovak Republic. Šaca, Košice District; June 1990 (1F). Hraň, Trebišov District; June 1990 (7F, 17M). Hungary. Bar at Mohács; October 1979 (1F, 4M). Slovenia. Radenci, Prekmurje, Murska Sobota; May 1988 (1M). Croatia. Ilok, Slavonia; October 1979 (2F, 2M). Serbia. Apatin, Vojvodina; October 1979 (1F, 1M). Ritopek, Vojvodina; October 1979 (1F). Greece. Thrace; September 1988 (1F, leg. V. Vohralík). Romania. Giurgeni, Danube River; October 1979 (1M). Crisan, Danube Delta; October 1979 (1F, 3M). Lake Lacul Rosu, Danube Delta; October 1979 (2F, 2M). Mila 23, Danube Delta; October 1979 (1F). Ukraine. Chernomorski zapovednik Reserve, Cherson Province; September 1989 (3F). Kiev – Teremki; October 1989 (2F). European Turkey. Igneada, Istranca Mts.; June 1994 (1F, 1M).