Theor Appl Genet (1983) 67:59–65

Chromosome localization of the genes for ENO1, HK1, ADK, ACP2, MPI, ITPA, ACON1 and α-GAL in the American mink (*Mustela vison*)

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Received March 7, 1983
Communicated by Y. Gleba

Summary. Twenty-eight American mink × Chinese hamster somatic cell hybrids were analysed for the expression of mink enzymes and the segregation of mink chromosomes. The results demonstrated that the gene for enolase-1 is located on the long arm of mink chromosome 2, and those for hexokinase-1 and adenosine kinase, on its short arm. Segregation analysis of mink chromosomes and mink acid phosphatase-2, mannose phosphate isomerase, inosine triphosphatase and aconitase-1 provided data allowing us to assign the genes for these markers to mink chromosomes 7, 10, 11 and 12, respectively. The expression of mink α-galactosidase was highly coincidental with mink X chromosome as well as with its markers: hypoxanthine-phosphoribosyltransferase, glucose-6-phosphate dehydrogenase and phosphoglycerate kinase-1. This result confirms the assignment of the gene for α-galactosidase to the mink X chromosome.

Key words: Gene maping – Somatic cell hybrids – Enolase-α-galactosidase – American mink – Chinese hamster

Introduction

Techniques of somatic cell hybridization have been extensively used for gene assignment. Mapping of human and mouse genomes have been successful (McKusick 1980; Womack 1982), however, relatively less information has been obtained for gene mapping in other mammals (Pearson et al. 1982). The building of chromosome maps by the use somatic cell hybrids has basic and applied implications. It would give insight into the evolution of the mammalian genome and contribute to the development of genetics of species – those of commercial importance in particular.

Somatic American mink × Chinese hamster hybridization has been used in this laboratory during the last years for the assessment of the American mink chromosome. We have succeeded in assigning 20 genes of biochemical traits to 11 chromosomes in the American mink (Rubtsov et al. 1981a, b, 1982a, b). This report presents our results with the mapping of an additional 8 gene loci for enolase-1, hexokinase-1, adenosine kinase, acid phosphatase-2, mannosephosphate isomerase, inosine triphosphatase, aconitase-1 and alpha-galactosidase.

Materials and methods

The following cell lines were used in the experiments: a cell line of the Chinese hamster, B14 (previously designated as M-15-1), an established cell line of the American mink, MV, and 28 American mink × Chinese hamster hybrid clones of independent origin. The generation of hybrid cell clones by means of a fusion of the B14 cells with mink bone marrow cells or mink white blood cells has been previously described (Rubtsov et al. 1981a). For details concerning the production of the cell hybrids and their karyological characterization, see Rubtsov et al. (1981a, 1982a). The cytogenetic and biochemical analyses of the hybrid cells were done within the same passage to insure uniformity.

Extracts from the cell cultures were prepared according to a standard method (Rubtsov et al. 1981a). Electrophoresis of the cell extracts was conducted in 14% starch gel with the addition of 10% sucrose.

Electrophoresis of enolase (ENO; EC 4.2.1.11), hexokinase (HK; EC 2.7.1.1), mannosephosphate isomerase (MPI; EC 5.3.1.8) and inosine triphosphatase (ITPA; EC 3.6.1.19) was carried out utilizing a Tris-EDTA-borate buffer system (Rubtsov et al. 1981a) whose gel buffer additionally contained 1% Triton X-100 and 0.1% beta-mercaptoethanol for ITPA or 1% Nonidet NP-40 for all the other enzymes. ITPA was

visualized by histochemical staining of the gels according to Van der Heiden (1969), and staining by the method of Harris and Hopkinson (1976) was used to identify ENO, HK and MPI.

A Tris-citrate buffer system (Shows and Ruddle 1968) was utilized for the electrophoresis of adenosine kinase (ADK; EC 2.7.1.20). The supplements to the gel buffer were Nonidet NP-40 (to a final concentration of 1%) and 0.0015 M of beta-mercaptoethanol. Autoradiographic procedures for the visualization of ADK were as previously described (Leinwand et al. 1978) but with a few modifications. Ten mg of ATP, 0.02 ml of adenosine-C^{14} (0.2 MBq) and 0.1 ml of 3 M $MgCl_2$ were mixed in 6 ml of 0.5 M Tris-HCl buffer, pH 7.5, and then mixed with 6 ml of 2% agarose (at 42 °C). This mixture was poured into the gels and incubated at 37 °C for 1 h. Subsequently, 0.01 M of $(CH_3COO)_3La$ in 0.05 M Tris-HCl buffer, pH 7.5, was poured into the gels, and the gels were allowed to stand for 10–12 h. The agarose layer was removed and thoroughly rinsed three times with water for 30 min. The agarose gels were then placed on slides and dried at 40 °C. The dried gels were coated with a RF-3 film (USSR) and exposed for 15–20 days.

Electrophoresis of acid phosphatase-2 (ACP2; EC 3.1.3.2) was done in a Tris-citrate buffer (Rubtsov et al. 1981a). The gel buffer was supplemented with 1% Triton X-100. ACP2 activity was detected as described by Harris and Hopkinson (1976) employing alpha-naphthyl phosphate as substrate.

Aconitase (ACON; EC 4.2.1.3) was subjected to electrophoresis in a Tris-citrate buffer (Shows and Ruddle 1968). The supplement to the gel buffer was 1% Triton X-100. Staining for visualization of ACON was done according to Harris and Hopkinson (1976).

Electrophoresis of alpha-galactosidase (αGAL; EC 3.2.1.22) was done using a phosphate-citrate buffer system: the electrode buffer was 0.2 M phosphate-citrate, pH 7.4, and the gel buffer was a 1:20 dilution of the electrode buffer plus 1% Nonidet NP-40. αGAL was visualized by staining the gels according to Harris and Hopkinson (1976).

Results and discussion

Figure 1 presents patterns of HK isozymes from cells of the American mink, Chinese hamster and several hybrid clones. Chinese hamster and mink cells displayed 2 HK bands, referred to as HK1 and HK2 in order of decreasing anodal mobility (Fig. 1). Under the electrophoretic conditions used, mink and hamster HK1's differed in their anodal mobilities, and this property made them easily identifiable in mixed extracts of mink and Chinese hamster cell cultures (Fig. 1). In contrast, mink and hamster HK2's differed slightly in electrophoretic mobilities and, hence, they were not consistently identified in hybrid clones.

Figure 2 presents the phenotypes observed following electrophoresis and staining for ACP2 in mink and hamster cells and hybrid clones. Mink ACP2 is represented by a single blurred band which is more mobile than hamster ACP2 (Fig. 2). Chinese hamster ACP2 is composed of two bands. One band is distinct and more active near the line of origin; the other less active and more anodal band is intermediate with respect to mink and the first Chinese hamster band (Fig. 2). In hybrid clones, which were positive for mink ACP2, staining intensity was increased in the zone comprised within the limits of the mink fraction and the first ACP2 fraction of the Chinese hamster (Fig. 2). This fraction probably represents heteropolymeric ACP2 isozyme. It is composed of mink and hamster subunits because mammalian ACP2 is a dimeric enzyme (Swallow and Harris 1972; Jones and Kao 1978).

Figure 3 presents an ACON pattern yielded by cells of the American mink, Chinese hamster and their hybrid clones. The pattern is composed of two fractions, ACON1 and ACON2. A comparison of the pattern shown by the MV cells with that obtained from ACON of various mink tissues demonstrates that ACON1 corresponds to the soluble form, and ACON2 to the mitochondrial form, of the enzyme. Under the

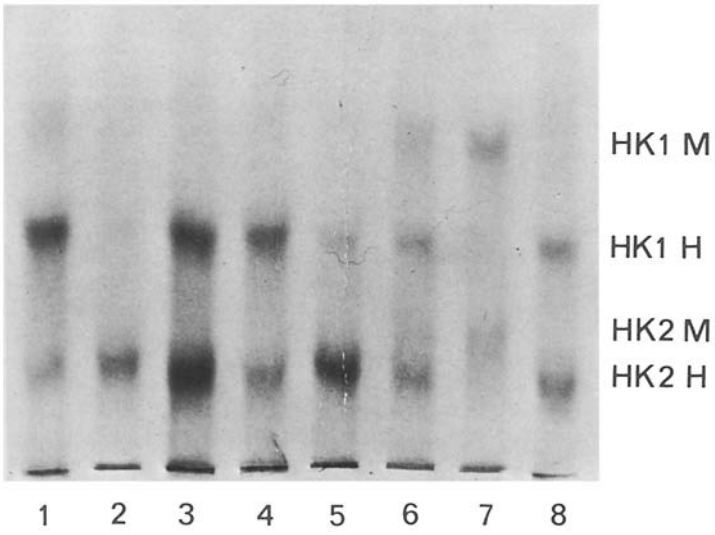

Fig. 1. Electrophoretic HK patterns obtained from parental species and their hybrid cells. *Channel 1* clone RO1; *channel 2* clone CO113; *channel 3* clone KO5; *channel 4* clone K11; *channel 5* clone K12; *channel 6* clone RO9; *channel 7* mink fibroblasts, MV cells; *channel 8* Chinese hamster fibroblasts, B14 cells. HK1 M and HK2 M are HK isozymes of mink, and HK1 H and HK2 H are HK isozymes of hamster

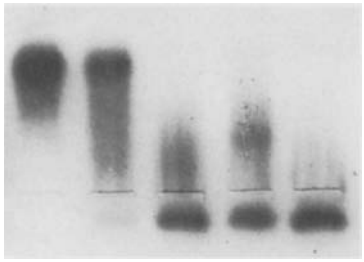

Fig. 2. Electrophoretic ACP2 patterns obtained from parental species and their hybrid cells. *Channel 1* MV cells; *channel 2* mixture (1 : 1) of mink and hamster fibroblasts; *channel 3* B14 cells; *channel 4* clone L15; *channel 5* clone RO1

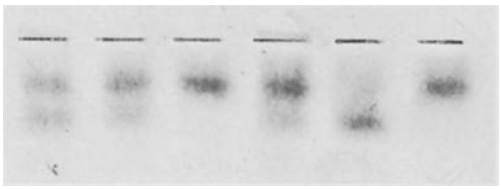

Fig. 3. Electrophoretic ACON patterns obtained from parental species and their hybrid cells. *Channel 1* clone K11; *channel 2* clone K12; *channel 3* clone RO1; *channel 4* mixture (1 : 1) mink and hamster fibroblasts; *channel 5* mink MV cells; *channel 6* hamster B14 cells

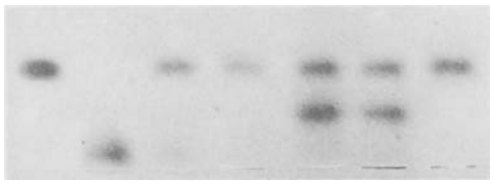

Fig. 4. Electrophoretic ENO patterns obtained from parental species and their hybrid cells. *Channel 1* hamster B14 cells; *channel 2* mink MV cels; *channel 3* mixture (1 : 1) of mink and hamster fibro blasts; *channel 4* clone L26; *channel 5* clone F6B; *channel 6* clone CO113; *channel 7* clone M1123

electrophoretic conditions used, mink and hamster ACON1 are readily separable, while the ACON2 from the two species differs less distinctly in electrophoretic mobility. Clones positive and negative for mink ACON1 are shown in Fig. 3.

The electrophoretic patterns of ENO, ADK, MPI, ITPA and αGAL for mink, Chinese hamster and some of the hybrid clones are shown in Figs. 4–8. The hybrid clones, which were positive for mink ENO1 and IPTA, contained a heteropolymeric isozyme with mobility intermediate with respect to the parental homopolymeric isozymes (Figs. 4 and 7). Thus, electrophoretic analysis made it possible to reliably identify enzymes of American mink and Chinese hamster origin in the hybrid clones (Figs. 4–8).

Table 1 contains data on the distribution of ENO1, HK1, ADK, ACP2, MPI, ITPA, ACON1 and αGAL in the 28 American mink × Chinese hamster clones. Clones M1110, MA10 and L14, containing all mink chromosomes with the exception of the Y, correlated positively with markers of mink origin.

The data on the segregation of mink chromosomes and mink ENO1, HK1, ADK, ACP2, MPI, ITPA, ACON1 and αGAL in 25 hybrid clones are summarized in Table 2. These data indicate that ACP2, MPI, ITPA, ACON1 and αGAL segregate independently in the clones studied, while ENO1, HK1 and ADK segregate together in the majority of the clones.

From the data of Tables 1 and 2, it follows that the genes for ENO1, HK1 and ADK are syntenic and that they are located on mink chromosome 2. Of interest are the data regarding these markers in clone CO113. It contains the long arm of mink chromosome 2 only (Rubtsov et al. 1981a, b) and possesses mink ENO1 but not HK1 and ADK (Table 1). It should be recalled that

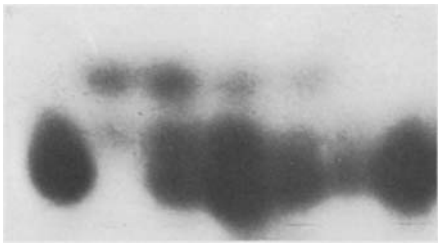

Fig. 5. Electrophoretic ADK patterns obtained from parental species and their hybrid cells. *Channel 1* hamster B14 cells; *channel 2* mink MV cells; *channel 3* mixture (1 : 1) of mink and hamster fibroblasts; *channel 4* clone RO9; *channel 5* clone RO1; *channel 6* clone K14; *channel 7* clone K15

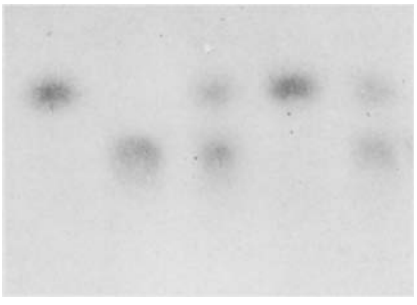

Fig. 6. Electrophoretic MPI pattern obtained from parental species and their hybrid cells. *Channel 1* hamster B14 cells; *channel 2* mink MV cells; *channel 3* mixture (1 : 1) of mink and hamster fibroblasts; *channel 4* clone KO5; *channel 5* clone K11

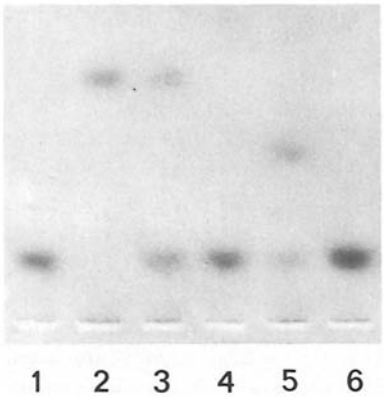

Fig. 7. Electrophoretic ITPA pattern obtained from parental species and their hybrid cells. *Channel 1* hamster B14 cells; *channel 2* mink MV cells; *channel 3* mixture (1 : 1) of mink and hamster fibroblasts; *channel 4* clone L25; *channel 5* clone L26; *channel 6* clone F6B

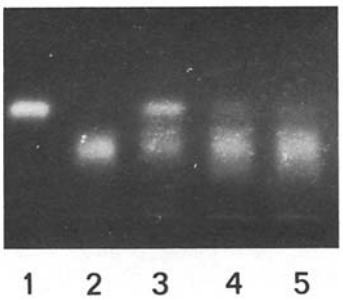

Fig. 8. Electrophoretic αGAL pattern obtained from parental species and their hybrid cells. *Channel 1* hamster B14 cells; *channel 2* mink MV cells; *channel 3* mixture (1 : 1) of mink and hamster fibroblasts; *channel 4* clone RO1; *channel 5* clone RO9

the syntenic pair of genes for 6-phosphogluconate dehydrogenase (PGD) and phosphoglucomutase-1 (PGM1) is located on the long arm of mink chromosome 2 (Rubtsov et al. 1981 b). As shown in Table 1, clone CO113 is positive for mink PGD and PGM1. There is, thus, reason for suggesting that the gene for ENO1 is located on the long arm of chromosome 2. The syntenic relationships of the genes for ENO1, PGD, and PGM1 has been described in many mammalian species: man (Lalley et al. 1978 a), rhesus monkey, African green monkey, baboon, gorilla, orang utang (Garver et al. 1977), chimpanzee (Rebourcet et al. 1975; Garver et al. 1977), *Cebus capucin* (Créau-Goldberg et al. 1981), mouse (Lalley et al. 1978 a) and Chinese hamster (Lasserre et al. 1981; Stallings and Siciliano 1982). Synteny of PGD-ENO1 has been established in cattle (Heuertz and Hors-Cayla 1981) and sheep (Säidi-Mehtar et al. 1981), and that of PGD-PGM1 in cat (Nash and O'Brien 1982). The linkage of the autosomal genes for PGD, PGM1 and ENO1 appears to be well preserved during mammalian evolution.

Mink HK1 was not observed in clone CO113 (Table 1), but it was found to be present in all the clones (with the exception of clone F10B) having the entire mink chromosome 2. It has been shown earlier that the gene for inorganic pyrophosphatase (PP) is located on the short arm of mink chromosome 2 (Rubtsov et al. 1982 b). Because HK1 and PP are syntenic (Table 1), it appears very likely that the gene for HK1 is located on the short arm of mink chromosome 2. The genes for HK1 and PP are syntenic in man (McKusick 1980) and mouse (Lalley et al. 1978 b; Womack 1982), but not in cat (O'Brien and Nash 1980).

According to the data of Table 2, the gene for ADK is most likely located on the short arm of chromosome 2. Two discordant clones, L15 and F10B chromosome"+"/ADK"–"), presumably contain chromosome 2 with a small deletion. This appears to be so because several other enzyme markers of mink chromosome 2 are present in these clones (Table 1). It should be also noted that clone L15 is devoid of glutamate-oxaloacetate transaminase-1 (Rubtsov et al. 1982 b), and clone F10B is devoid of HK1 (Table 1). Inasmuch as two other enzyme markers of the short arm of mink chromosome 2, namely PP and purine nucleoside-phosphorylase, are present in these discordant clones (Table 1; Rubtsov et al. 1982 b), it may be suggested that the putative deletions of mink chromosome 2 in the discordant clones affect the terminal region of its short arm.

Judging by the segregation data on mink chromosomes and mink ACP2 (Table 2), the gene for ACP2 may be with confidence assigned to mink chromosome 7. The only discordant clone CO113, chromosome 7"–"/ACP2"+", seems to contain a small cytogenetically undetectable fragment of mink chromosome 7. This appears likely when recalling that mink glucose phosphate isomerase (GPI) and lactate dehydrogenase-A (LDHA), which are markers of mink chromosome 7 (Rubtsov et al. 1981 b), are missing in this discordant clone. Recently, we succeeded in locating the gene for pyruvate kinase on mink chromosome 7, but clone CO113 is devoid of mink pyruvate kinase. In man, the genes for ACP2 and LDHA are located on chromosome 11, and the gene for GPI on chromosome 19 (McKusick 1980). In mouse, the gene for LDHA is syntenic with that for GPI (both being located on chromosome 7), while the gene for ACP2 is located on chromosome 2 (Womack 1982). It appears that the syntenic association of these genes has not been a stable during mammalian evolution.

As is evident from Table 2, the most likely candidates for the assignment of the genes for MPI and ITPA are mink chromosomes 10 and 11, respectively. This gene assignment is tentative because there were

Table 1. Distribution of mink EN01, HK1, ADK, ACP2, MPI, ITPA, ACON1, and GAL in 28 American mink × Chines hamster cell clones

Clone	American mink enzyme													
	EN01	HK1	ADK	PGD/ PGM1[a]	PP[b]	ACP2	LDHA[c]	MPI	IDH2[d]	ITPA	MOR1[e]	ACON1	αGAL	G6PD/ PGK1/ HPRT[f]
MA10	+	+	+	+	+	+	+	+	+	+	+	+	+	+
M1110	+	+	+	+	+	+	+	+	+	+	+	+	+	+
L14	+	+	+	+	+	+	+	+	+	+	+	+	+	+
CO113	+	–	–	+	–	+	–	+	+	+	+	+	+	+
M1123	–	–	–	–	–	–	–	+	+	–	–	–	–	–
KO2	–	–	–	–	–	–	–	+	+	–	–	+	+	+
KO4	–	–	–	–	–	–	–	–	–	–	–	–	+	+
KO5	–	–	–	–	–	–	–	–	–	–	–	–	+	+
K11	–	–	–	–	–	+	+	+	+	+	+	+	+	+
K12	–	–	–	–	–	+	+	+	+	+	+	+	+	+
K14	–	–	–	–	–	–	+	–	+	–	–	+	+	+
K15	–	–	–	–	–	–	–	+	+	+	+	–	+	+
L12	–	–	–	–	–	–	–	+	+	–	–	–	+	+
L15	+	+	–	+	+	+	+	–	+	+	+	–	+	+
L18	–	–	–	–	–	–	–	–	–	–	–	–	+	+
L22	–	–	–	–	–	+	+	–	–	–	–	+	+	+
L25	–	–	–	–	–	–	–	+	+	–	–	+	+	+
L26	–	–	–	–	–	–	–	+	+	+	+	–	+	+
R01	+	+	+	+	+	–	–	+	+	+	+	–	+	+
R09	+	+	+	+	+	–	–	+	+	–	–	–	+	+
R13	–	–	–	–	–	–	–	–	–	–	–	–	+	+
R14	–	–	–	–	–	–	–	+	+	–	–	+	+	+
D7B	–	–	–	–	–	–	–	+	+	–	+	+	+	+
D11B	–	–	–	–	–	+	+	–	–	–	–	–	+	+
FD16B	–	–	–	–	–	–	–	–	–	–	–	–	+	+
F6B	+	+	+	+	+	–	–	–	–	–	+	+	+	+
F10B	+	–	–	+	+	+	+	+	+	–	–	+	+	+
F12B	+	+	+	+	+	–	–	+	+	–	–	+	+	+

[a] PGD (6-phosphogluconate dehydrogenase) and PGM1 (phosphoglucomutase-1) are markers of the long arm of mink chromosome 2
[b] PP (inorganic pyrophosphatase) is a marker of the short arm of mink chromosome 2
[c] LDHA (lactate dehydrogenase-A) is a marker of mink chromosome 7
[d] IDH2 (isocitrate dehydrogenase-2) is a marker of mink chromosome 10
[e] MOR1 (malate dehydrogenase-1) is a marker of mink chromosome 11
[f] G6PD (glucose-6-phosphate dehydrogenase), PGK1 (phosphoglycerate kinase-1) and HPRT (hypoxanthine-phosphoribosyltransferase) are markers of the mink X chromosome

two discordant clones of chromosome"+"/marker"–" type in both cases (Table 2). We have earlier discussed the merits and disadvantages of the use of this clone panel (Rubtsov et al. 1981a). According to the criteria of Comeadow and Ruddle (1978) and Wijnen et al. (1977), the assignment of a gene for a marker is tentative when more than a single clone of chromosome"+"/marker"–" type is observed in the clone panel (Rubtsov et al. 1981a). It will be emphasized, however, that there are no other alternative candidates for the assignment of the genes as judged by the data of Table 2.

A noteworthy point is that discordant clones K14 and L15 MPI"–"/chromosome"+" contain isocitrate dehydrogenase-2, which is another marker of this chromosome (Table 1). This suggests that chromosome 10 has a small deletion involving the gene for MPI and unidentifiable cytogenetically. The same may be true for discordant clones D7B and F6B (ITPA"–"/chromosome 11"+") containing malate dehydrogenase-1 (NAD dependent), a marker of this chromosome (Table 1).

The most likely candidate for the assignment of the gene for mink ACON1 is mink chromosome 12 (Table 2). This is the first marker to be assigned to this particular mink chromosome. In the single discordant clone KO5, chromosome 12'+"/ACON1"–", contains probably chromosome 12 comprising a small unidentified deletion.

Another interference to be drawn from Table 1 is that αGAL is completely syntenic with the markers glucose-6-phosphate dehydrogenase (G6PD), phospho-

Table 2. Segregation of mink chromosomes and mink EN01, HK1, ADK, ACP2, MPI, ITPA and αGAL in 25 hybrid cell clones[a]

Chromosome	American mink enzyme															
	EN01		HK		ADK		ACP2		MPI		ITPA		ACON1		αGAL	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
1+	3	7	2	8	2	8	4	6	6	4	5	5	7	3	10	0
−	4	11	4	11	2	13	3	12	9	6	2	13	5	10	14	1
2+	7	0	5	1	4	2	3	3	4	2	2	4	3	3	6	0
−	0	18	0	19	0	19	4	15	11	8	5	14	9	10	18	1
3+	4	6	3	7	2	8	4	6	8	2	4	6	8	2	10	0
−	3	12	3	12	2	13	3	12	7	8	3	12	4	11	14	1
4+	4	7	3	8	2	9	4	7	7	4	5	6	7	4	11	0
−	3	11	3	11	2	12	3	11	8	6	2	12	5	9	13	1
5+	3	7	2	8	2	8	4	6	8	2	4	6	8	2	9	1
−	4	11	4	11	2	13	3	12	7	8	3	12	4	11	15	0
6+	4	11	3	12	3	12	5	10	10	5	5	10	9	6	15	0
−	3	7	3	7	1	9	2	8	5	5	2	8	3	7	9	1
7+	2	4	2	4	0	6	6	0	3	3	3	3	4	2	6	0
−	5	14	4	15	4	15	1	18	12	7	4	15	8	11	18	1
8+	4	3	3	4	2	5	2	5	4	3	2	5	5	2	7	0
−	3	15	3	15	2	16	5	13	11	7	5	13	7	11	17	1
9+	6	11	5	12	4	13	5	12	11	6	5	12	8	9	16	1
−	1	7	1	7	0	8	2	6	4	4	2	6	4	4	8	0
10+	6	11	5	12	3	14	5	12	15	2	7	10	10	7	16	1
−	1	7	1	7	1	7	2	6	0	8	0	8	2	6	8	0
11+	4	5	3	6	2	7	4	5	7	2	7	2	5	4	9	0
−	3	13	3	13	2	14	3	13	8	8	0	16	7	9	15	1
12+	4	9	3	10	2	11	5	8	9	4	3	10	12	1	13	0
−	3	9	3	9	2	10	2	10	6	6	4	8	0	12	11	1
13+	3	11	3	11	2	12	2	12	7	7	4	10	7	7	14	0
−	4	7	3	8	2	9	5	6	8	3	3	8	5	6	10	1
14+	7	9	6	10	4	12	6	10	10	6	7	9	8	8	16	0
−	0	9	0	9	0	9	1	8	5	4	0	9	4	5	8	1
X+	7	16	6	18	4	19	7	16	13	10	6	17	12	11	23	0
−	0	2	0	2	0	2	0	2	2	0	1	1	0	2	1	1

[a] Clones MA10, M1110 and L14, which retained all the mink chromosomes except for the Y, are not included in this table

glycerate kinase-1 (PGK1) and hypoxanthinephosphoribosyltransferase (HPRT), whose genes are located on mink X chromosome (Rubtsov et al. 1981a, 1982a). There is supporting evidence for this linkage. Thus, the previously described hybrid clone FD2M-4, which contains just one whole mink chromosome, the X (Rubtsov et al. 1982a), is positive for mink αGAL as well as for G6PD, PGK1 and HPRT. Recently, a derivative of this clone was obtained by its back-selection against 8-azaguanine in which mink X chromosome is undetectable. Analysis of this clone demonstrated that it lacks mink αGAL, G6PD, PGK1 and HPRT. This supports the idea that the gene for αGAL is located on the mink X chromosome. The assignment of the loci αGAL, G6PD, PGK1 and HPRT to the mink X chromosome (Rubtsov et al. 1981a, 1982a; present communication) is consistent with Ohno's assumption (Ohno 1974) that the set of genes in mammalian X chromosomes remained conservative during evolution.

Acknowledgements. The authors are indebted to Miss A. Fadeeva for translating the paper from Russian into English and to V. Prasolov for preparation of the photographs.

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