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STUDIES ON THE KARYOTYPE DIFFERENTIATION OF THE NORWAY RAT, IV. SEGREGATION AND FERTILITY OF THE NORWAY RATS WITH INVERSION PAIR NO. 1[1)]

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A female LEW (Lewis) strain rat with the chromosome mosaic consisting of two types was originally obtained; from this rat offspring with the normal and the inversion pair no. 1 (+/i) were obtained. By use of the latter rats, the segregation of the inversion pair no. 1 was examined by the following combination of matings; inversion heterozygous females and normal males (+/i♀×+/+♂), its reciprocal (+/+♀×+/i♂), and female and male inversion heterozygotes (+/i♀×+/i♂). Inversion heterozygotes and homozygotes were segregated in their offspring as we expected, but the number of inversion homozygotes was slightly smaller than the expected one, although there is no significant difference. Based on the litter size in the offspring, the fertility of the inversion heterozygotes and homozygotes were examined. The litter size from the inversion heterozygotes was slightly smaller than the control, but that from the inversion homozygotes was not different from the control one. This means that the fertility of the Norway rat with inversion pair no. 1 was normal.

INTRODUCTION

Occurrence of a female LEW (Lewis) strain rat with the karyotype characterized by 1/12 translocation heterozygous pairs has already been reported (Yosida 1980a). The female rat was mated to the normal LEW strain rat and 17 offspring from 3 litters were obtained. Among them 9 rats showed normal homomorphic pairs, but the remaining 8 rats showed heteromorphic pair nos. 1 and 12. Somatic and germ cells of one female among the latter rats were remarkable by showing the mosaic condition consisting of two cells types; one of them was the translocation and normal pair no. 1, while the other the translocation and inversion pair no. 1. This female mosaic rat was crossed to the normal male rat and 6 offspring were segregated as we expected;

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one rat had the normal pair no. 1, 3 rats had the normal and translocation pair no. 1, and the remaining 2 showed the normal and inversion pair no. 1 (Yosida 1980b). From the latter rats many offspring with inversion pair no. 1 were obtained by mating between them.

The present paper deals with the segregation of the rat with the inversion pair no. 1 obtained by mating between the inversion heterozygotes and normal homozygotes, and also between the female and male inversion heterozygotes. The fertility (litter size) of the inversion heterozygotes and homozygotes is also investigated with a special interest on differentiation of the karyotype in the Norway rat.

MATERIALS AND METHODS

LEW (Lewis) strain rats (*Rattus norvegicus*) used for the study were originally obtained from the Ohmura Experimental Animal Institute, Kanagawa, Japan, in 1978. To maintain the mutant chromosome the female mosaic rat was crossed to the LEJ (Long Evans) male rat, and from the hybrids between these two strains the segregation ratio of the inversion chromosome was examined. The rats without the inversion were selected from the segregants in the hybrids, and they were used as control rats.

The chromosomes were investigated in primary cultured cells from the tail tissues by our routine procedure (Yosida 1980c).

RESULTS

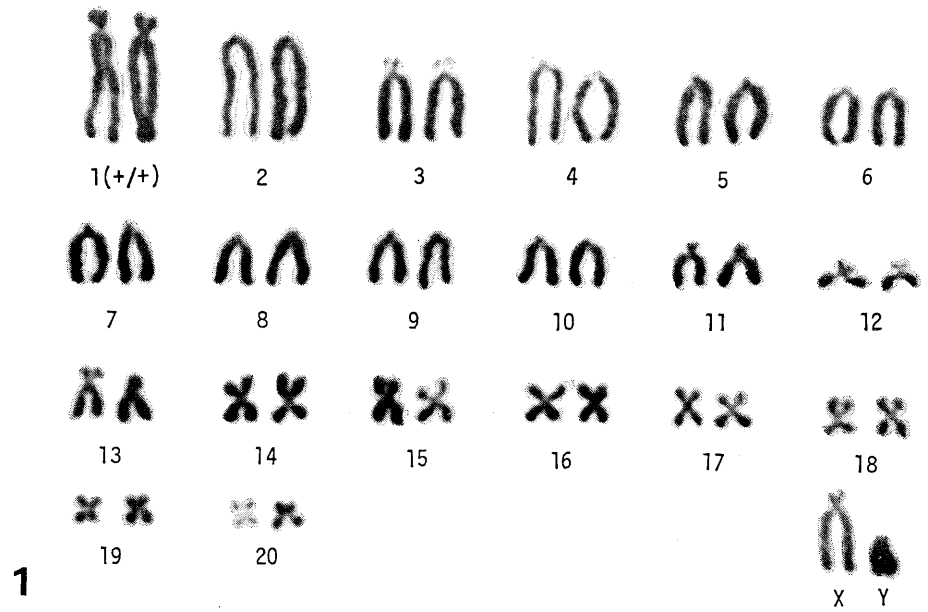
1. *Segregation of the rat with inversion pair no. 1*

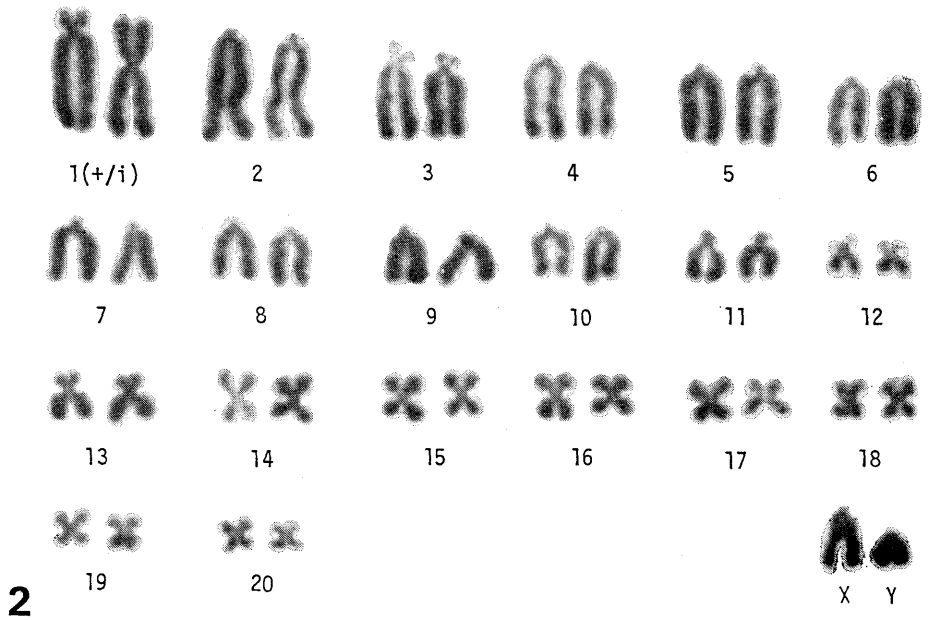
By mating between the inversion heterozygous female (i/+) and the normal male (+/+), 18 offspring (9 females: 9 males) were obtained (Table 1). They segregated into 7 normal (+/+) (Fig. 1) and 11 translocation heterozygotes (i/+) (Fig. 2). Thirty-two offspring (9 females: 23 males) obtained by the reciprocal matings (+/+ females $\times$ i/+ males) segregated into 13 normal (+/+) and 19 heterozygotes (i/+). Total 50 rats (18 females and 32 males) segregated into 20 (+/+) and 30 (i/+). Segregation ratio between the normal and heterozygous rats was not significantly different from that of the expected one ($\chi^2=2.1$, $p<0.1$).

Based on the mating between the female and male inversion heterozygotes, 50 rats (♀ 23: ♂ 27) were also obtained. They segregated into three types; 19 rats with normal pair no. 1 (+/+), 22 heterozygotes (i/+) and 9 inversion homozygotes (i/i) (Figs. 3 and 4). Although the number of rats with the normal karyotype was slightly larger and that of inversion homozygotes was slightly smaller than the expected ones, the χ^2 test showed that there is not significant difference between observed and expected values.

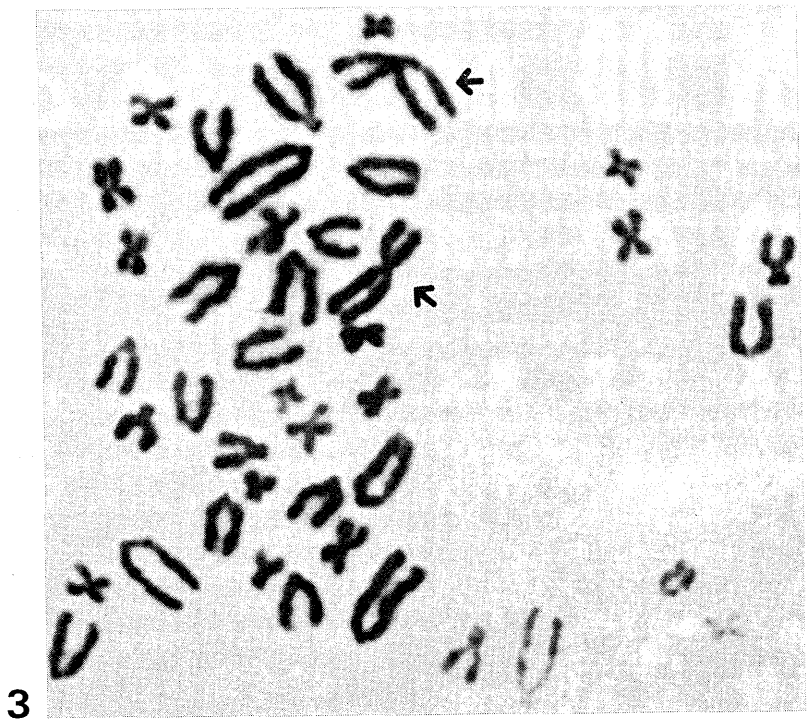
2. *Fertility of the rats with inversion pair no. 1*

Fertility of the rats with inversion pair no. 1 was examined based on the litter size of offspring (Table 2). As seen in the table, the average litter size was almost normal in all matings, although it was slightly smaller in the case of mating between





Figs. 1–2. 1, Normal karyotype of the Lewis strain rat. Pair no. 1 is normal consisting of the subtelocentric pair (+/+). 2, Karyotype with a heterozygous pair no. 1 consisting of normal subtelocentric and submetacentric chromosomes (+/i).



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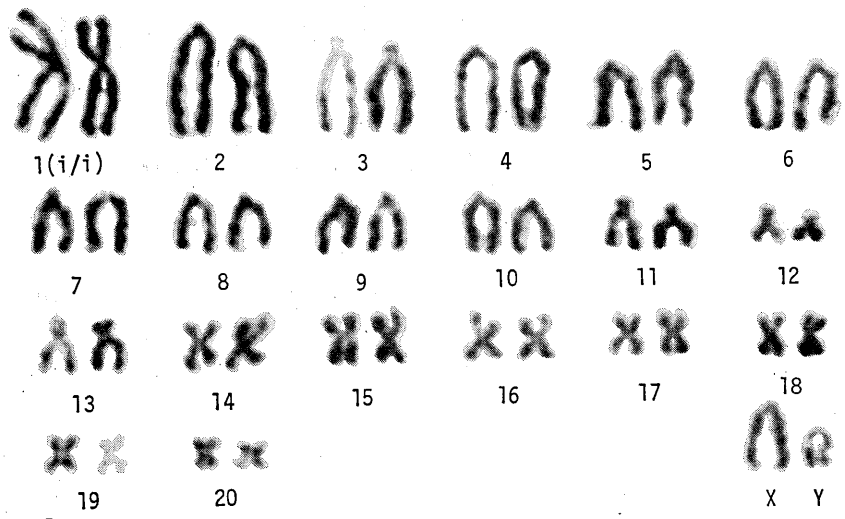

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Figs. 3 and 4. Metaphase and its karyotype with homologous submetacentric pair no. 1 occurred by pericentric inversion. 3, Metaphase. Arrows indicate the submetacentric pair no. 1. 4, Karyotype. Submetacentric pair no. 1 is shown by (i/i).

Table 1. Segregation of inversion pair no. 1 in Norway rats*

Parents ♀ × ♂	+/+	i/+	i/i	Total (♀ : ♂)
i/+ +/+	7	11	0	18 (9: 9)
+/+ i/+	13	19	0	32 (9:23)
Total	20 (25)	30 (25)	0	50 (18:32) $\chi^2=2.1$ $p<0.1$
i/+ i/+	19 (12.5)	22 (25)	9 (12.5)	50 (23:27) $\chi^2=1.36$ $p<0.5$

* +/+, i/+ and i/i indicate the normal homozygous, inversion and normal heterozygous and inversion homozygous pair no. 1, respectively.

Table 2. Litter size and sex ratio in the offspring of the Norway rats with inversion pair no. 1

Matings	Litters examined	Tot. no. of rats	Sex ratio (♀ : ♂)	Average litter size
Hetero. × Norm.	9	57	19 : 38	6.3±3.3
Hetero. × Hetero.	22	126	58 : 68	5.7±2.3
Homo. × Homo.	13	97	47 : 50	7.4±2.8
Norm. × Norm.	11	81	41 : 40	7.4±3.3

Hetero., Homo. and Norm. indicate the inversion heterozygotes, inversion homozygotes and normal homozygotes for pair no. 1.

inversion heterozygotes and normal rats (6.3±3.3), and also between inversion heterozygotes (5.7±2.3). By mating between the inversion homozygous rats, 97 offspring (47 females: 50 males) were obtained from 16 litters. All of the offspring showed the inversion homologous pair no. 1, and no any other karyotype was obtained. Average litter size of the offspring from the inversion homozygotes was 7.4±2.8. In the control rats with normal pair no. 1 which were established from segregants of the offspring obtained by mating between the inversion heterozygotes, the litter size was 7.4±3.3 in an average of 11 litters, which was very similar to that of the inversion homozygous rats.

DISCUSSION

Inversion of chromosomes has often been found in *Drosophila* and orthopteran insects (ref. White 1973). In the rodents, the pericentric inversion has been reported in *Mus minutoides* (Matthey 1963, 1966a), *Mastomys natalensis* (Matthey 1966b), *Peromyscus* (Ohno *et al.* 1966; Sperker and Arakaki 1966), *Ctenomys* (Reg and Kiblisky 1969) and some others. In *Peromyscus* all nineteen species showed the same chromosome number

($2n=48$), but there was much interspecific variation karyotypes (Hsu and Arrighi 1968). Chromosome changes by inversion from telocentric to subtelocentrics have often been found in pair nos. 1, 9 and 13 in the black rats (*R. rattus*) (Yosida 1980c). A similar inversion from the telocentric to subtelocentric in the Norway rat has been found in pair no. 3 (Yosida and Amano 1965), and from subtelocentric to telocentric in pair no. 12 (Masuji 1970) and pair no. 1 (Tsuchiya 1979), although it is questionable whether they have occurred by real inversion or not as discussed by Sasaki *et al.* (1979). The pericentric inversion in the chromosomes in the black and Norway rats occurred always in a small region near the centromere so far as they observed. Occurrence of a large inversion of pair no. 1 in which the subtelocentric changed to submetacentric has not yet been observed in the black and Norway rats.

In the black rat the fertility of the individuals with subtelocentric pair no. 1, which occurred by pericentric inversion of the original acrocentric member, did not change from that of the original telocentric one when they were bred in the laboratory which was controlled by air conditioning, but the black rats with subtelocentric no. 1 seemed to be non-adaptive to the cold weather in natural population (Yosida *et al.* 1971) and in the population breeding experiment (Yosida 1976). In the Norway rat the individuals with metacentric pair no. 1 by pericentric inversion seemed to exert no effect on the fertility so far as the breeding has been taken in the laboratory, although the fertility seemed to be slightly decreased in the case of matings of rats having inversion heterozygotes. This may be due to the non-disjunction of the heteromorphic chromosome pair in meiosis. We do not know whether the Norway rats with the submetacentric pair no. 1 occurred by inversion are adaptive in the natural condition. This problem will be resolved by an experiment on the population breeding set in the wild condition as we did in the black rats (Yosida 1976).

Concerning the establishment of the homozygotes in the inversion pair no. 1 of the Norway rat, the homozygotes with the translocation between pair nos. 1 and 12 have been established by the present author (Yosida 1980d). In that case the fertility of the translocation homozygotes was rather better than the control rats with the normal karyotype. If such karyotype rearrangements occurred in natural population and they have the stronger competitive ability than the other rats, the rats with the altered karyotype might be taken over those with the normal karyotype.

Appendix: The Norway rats with the 1/12 translocation homozygous pair established by the present author were named the LET-stock (Yosida 1980d). The present rats with the submetacentric homologous pair no. 1 derived from the pericentric inversion will be named the LEM-stock hereafter. The control rats without the translocation and inversion which were established from the rats with heterologous pair no. 1 are named the LEO-stock.

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