Inherited Semisterility for Control of Harmful Insects. II. Degree of Sterility and Types of Translocations in the Mosquito *Culex pipiens* L.

In the first paper of this series[1] basic figures have been presented on the production of translocations by X-ray irradiation in the mosquito *Culex pipiens* L. As outlined there the occurrence of semisterility in the F_1 offspring of irradiated males, outcrossed to normal females, was taken as evidence for the presence of a translocation. This has been confirmed by cytological investication in several semisterile lines. Only in one case investigated in this way was the observed semisterility due to a pericentric inversion instead of a translocation. For the practical application of semisterility as a measure for control of harmful animals it seems be of no importance whether it is due to a translocation or a pericentric inversion. In both cases the heterozygotes are semisterile to a certain degree and the semisterility is inherited.

However, two other characteristics of the semisterility produced in this way are of paramount importance for practical application, namely the degree of the sterility and the kind of chromosomes involved in the translocation or inversion.

We have tested by now all in all 401 sperms, exposed in adult males of the mosquito *Culex pipiens* L. to various dosages of irradiation and screened in the F_1 for semisterility. Most of the tested F_1 animals revealed in the F_2 eggs a lethality of under 10%. 277 of the 401 tested F_1 animals laid egg batches with a lethality of under 10% (Figure 1). These animals are regarded as normal without a translocation, although the lethality in crosses between normal strains is somewhat lower (around 3%).

The rest of the tested F_1 animals, 124 in all, produced egg rafts with lethalities higher than 10% and up to 85%. As may be seen from the graph the values are almost equally distributed between 10% and 50% (10–20%: 28 cases; 20–30%: 21; 30–40%: 24; 40–50%: 28). There was no accumulation of lethality values either around 50% or 66%. A preponderance of lethality values around 50% would be expected, if during meiosis I in translocation heterozygotes the separation of alternate chromosomes prevailed. 66% lethality would be expected, if all 3 possibilities of separation of chromosomes had the same chance. Out of the total of 124 lethality values most are between 10 and 50% ($N = 101$) and only less than $^1/_5$ ($N = 23$) over 50%.

From these figures it becomes obvious that all desired degrees of lethality up to 85% can be isolated from a series of tests of this size. Accordingly the extent of the influence of the semisterility principle on a natural population in practical application for control can be fixed at any level.

The values in Figure 1 represent lethality in a single or at the maximum two F_2 offspring. Many lines have been maintained for further generations. In each line a variability of lethality values of $\pm 10\%$ with normal distribution around a mean was observed. Therefore each translocation produces a fixed mean of lethality which does not change from generation to generation. What determines the characteristic value of lethality for each translocation is still a matter of speculation. It might be connected with the size of the translocated chromosome segments, with the distance of the break points to the centromere or with the incidence of chiasmata in the altered chromosomes.

From a practical standpoint, translocations with a high degree of lethality would be desirable. Whether the lethalities of 60% and more, as reported here, are due to a single translocation has not been investigated. Recent experiments have shown that double translocations will enhance the lethality to 80% and up to 93%. The results on the development of translocation lines with such high degrees of lethality will be presented in another part of this series.

The mosquito *Culex pipiens* has, as most other mosquito species, 3 pairs of almost metacentric chromosomes. One of these pairs, probably the smallest one, contains the sex-determining factors. The male is the heterozygous sex with the factor M for maleness and the factor m for femaleness. Females are homozygous m/m. With a chromosome complement of 1 sex chromosome pair and 2 autosomal pairs, 3 types of reciprocal translocations can be expected. The first type of translocation is the one with an exchange

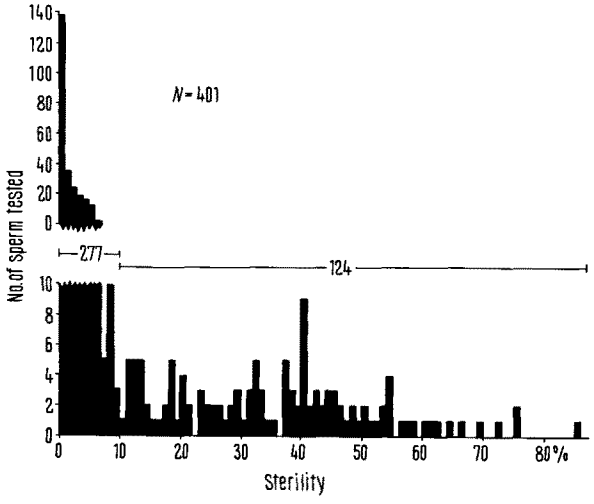

Fig. 1. Distribution of percentage of sterility of F_1 individuals of *Culex pipiens* L., derived from crosses of irradiated P males with normal P females.

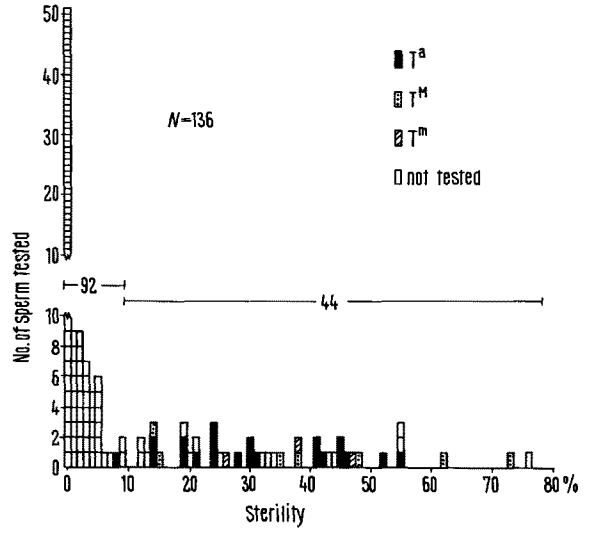

Fig. 2. Types of translocations produced with X-ray irradiation. For further explanation see text.

[1] H. LAVEN and E. JOST, Experientia *27*, 471 (1971).

of chromosome segments between the M-chromosome and an autosome (= T^M). The second type has an exchange between the m-chromosome and an autosome (= T^m), and in the third type exchange has taken place between 2 autosomes (= T^a). If exchanges occurred at random between the 3 chromosomes in an irradiated sperm, the T^M- and T^m-translocations would be almost twice as frequent as T^a-translocations according to the length of the 3 chromosomes (I = M or m = 5.6 µm; II = 7.4 µm; III = 8.1 µm). Our observations did not confirm such an expectation (Figure 2 and Table). In all experiments T^a-translocations were more numerous than the 2 other types.

For the time being the most useful translocation is the T^M type. First, it is inherited from the father to all sons. Therefore the selection of males in a translocation strain of this type guarantees that all selected animals carry the translocation. In the 2 other translocation types the translocation is transmitted from the parents to half of the offspring in either sex. The separation of animals with or without translocation in such lines is very difficult or impossible. Second, the T^M translocation can hardly become homozygous because it is linked with the M factor which is always heterozygous in the males. There is the possibility that the T^M translocation can become a T^m translocation, if crossing over occurs between the break point and the M factors. Such an event has so far not been observed in 5 selected T^M strains for over 20 generations and a total of 500–1,000 offsprings. The transformation of a T^M into a T^m translocation would have as a single event no serious influence on a control experiment. Only if the combination of T^M/T^m or T^m/T^m were viable, the depressing influence of the translocation upon a natural population would finally be cancelled. This can happen much earlier with a T^m or a T^a translocation. Therefore we regard T^M translocations at present as the most useful and safe type for practical purposes. That does not exclude the possibility of using an integrated system of one or several translocations, which are viable in homozygous condition, combined with a T^M translocation as a safety measure to prevent the fixing of homozygous translocations in natural populations. We are at present exploring the possibilities of developing such multiple translocation strains.

Frequency of different translocations in *Culex pipiens* in 4 series of tests

Series	No. of translocations	T^M	T^m	T^a
1	31	7	3	21
2[a]	12	5	–	7
3[a]	21	8	–	13
4[b]	17	–	7	10
Total	81	20	10	51

[a] Only sperms with a M-chromosome tested. [b] Only sperms with a m-chromosome tested.

Zusammenfassung. Für die Anwendung von Semisterilität infolge von Translokationen zur Bekämpfung schädlicher Insekten ist der Grad der Semisterilität und die Art der zugrundeliegenden Translokation von Bedeutung. Von den bisher untersuchten 124 Translokationen hatten 101 einen Sterilitätsgrad zwischen 10 und 50%, 23 über 50 bis zu 85%. Mit dem männlichen Geschlechtsfaktor M gekoppelte Translokationen sind zur Zeit die für die Praxis am nützlichsten. Sie treten nicht so häufig auf als erwartet, machen aber doch rund $^1/_4$ aller getesteten Translokationen aus. Es werden Gründe angeführt, weshalb M-gekoppelte Translokationen nützlicher sind.

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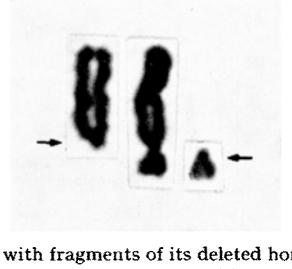
A Possible Case of Centric Fission in a Primate

The main mechanisms in the evolution of mammalian karyotypes have been centric (Robertsonian) fusion and pericentric inversion (Benirschke[1]). However, the origin of some complements with high diploid numbers and a predominance of acrocentric chromosomes is difficult to explain (e.g. Tarsius, Cercopithecus, Canis, Bos, etc.).

In 1967, Todd[2] (v. also[3–5]) put forward a hypothesis of karyotype evolution through succesive cycles of chromosomal fission (explosive or eruptive speciation[6,7]) and chromosomal stabilization by centric fusion and pericentric inversion (adaptive radiation). As we have indicated before[8], the theory is extremely appealing, but although Todd[2] states that 'The fissioning postulated here must be meiotic in vivo, and the negative 'evidence' against it which is principally based on direct somatic or tissue culture preparations is inadmissible', the main objection to the theory has been, precisely, that chromosomal fission has never been observed in a mammal, although it is known to occur in other organisms (Southern[9]).

Recently, we had the opportunity to analyze the chromosomal complement of the same male *Presbytis entellus* studied by Ushijima et al.[10]. The animal had 1 pair of unmatched chromosomes, which had been interpreted as the *X* and the *Y*. However, existing information on the chromosomes of *Presbytis*[11–16] indicates that these chromosomes are really autosomes, and that in our animal one of them must have undergone a deletion of the short arms. In a detailed study of the available pictures from the male *Presbytis* (kindly given to us by Dr. Ushijima), we were able to find 3 metaphases (25%) in which the deleted short arms had not been lost. Morphologically, both autosomal arms seem to have a centromere (Figure). The fissioning event would, then, have produced a stable, long telocentric (present in all metaphases) and a rather un-



Normal autosome, with fragments of its deleted homologous on both sides to show length similarity of short and long arms. Arrows point to centromeres on both fragments.