From the beginning of cytology liliaceous plants have been repeatedly studied from various points of view as favorable material on account of their large-sized chromosomes and of easiness in cytological treatments. However, as far as the writer is aware, reciprocal translocation or interchange of chromosome segments is not reported hitherto in Lilium, although Levan (1935 and 1939) noted a case of reciprocal translocation each in Allium ammophilum and in Allium cernuum. The present writer happened to meet a similar case in Lilium Hansonii Leicht. (Haga 1938), and aims in the present paper, to give a full account of the findings.

Cytological observations were made wholly with the permanent smear preparations of PMCs fixed with La Cour 2BE and stained with gentian-violet according to Newton's procedure.

Meiosis

Generally saying meiosis proceeds quite usually up to the pollen-tetrad stage (Fig. 1). Therefore only specific points will be mentioned below. In PMCs of normal plants twelve bivalents are regularly formed, in this respect no irregularity being observed in 200 first metaphases (Figs. 1a and 2). A plant heterozygous for a reciprocal translocation, which is referred hereinafter as the interchange plant, showed invari-
ably one quadrivalent and ten bivalents. This was ascertained in 342 first metaphase plates (Figs. 1b and 3–8). The metaphase configuration of the quadrivalent pairing was a ring modified by a number of interstitial chiasmata. This mode of pairing of four chromosomes is a conclusive evidence that the translocation is reciprocal. It is quite worth noticing that the quadrivalent shows always two distinct arm pairs, i.e. a pair of very minute arms and a pair of somewhat larger-sized ones. The sizes of these arm pairs correspond exactly with the short arm sizes of A- and B-type chromosomes respectively (Figs. 2–8, cf. Fig. 9). The size of each of these arm pairs was invariable regardless of the number and position of chiasmata formed (Figs. 3–8). This is a clear evidence for the ‘kinetochore pairing’ which is brought about by the kinetochore pair that remains synapsed until metaphase (cf. Matsuura 1935, 1937a, 1938, 1941, et al.). This type of metaphase pairing seems to take place generally, at least before anaphase, notwithstanding the valency of pairing. Really the quadrivalent configuration was always a closed ring except only one case in which the kinetochore pair bearing the larger-sized short arm is appeared separated (Fig. 5, bottom in right column). This constant formation of a ring of four chromosomes is readily and solely explicable with the effect of constant occurrence of kinetochore pairing. Otherwise the quadrivalent should frequently dissolve into a chain of four chromosomes, or of three chromosomes and an univalent, or even into two bivalents. For, the interchange had taken place between major portions
of long arms of two non-homologous A- and B-type chromosomes, both having very minute short arm (cf. Fig. 9). The last fact, that the interchange involves two major portions of chromosomes, is confirmative with the quadrivalent configuration in which the chromosome portion between the synapsed kinetochore and the chiasma nearest to it is remained very short (Figs. 5–8).

In normal plants 2.1 per cent of a total of 240 PMCs and in the interchange plant 2.2 per cent of a total of 831 PMCs showed a chromatid bridge or bridges at first anaphase (Figs. 1f and 10). A majority of bridges were those which do not accompany akinetic (acentric) fragments, two separating sister chromatids being entangled at an interstitial position. Two chromatid portions distal to this position are of equal length (Fig. 10, a–c and g). These entangles are seen to be cancelled out after some unravelling attenuation of the spiralized chromonemata (Fig. 10, d–f and h–i). A similar phenomenon has been illustrated by Richardson (1936) in a hybrid *Lilium Martagon album* × *L. Hansonii*, who inter-
interpreted it as the "drawn-out constriction" of chromatid interlocking which is caused by chiasmata. Further, Darlington (1939) has interpreted the same configuration in *Fritillaria kantshatkensis* as due to "delayed lapse of chromatid attraction." However, in the writer's view such an attachment of the separating sister chromatids as just mentioned above seems to appear as a consequence of half-twisting of the spiralized chromonemata. Anaphase strain between the kinetochore and the twist would unravel and attenuate the spiralized chromonemata. Later the twist would be cancelled by a half turn of the distal portions around themselves, leaving a stretched chromonema portions.

The remainings were bridges accompanying an akinetic fragment (Fig. 10, j–k). Most of the recent cytologists seem to believe the similar bridge as an evidence for crossing-over in an inverted region in organisms heterozygous for it (cf. Darlington 1937). However, here will be emphasized that such bridges may also be originated in chromatid break and fusion, comparable with those induced by X-rays, not in relation to the crossing-over in an inverted region. At least certain proportion of the bridges of this type should be an indication of the new structural reorganization of the chromosomes instead of the evidence for pre-existence of inversions (cf. Haga 1944).

**Fertility**

Pollen of normal individuals of the present *Lilium* plant is uniform in size and structure and is stained deeply with aceto-carmine. These pollen grains apparently represent functional ones. Proportion of these good pollen was 94.6 per cent in a total of 1000 pollen grains. Remaining pollen (5.4 per cent) was shrivelled empty. The latter represents
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doubtlessly the sterile pollen. Whereas pollen grains of the interchange plant was nearly totally shrivelled ones, rarely occurring plump pollen being also abnormal in their stainability. The proportion of these bad pollen had amounted to as high as 99.8 per cent in a total of 1000 pollen grains, only 2 (0.2 per cent) being seemingly normal in appearance (Fig. 11).

Usually interchange heterozygotes are known to show 50 per cent pollen sterility. Therefore such an extraordinary high pollen abortion as in the present case is exceptional, representing an extreme against several interchange heterozygotes in *Triticum monococcum* and *T. durum* which show "nearly normal fertility, both of seeds and pollen" (Thompson and Thompson 1937). Yet the present case will be properly explained assuming the following mechanism of the meiotic segregation of the ring of four chromosomes. As above mentioned kinetochores located on the homologous parts of the ring maintain their synapsis up to the metaphase, so a pair of synapsed kinetochores in a ring—a repulsion system—will orientate itself along the spindle axis at full metaphase. This was confirmed in side views of several first metaphases (Figs. 4 and 8). From this type of metaphase orientation of the ring only unbalanced pollen will be resulted as the two adjacent chromosomes paired by kinetochores pass to the same pole (cf. Matsuura 1937b). The degree of pollen abortion in the present interchange plant suggests that in almost all of the cases a pair of synapsed kinetochores of the quadrivalent ring orientates itself along the spindle axis at full metaphase. Contrarily to the present *Lilium* case, the complete fertility in the *Triticum* cases above cited is revealed cytologically as due to the constant alternate or zig-zag orientation of the four chromosomes.

Normal as well as interchange plants do not set seeds by natural pollination or even by the carefully made intra- and inter-individual artificial pollination. This fact was experienced with several dozens of plants which were observed yearly from 1938 to 1941. Exceptionally two plants yielded some fully developed capsules in autumn of 1940 though
Fig. 12. Capsules at autumn. a, two normal plants. b, two interchange plants. Note the shrivelled capsules showing no development and exceptional individual bearing some fully developed capsules containing certain proportion of good seeds. ×1/4.

majority of seeds were empty (Fig. 12). One of these two plants was normal individual and the other the interchange plant. The reason for the nearly complete defect in seed production of the present *Lilium*, including normal individuals, is not clear as yet. Exceptional capsule development just above mentioned seems to suggest the physiological cause, but the conclusion must be left for further investigations.

**Summary**

1. A plant heterozygous for a reciprocal translocation was found in *Lilium Hansonii* Leicht. Metaphase pairing of the four chromosomes was nearly always a ring modified by a number of interstitial chiasmata.

2. Kinetochores of homologous chromosomes or of homologous segments maintain their prophase synapsis up to the first metaphase.

3. At first anaphase two types of chromatid bridges were observed, viz. bridges accompanying akinetic (acentric) fragments and those not accompanying them. These bridges occur in normal as well as in the interchange plant. The latter type of the bridges is interpreted as those caused by a half-twist around the spiralized sister chromonemata.

4. Pollen of the normal individual is of quite normal appearance (94.6 per cent). In the interchange plant pollen is nearly totally abortive (99.8 per cent). Such an unusually high pollen abortion was explained as follows: A pair of synapsed kinetochores in the ring of four chromo-
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somes—a repulsion system—orientates itself along the spindle axis at full metaphase. Consequently two adjacent chromosomes pass to the same pole, leading to the unbalance of chromosome set of all the pollen.

5. Normal plants as well as the interchange plant were completely defective in seed production except the two exceptional cases in which some capsules containing some good seeds were developed. The reason for this remains for further investigations.

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