FROM the observation that broken ends of chromosomes will seek to unite with other broken ends rather than become healed MULLER (1932) concluded that the free ends of chromosomes must contain a structural element necessary for the existence of the chromosome as a unit, which he called a telomere. If this is true, the existence of deficiencies or inversions at the tip of the chromosome becomes an impossibility. There are some exceptions which Muller concedes and considers to be “mutations of an interstitial gene into a terminal one.” (This is not the place to criticize this use of the words gene and mutation for a chromosomal structure and its change; it is objectionable, we think, to speak of a structural feature like the telomere in terms of genes, whatever idea of the gene we may entertain.) Actually, truly terminal deficiencies have been found not only in maize but also in Drosophila (DEMEREC and HOOVER 1936, SUTTON 1940), some of Drosophila deficiencies being in use as standard tester stocks. The salivary structure is in these cases (re-checked by us, though this was unnecessary) unequivocal (about others see below).

Meanwhile the junior author (KODANI 1942) demonstrated the actual existence of a visible structure at all free ends of the salivary chromosomes in D. melanogaster which might represent MULLER’S theoretical telomeres. By proper chemical treatment the end disk uncoils—as all bands do—into a number of so-called perultimate chromomeres which are distinguishable from those of other bands by their size, smaller number, and different solubility. These findings drew our attention to the general problem of the telomere and made us reconsider the interpretation of a set of observations which we had made in another line of work and had originally interpreted as small terminal deficiencies and translocations. This reconsideration was also favored by the work of HINTON and ATWOOD (1941) who described terminal adhesions of the free ends of the salivary chromosomes as a typical feature with varying percentages for different chromosomes and stocks. The junior author had frequently seen the same thing and we could now attribute the phenomenon to a special property of the visible telomeres, which one might call stickiness (see GOLDSCHMIDT and KODANI 1942).

The facts to be reported here were found when certain stocks belonging to or derived from a mutable stock were carefully scrutinized for the smallest rearrangements. What looked like terminal deficiencies and small translocations were found in different chromosomes of this stock as a typical feature (they were also found in a homozygous condition), and we tried in vain to relate them to definite genetical facts. The most frequent case was a deficiency of the first four bands in the X chromosome accompanied by a small translocation to the
tip of IIIR. As Sutton (1940) had found that even a two-band deficiency here had a yellow heterozygous effect (if opposite yellow), numerous tests were made for y and ac (actually before Sutton's paper had appeared, and repeated afterwards), which were always negative. However Demerec and Hoover found a four-band deficiency, morphologically identical to the one mentioned above, which had no visible effect; a strange and unusual disagreement with Sutton's findings—the importance of which has been discussed in a paper now in press. Our suspicions were aroused when we found the same tip deficiencies in other stocks, even in wild stock though less frequently, and we finally came to the conclusion that we were studying pseudo-deficiencies, caused by mechanical breakage of attached tips during the procedure of smearing. This interpretation would throw suspicion upon apparently similar cases described by others, as will be discussed below. The following observations suggest that no special explanation may be needed for such cases.

**Table 1**

<table>
<thead>
<tr>
<th>STOCKS</th>
<th>px bl</th>
<th>poi</th>
<th>poi px bl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heterozygous matings</td>
<td>17</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>Homozygous matings</td>
<td>6</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Slides heterozygous ♀</td>
<td>49</td>
<td>59</td>
<td>20</td>
</tr>
<tr>
<td>Slides homozygous ♀</td>
<td>18</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Slides heterozygous ♂</td>
<td>30</td>
<td>26</td>
<td>10</td>
</tr>
<tr>
<td>Slides homozygous ♂</td>
<td>12</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

Rearrangement in heterozygous ♀ found in n glands (but not all nuclei), ♂ glands in parentheses.

1. Df(1)1A1-4 22 glands 42 glands 5 glands
2. Df(2R)6oF4-5 20(8) 9(4) 2(2)
3. T(3L)6tA 7(1) 17(2) 2
4. T(3R)10cF 10(5) 38(13) 5(4)

Rearrangement in homozygous ♀ (♂)
3. T(3L)6tA 5(1)
4. T(3R)10cF 3 1

Together in same gland, rearrangement No.
1, 2, 3, 4 3 times 3 times
1, 2, 3 1 2
1, 2, 4 3 — 1
2, 3, 4 6 1
1, 3, 4 — 4
1, 2 4 1 1
2, 3 1 1
2, 4 3 4
1, 3 1 3
1, 4 2 25

Table 1 contains the results of a statistical survey carried out for three stocks marked px bl, poi, and poi px bl. In this survey the four types mentioned in the tables were found: (1) Df(1)1A1-4, absence of the first four bands at the tip of the X chromosome; (2) Df(2R)6oF4-5, absence of two bands at the tip of IIIR; (3) T(3L)6tA, an apparent translocation of the tip of the X chromosome to the end of IIIL, that is, the same as described by Muller; and (4)
T(3R)100F, that is, the same attachment to IIIR. In other slides, not belonging to the series made for statistical study and thus not contained in the table, tip deficiencies for III, IIIR, and IV were also found. These are pictured in figures 4, 9, 11. The procedure in the study to which the table refers was this: A number of crosses were made in both directions between the three stocks and Oregon wild. For each cross a number of one-gland slides were made, using female as well as male larvae. Further, a number of pairs of the pure stock were mated and handled in the same way, and for all these slides the presence of the four types of "deficiencies" or "translocations" in any nucleus of a gland was marked. All those reported in the table, including those marked in the column of homozygous slides, were heterozygous, that is, one tip only was affected. However, the homozygous condition (both tips) was frequently found, though less so than the heterozygous condition (see figs. 6, 8, 12). This difference may not be significant, as the homozygous condition might be overlooked in more contracted chromosomes.

The number of nuclei within one gland which showed the deficiencies and translocations was highly variable, as was also the number of these aberrations in a single nucleus. The most frequently found types (Df(1) and T(3R)) occurred in most nuclei of a gland simultaneously but normal nuclei were always found (about 10 percent). The less frequent types (2, 3 in table 1) were less often found together. Again the combinations of Df(1) and T(2)R or T(3L) were more frequent.

Table 1 shows a very high incidence of the pseudo-deficiencies and translocations of the type 1 and 4. Whether the differences between the stocks are significant is difficult to tell. It is remarkable that the heterozygous changes were rather rare in the homozygous stocks though the homozygous condition was present (not marked in the table). This indicates that breakage is more easily accomplished in our mutant stocks than in the wild stock.

We anticipated the conclusion that we were dealing with pseudo-deficiencies and translocations. Our conclusion is that the cohesion of the chromosome tips (by stickiness of the telomeres) is stronger than the cohesion within the chromosome itself near the tip and that therefore, in smearing the preparations, the tips with two to four bands are broken off and become stuck to the ends of

**Explanation of Figures 1-12**

**Figure 1.**—Association and pulling apart of tips of X and IIIR (poi/+).
**Figure 2.**—Pseudo-deficiency of X A1-4 with thick terminal band (poi/+).
**Figure 3.**—The same.
**Figure 4.**—Pseudo-deficiency tip III (new dp/+).
**Figure 5.**—Pseudo-translocation to tip of III (poi/+).
**Figure 6.**—Homozygous pseudo-deficiency tip of X (poi).
**Figure 7.**—Pseudo-deficiency IIIR tip (poi/+).
**Figure 8.**—Homozygous pseudo-translocation to IIIIR tip (px bl).
**Figure 9.**—Pseudo-deficiency tip IIIIR in wild stock (Canton × Oregon).
**Figure 10.**—Pseudo-translocation X to IIIIR (poi/+).
**Figure 11.**—Pseudo-deficiency tip of IV (new giant/+).
**Figure 12.**—Homozygous pseudo-translocation to tip of X (px bl).
other chromosomes. The data of the table indicate the highest degree of stickiness between X and IIIR, and the lowest cohesion within the chromosome near the tip of X. If this interpretation is correct, the apparent translocations ought to be always in inverted position. Unfortunately this could not be checked since the bands in the "translocated" piece of the X chromosome were too faint for reliable seriation. But a condition such as is pictured in figure 5 looks like an inverted translocation.

Such pictures as the one figured in figure 1 seem to show how the tip of a chromosome is pulled off under mechanical stress after sticking to another tip. In figures 2–10 the appearances of these pseudo-deficiencies and translocations are reproduced (for description of aberrations see explanation of figures). It was observed that rather frequently, though not always, the half-band adjoining the break was much thicker than the other half. Muller might have interpreted this (in case of a genuine deficiency) either as a translocation of a telomere from another chromosome or as a "mutation" of an ordinary band into a telomere. What the phenomenon means in our case of pseudo-deficiency is difficult to say. We assume that in such a case only three bands have been broken off and that the interval between the fourth and fifth was ruptured by the stress and consequently the fourth and fifth bands appear as a single thick one. We shall try to make special checks on the telomeres with Kodani's method, if this is technically possible. The illustrations contain also a number of heterozygous and homozygous pseudo-deficiencies and translocations not found in the table. They are described in the explanation of the figures.

DISCUSSION

The interpretation of our findings as pseudo-deficiencies or translocations is based upon the frequency of these tip changes in many unrelated stocks, the certainty of their presence in only a part of the nuclei of a gland, Hinton and Atwood's findings concerning the union of chromosome tips, and upon such pictures as are presented in figure 1. (To this might be added that Bridges once told the senior author, when discussing the variable aspect of the tip of X in standard slides, that in his experience this tip was easily broken off in the handling of the chromosomes.) It may be asked whether our conclusion can be extended also to cases described as real rearrangements. Thus, Muller (1941) found a scute-J4 with a terminal deficiency and the missing piece apparently attached to the end of IIIL. Muller calls this a double miracle (from the standpoint of his theory of the telomere) and postulates that a minute and invisible end piece of II must have been attached to the tip of X. We suspect this case to be in the same category as ours. Demerec and Hoover's four-band deficiency of the X is present in all nuclei. This is a genuine deficiency if there is no indication that the missing four bands have been translocated to the tip of IIIR. Among the tip deficiencies described by Bridges in D.I.S. No. 9 one, Df(2)OreR, is described as "apparently" homozygous, two others are described as homozygous (Df(2)SwL and Df(2)SwR), and two others (Df(3)D3H and Df(3)MzL) are mentioned only as observed in slides. All of these ought
to be rechecked nucleus by nucleus, as a number of clear findings in one gland might have prevented searching for normal nuclei.

SUMMARY

Apparent small endwise deficiencies and translocations in Drosophila were found to be only pseudo-deficiencies and translocations, produced by mechanical breaks near the chromosome tip following cohesion of the telomeres at the tips of two chromosomes. Different chromosomes and strains are more or less apt to undergo such subterminal breaks.

LITERATURE CITED