Relational Coiling in *Tradescantia*, *Allium* and *Vicia Faba*

By

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At earliest prophase of the microspore mitosis in *Tradescantia*, *Allium*, and *Vicia* the minor spirals of the previous anaphase chromosomes are still present, although somewhat relaxed. As prophase advances the old minor, or relic spirals, relax more completely and the gyres of these spirals increase in diameter and decrease in number as new minor spirals are formed in each chromatid. When the relic spirals have been eliminated, new minor spirals are well developed, and the two chromatids of each chromosome tend to be relationally coiled (twisted or bent around each other). The chromosomes become shortened and the gyres of the new minor spirals (in *Tradescantia*), like the gyres of the relic spirals, increase in diameter and decrease in number until 20–25 remain in each chromatid. The amount of relational coiling is reduced as the chromosomes are shortened during late prophase and little remains at metaphase.

In meiotic prophase new minor spirals are not formed until the minor spirals of the premeiotic anaphase chromosomes have been eliminated and homologous chromosomes have become intimately associated throughout a part or all of their length. At diplotene, the stage when minor spirals have formed in meiosis, homologous chromosomes appear to be associated by means of chiasmata and often relationally coiled.

A study of relational coiling in the somatic prophase and gametophytic mitosis of *Fritillaria* has been reported by Darlington (1935). The two chromatids at early prophase of these divisions are closely associated, have relic and super-spirals in common, and “are tightly coiled round one another.” The number of relic spirals and the amount of relational coiling of chromatids decrease as prophase advances. The relational coiling of chromatids and the super-spirals correspond approximately in number and sometimes in direction. According to Darlington (1936), the direction of relational coiling “shows no consistency” at mitotic metaphase in *Spironema*, *Crocus graveolens*, *Pushkinia libanotica*, and some in *Nomocharis saluenensis*. At early anaphase in *Fritillaria Elwesii*, *F. verticillata*, *F. pluriflora*, and *F. recurvata* the two pairs of “M” chromosomes have
the consistent property (with 1 exception) of one arm's coiling left and the other right. In *F. Elwesi* the longer arm of each "M" chromosome coils left. Two of the "M" chromosomes have a shorter arm with a secondary constriction. This arm always shows coiling in the right-hand direction. In the 5 pairs of "M" chromosomes of *F. ruthenica* the direction of coiling appears to be at random.

Sax (1936) has analysed the relational coiling of chromatids in the somatic chromosomes of *Trillium grandiflorum* and *Vicia faba*. The direction of relational coiling is found to be approximately at random for the 2 arms of a chromosome and for identical arms of homologous chromosomes; in any one chromosome arm it is rarely reversed, and there is no evidence that it is transferred from one arm to the other of the same chromosome.

Darlington (1936) considers that the chromosome split takes place along a surface which will divide the spiral chromosome in such a manner that when the halves are straightened out without rotation of their ends, they will lie parallel, in one plane; and that the relational coiling of chromatids at mitotic metaphase is "due to the chromatids being dragged round one another during spirilisation..." Relational coiling at mitotic prophase is thought likewise by Husted (1936) to be a result of the formation of new minor spirals.

It is probable that the tendency to twist or bend around each other, which chromatids in mitosis and paired chromosomes in meiosis exhibit, is basically the same phenomenon and inherent, to a variable degree, in all chromosomes. The part relational coiling may play in the process of chiasma formation is not clearly understood (cf. Darlington, 1935; Sax, 1936). Sax and Sax (1935) have observed that the chromatids of *Vicia faba* (chiasma frequency of "m" chromosome = 2.63) in root tip cells are twisted about each other to a greater extent than the chromatids of *Tradescantia paludosa* (chiasma frequency = 1.87) in the microspore mitosis. In view of this observation it is desirable that a study be made of the amount of relational coiling in plants with different chiasma frequencies at the prophase of mitotic divisions which are comparable.

Microspores of *Tradescantia paludosa*, *Allium cepa*, and *Vicia faba* were fixed in Farmer's solution (Chamberlain, 1924) at a temperature slightly below 0°C. for 15 hours or longer. The first gametophytic mitosis was studied in somewhat flattened aceto-carmine smear of the previously fixed material. The cold fixation resulted in more sharply differentiated chromatids. It eliminated the tendency for chromatids and chromosomes to "run together", which is so often encountered in aceto-carmine preparations of *Allium* chromosomes.
Amount of Relational Coiling

The haploid complement \textit{T. paludosa}, as seen at metaphase in the first mitosis of the microspore, is made up of 6 chromosomes with median or submedian attachments. The chromosomes average approximately 12 $\mu$ in length and the chromatids 1.5 $\mu$ in diameter at metaphase of this division. At pachytene they average ca. 81 $\mu$ in length, and at meiotic metaphase ca. 9 $\mu$ (Sax and Sax, 1935). The chiasma frequency varies considerably in different plants of the species. In the plant used for this study (13-1), 191 chiasmata were found in 17 pollen mother cells at metaphase, or 1.87 chiasmata per bivalent. This agrees with the chiasma frequency of 1.9 reported for \textit{T. paludosa} (plant 13-1) by Anderson and Sax (1936).

Table 1. Amount of relational coiling in half turns or overlaps at mid-prophase of the microspore mitosis

<table>
<thead>
<tr>
<th>Species</th>
<th>Half turns per chromosome</th>
<th>Average number of half turns per chromosome</th>
<th>Number of chromosome</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>\textit{V. faba}</td>
<td>4</td>
<td>31</td>
<td>42</td>
</tr>
<tr>
<td>\textit{A. cepa}</td>
<td>6</td>
<td>19</td>
<td>28</td>
</tr>
<tr>
<td>\textit{T. paludosa}</td>
<td>3</td>
<td>8</td>
<td>18</td>
</tr>
</tbody>
</table>

At the prophase of the first microspore mitosis, when the relic spirals have been practically eliminated and new minor spirals are well formed, the two chromatids of each chromosome are seen to be independently spiralled and usually relationally coiled. At this stage (fig. 1) the chromosomes are approximately 3 times their shortest length as seen at late metaphase (fig. 3). The chromatids make 0–6 half turns around each other, 2 or 3 half turns being the most often encountered numbers (table 1). The mean number of half turns per chromosome at this stage is 2.32. As the chromatids increase in diameter and decrease in length, the amount of relational coiling is decreased. At late prophase or early metaphase (fig. 2) the chromatids, for the most part, lie parallel, but overlaps and an occasional complete half turn are found. At late metaphase (fig. 3) overlaps are present but no complete half turns. The average number of overlaps per chromosome is 0.56 (table 2) at this stage.

The haploid complement of \textit{A. cepa} is composed of eight chromosomes. Seven have median or submedian attachments. The attachment of 1 is subterminal. The chromosomes average approximately 8 $\mu$ in the length and the chromatids 1.5 $\mu$ in diameter at the meta-
phase of the microspore mitosis. At pachytene they average approximately 69 μ and at meiotic metaphase approximately 9 μ (Sax and Sax, 1935). One hundred sixty-one chiasmata were found in 10 pollen mother cells at metaphase, a mean chiasma frequency of 2.01 per bivalent.

Text-figs. 1–9. Prophase, early and late metaphase chromosomes as seen at the first mitosis in the microspores of Tradescantia paludosa, Allium cepa, and Vicia faba. 1–3, T. paludosa; 4–6, A. cepa; 7–9, V. faba. The chromosomes in figs. 3, 5, 8 and 9 have been spaced for clearness. × ca. 1570.

When the relic spirals are practically eliminated from the chromosomes and the new minor spirals are well developed, (fig. 4), the chromosomes are approximately twice their shortest length as seen at late metaphase (fig. 6). At this stage the chromatids make 0–5 or 6 half turns around each other, 2 half turns being the number most often found (table 1). The mean number of half turns per chromosome is 2.07. At a later prophase stage when the chromatids have increased in diameter and decreased in length, 117 half turns
or overlaps were found in 94 chromosomes; an average number of 1.2 half turns or overlaps per chromosome. At late metaphase (fig. 6) no complete half turns and few overlaps were found. The average number of overlaps at this stage was 0.26 per chromosome (table 2).

The haploid complement of *Vicia faba* is made up of 1 "M" chromosome with an approximately median attachment and a secondary constriction in one arm, and 5 "m" chromosomes which are indistinguishable and have subterminal attachments. The "M" chromosome measures ca. 21 μ in length at metaphase of the first mitosis in the microspore, and the "m" chromosomes average ca. 10 μ. The chromatids at this stage are ca. 1.2 μ in diameter. At pachytene the "m" bivalent averages ca. 84 μ in length and at meiotic metaphase ca. 8 μ (calculated from data of Sax and Sax, 1935). The mean chiasma frequencies reported for the "M" bivalent at meiotic metaphase are 8.10 (Maeda, 1930), 6.75 (Sax, 1935), and 7.06 (Mather and Lamm, 1935). The "m" bivalents have mean chiasma frequencies of 3.5 (Maeda, 1930), 2.63 (Sax, 1935), and 3.42, according to Mather and Lamm (1935). The chiasma frequency of the "M" bivalent recorded by the three authors is over twice that of an "m" bivalent. Although the frequencies reported by Maeda, Sax, and Mather and Lamm do not agree perfectly, they are significantly higher than the chiasma frequency at metaphase in *T. paludosa* and *A. cepa*.

When the relic coils have been practically eliminated at prophase of the microspore mitosis in *Vicia*, the "m" chromosomes (fig. 7) are approximately twice their metaphase length (fig. 9). This appears to be at a somewhat later period than is the case in *A. cepa* and *T. paludosa*. The chromatids of the long arm of the "m" chromosomes at this (fig. 7) and a slightly earlier stage make 0–6 half turns about each other, 3 half turns being the most common number encountered (table 1). The mean number of half turns per "m" chromosome (long arm) at this prophase period is 2.40. As the chromatids become shortened and their diameter increased, the amount of relational coiling is decreased. At late metaphase the chromatids of both "M" and "m" chromosomes may lie parallel.
Complete half turns as well as overlaps, however, are found at this stage (fig. 9). The chromatids of the longer "M" chromosome average 1.92 half turns or overlaps, while the chromatids of the long arm of the "m" chromosome average 0.6 per chromosome (table 2). The average amount of relational coiling in the "M" chromosomes of *Vicia* is over twice the average amount in the shorter chromosomes. The chromatids of the "m" as well as the "M" chromosomes may make complete half turns around each other at late metaphase. In *A. cepa* and *T. paludosa*, where the chromosome arms are shorter than the long arm of the "m" chromosome of *Vicia* only overlaps are found at this stage.

**Direction of Relational Coiling**

The results of an analysis of the direction of relational coiling in the two arms of 90 chromosomes of *Tradescantia*, 23 "M" chromosomes of *Vicia*, and 94 chromosomes of *Allium* are shown in table 3. The direction of coiling appears to change at the attachment point in approximately a third of the chromosomes in *Tradescantia* and *Allium*. In *Vicia* the direction seems to be more nearly random as reported by Sax (1936). The data in *Allium* were taken at prophase or very early metaphase. It is doubtful if external influences such as cytoplasmic streaming, a possibility pointed out by Darlington (1936), have removed old coils and formed new ones.

**Table 3.** Direction of relational coiling at prophase or early metaphase

<table>
<thead>
<tr>
<th>Species</th>
<th>RR</th>
<th>RL</th>
<th>LL</th>
<th>RO</th>
<th>LO</th>
<th>R</th>
<th>L</th>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>V. faba</em></td>
<td>××3</td>
<td>8</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>52</td>
<td>×××</td>
<td>× Present but not recorded</td>
</tr>
<tr>
<td><em>A. cepa</em></td>
<td>14</td>
<td>22</td>
<td>35</td>
<td>85</td>
<td>85</td>
<td>95</td>
<td>85</td>
<td>××&quot;M&quot; chromosome</td>
</tr>
<tr>
<td><em>T. paludosa</em></td>
<td>30</td>
<td>35</td>
<td>25</td>
<td>×</td>
<td>×</td>
<td>95</td>
<td>85</td>
<td>×××Long arm,&quot;m&quot; chromosome</td>
</tr>
</tbody>
</table>

The direction of relational coiling in 100 long arms of the "m" chromosomes of *Vicia* is also shown in table 3, together with figures on the coiling in single arms of *Tradescantia* and *Allium* chromosomes, derived from the study of relational coiling in whole chromosomes. In the three species approximately half of the arms show right-hand relational coiling and half are coiled in the opposite direction.

**Discussion**

The chromosomes of *Tradescantia* and the "m" chromosomes of *Vicia* have approximately the same expanded length at pachytene
and contracted length at metaphase of the microspore division. The chromatids of *Vicia* at metaphase are slightly more slender than the chromatids of *Tradescantia*. The expanded and contracted lengths of the *Allium* chromosomes are roughly proportional to, but less than, the expanded and contracted lengths in *Tradescantia*. Their diameters at metaphase are the same. (See table 4).

The average number of half turns per chromosome in *Allium* and *Tradescantia*, and in the long arm of the “m” chromosome of *Vicia* are not significantly different. In *Tradescantia* the chromosomes are long at the prophase stage studied. It is doubtful if the amount of relational coiling is greatly reduced in these chromosomes, prior to the stage illustrated in fig. 1. In *Allium* the chromatids, at a prophase stage which is considered comparable to the *Tradescantia* prophase, are relationally coiled to the same extent as those in *Tradescantia*, but the chromosomes are half as long. It is possible, because of the greater contraction, that even more relational coiling than has been demonstrated in *Allium* may exist at an earlier prophase stage. The average amount of relational coiling in the long arm of the “m” chromosome of *Vicia* is the same as the amount found in the entire chromosome of *Tradescantia*. The long arm of the “m” chromosome of *Vicia*, however, is shorter than the length of the average *Tradescantia* chromosome at metaphase. It is possible that in *Vicia*, for the same reason given for *Allium*, more relational coiling than has been shown to exist is present at an earlier prophase stage.

The average chiasma frequency per bivalent at metaphase is 1.87 in *T. paludosa*. Although the chromosome length which may associate at meiotic prophase in *A. cepa* is less than the length in *Tradescantia*, the chiasma frequency in *A. cepa* is slightly higher —2.01 per bivalent. In *A. cepa* the amount of relational coiling per

### Table 4. Summary of data on chromosome length, diameter, relational coiling of chromatids, and chiasma frequency

<table>
<thead>
<tr>
<th>Species</th>
<th><em>Vicia faba</em></th>
<th><em>Allium cepa</em></th>
<th><em>Tradescantia paludosa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Average amount of relational coiling in half turns</td>
<td>2.40**</td>
<td>2.07</td>
<td>2.32</td>
</tr>
<tr>
<td>Average length of pachytene chromosomes</td>
<td>84μ</td>
<td>69μ</td>
<td>81μ</td>
</tr>
<tr>
<td>Average length of mitotic metaphase chromosomes</td>
<td>10μ</td>
<td>8μ</td>
<td>12μ</td>
</tr>
<tr>
<td>Average diameter of metaphase chromatids</td>
<td>1.2μ</td>
<td>1.5μ</td>
<td>1.5μ</td>
</tr>
<tr>
<td>Average chiasma frequency per bivalent</td>
<td>2.63-3.5</td>
<td>2.01</td>
<td>1.87</td>
</tr>
</tbody>
</table>

* “m” chromosomes. ** Long arm only.
unit of chromosome length is greater than in Tradescantia. The average chiasma frequency per “m” bivalent at metaphase in V faba grown at the Arnold Arboretum is 2.63. In these bivalents terminal associations are often found between the short arms of the homologous chromosomes and have been classed as chiasmata (Sax, 1935). The terminal association between short arms seems to be present in at least a half of the “m” bivalents. The chiasma frequency between the long arms of this chromosome is probably more nearly 2 per bivalent. This frequency corresponds with the chiasma frequency in A. cepa. The average amount of relational coiling in an Allium chromosome and the average amount in the long arm of the “m” chromosomes of Vicia are the same. The average length of the Allium chromosomes and the long arm of the “m” chromosomes are nearly the same. Their lengths might be more nearly identical if the diameter of the chromatids in Vicia was greater. In V faba, as in A. cepa, the amount of relational coiling per unit of chromosome length is greater than in T. paludosa.

The results given here are suggestive, but no very definite conclusions can be drawn at present. The differences in chromosome length and chiasma frequency are small. The pachytene lengths are only approximate. Sax and Sax (1935), whose data have been used, experienced difficulty in selecting strictly comparable stages and in accurate measurement of the stages selected. Pachytene pairing is not known to be complete in all the forms studied. Approximately the same amount of relational coiling exists in a prophase chromosome of T. paludosa, A. cepa, and in the long arm of an “m” chromosome of V. faba. If metaphase lengths are an indication of expanded lengths, or if the pachytene measurements are relatively correct, the amount of relational coiling at mitotic metaphase per unit of chromosome length is greater in the species with the higher chiasma frequencies, A. cepa and V faba. In these plants with higher chiasma frequencies the paired chromosomes at pachytene may be shorter, but the tendency to become relationally coiled, twisted, or bent around each other, may be greater. This more pronounced tendency seen at mitotic prophase may be a factor operative at meiotic prophase and resulting in the higher chiasma frequencies at metaphase.

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Literature Cited


