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On the Correlation between the Satellite of Chromosome and the Leaf Shape in Parideae from Hokkaido

By

ISAMU STOW

The correct basic number of chromosomes of Parideae was determined as five by Gotoh and Stow (1930) who found that these five chromosomes of each species are different in size and shape from each other. Moreover, four of these five types of chromosomes are like not only among the different species of the same genus, but also in the two different genera, Paris and Trillium. The fifth chromosome type of Paris, however, differs in each species respectively, while in Trillium it is always almost similar in shape. Gotoh (1933) studied further this relation with an American species of Trillium and found that its basic number of chromosomes is also five and that the types of these five chromosomes are similar to those of the Japanese Trillium. Haga (1934) made a very close investigation with Japanese Parideae and confirmed the results of Gotoh and Stow (1930).

Satellites were first reported by S. Nawaschin (1912) in Galtonia candicans, and afterwards many other plants1) were found, which carry satellites of various types.2) The asymmetry3) of nuclei in connection with the occurrence of satellites was also ascertained by the same author (1912) in Galtonia and in Muscari by Delaunay (1915). Such asymmetry or elimination of satellites is often accompanied by deviation of some physiological or morphological characters as seen in Galtonia (S. Nawaschin 1915), Muscari (S. Nawaschin 1915, Delaunay 1915) or Crepis (M. Nawashin 1925, 1926) etc.

Although there have been many cytological investigations on Parideae4), the relation between the chromosome types and the morphological characters of these plants have been studied very

1) See Kuhn (1928).
2) See Delaunay (1929).
3) The term “asymmetry and symmetry” of nuclei is used in the same sense as by S. Nawaschin.
4) See Haga (1934), Huskins and Smith (1935), Smith (1935) and Matsuura (1935).

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rarely. In a joint work with Gotoh (1930), the present writer reported that the diploid plant of Paris of the asymmetrical type with regard to the satellite grows more vigorously than the symmetrical ones, as confirmed in Galtonia (S. Nawaschin 1912) or Muscari (S. Nawaschin 1915, Delaunay 1915) and that the ratios of the breadth to the length of the laminae of the asymmetrical type are greater than those of the symmetrical ones. By a re-examination of the results of the former investigation and by further studies, the writer has found a noticeable relation between the satellites and an outer morphological character of the leaf.

Material and method

The materials used in the present investigation are as follows: Paris hexaphylla Cham., Paris tetraphylla A. Gray, Trillium kamtschaticum Pall., Trillium Tschonoskii Maxim. and Trillium Smallii Maxim. The majority of these materials were collected in the vicinity of Sapporo, and some of them in the Botanical Garden of the university, where they grew under the wild condition.

Flemming-Bonn and Navashin's fluids were employed for the fixation of the root-tip, both normal and chloralized materials, after Sakamura's procedure (1920). The microtome sections were stained with HEIDENHAIN's iron-alum hematoxylin or with MACCLINTOCK's iodine crystal violet; in both cases the results were satisfactory. For the fixation of the anther, in which the reduction division in the pollen-mother cells occurred, Flemming-Bonn solution was chiefly employed and the sections were stained with HEIDENHAIN's iron-alum hematoxylin with fairly good results. The most satisfactory result, however, was obtained with the iron-acetocarmine method.

The size of the angle between the two edges of the leaf margin at the base was calculated in a simple geometrical way. No doubt the leaf margin does not show a straight, but a curved line. In order to simplify the calculation, the writer treated it as a straight line, for its curvature is not remarkably great. Now let us consider a triangle \( \triangle OBC \) (Fig. 1) whose base BC is the maximum width of laminae and the apex O is the leaf base. It is easy to measure the size of the angle between the two edges of the leaf margin at the base, which will be

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1) In the previous paper (Gotoh & Stow 1930) the synonymous name T. apetalon Makino was used.
2) The formalin is reduced to 1/4 of the original receipt.
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indicated hereafter by $\theta$ for simplifying the description, assuming it to be approximately equal to the angle $\angle BOC$. Measuring the length BC, the maximum width of the laminae, and the height OD, the vertical line from O to BC, one can obtain the value of $\theta$ from the following formula:

$$\tan \frac{\theta}{2} = \frac{BC}{2 OD}$$

In some materials the mean values of both BC and OD from many leaves were used for the calculation of $\theta$, while in the others the calculation was made with each leaf separately and then the mean value of $\theta$ was obtained.

The $\theta$ value thus obtained is somewhat smaller than the value of the angle between two tangent lines (OB' and OC') and this error becomes larger, the wider the laminae. Nevertheless there is no marked objection to assuming $\angle BOC$ as equal to $\theta$, because this error does not extend beyond the limit of the purpose of the present investigation.

Results

The chromosome set of Parideae consists of five chromosomes having different size and shape (Fig. 2).

a-chromosome: The largest V-shaped chromosome with a median attachment (52% of the total length from one end).

b-chromosome: A V-shaped chromosome about 2/3 as long as the a-chromosome with a submedian attachment (58%–62% of the total length from one end).

c-chromosome: A J-shaped chromosome with an atelomitic attachment (70%–74% of the total length from one end), somewhat shorter than the b-chromosome.

1) The size of the leaves was measured with the materials in bloom except T. Smallii, which was measured after bloom. The angle $\theta$ becomes somewhat smaller, when the material bears the berry.

2) See also Gotoh and Stow (1930), Gotoh (1933), Haga (1934 a and b), Matsuura (1934), Huskins and Smith (1935).
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**d-chromosome:** The shortest V-shaped chromosome, about half as long as the a-chromosome, with a submedian attachment (60%–64% from one end).

**e-chromosome:** A J-shaped chromosome with a subterminal attachment, of median length between the c- and d-chromosome. In the case of *Paris*, it carries a satellite on the proximal knob, while in *Trillium* it has no satellite.

There are slight differences between the chromosomes of the same type among the different species except in the e-chromosome, so the chromosomes can be distinguished by precise measurement and observation. In the case of the e-chromosome, especially in *Paris*, however, there are characteristic differences between one species and another. The e-chromosome of *Paris hexaphylla* has a somewhat large oblong satellite on the proximal knob with a short connecting filament, and that of *P. tetraphylla* has a relatively large stick shaped satellite, which is thicker than a mere connecting filament. In the first nuclear division of the pollen grain, one can find a spiral with long pitch, deeply stained with iron-acetocarmine, and embedded in the weak stained ground matrix substance¹ (Figs. 11a and b). Therefore, the stick shaped portion may be considered as an elongated satellite². The satellite of the e-chromosome of *P. japonica* is of a characteristic tandem shape (Haga 1934a). In the case of *Trillium*, however, the e-chromosome has only a knob, but no satellite, and only slight differences in the size of the knob or the limb can be recognized between the different species. The e-chromosome of *Trillium kamtschaticum*, first nuclear division in the pollen grain, anaphase, e-chromosomes indicated by solid black. 1000x

¹ At the kinetic constriction of the chromosome of *Paris* this deeply stained spiral structure disappears, and it seems that it is broken at this portion. The connecting filament of the satellite is constructed with a deeply staining thin thread, and the spiral seems to be stretched to a thread without any matrix.

² Haga (1934a) has studied the somatic chromosomes especially in the root-tip fixed with modified Flemming's solution and stained with iodine-gentian violet after Newton. He stated that the e-chromosome of *P. tetraphylla* (dt after Haga) has a small satellite on the proximal knob with a long connecting filament, and that on some occasions its form changes into a long thread, especially at anaphase.
T. kamtchaticum has a knob of almost the same size as Paris, and the part of its limb nearer to the knob is somewhat more slender than the other part. This character does not appear in other species of Trillium and Paris, and it is clearly visible in the first nuclear division of the pollen grain especially at anaphase (Figs. 3 and 15). The knob of the e-chromosome of T. Smallii is somewhat larger than in the other species.

In some individuals of Paris, the satellite of the e-chromosome is reduced; in the materials studied, one of two e-chromosomes of the diploid plant of P. hexaphylla and P. tetraphylla, and one or two of the e-chromosomes of the triploid plant of P. hexaphylla do not carry a satellite. Now we can suppose the existence of several caryotypes in Paris and Trillium from Hokkaido regarding the elimination of the satellite of the e-chromosome as follows:

The chromosome value of a nucleus is indicated by Roman numerals II or III..., and the number of satellites of the e-chromosome in a nucleus is indicated by arabic numerals 0, 1, 2, ...

<table>
<thead>
<tr>
<th>Chromosome Type</th>
<th>Chromosome Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paris hexaphylla Cham.</td>
<td>II₂, II₁, II₀</td>
</tr>
<tr>
<td>&quot;</td>
<td>II₂, II₁, II₀</td>
</tr>
<tr>
<td>&quot;</td>
<td>II₂, II₁</td>
</tr>
<tr>
<td>&quot;</td>
<td>II₂, II₁, II₀</td>
</tr>
<tr>
<td>&quot;</td>
<td>III₃</td>
</tr>
<tr>
<td>&quot;</td>
<td>III₂</td>
</tr>
<tr>
<td>&quot;</td>
<td>III₁, III₀</td>
</tr>
<tr>
<td>&quot;</td>
<td>III₀</td>
</tr>
<tr>
<td>Paris tetraphylla A. Gray</td>
<td>II₂, II₁, II₀</td>
</tr>
<tr>
<td>&quot;</td>
<td>II₂, II₁, II₀</td>
</tr>
<tr>
<td>&quot;</td>
<td>II₂, II₀</td>
</tr>
<tr>
<td>Trillium kamtchaticum Pall.</td>
<td>II₀</td>
</tr>
<tr>
<td>T. Tschonoskii Maxim.</td>
<td>IV₄ ¹</td>
</tr>
<tr>
<td>T. Smallii Maxim.</td>
<td>VIₒ</td>
</tr>
</tbody>
</table>

Among these caryotypes, P. hexaphylla II₀, III₀ and P. tetraphylla II₀, those marked with an *, have not been found, but are expected to exist. The plant of each caryotype, which was found actually, has a different morphological appearance, especially in the leaf character (Figs. 6–10). The writer reported in a joint work with GOTOH (1930) that the ratios of breadth to length of the laminae of P. hexaphylla II₂, II₁ and III₀² are different from each other.

¹) T. Tschonoskii f. violaceum Makino has two kinds of the c- and e-chromosomes (Fig. 4), and it seems to be a hybrid plant between T. Tschonoskii and T. Smallii.

²) Described as types 1, 2 and 3 respectively in the paper of GOTOH and STOW (1930).
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Fig. 4. *Trillium Tschonoskii* f. *violaceum*; root-tip, showing two kinds of c- and e-chromosomes. c-chromosome dotted and e-chromosome solid black. 1000×

Similar studies with other caryotypes, *P. hexaphylla* III₂, III₃ and *P. tetraphylla* II₂ and II₁, show the results indicated in Table 1. As the differences between the above mentioned ratios in respect to the leaf character in each caryotype are larger than 5 times their probable errors, it is not probable that such differences are a matter of chance.

Table I.

<table>
<thead>
<tr>
<th></th>
<th>Breadth (mm)</th>
<th>Length (mm)</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paris hexaphylla</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II₁</td>
<td>16.975±0.168</td>
<td>63.422±0.819</td>
<td>0.278±0.0025</td>
</tr>
<tr>
<td>II₂</td>
<td>24.315±0.343</td>
<td>66.489±0.639</td>
<td>0.365±0.0016</td>
</tr>
<tr>
<td>III₁</td>
<td>31.061±0.394</td>
<td>78.073±1.000</td>
<td>0.399±0.0038</td>
</tr>
<tr>
<td>III₂</td>
<td>31.780±0.232</td>
<td>74.870±0.705</td>
<td>0.427±0.0035</td>
</tr>
<tr>
<td>III₃</td>
<td>35.076±0.302</td>
<td>77.557±0.439</td>
<td>0.452±0.0033</td>
</tr>
<tr>
<td><em>Paris tetraphylla</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II₁</td>
<td>38.645±0.479</td>
<td>68.458±0.842</td>
<td>0.560±0.0042</td>
</tr>
<tr>
<td>II₂</td>
<td>32.875±0.816</td>
<td>67.209±1.294</td>
<td>0.495±0.0056</td>
</tr>
</tbody>
</table>

The most probable reason for such differences of the ratios is the elimination of the satellite of the e-chromosome. By a further investigation, the writer ascertained that the elimination of the satellite is more closely related to the angle between the two edges of the leaf margin at the base (θ) than it is to the ratio of the breadth to length of the laminae. The angle θ in *Paris* was measured and the results obtained are shown in Table 2.
Table II.

Angle between the two edges of leaf margin at the base ($\theta$), quotient $360^\circ$/leaf number ($d$) and degree of decrease of $\theta$ ($\lambda$) of the different caryotypes of Paris.

<table>
<thead>
<tr>
<th></th>
<th>ratio of breadth to length of lamina (%)</th>
<th>$\theta$</th>
<th>$\frac{d}{n}$</th>
<th>$\lambda = \frac{d - \theta}{d}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. hexaphylla</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II$_2$</td>
<td>27.81 ± 0.245</td>
<td>28°20'</td>
<td>$\frac{360^\circ}{n} = 45^\circ$</td>
<td>0.372</td>
</tr>
<tr>
<td>II$_1$</td>
<td>36.51 ± 0.159</td>
<td>36°21'</td>
<td>&quot;</td>
<td>0.189</td>
</tr>
<tr>
<td>III$_3$</td>
<td>39.91 ± 0.375</td>
<td>38°18'</td>
<td>&quot;</td>
<td>0.149</td>
</tr>
<tr>
<td>III$_2$</td>
<td>42.71 ± 0.345</td>
<td>41°12'</td>
<td>&quot;</td>
<td>0.088</td>
</tr>
<tr>
<td>III$_1$</td>
<td>45.21 ± 0.331</td>
<td>43°24'</td>
<td>&quot;</td>
<td>0.035</td>
</tr>
<tr>
<td>P. tetraplylla</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II$_2$</td>
<td>56.50 ± 0.420</td>
<td>52°35'</td>
<td>$\frac{360^\circ}{4} = 90^\circ$</td>
<td>0.355</td>
</tr>
<tr>
<td>II$_1$</td>
<td>49.50 ± 0.560</td>
<td>52°31'</td>
<td>$\frac{360^\circ}{6.62} = 54°34'$</td>
<td>0.183</td>
</tr>
</tbody>
</table>

It is a remarkable fact that the differences of the values of $\theta$ between the different caryotypes III$_1$, III$_2$ and III$_3$ of the triploid Paris are nearly equal:

III$_2$–III$_3$=41°12′–38°18′=2°54′

III$_1$–III$_2$=43°24′–42°12′=2°12′.

As the caryological difference of these plants is seen in the number of the eliminated satellites, it may be suggested that the difference between the III$_1$ and III$_2$ plant or between the III$_2$ and III$_3$ plant indicates the degree of increase of the $\theta$ value, when a satellite is eliminated. If all e-satellites were eliminated, as in the case of the assumed III$_0$ plant, the $\theta$ value is expected to become equal to the sum of the $\theta$ value of the III$_1$ plant and the average of the difference of the $\theta$ value between the III$_2$ and III$_3$ plant, or between the III$_1$ and III$_2$ plant. It indicates:

$43°24′ + \frac{2°12′ + 2°54′}{2} = 45°57′$

In the same way the $\theta$ value of the assumed II$_0$ plant is expected to be equal to the sum of the $\theta$ value of the II$_1$ plant and the difference of the $\theta$ value between the II$_1$ and II$_2$ plant, thus:
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\[ 36°30' + (36°30' - 28°20') = 44°40' \].

In both cases, diploid and triploid, the \( \theta \) values of the plants without any satellite approximate to 45°. The leaves of Parideae are verticillate and arranged on a horizontal plane, and in Paris hexaphylla the leaf number of the well developed plant is 8\(^{1)}\). Therefore, 45° is the maximum value of \( \theta \), assuming that 8 leaves grow radiating from an axis and are arranged on a plane without covering each other, because 45° is the quotient \( \frac{360°}{8} \), where 360° is the angle surrounding a point on a plane and 8 is the leaf number.

In the case of \( P. \) tetraphylla, the leaf number of the II\(_2\) plant is always 4 and its mean \( \theta \) value is 58°35'. Comparing these results with those of \( P. \) hexaphylla II\(_2\), we can find that the leaf number of the former is just a half of the latter, while the \( \theta \) value of the former is almost twice that of the latter. In the case of the II\(_1\) plant of \( P. \) tetraphylla, however, the leaf number varies from 4 to 7 and averages 5.62. In the same plant the mean value of \( \theta \) is 52°21', which is smaller than the \( \theta \) value of the II\(_2\) plant. On the other hand, the mean value of \( \theta \) of \( P. \) hexaphylla with less leaves is larger than that of the normal eight leaved plant. Moreover, in case of one individual\(^2\) of \( P. \) tetraphylla, the leaf number varies from 4 to 6, so the mean value of \( \theta \) in the four leaved plant is 83°18', while it is 68°40' in the five leaved one\(^3\). In this case, we can find that the ratio \( \frac{83°18'}{68°40'} = 1.214 \), to be approximately equal to the inverse ratio of the leaf number \( \frac{5}{4} = 1.25 \). From these facts, it follows that the \( \theta \) value varies proportionally to the reciprocal of the leaf number.

Applying this idea to the case of \( P. \) tetraphylla II\(_1\) plant, the calculated value of \( \theta^4 \) of the 4-leaved plant can be obtained, multiplying 52°21' (the \( \theta \) value of the II\(_1\) plant with an average leaf number 5.62) by the inverse ratio of the leaf number; thus

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1) Well developed \( P. \) hexaphylla has 8 leaves, and in the young or poorly developed ones there are less than 8, sometimes even 4. When the leaf number is less than 8 especially in young ones, the width of laminae is larger than in the 8 leaved.

2) Caryological study is not yet finished.

3) The \( \theta \) value of the 6 leaved plant is omitted, because only one came to the writer's observation.

4) This is indicated by \( \theta' \).
\[ \theta' = 52^\circ 21' \times \frac{5.62}{4} = 73^\circ 33' \]

this calculated value of \( \theta' \) for the 4 leaved \( P. \text{tetraphylla} \) II, plant is almost twice that of the II, plant of \( P. \text{hexaphylla} \) (36°21'), while the leaf number of the former is a half that of the latter. Now we can calculate the \( \theta \) value of the assumed \( P. \text{tetraphylla} \) IIo plant with four leaves, in which all satellites are eliminated, according to the following formula:

\[ 73^\circ 33' + (73^\circ 33' - 53^\circ 35') = 88^\circ 31', \]

where 58°35' is \( \theta \) of the four leaved II2 plant, and 73°33' is \( \theta \) of the four leaved II, plant. This \( \theta \) value of \( P. \text{tetraphylla} \) IIo plant is almost twice that of \( P. \text{hexaphylla} \) IIo and IIIo plant, and it is nearly equal to the quotient \( \frac{360^\circ}{4} = 90^\circ \), where 4 is the leaf number of this plant.

From the above mentioned results in Paris, it can be expected that the \( \theta \) value becomes larger and approximates to the quotient \( \frac{360^\circ}{\text{leaf number}} \), proportionally to the increase of the satellite elimination. If all satellites were eliminated, it will become equal to the quotient, which will be indicated hereafter by \( \Delta \) for simplifying the description. So one can say that the \( \theta \) value is limited below \( \Delta \) by the presence of the satellite and then the degree of decrease of \( \theta \) (indicated by \( \lambda \)) will be expressed by the following formula:

\[ \lambda = \frac{\Delta - \theta}{\Delta} = 1 - \frac{\theta}{\Delta} \]

or

\[ \frac{360^\circ - \theta}{360^\circ} = 1 - \frac{n\theta}{360^\circ}, \]

where \( n \) is the leaf number.

A remarkable similarity of the \( \lambda \) value between the same kinds of caryotype of both \( P. \text{hexaphylla} \) and \( P. \text{tetraphylla} \) is recognized (Table 2). The \( \lambda \) value of the II2 plant in both Paris species is 0.372 and 0.355 respectively, and in the II, plants it is 0.189 and 0.183.
Therefore, it may be assumed that the $\lambda$ value is closely related with the elimination of the satellite equally among the plants of different species used. On the other hand, as no decrease of the $\theta$ value would take place in the case of the $I_{0}$ or $II_{0}$ plant without satellite, one can expect that the $\theta$ value of these plants will become equal to $A$, namely that the $\lambda$ value becomes equal to zero. This relation is easily recognized in a graph in which the $\lambda$ values are taken as the co-ordinate, and the quotient, that is the number of eliminated satellites is divided by the number of the e-chromosomes, as the abscissa. Two lines of $P. hexaphylla$ (diploid and triploid) and the line of $P. tetraphylla$ converge near the point $A$, where $\lambda = 0$ and the quotient is 1 (Fig. 5). But, as no material without a satellite, neither diploid nor triploid of both $Paris$ species, came within the observation

![Graph](image-url)

Fig. 5. Close relation between the angle of the two edges of the leaf margin at the base and the elimination of the satellite as indicated by a graph. Ph, $P. hexaphylla$. Pt, $P. tetraphylla$. Tk, $Trillium kamtschaticum$. TT, $T. Tschonoskii$. TS, $T. Smallii$. 
of the writer, it is impossible to ascertain the presence of the point of the coincidence in Paris. *Trillium* has not only very similar chromosomal elements to those of *Paris*, but also the e-chromosome of the former genus is closely similar to the e-chromosome without satellite of *Paris*. So it may not be impossible to confirm the assumed relation, that the $\lambda$ values become zero in the absence of a satellite, by the use of *Trillium* instead of *Paris*. In reality it was found that the $\lambda$ values of *T. kamtschaticum*, *T. Tschonoskii* and *T. Smallii* are 0.032, 0.025 and 0.178 respectively (Table 3), where $\lambda$ of all *Trillium*

**Table III.**

Ratio of breadth to length of laminae, value of $\theta$ and degree of decrease of $\theta (\lambda)$ in *Trillium*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ratio of breadth to length of lamina (%)</th>
<th>$\theta$</th>
<th>$\lambda = \frac{360^\circ}{n}$</th>
<th>$\lambda = \frac{\theta - \theta}{\lambda}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. kamtschaticum</em> II$_0$</td>
<td>106.90±0.558</td>
<td>116° 3'±16'.5</td>
<td>$\frac{360^\circ}{3} = 120^\circ$</td>
<td>0.032</td>
</tr>
<tr>
<td><em>T. Tschonoskii</em> VI$_0$</td>
<td>106.22±0.622</td>
<td>116°26'±54'.9</td>
<td>,,</td>
<td>0.027</td>
</tr>
<tr>
<td><em>T. Smallii</em> IV$_0$</td>
<td>106.28±0.467</td>
<td>98°37'±21'.1</td>
<td>,,</td>
<td>0.178</td>
</tr>
</tbody>
</table>

plants is equally $120^\circ$. Thus the results obtained with *T. kamtschaticum* and *T. Tschonoskii* agree almost with the expectation, but in the case of *T. Smallii* the result is entirely contrary to it and the $\lambda$ value is nearly equal to that of the II$_1$ plant of *Paris* (0.189 or 0.183). But it is a noticeable fact that the mean values of the ratio of the breadth to the length of the laminae of these three *Trillium* species nearly agree with each other, that is 106.90±0.558 and 106.22±0.622, 106.28±0.467, respectively (Table 3). So the writer inclines to assume that a certain unknown factor, instead of the satellite, may exist, which is related with the value of $\theta$ at least in the case of *T. Smallii*.

**Conclusion**

With the recent advance of cytological investigations nuclear polymorphism was found in many plants and sometimes an interesting relation between the caryotypes and morphological character was ascertained. Certainly, this character can be distinguished both in the qualitative and the quantitative sense. The former is recogni-
zable rather easily, but in the latter case it is a matter of difficulty, because it needs many statistical studies even for a single character and sometimes it is rather difficult to find out its mode. Therefore, the investigations, undertaken hitherto in this direction, have been mostly of qualitative nature. The case of Paris is an example of the latter; the different caryotypes have different quantitative morphological characters\footnote{1).\ It is not necessary to consider that these characters develop from the genes located on the chromosome.}. The $\theta$ value, the angle between the two edges of the leaf margin at the base, is closely related to the satellite of the e-chromosome, and the $\lambda$ value, the decrease of the $\theta$ value, is proportional to the presence of the satellite. It can be expected that $\theta$ reaches the maximum value and becomes equal to $\Delta$, when all satellites are eliminated, where $\Delta$ is the quotient; \(\frac{360^\circ}{\text{leaf number}}\). This expectation is supported powerfully by the fact, that $\theta$ of two species of Trillium are nearly equal to their $\Delta$, where the chromosomal elements are similar to those of Paris, especially when there is an e-chromosome without satellite.

It is a noticeable fact that the maximum value of $\theta$ becomes equal to $\Delta$, because the latter is the maximum size of the angle between the two edges of the leaf margin at the base, assuming that they do not cover each other, radiating from an axis and arranged on a plane. As the $\theta$ value will never become larger than $\Delta$, even if all satellites were eliminated, the presence of the satellite may be considered as the secondary factor related to the decrease of the $\theta$ values, and one should probably assume a certain unknown primary factor which restricts the $\theta$ value below $\Delta$. If one could suppose the primary existence of a satellite, it is impossible to explain why the $\lambda$ values of those plants, in which all the e-chromosomes have satellites, are different and those of the plants with no satellite converge nearly to a point. So it is rather natural to expect that the satellite of the e-chromosome of Paris has been derived secondarily. It is not difficult to consider that the e-chromosome of Paris might be derived from a chromosome without satellite as in Trillium, having obtaining a mass of chromatin at the proximal end, as in the case of Crepis\footnote{2) M. Navashin (1931, b and 1932), Schkwarnikow u. M. Navashin (1934).} where a fragment of a chromosome or satellite alone translocated to another chromosome. One might suppose that an e-chromosome with
satellite had been derived from a J-shaped chromosome, a constriction being newly produced in its shorter arm and its terminal portion being changed into a satellite. But it is not probable that such a change, which does not accompany the loss or gain of chromatin substance, is related with the change of the morphological character.

Summary

1) The satellite of the e-chromosome of *Paris hexaphylla* and *P. tetraphylla* is sometimes eliminated. The size of the angle between the two edges of the leaf margin at the base (θ) is closely related with this elimination of the satellite; the increase of the former is proportionate to that of the latter. The θ value approaches to the quotient: \( \frac{360°}{\text{leaf number}} = \Delta \) in accordance with the elimination of the satellite.

2) No plant of *Paris*, in which all satellites of the e-chromosomes are eliminated, is found. But it is expected that the angle between the two edges of the leaf margin at the base of such a plant will become equal to the quotient \( \Delta \), which is the maximum value of the angle between the two edges of the leaf margin at the base.

3) The chromosomal elements of *Trillium* are closely similar respectively to those of *Paris*, and especially the e-chromosome of the former strikingly resembles the e-chromosome without satellite of the latter. In *T. kamtschaticum* and *T. Tschonoskii*, the θ values are nearly equal to the calculated value \( \Delta = \frac{360°}{3} = 120° \), where 3 is the leaf number. This fact is a powerful support for the expectation that the θ value of *Paris* without satellite will become equal to the quotient \( \Delta \).

4) It may be considered that the e-chromosome of *Paris* was derived from a chromosome without satellite, such as that of *Trillium*, by the addition of a chromatid to its proximal end.

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Correlation between Satellite and Leaf Shape

Literature

—— (1915): (cited after DELAUNAY, 1929).
Explanation of Plates

Plate I

Figs. 6–9. Direct print of leaves. Fig. 10. Photograph. Reduced size $\frac{1}{2} \times$.
Fig. 11 a & b. Photomicrograph, iron-acetocarmine preparation, ca. 500 $\times$.

6. Paris hexaphylla II.
7. " " II.
8. " " III.
9. Paris tetraphylla II.
10. " " II.
11. Paris tetraphylla, first nuclear division in the pollen grain, showing the stick shaped satellite. 750 $\times$.

Plate II

Figs. 12–14. Direct prints of leaves, reduced size $\frac{1}{3} \times$.
Fig. 15. Photomicrograph, iron-acetocarmine preparation.
12. Trillium kamtschaticum.
13. Trillium Tschonoskii.
15. Trillium kamtschaticum, first nuclear division in the pollen grain. 750 $\times$. 
Stow: Correlation between Satellite and Leaf Shape.
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