The Comparative Morphology of the Chromosome Complement in the Tribe *Parideae*

By

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(With 24 Text-figures and 1 Plate)

Introduction

The tribe *Parideae* which comprises two closely related genera, *Paris* and *Trillium,* offers very favourable material for karyological investigations, because of the exceedingly large dimension of the chromosomes and their relatively small number. Furthermore the tribe seems to constitute a comparium-population; in reality the writer obtained some good seeds from certain interspecific crosses within the genus *Paris*. These facts led the writer to an investigation involving the interrelations of cytological features with genetical ones. Describing a part of this plan of investigation, the present paper deals with the morphology of the somatic chromosomes and the comparison of the species from a phylogenetic point of view.

Concerning the chromosome number in these genera, some earlier workers concluded that the basic number is 6 (ATKINSON 1899, COULTER and CHAMBERLAIN 1902, ERNST 1902, GRÉGOIRE 1912, KOMURO 1924, SPANGLER 1925, LEE 1925, and JOHANSEN 1932), whereas GOTOH and STOW (1930) examining several Japanese and two foreign species found the basic number to be 5 with which the tribe constitutes di-, tri- and tetraploid species. In the present study, the writer using 3 species of *Trillium* and 2 species and one variety of *Paris* confirmed the results obtained by GOTOH and STOW. Of these species studied *Paris japonica* was not dealt with by them. It proved now to be an octoploid species, i.e., to have 40 chromosomes in its somatic cells.

Of these two different views on the chromosome number, we might interpret them as the results of fusion or fragmentation of a chromosome

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pair, as is well known in some instances, e.g. *Vicia* (SWESCHNIKOWA 1928), *Secale* (GOTOH 1924, 1932), etc. However, reinvestigations on the species reported to have 12 or 24 somatic chromosomes are desirable, because their counts of chromosomes were made without any reliable figure. Indeed in many figures of ATKINSON one can clearly identify 5 elements instead of 6. Furthermore in two foreign *Trillium* species, although their names were uncertain, GOTOH and STOW (1930) also determined 10 and 20 somatic chromosomes, and very recently GOTOH (1933) reported that *Trillium sessile* var. *californicum* contains 5 gametic and 10 somatic chromosomes.

Materials and Methods

The materials used were all collected in the suburbs of Sapporo with the exception of *Paris japonica* which was collected on Mt. Gassan in Yamagata prefecture.

For the determination of somatic complements the root-tip cells were employed. They were fixed in the Flemming's solution modified in our laboratory with good result; its formula is as follows:

10% Chromic acid	5 c.c.
10% Gracial acetic acid	20 c.c.
2% Osmic acid	15 c.c.
Distilled water	80 c.c.

They were then sectioned in paraffin at a thickness of 26 microns. The preparations were stained after Newton's iodine-gentian-violet method. In some cases chloralisation was tried according to SAKAMURA's procedure (1920). On those occasions root-tips were fixed in 2 BE (LA COUR 1931) 4–6 hours after treatment with 1 per cent solution of chloralhydrate. By this treatment the chromosomes become straight with constrictions very pronounced, making the identification of different chromosome types in a complement very easy (cf. Figs. 10, 12 and Pl. 1). Chromosome conditions in pollen mother-cells and pollen grains were studied employing BELLING's iron aceto-carmine method.

Drawings were made with a Leitz Abbe camera lucida using a Leitz $\frac{1}{12}$ oil immersion in combination with an eye piece $15\times$, giving a magnification of $1750\times$ diameters. They were reduced for reproduction to the scale indicated.

As the chromosomes in the present materials are exceedingly large, it is unusual to find them lying on one horizontal plane—any plane perpendicular to the microscopic axis—along their entire lengths. They are usually inclined to this plane, sometimes with a complex curvature. The length of a chromosome drawn on the paper as its plan figure is necessarily shorter than its actual length. To measure the true length of such a chromosome the writer used HASEGAWA's method (1932) with some modifications.

Firstly a chromosome to be measured is divided into several portions in which the foci change uniformly in only one direction, upwards or downwards; thus each portion in an ideal case takes a straight line when it is propected on the vertical plane. In Figure 1 *B*, the curve *ab* represents a plan figure of the chromosome part thus divided, and Figure 1 *A* represents its inclination from the horizontal plane *ab″* through the lower turning point *a*. The vertical distance between *a* and *b* is indicated by *h* and is measured by reading the scale difference of the fine adjustment screw of the microscope. The practical method for the measurement of the portion *ab* (Fig. 1, *B*) is as follows: (1) take *h* from *b* perpendicular to line *ab*, (2) take any desirable points on the curve *ab* (e.g., *c*, *d*, *e*) and draw parallel lines from them to *h* (*bb′*), (3) then draw lines from the points of their intersection with *ab* perpendicularly to the latter and on each line take the corresponding distances between the line *ab* and the curve *ab* ($c_1=c_2$, $d_1=d_2$, $e_1=e_2$). The curve *ab′* passing *c′*, *d′*, *e′* will be of the approximate length of the forshortened part *ab*. Of course, relatively small errors may result from neglecting the differences $h_c \sim h_c'$, $h_d \sim h_d'$ and $h_e \sim h_e'$, where h_c, h_d and h_e represent the true heights of the points corresponding to their suffixes from the horizontal plane *ab″*. But such errors may be avoided if the measurement is very carefully made. It may be mentioned here that in order to make the measurement more easily and correctly the original figures were enlarged two times with the

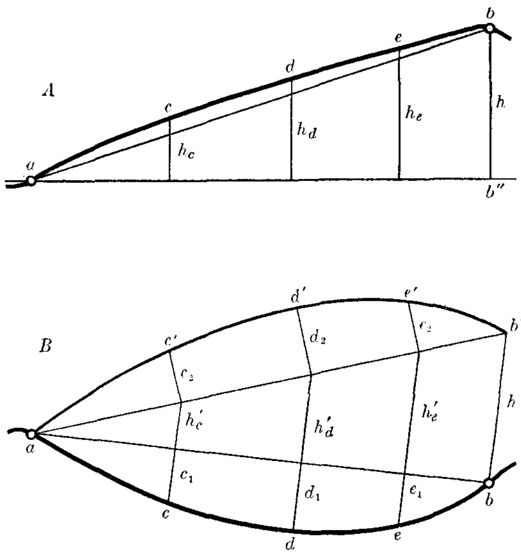


Fig. 1. Diagramatic representation of chromosome measurement. Explanation in text.

aid of a Leitz projecting apparatus, giving a magnification of 3500× diameters.

Observations

In the following descriptions the writer has used the terms "length per cent" and "form per cent" to express the relative lengths in a complement and the relative positions of constrictions of the different chromosome types, the former representing the whole length of a chromosome in per cent of the total sum of chormosome lengths in a complement and the latter the short arm length in per cent of the whole length of a chromosome.

Chromosomes in every plant investigated were classified into five general types *A, B, C, D,* and *E* according to their length and form per cents. And when they were applied within a species, they were represented by the small letters *a, b, c, d,* and *e* respectively. With regard to the widths of the chromosomes, there is no significant difference among all the constituents in a chromosome complement of a species or between the chromosomes of different species, e. g., diameters of the single metaphasic chromatids of *Trillium kamtschaticum* are *ca.* 0,9 microns in all five chromosome types. So that no attention was paid to this respect.

1. *Trillium kamtschaticum* PALL. n=5, 2n=10

As already counted by GOTOH and STOW, the gametic and the somatic chromosome number of this species has been determined as 5 and 10 respectively. The 10 somatic chromosomes are classified into five types designated as *a, b, c, d,* and *e,* each containing two members (Figs. 2 and 3). These

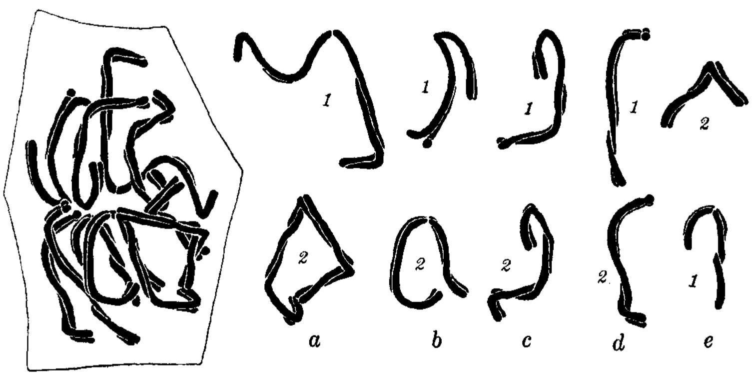


Fig. 2. *Trillium kamtschaticum.* Left, somatic metaphase showing 10 chromosomes. Right, chromosomes classified from the left; numerials indicate chromosome individuals. 1220×.

five types are very clear at the metaphase of the first division in pollen grains (Pl. 2 and 8), and are also easily identified in the meiotic divisions (Pl. 4).

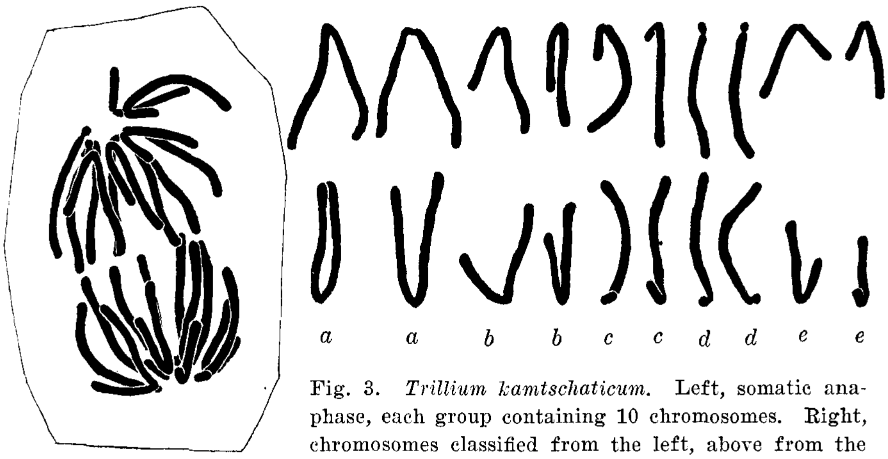


Fig. 3. *Trillium kamtschaticum.* Left, somatic anaphase, each group containing 10 chromosomes. Right, chromosomes classified from the left, above from the upper group and below from the lower, facing the daughter halves to each other. 1220×.

The results of measurements of the metaphase chromosomes in a somatic complement shown in Figure 2 are given in Table 1 and represented diagrammatically in Figure 4.

Table 1.

Lengths and positions of constrictions of metaphase chromosomes in a somatic cell of *Trillium Kamtschaticum.*

Chromosome Type	Individual	Whole length in μ	Position of constriction (–) in μ	Form percent	Length percent
a	1	36,3	18,3-18,0	49,6	15,3
	2	35,7	18,0-17,7	49,6	15,0
b	1	23,7	14,6-9,1	38,6	10,0
	2	23,2	14,3-8,9	38,3	9,7
c	1	22,3	17,4-4,9	21,8	9,4
	2	21,8	16,9-4,9	22,1	9,1
d	1	21,1	20,0-1,1	5,4	8,9
	2	20,5	19,4-1,1	5,6	8,6
e	1	16,9	10,6-6,3	37,3	7,1
	2	16,3	10,3-6,0	36,9	6,9
Total sum		237,8			100,0

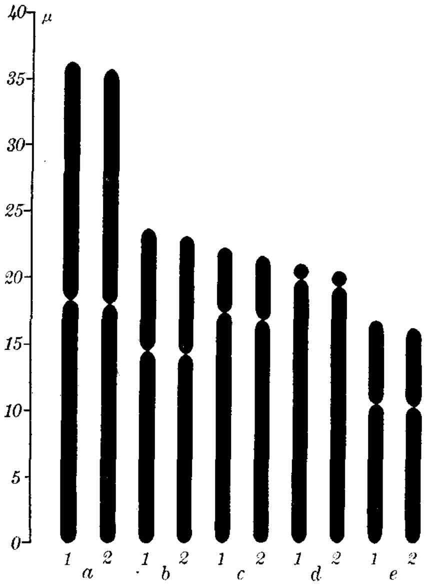


Fig. 4. *Trillium kamtschaticum.* Diagramatic representation of a somatic complement drawn in Figure 2 and measured in Table 1; chromosome individuals are indicated by numerals.

Description of chromosome types.

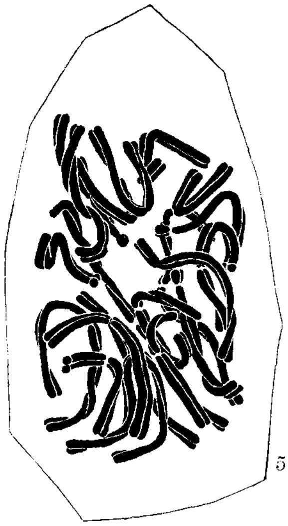
Type *a*, Longest in a complement with a quite median constriction.

Type *b*, Fairly short as compared with type *a* and having a submedian constriction.

Type *c*, Length a little shorter than type *b* and having a subterminal constriction separating a comparatively long segment.

Type *d*, Fourth in length, having a small spherical segment formed by a subterminal constriction.

Type *e*, Resembling type *b* in the relative position of a constriction, but readily distinguishable from the latter by its being the shortest in a complement.



5

6

Figs. 5–6. *Trillium Smallii.* 5, somatic metaphase showing 20 chromosomes. 6, somatic anaphase, each group containing 20 chromosomes. 1220×.

2. *Trillium Smallii* MAXIM.[1] n=10,[2] 2n=20.

In agreement with the data of GOTOH and STOW, this species was found to show a tetraploid number in its somatic cells. The gametic number of this species has not been studied as yet. Figure 5 and 6 represent 20 somatic chromosomes at metaphase and anaphase respectively. The results of measurements in a somatic metaphase shown in Figures 5 and 7 are given in Table 2 and in the diagrams of Figure 9.

From these measurements, we can identify five types *a*, *b*, *c*, *d*, and

Table 2.

Lengths and positions of constrictions of metaphase chromosomes in a somatic cell of *Trillium Smallii*.

Chromosome Type	Individual	Whole length in μ	Position of constriction (–) in μ	Form percent	Length percent
a	1	31,7	16,6-15,1	47,8	7,8
	2	31,1	15,7-15,4	49,6	7,7
	3	30,8	15,7-15,1	49,1	7,6
	4	30,8	15,4-15,4	50,0	7,6
b	1	22,0	14,0-8,0	36,4	5,4
	2	21,7	14,0-7,7	35,5	5,4
c	1	20,9	16,9-4,0	19,2	5,1
	2	20,3	16,6-3,7	18,3	5,0
b'	1	19,7	12,0-7,7	39,1	4,9
	2	19,7	11,7-8,0	40,6	4,9
c'	1	16,8	13,7-3,1	18,7	4,2
	2	16,8	13,4-3,4	20,3	4,2
d	1	16,8	15,7-1,1	6,8	4,2
	2	16,5	15,4-1,1	6,9	4,1
	3	16,5	15,4-1,1	6,9	4,1
	4	16,0	14,9-1,1	7,1	3,9
e	1	15,6	9,0-6,6	40,7	3,8
	2	14,7	9,0-5,7	38,5	3,7
e'	1	13,4	8,5-4,9	36,2	3,3
	2	13,4	8,3-5,1	38,3	3,3
Total sum		405,2			100,2

1) Synonymous with *T. apetalon* MAKINO.

2) This number was confirmed at the meiotic divisions when the MS was in the press.

e closely resembling those of *T. kamtschaticum* and three dissimilar types *b′*, *c′*, and *e′* (Figs. 7, 8 and Pl. 1).

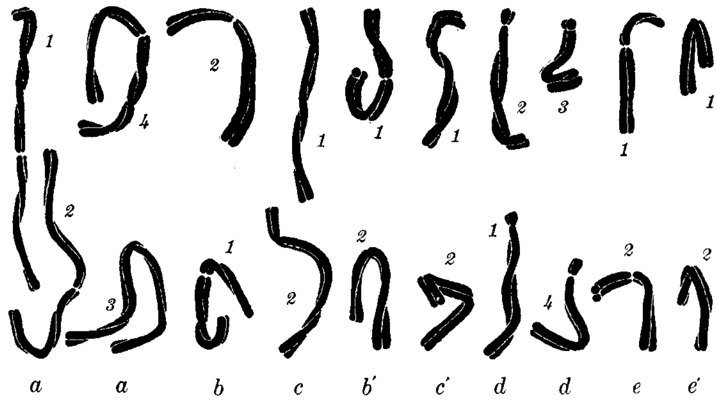


Fig. 7. *Trillium Smallii.* Chromosomes classified from Figure 5; numerals indicate chromosome individuals. 1220 ×.

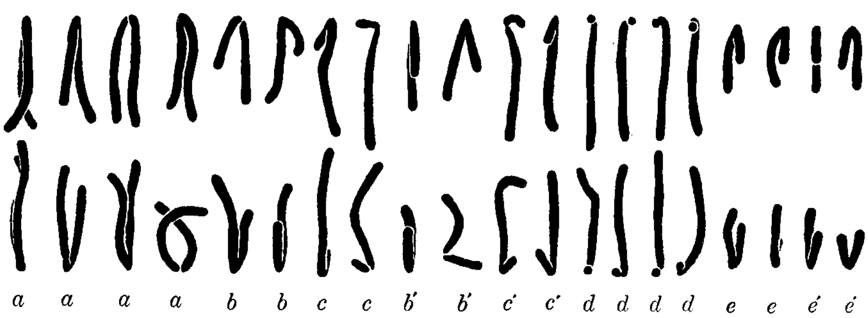


Fig. 8. *Trillium Smallii.* Chromosomes classified from Figure 6, above from the upper group and below from the lower, facing the daughter halves to each other. 1220 ×.

Description of chromosome types.

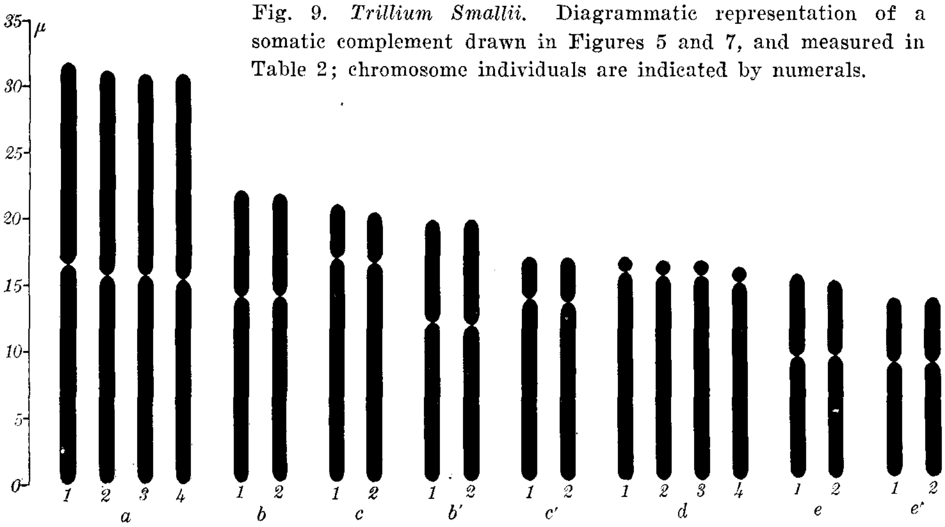
Type *a*, In every respect the same as type *a* of *T. kamtschaticum*, but composed of four members.

Type *b*, Fairly corresponding to type *b* of the former species; two members.

Type *c*, Somewhat low in form per cent as compared with the corresponding type of the former plant; two members.

Type *b′*, Considerably shorter than types *b* and *c*, with somewhat higher form per cent as compared with type *b*; two members.

Fig. 9. *Trillium Smallii.* Diagrammatic representation of a somatic complement drawn in Figures 5 and 7, and measured in Table 2; chromosome individuals are indicated by numerals.



Type *c′*, Much shorter than type *c*, but with similar form per cent; two members.

Type *d*, Similar to the corresponding type of *T. kamtschaticum*, having four members. But the relative length in a complement is much shorter than that of the former plant (cf. Figs. 4 and 9).

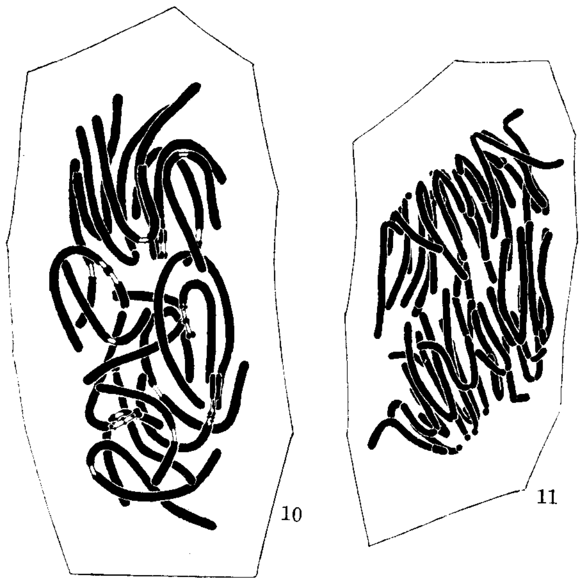
Type *e*, Closely resembling type *e* of the former species; two members.

Type *e′*, Slightly shorter than type *e*; two members.

3. *Trillium Tschonoskii* Maxim. n=10, 2n=20

This species has been reported by Gotoh and Stow to be a tetraploid plant with 20 somatic chromosomes. The writer also observed the same number in its root-tip cells and further determined the gametic number 10 at meiotic metaphase (Figs. 10, 11 and Pl. 5).

To the writer's deep regret, however he has not been able to find any good metaphasic figure adequate for chromosome measurements. Consequently measurements were made with a metaphasic figure of chloral-hydrate material drawn in Figures 10 and 12, so some disagreement from a natural complement may be necessarily involved in this case. In the calculation of length and form per cent the lengths of the threads connecting broken pieces or found in the region of constriction were neglected (Table 3 and Fig. 14).



Figs. 10–11. *Trillium Tschonoskii.* 10, somatic metaphase of a chloralhydrate material showing 20 chromosomes. 11, somatic anaphase, each group containing 20 chromosomes. 1220 ×.

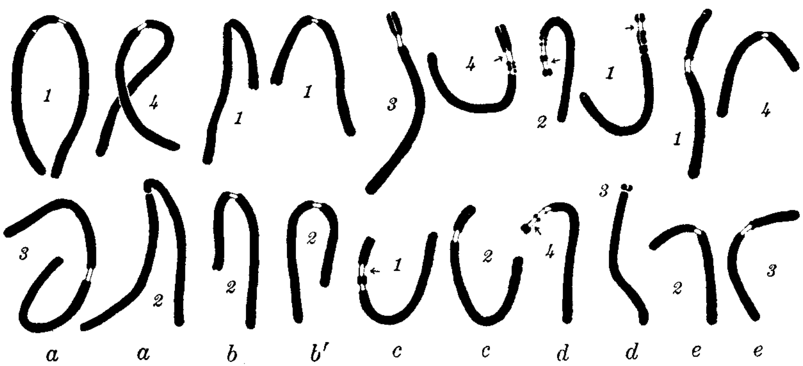
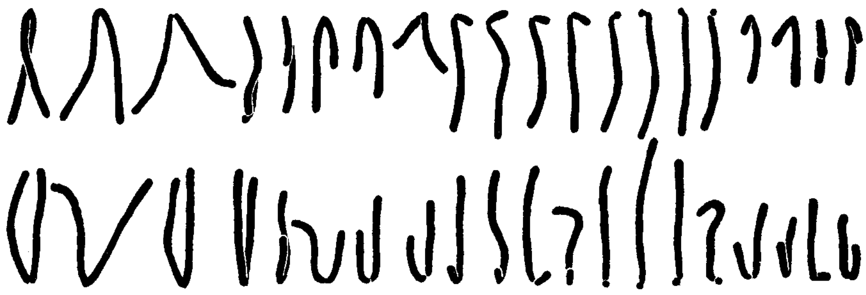


Fig. 12. *Trillium Tschonoskii.* Chromosomes classified from Figure 10; numerals indicate chromosome individuals and supposed true contrictions are indicated by arrows. 1220 ×.

In this plant there can also be identified five chromosome types *a, b, c, d,* and *e* closely resembling those in the *kamtschaticum* complement. One exceptional type *b′* was found, which has some resemblance to type *b′* of *T. Smallii* (Figs. 12 and 13).



a a a a b b b' b' c c c c d d d d e e e e

Fig. 13. *Trillium Tschonoskii.* Chromosomes classified from Figure 11, above from the upper group and below from the lower, facing the daughter halves to each other. 1220×.

Table 3.

Lengths and positions of constrictions of metaphase chromosomes in a somatic cell of *Trillium Tschonoskii.*

Chromosome Type	Individual	Whole length in μ	Position of constriction (–) in μ	Form percent	Length percent
a	1	37,7	19,4–18,3	48,5	8,0
	2	36,9	18,6–18,3	49,6	7,8
	3	36,3	18,6–17,7	48,8	7,7
	4	35,2	18,0–17,2	49,2	7,5
b	1	24,5	15,1–9,4	38,4	5,2
	2	24,2	15,1–9,1	37,7	5,1
b'	1	22,5	13,4–9,1	40,5	4,8
	2	22,5	13,4–9,1	40,5	4,8
c	1	22,0	18,6–3,4	15,6	4,7
	2	21,7	18,6–3,1	14,5	4,6
	3	21,4	18,3–3,1	14,7	4,5
	4	21,1	18,0–3,1	14,9	4,5
d	1	19,6	18,9–0,7	3,7	4,1
	2	19,3	18,6–0,7	3,7	4,1
	3	19,3	18,6–0,7	3,7	4,1
	4	18,7	18,0–0,7	3,8	4,0
e	1	17,4	11,4–6,0	34,4	3,7
	2	17,4	11,4–6,0	34,4	3,7
	3	17,1	11,4–5,7	33,5	3,6
	4	17,1	11,1–6,0	35,0	3,6
Total sum		471,9			100,1

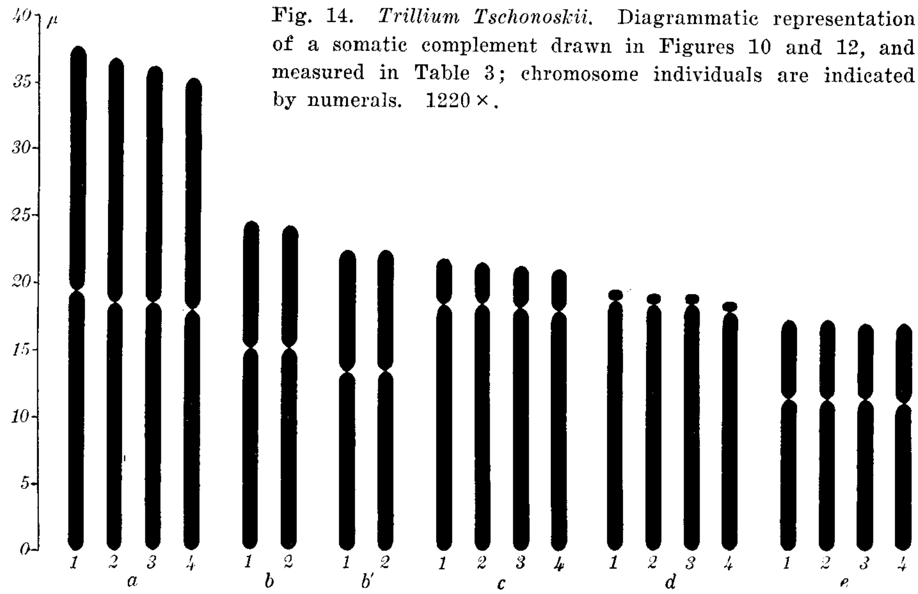


Fig. 14. *Trillium Tschonoskii.* Diagrammatic representation of a somatic complement drawn in Figures 10 and 12, and measured in Table 3; chromosome individuals are indicated by numerals. 1220 ×.

Description of chromosome types.

Types *a* and *b*, Corresponding to those in *kamtschaticum* and *Smallii* complement without any marked difference; the former including four members and the latter two.

Type *b'*, Bearing resemblance to type *b'* of *T. Smallii*; slightly shorter than type *b*, and a constriction rather more median than that of the latter; two members.

Type *c*, Considerably low in form per cent as compared with that of type *c* of *T. kamtschaticum*, *c* and *c'* of *T. Smallii*; consisting of four members.

Type *d*, Similar to the corresponding type of *T. kamtschaticum* and *T. Smallii*, but with a smaller terminal segment; four members.

Type *e*, Almost the same as type *e* of the two former species; four members.

4. *Paris quadrifolia* L. var. *obovata* REGEL et TIL.

n=5, 2n=10, 3n=15

This variety shows 5 bivalents at meiotic metaphase and 10 chromosomes at somatic divisions as already observed by GOTOH and STOW. In this case too, the 10 chromosomes in a somatic complement fall into five types *a*, *b*, *c*, d_T, and *e*, each comprising two members (Figs. 15 and 16). Excluding the new type d_T, four of the five are closely similar to those of *Trillium* species. The type d_T represents the chromosomes with a primary constriction separating a spherical segment, on which a large proximal

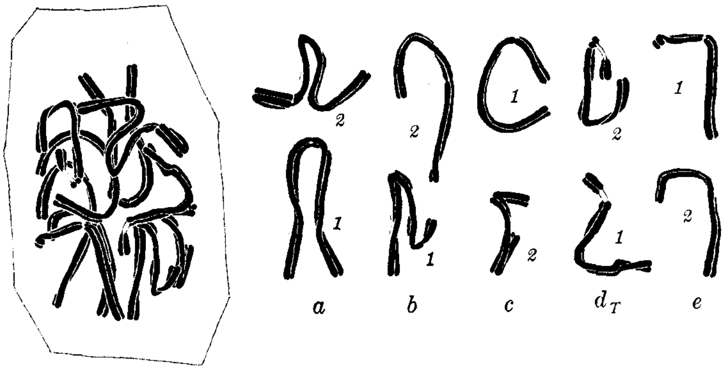


Fig. 15. *Paris quadrifolia* var. *obovata*. Left, somatic metaphase showing 10 chromosomes. Right, chromosomes classified from the left. Numerals indicate chromosome individuals. 1220. ×.

Table 4.

Lengths and positinos of constrictions of metaphase chromosomes in a somatic cell of *Paris quadrifolia* var. *obovata*.

Chromosome Type	Individual	Whole length in μ	Position of constriction (−) in μ	Form percent	Length percent
a	1	33,5	16,9-16,6	49,6	13,5
	2	32,9	16,6-16,3	49,6	13,3
b	1	26,6	16,0-10,6	39,8	10,8
	2	25,5	15,5-10,0	39,3	10,3
c	1	22,8	17,1-5,7	25,0	9,3
	2	22,5	17,1-5,4	24,1	9,1
d_T	1	22,3	18,9-1,1-*1,7*-2,3[1]	5,1; 10,3[2]	9,0
	2	22,0	18,6-1,1-*1,7*-2,3	5,2; 10,4	8,9
e	1	19,4	11,1-8,3	43,0	7,9
	2	19,4	11,1-8,3	43,0	7,9
Total sum		246,9			100,0

1) The number in italics represents the length of the connecting filament.

2) The former represents the length of the spherical head, and the latter that of the trabant.

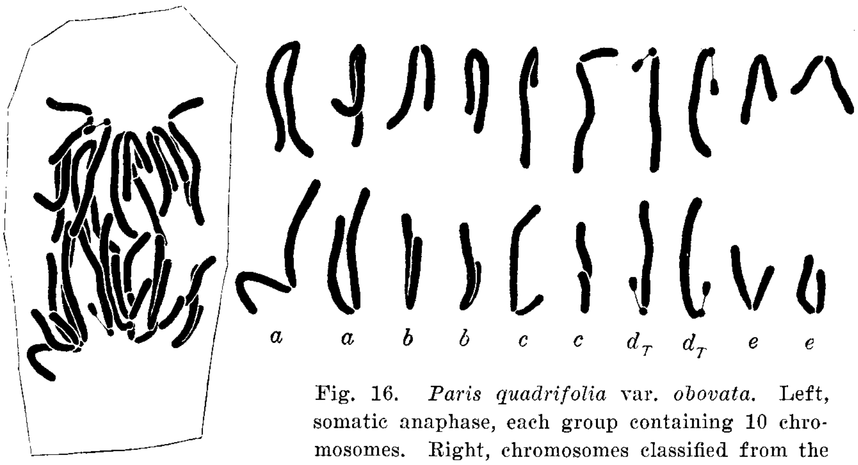


Fig. 16. *Paris quadrifolia* var. *obovata.* Left, somatic anaphase, each group containing 10 chromosomes. Right, chromosomes classified from the left, above from the upper group and below from the lower. facing the daughter halves to each other. 1220 ×.

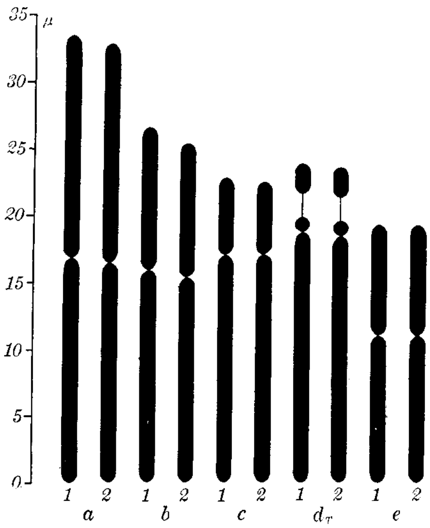


Fig. 17. *Paris quadrifolia* var. *obovata.* Diagrammatic representation of a somatic complement drawn in Figure 15 and measured in Table 4. Chromosome individuals are indicated by numerals.

trabant is attached. These five types are easily recognized at meiotic divisions and very clearly at mitosis in pollen grains (Pl. 6 and 7).

The chromosome measurements were undertaken at somatic metaphase shown in Figure 15, from which Table 4 and the diagrams of Figure 17 were made. In the calculation of length and form per cent of type d_T, the length of the filament connecting the trabant to the main chromosome body was not considered.

In this plant a heterozygous and a triploid form have been found by GOTOH and STOW and again by the present writer. The first form contains a d_T and a d_0 chromosome (d_T chromosome deprived of its trabant) instead of a d_T chromosome pair, and the triploid form also includs two d_0's among three of its D type chromosomes (cf. Pl. 6). Since critical observations are now in progress on these two forms, no further description will be given in this paper (see HAGA 1934).

Description of chromosome types.

With the exception of type d_T, all other types are almost the same as those of *T. kamtschaticum*, differing only in a somewhat higher form per cent of type *e*.

Type d_T, Fourth in length. This is an interesting type with an extremely large trabant connected to a small segment under which a primary constriction is located, the former being twice as long as the latter. The length per cent as a whole coinsides with that of *d*-chromosome in *T. kamtschaticum* complement, but the main body is almost equal to the length of type *e*.

5. *Paris tetraphylla* A. GRAY n=5, 2n=10

In agreement with the previous observation by GOTOH and STOW, there have been counted 5 bivalents at meiotic metaphase and 10 somatic chromosomes. Here also five types *a, b, c,* d_t, and *e* are easily distinguished at somatic, meiotic, and post meiotic divisions (Figs. 18, 19, Pl. 3 and 9).

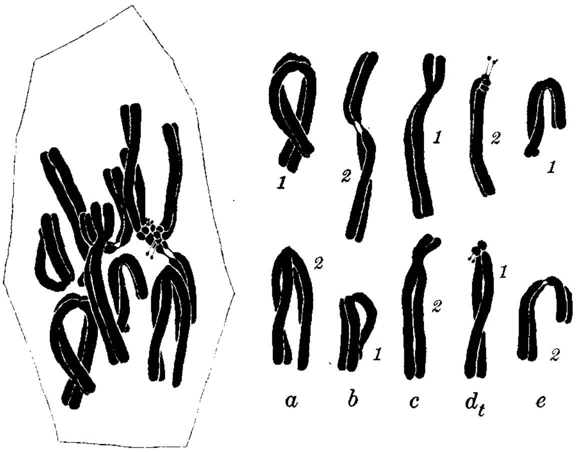


Fig. 18. *Paris tetraphylla.* Left, somatic metaphase showing 10 chromosomes. Right, chromosomes classified from the left. Numerals indicate chromosome individuals. 1220×.

Each type contains two members in a somatic complement. The *D* type chromosome of this plant possesses a very small trabant at somatic metaphase, which was designated as d_t. It is interesting to note that this small trabant behaves variously at the anaphase, appearing sometimes as a thin thread of variable length which is no more distinguishable from the connecting filament (Fig. 19). Such an anaphasic transformation of the trabant was not the same even between the daughter halves of a metaphase chromosome (Pl. 11).

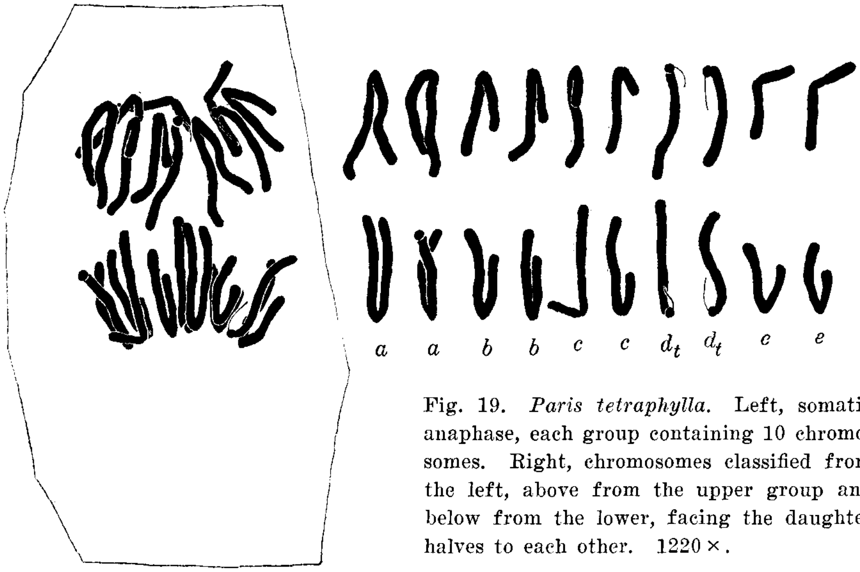


Fig. 19. *Paris tetraphylla.* Left, somatic anaphase, each group containing 10 chromosomes. Right, chromosomes classified from the left, above from the upper group and below from the lower, facing the daughter halves to each other. 1220 ×.

Table 5.

Lengths and positions of constrictions of metaphase chromosomes in a somatic cell of *Paris tetraphylla.*

Chromosome Type	Individual	Whole length in μ	Position of constriction (–) in μ	Form percent	Length percent
a	1	27,1	13,7–13,4	49,5	14,2
	2	27,1	13,7–13,4	49,5	14,2
b	1	20,6	12,3–8,3	40,3	10,7
	2	19,7	11,7–8,0	40,6	10,3
c	1	17,1	13,4–3,7	21,7	9,0
	2	16,6	13,2–3,4	20,6	8,7
d_t	1	16,0	14,9–1,1–*1,7*–0,2[1)]	7,1	8,4
	2	15,7	14,9–1,1–*1,7*–0,2	7,3	8,2
e	1	15,7	9,7–6,0	38,2	8,2
	2	15,7	9,7–6,0	38,2	8,2
Total sum		191,3			100.1

1) The number in italics represents the length of the connecting filament.

In the present species the somewhat abnormal metaphase plate, which was fixed on a late autumn day, shown in Figure 18 was subjected to chormosome measurements. The chromosomes are shorter but somewhat broader than those in ordinary plates in which the writer could not obtain any good figure suitable for measurement. Perhaps low temperature may be responsible for such abnormality, as suggested by analogous alterations caused experimentally by O. HARTMANN (1919 b, cited after TISCHLER 1921–22) and recently by DELAUNAY (1930, cited after DARLINGTON 1932). Such alterations were observed by MEURMAN (1928) under natural conditions in *Ribes*. The results of measurements are presented in Table 5 and diagrammatically in Figure 20. In the calculation of length and form per cent of type d_t, the length of the filament connecting the trabant and that of the trabant itself were not considered.

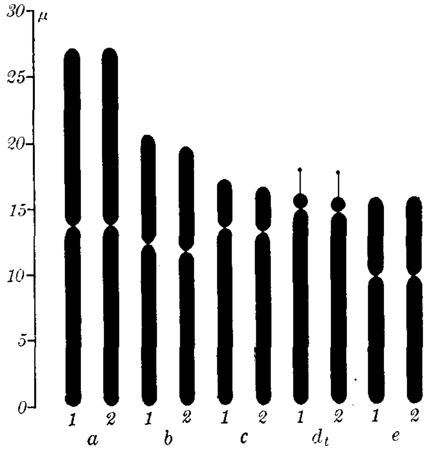


Fig. 20. *Paris tetraphylla.* Diagrammatic representation of a somatic complement drawn in Figure 18 and measured in Table 5; chromosome individuals are indicated by numerals.

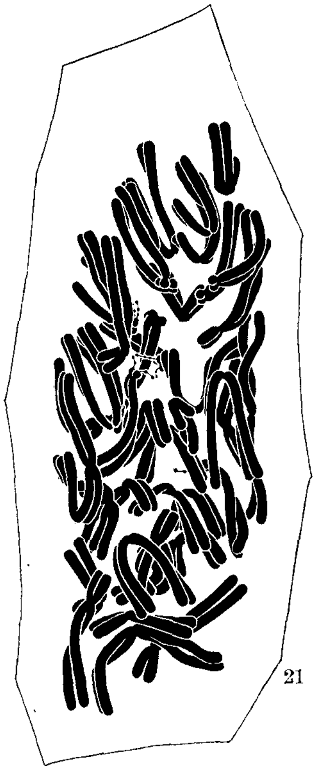
Description of chromosome types.

In general the chromosomes measured are considerably shorter than those of any of the preceding plants, but it is most probable that such differences are not of prime significance judging from their widths and from observations on normal metaphase chromosomes. The length and the form per cent of types *a, b, c,* and *e* are almost the same as those of *T. kamtschaticum* and *P. quadrifolia* var. *obavata.*

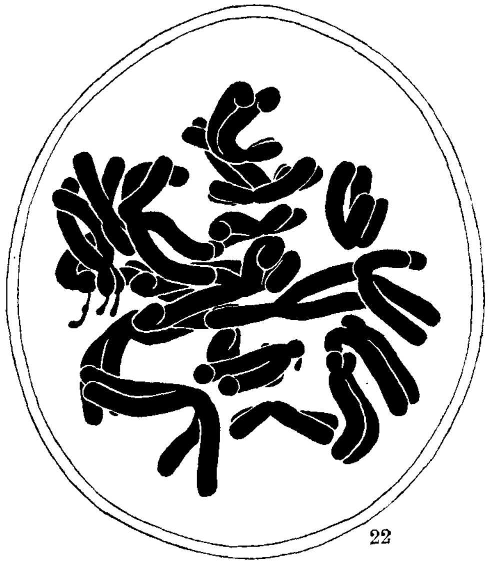
Type d_t. Fourth in length; in length per cent resembling closely *d*-chromosome of *T. kamtschaticum* and d_T of *P. quadrifolia* var. *obovata,* but possessing a small trabant connected to a spherical segment under which a primary constriction is located.

6. *Paris japonica* FRANCH. n=20, 2n=40

Up to the present this plant has not been investigated cytologically. The writer found that tihs species is octoploid; i. e., it contains 20 gametic



21



22

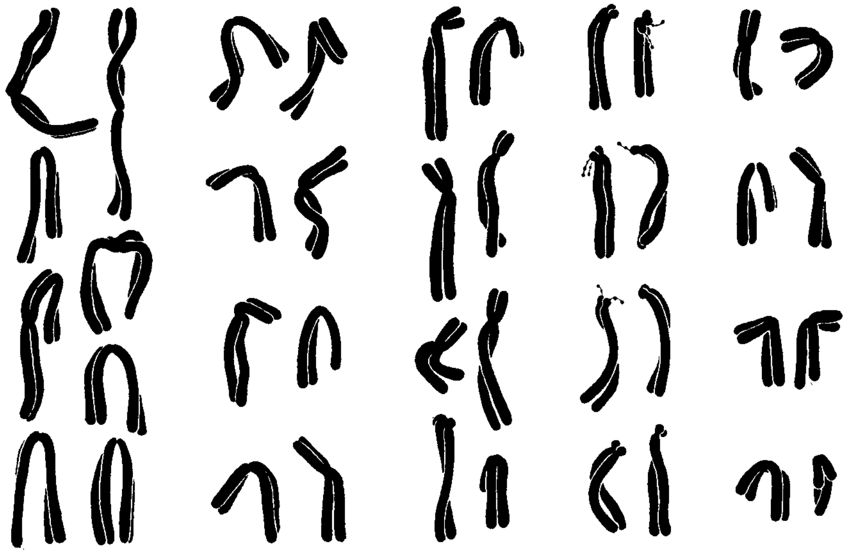
Figs. 21–22. *Paris japonica.* 21, somatic metaphase showing 40 chromosomes. 22, first metaphase in a pollen grain. 1220×.

and 40 somatic chromosomes (Figs. 21 and 22). In the present case the gametic number was determined at first metaphases in pollen grains, and it seems highly probable that the number thus determined represents the number of bivalents in the pollen mother-cells.[1]

Although measurements were not attempted owing to the complexity of the metaphase plate, the five general chromosome types *A, B, C, D,* and *E* closely resembling those of the preceding plants were identified with certainty, each comprising four members in a gametic and eight in a somatic complement (Figs. 23 and 24). In one pollen grain three of the four *D* type chromosomes were found to be accompanied by a tandem trabant, probably the absence in the fourth being only apparent because of its inconspicuous position. Presumably then eight *D* type chromosomes would be satellited in a somatic complement (Figs. 21, 23 and Pl. 10). As already described in none of the preceding plants was a tandem trabant found.

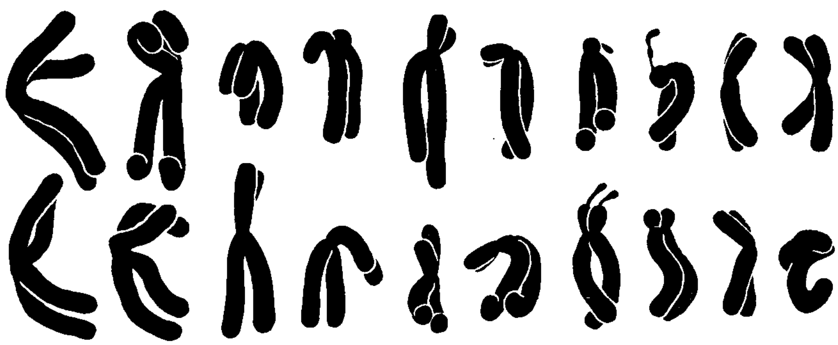
Metaphase chromosomes drawn in Figure 21 are shorter and broader

1) Very recently the same gametic number 20 was counted at the meiotic divisions.



A *B* *C* *D* *E*

Fig. 23. *Paris japonica.* Chromosomes classified from Figure 21. 1220 ×.



A *B* *C* *D* *E*

Fig. 24. *Paris japonica.* Chromosomes classified from Figure 22. 1220 ×.

as compared with those in a normal plate (cf. Fig. 23, *D* and Pl. 10). Basing one's considerations upon the ordinary chromosome lengths in the somatic cells, one may conclude that there are no great differences in the chromosome sizes between the present species and the preceding diploid or tetraploid ones.

In the present study, the comparison of the chromosomes was made on data obtained by measuring chromosome lengths in only one complement of each species. Now a question may arise as to the degree of reliability of the data thus acquainted. To what extent is any one chromosome complement to be considered as the representative of the species? In this connection, the writer has chosen *T. kamtschaticum* as suitable material and determined the length and the relative positions of constrictions of the five chromosome types at both metaphase and anaphase, selecting at random chromosomes lying flat. At metaphase 10 chromosomes and at anaphase 30 chromosomes were chosen for each type; the results of the measurements are given in Tables 6, 7 and 8. Length per cents in these Tables were calculated as the two times of the total sum of the mean lengths of 5 chromosome types corresponding to a somatic complement, i.e., $2(a+b+c+$

Table 6.[1)]

Lengths and positions of constrictins of each 10 metaphasic chromosomes of the 5 chromsome types in the somatic cells of *Trillium kamtschaticum*.

Type *a*

Chromosome individual	Whole length in μ	Position of constriction (—) in μ	Form %	Length % as a diploid set
1	37,8 *m*	18,9–18,9	50,0 *m*	
2	37,8	18,9–18,9	50,0	
3	37,2	18,3–18,3	50,0	
4	36,6	18,9–18,3	49,2	
5	34,9	17,8–17,1	49,2	
6	34,9	17,8–17,1	49,2	
7	34,2	17,1–17,1	50,0	
8	34,2	17,1–17,1	50,0	
9	31,4 *n*	16,0–15,4	49,1	
10	31,4	16,0–15,4	49,1 *n*	
Mean value	35,0	17,7–17,3	49,4	14,8

Type *b*

Chromosome individual	Whole length in μ	Position of constriction (—) in μ	Form %	Length % as a diploid set
1	26,8 *m*	17,1–9,7	36,2	
2	25,7	16,0–9,7	37,8	
3	25,7	16,6–9,1	35,6 *n*	
4	24,5	15,4–9,1	37,2	
5	24,5	15,4–9,1	37,4	
6	24,5	15,4–9,1	37,2	
7	22,9	14,3–8,6	37,5	
8	22,3	13,7–8,6	38,5 *m*	
9	21,7	13,7–8,0	36,9	
10	20,5 *n*	13,1–7,4	36,1	
Mean value	24,0	15,1–8,9	37,1	10,2

1) *m* indicates maximum value, and *n* minimum value.

Type *c*

Chromosome individual	Whole length in μ	Position of constriction (–) in μ	Form %	Length % as a diploid set
1	26,8 *m*	21,1–5,7	21,3	
2	25,1	19,4–5,7	22,7	
3	24,0	18,3–5,7	23,8	
4	24,0	18,3–5,7	23,8	
5	23,4	18,3–5,1	21,9	
6	22,4	17,8–4,6	20,5 *n*	
7	21,2	16,6–4,6	21,6	
8	21,1	16,0–5,1	24,3 *m*	
9	21,1	17,1–4,0	18,9	
10	20,6 *n*	16,0–4,6	22,2	
Mean value	23,0	17,9–5,1	22,2	9,7

Type *d*

Chromosome individual	Whole length in μ	Position of constriction (–) in μ	Form %	Length % as a diploid set
1	21,1 *m*	20,0–1,1	5,4 *n*	
2	20,5	19,4–1,1	5,6	
3	20,5	19,4–1,1	5,6	
4	20,5	19,4–1,1	5,6	
5	19,4	18,3–1,1	5,9	
6	19,4	18,3–1,1	5,9	
7	18,9	17,8–1,1	6,1	
8	18,9	17,8–1,1	6,1	
9	18,2 *n*	17,1–1,1	6,3 *m*	
10	18,2	17,1–1,1	6,3	
Mean value	19,6	18,5–1,1	5,9	8,3

Type *e*

Chromosome individual	Whole length in μ	Position of constriction (–) in μ	Form %	Length % as a diploid set
1	18,8 *m*	11,4–7,4	39,4 *m*	
2	17,8	10,9–6,9	38,7	
3	17,8	10,9–6,9	38,7	
4	17,8	10,9–6,9	38,7	
5	17,8	10,9–6,9	38,7	
6	17,2	10,9–6,3	36,7 *n*	
7	16,6	10,3–6,3	38,0	
8	15,4	9,7–5,7	37,0	
9	14,8 *n*	9,1–5,7	38,5	
10	14,8	9,1–5,7	38,5	
Mean value	16,9	10,4–6,5	38,5	7,1

$d+e)=100$.

From the tables, it will be seen that there are certain variations in the absolute length and also in the position of the constriction in different chromosome individuals belonging to the same chromosome type. The

Table 7.[1]

Lengths and positions of constrictions of each 30 anaphasic chromosomes of the 5 chromosome types in the somatic cells of *Trillium kamtschaticum*.

Type *a*

Chromosome individual	Whole length in μ	Position of constriction (–) in μ	Form %	Length % as a diploid set
1	28,6 *m*	14,3-14,3	50,0 *m*	
2	28,6	14,3-14,3	50,0	
3	28,0	14,3-13,7	49,0	
4	27,4	13,7-13,7	50,0	
5	27,4	13,7-13,7	50,0	
6	27,4	13,7-13,7	50,0	
7	27,4	13,7-13,7	50,0	
8	27,4	13,7-13,7	50,0	
9	27,4	13,7-13,7	50,0	
10	27,4	13,7-13,7	50,0	
11	26,8	13,7-13,1	49,8	
12	26,8	13,7-13,1	49,8	
13	26,8	13,7-13,1	49,8	
14	26,8	13,7-13,1	49,8	
15	26,8	13,7-13,1	49,8	
16	26,8	13,7-13,1	49,8	
17	26,2	13,1-13,1	50,0	
18	26,2	13,1-13,1	50,0	
19	25,7	13,1-12,6	48,9	
20	25,7	13,1-12,6	48,9	
21	25,2	12,6-12,6	50,0	
22	25,2	12,6-12,6	50,0	
23	25,2	12,6-12,6	50,0	
24	25,2	12,6-12,6	50,0	
25	24,6	12,6-12,0	48,8 *n*	
26	24,6	12,6-12,0	48,8	
27	24,6	12,6-12,0	48,8	
28	24,0 *n*	12,0-12,0	50,0	
29	24,0	12,0-12,0	50,0	
30	24,0	12,0-12,0	50,0	
Mean value	26,3	13,2-13,1	49,6	14,5

1) *m* indicates maximum value, and *n* minimum value.

Type *b*

Chromosome individual	Whole length in μ	Position of constriction (−) in μ	Form %	Length % as a diploid set
1	18,8 *m*	11,4-7,4	39,4	
2	18,8	11,4-7,4	39,4	
3	18,8	11,4-7,4	39,4	
4	18,3	10,9-7,4	40,6 *m*	
5	18,3	11,4-6,9	37,5	
6	18,3	10,9-7,4	40,6	
7	18,3	10,9-7,4	40,6	
8	18,3	11,4-6,9	37,5	
9	18,3	11,4-6,9	37,5	
10	18,3	11,4-6,9	37,5	
11	18,3	11,4-6,9	37,5	
12	18,3	11,4-6,9	37,5	
13	18,3	11,4-6,9	37,5	
14	18,3	11,4-6,9	37,5	
15	18,3	11,4-6,9	37,5	
16	18,3	11,4-6,9	37,5	
17	18,3	11,4-6,9	37,5	
18	18,3	10,9-7,4	40,6	
19	17,8	10,9-6,9	38,7	
20	17,8	10,9-6,9	38,7	
21	17,8	10,9-6,9	38,7	
22	17,8	10,9-6,9	38,7	
23	17,8	10,9-6,9	38,7	
24	17,8	10,9-6,9	38,7	
25	17,7	11,4-6,3	35,5 *n*	
26	17,2	10,9-6,3	36,7	
27	17,2	10,9-6,3	36,7	
28	16,5 *n*	10,8-5,7	35,7	
29	16,5	10,8-5,7	35,7	
30	16,5	10,8-5,7	35,7	
Mean value	17,9	11,1-6,8	38,0	9,9

Type *c*

Chromosome individual	Whole length in μ	Position of constriction (–) in μ	Form %	Length % as a diploid set
1	18,3 *m*	14,3–4,0	21,9	
2	18,3	14,3–4,0	21,9	
3	18,3	14,3–4,0	21,9	
4	18,3	14,3–4,0	21,9	
5	18,3	14,3–4,0	21,9	
6	17,7	13,7–4,0	22,6	
7	17,7	13,7–4,0	22,6	
8	17,7	13,7–4,0	22,6	
9	17,7	13,7–4,0	22,5	
10	17,7	13,7–4,0	22,6	
11	17,7	13,7–4,0	22,6	
12	17,7	13,7–4,0	22,6	
13	17,7	13,7–4,0	22,6	
14	17,7	13,7–4,0	22,6	
15	17,7	13,7–4,0	22,6	
16	17,7	13,7–4,0	22,6	
17	17,7	13,7–4,0	22,6	
18	17,7	13,7–4,0	22,6	
19	17,1	13,7–3,4	20,0	
20	17,1	13,1–4,0	23,3	
21	17,1	13,1–4,0	23,3	
22	17,1	13,1–4,0	23,3	
23	17,1	13,7–3,4	20,0 *n*	
24	17,1	13,1–4,0	23,3 *m*	
25	16,5	13,1–3,4	20,7	
26	16,5	13,1–3,4	20,7	
27	16,5	13,1–3,4	20,7	
28	16,5	13,1–3,4	20,7	
29	16,0 *n*	12,6–3,4	21,4	
30	16,0	12,6–3,4	21,4	
Mean value	17,5	13,6–3,9	22,3	9,6

Type *d*

Chromosome individual	Whole length in μ	Position of constriction (−) in μ	Form %	Length % as a diploid set
1	18,2 *m*	17,1–1,1	6,3 *n*	
2	17,1	16,0–1,1	6,6	
3	17,1	16,0–1,1	6,6	
4	17,1	16,0–1,1	6,6	
5	17,1	16,0–1,1	6,6	
6	17,1	16,0–1,1	6,6	
7	16,5	15,4–1,1	6,9	
8	16,5	15,4–1,1	6,9	
9	16,5	15,4–1,1	6,9	
10	16,5	15,4–1,1	6,9	
11	16,5	15,4–1,1	6,9	
12	16,5	15,4–1,1	6,9	
13	16,5	15,4–1,1	6,9	
14	16,5	15,4–1,1	6,9	
15	16,5	15,4–1,1	6,9	
16	16,0	14,9–1,1	7,1	
17	16,0	14,9–1,1	7,1	
18	16,0	14,9–1,1	7,1	
19	16,0	14,9–1,1	7,1	
20	16,0	14,9–1,1	7,1	
21	16,0	14,9–1,1	7,1	
22	16,0	14,9–1,1	7,1	
23	16,0	14,9–1,1	7,1	
24	16,0	14,9–1,1	7,1	
25	15,4	14,3–1,1	7,4	
26	15,4	14,3–1,1	7,4	
27	15,4	14,3–1,1	7,4	
28	14,8 *n*	13,7–1,1	7,7 *m*	
29	14,8	13,7–1,1	7,7	
30	14,8	13,7–1,1	7,7	
Mean value	16,2	15,1–1,1	7,0	9,0

Type *e*

Chromosome individual	Whole length in μ	Position of constriction (−) in μ	Form %	Length % as a diploid set
1	14,3 *m*	8,6–5,7	40,0	
2	14,3	8,6–5,7	40,0	
3	13,1	8,0–5,1	39,1	
4	13,1	8,0–5,1	39,1	
5	13,1	8,0–5,1	39,1	
6	13,1	8,0–5,1	39,1	
7	13,1	8,0–5,1	39,1	
8	13,1	8,0–5,1	39,1	
9	13,1	8,0–5,1	39,1	
10	13,1	8,0–5,1	39,1	
11	13,1	8,0–5,1	39,1	
12	13,1	7,4–5,7	43,5 *m*	
13	12,6	8,0–4,6	36,4 *n*	
14	12,6	8,0–4,6	36,4	
15	12,6	8,0–4,6	36,4	
16	12,5	7,4–5,1	40,9	
17	12,5	7,4–5,1	40,9	
18	12,5	7,4–5,1	40,9	
19	12,5	7,4–5,1	40,9	
20	12,5	7,4–5,1	40,9	
21	12,5	7,4–5,1	40,9	
22	12,5	7,4–5,1	40,9	
23	12,5	7,4–5,1	40,9	
24	12,5	7,4–5,1	40,9	
25	12,5	7,4–5,1	40,9	
26	12,5	7,4–5,1	40,9	
27	12,0 *n*	7,4–4,6	38,1	
28	12,0	7,4–4,6	38,1	
29	12,0	7,4–4,6	38,1	
30	12,0	7,4–4,6	38,1	
Mean value	12,8	7,7–5,1	39,8	7,0

maximum variation in absolute length is found in type *c* of Table 6, where $m:n=13:10$ and $m\text{-}n=6{,}2\,\mu$. The greatest difference in form per cent is $m\text{-}n=7{,}1\%$ in type *e* of Table 7. Such variations may be due to different grades of contraction of chromosome or to a different rate of contraction at either side of a constriction. Such variations are already established phenomena in *Crepis* (HOLLINGHEAD 1930) and *Allium* (Levan 1932).

Table 8.

Comparison of the mean values in Tables 6–7 and the contraction ratio at anaphase.

Chromosome type	Whole length in μ		Length % as a diploid set		Form %		Contraction ratio (Ana./Meta.)
	Meta.	Ana.	Meta.	Ana.	Meta.	Ana.	
a	35,0	26,3	14,8	14,5	49,4	49,6	0,75
b	24,0	17,9	10,2	9,9	37,1	38,0	0,75
c	23,0	17,5	9,7	9,6	22,2	22,3	0,76
d	19,6	16,2	8,3	9,0	5,9	7,0	0,83
e	16,9	12,8	7,1	7,0	38,5	39,8	0,76

It is important to notice, however, that the relative position of the constriction and, probably, the relative length of the chromosomes are nearly constant to each chromosome in a complement. With respect to the length per cent, that of the chromosomes at metaphase is thus the same as that of the chromosomes at anaphase. Furthermore with respect to the absolute length, the proportion of the length of the metaphasic to that of the anaphasic chromosome is constant for each chromosome type (see Table 8). Actually the chromatids increase their widths at anaphase. Average diameter of the 10 chromatids at metaphase is 0,86 microns, while that at anaphase 1,29 microns. Such a great increase in the diameters of the chromatids at anaphase can not be interpreted as the results of mere longitudinal contraction in classical sense.

In view of these findings it may be justifiable to take the relative (not absolute) length of the chromosomes in a single complement as the basis of comparison of the chromosome type in different species, on which the present study is made. Furthermore if one compares Table 1 with 8, one will find close parallelism between them. It may be therefore concluded that, if the measurement is adequetly made, reliance is to be placed on its results.

For convenience of further comparison of the chromosome types in different species, the mean values of each chromosome type shown in

Tables 1–5 are arranged in Table 9. In this table, the length per cent in tetraploid species are presented as a haploid set and that in diploid species as a diploid set to make the direct comparison between them possible.

Table 9.[1]

Comparison of the mean values of form and length per cents of the 5 chromosome types in different species shown in Tables 1–5.

Chromosome type		*T. kamtschaticum*	*T. Smallii*	*T. Tschonoskii*	*P. quadrifolia* var. *obovata*	*P. tetraphylla*
A	F%	49,6	49,1	49,0	49,6	49,5
	L%	15,2	15,4	15,6	13,4	14,2
B	F%	38,5	*b* 36,0 *b'* 39,9	*b* 38,0 *b'* 40,5	39,6	40,5
	L%	9,9	*b* 10,8 *b'* 9,8	*b* 10,3 *b'* 9,6	10,6	10,5
C	F%	22,0	*c* 18,8 *c'* 19,5	14,9	24,6	21,2
	L%	9,3	*c* 10,1 *c'* 8,4	9,2	9,2	8,9
D	F%	5,5	6,9	3,7	5,2 ; 10,4[2]	7,2
	L%	8,8	8,2	8,2	9,0	8,3
E	F%	37,1	*e* 39,6 *e'* 37,3	34,4	43,0	38,2
	L%	7,0	*e* 7,5 *e'* 6,6	7 3	7,9	8,2

Discussion

As above mentioned in the tests of measurement, it is hardly tenable to consider the slight differences in length and form per cents and in absolute lengths of the chromosomes found between different species as very significant. Furthermore technical errors in measurement may be somewhat large, so that, as we can see in Tables 1–5 and collectively in Table 9, it may be said that all the species examined contain in their somatic cells 2–8 multiples of the common basic complement or genome

1) F% indicates form per cent and L% length per cent.

2) The former represents the F% of the spherical segment, and the latter that of the trabant.

$(A+B+C+D+E)$. Consequently it is possible to represent the somatic complement of diploid, tetraploid and octoploid species with the general formulas:

Diploid	$2(A+B+C+D+E)$	= 10 chromosomes.
Tetraploid	$4(A+B+C+D+E)$	= 20 chromosomes.
Octoploid	$8(A+B+C+D+E)$	= 40 chromosomes.

The finest instances of such relationships between polyploidy and chromosome complements are seen, although they are autopolyploids, in 2n, 3n and 5n plants of *Crepis capillaris* and 2n, 3n and 4n plants of *Crepis tectorum* (NAWASCHIN 1927), and in an amphidiploid plant from the cross *Crepis capillaris* × *C. tectorum* (HOLLINGSHEAD 1930). Among the natural group of species, only the *Aconitum* species seem to bear some resemblance to the present case (DARLINGTON, cf. 1932).

Recent investigations have furnished several proofs on the origin of polyploids, revealing that many constant polyploid plants have been raised in several ways through interspecific hybridization (cf. WINGE 1932). On the bases of the following findings it seems to be highly pertinent to consider that the polyploids in the present tribe, although their parental plants are undeterminable, have originated through hybridization within existing or pre-existing plants with different genomes $(A+B+C+D+E)$ or between them.

1. As repeatedly mentioned, all the species contain the multiples of a very closely similar basic complement $(A+B+C+D+E)$.

2. The total sum of the chromosome lengths in a complement of the diploids is approximately the half of that of the tetraploid (cf. Table 1–5), and very probably such a relationship may be kept between tetraploid and octoploid.

3. In *Trillium Smallii* three dissimilar pairs of types in pair were found; i.e., b and b', c and c', e and e' among each four members of B, C, and E chromosome type respectively, and in *Trillium Tschonoskii* probably b and b' among four of its B type chromosomes.

4. Though extensive examination was not carried out there was observed no indication of multivalent association of chromosomes at meiosis in polyploid species.

As a matter of course, the present findings do not allow any conclusion as to the genetical relationships between the basic complements or genomes, but it is a very interesting fact that the D-chromosomes of *Trillium* species are always d type without any trabant, while those of *Paris* are in every case furnished with a trabant which is characteristic to the species or variety.

The writer wishes to express his heartiest thanks to Professor H. MATSUURA for his helpful suggestions and criticisms in the course of the work.

Summary

1. The number, size and shape of gametic and especially of somatic chromosomes in the following plants were investigated:

Species	n	2n	Chromosome constitution
Paris japonica FRANCH.	20	40	$= 8\ (A + B + C + D + E)$
Paris quadrifolia L. var. *obavata* REGEL et TIL.	5	10	$= 2\ (A + B + C + D + E)$
Paris tetraphylla A. GRAY	5	10	$= 2\ (A + B + C + D + E)$
Trillium kamtschaticum PALL.	5	10	$= 2\ (A + B + C + D + E)$
Trillium Smallii MAXIM.	10	20	$= 4\ (A + B + C + D + E)$
Trillium Tschonoskii MAXIM.	10	20	$= 4\ (A + B + C + D + E)$

2. A comparison of chromosome types was made among them, and hybridization within existing or pre-existing plants or between them was suggested as the possible process through which the present-day polyploids in this tribe may have arisen.

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Explanation of Plate

1. A complete set of the metaphase chromosomes of *Trillium Smallii* from a root-tip cell. Chromosomes marked with f are ones revealing their actual lengths; supposed true constrictions are indicated by arrows. Note *b* and *b′*, *c* and *c′*, *e* and *e′* chromosome. Chloralhydrate material. 1220×.

2. First metaphase in a pollen grain of *Trillium kamtschaticum*, *d*-chromosome being forshorten. From the left: *b, c, d*(upper), *c*(below), *a* chromosome. Photo. by Prof. Matsuura. 1220×.

3. Meiotic first metaphase in a P.M.C. of *Paris tetraphylla*, showing 5 bivalents. 430×.

4. Meiotic first metaphase in a P.M.C. of *Trillium kamtschaticum*, showing 5 bivalents. From the left: *dd, aa, ee, bb*(upper), *cc*(below). Photo. by Prof. Matsuura. 700×.

5. Meiotic first metaphase in a P.M.C. of *Trillium Tschonoskii*, showing 10 bivalents. 430×.

6. Meiotic first metaphase in a P.M.C. of the heterozygous form of *Paris quadrifolia* var. *obovata*, showing 5 bivalents. Note the association of d_T and d_0 chromosome. 430×.

7. First metaphase in a pollen grain of *Paris quadrifolia* var. *obovata*. 1220×.

8. First metaphase in a pollen grain of *Trillium kamtschaticum,* every chromosome lying almost flat. 990 ×.

9. First metaphase in a pollen grain of *Paris tetraphylla.* 1220 ×.

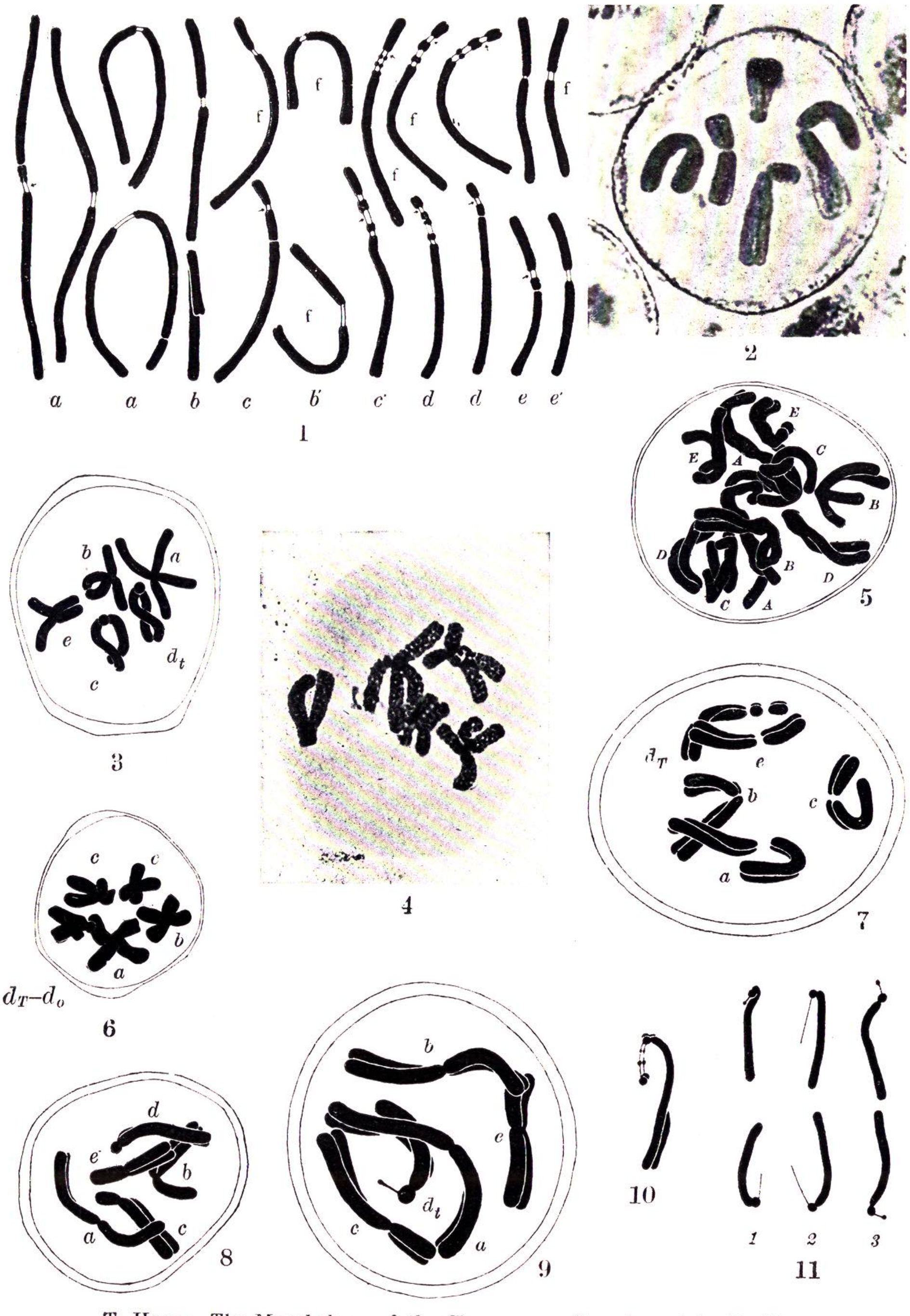
10. *D*-chromosome with a tandem trabant at a somatic metaphase of *Paris japonica,* showing the ordinary chromosome length. 1220 ×.

11. Anaphasic transformations of the trabants of d_t-chromosomes at somatic mitoes in an individual of *Paris tetraphylla,* facing the daughter halves to each other.

1. Above, ordinary in appearance; below, somewhat shorter thread.

2. Both, very long thread.

3. Both, somewhat greater in size. 1220 ×.



T. Haga: The Morphology of the Chromosome Complement in *Parideae*