The metamorphosis of floral organs in *Trillium amabile* MIYABE et TATEWAKI.

By

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(With 16 Text-figures)

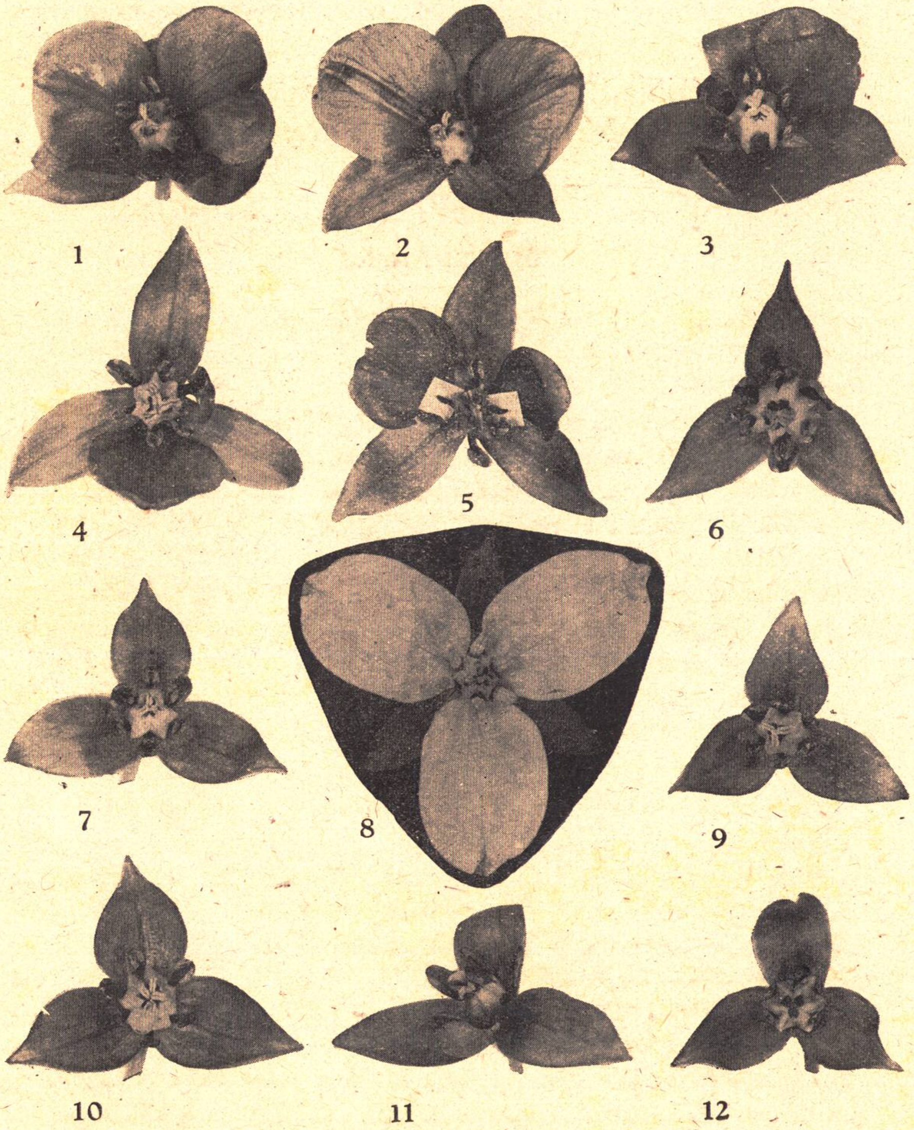
Introduction

The normal flower of *Trillium amabile* consists of three sepals, three petals, six stamens and an ovary formed by three carpels and three stigmata. The remarkable character of this plant is the habitual occurrence of metamorphosis in its petals and stamens, though the grades of metamorphosis are very variable.

At a lower degree of metamorphosis, a small patch of anther-sac appears on the petal margin and, as the metamorphosis advances, this comes up to a complete anther-sac and the petaline part coincidently converges into a filament. However, such a metamorphosed stamen is distinguishable from the true one by its broader filamental part (cf. HAGA '39 Fig. C). Figure 7 shows three petals which have converged into complete forms of stamens and do not show any parts of petaline rudiments. Such petals are classified into "staminoids" and the remaining ones into "antheroids" (HAGA '39).

Two directions of variation—metamorphosis and elimination—may take place on the stamen. The grades of metamorphosis are continuous up to the formation of complete carpels at its maximum. At first, only filamental parts adhere to a carpel and, in a more advanced form, filaments converge completely into carpellary tissues, notwithstanding the anther remains intact (Fig. 11). In the most advanced type of metamorphosis, the anther and filament of a stamen change into a stigma and a carpel respectively (Figs. 7 and 9–10). Of course, there are many intermediate forms between these types. Stamens which completely change to carpels, are classified as "carpeloids" and the rest of incomplete changes as "semicarpeloids", though such a classification is arbitrary.

The elimination of stamens occurs discontinuously. A filamental part without an anther is met with frequently (Fig. 5), and this is considered



Figs. 1–12. **1–4**, **6–7** and **10**, Abnormal flowers showing following metamorphosis. **1**, (1P+2a)+5S+3.5C+3Stig. **2**, (2P+1s)+5S+3.5C+3Stig. **3**, (2P+1a)+5S+4C+4Stig. **4**, (1P+1a+1s)+4S+3C+3Stig. **6**, 3s+4S+4C+4Stig. **7**, 3s+6S+3C+3Stig (balanced type). **10**, 3s+3S+5C+5Stig. **5**, Showing two filaments in an abnormal flower. **8**, a flower of *T. kamtschaticum*. **9**, An extreme metamorphosed type, "*Smallii* type". **11**, Showing semicarpeloid in an abnormal flower. **12**, A flower of *T. Smallii*.

as indicating the first step of the elimination. Figure 9 indicates three stamens eliminated.

A preliminary survey on this subject was done by HAGA ('39). The present study was planned as a succeeding work to his, to elucidate, on a larger scale, the mechanism of metamorphosis of the floral organ in this plant. The total 577 flowers on 398 plants were statistically treated in the present paper.

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Material

Material was taken from two different sources. The one is material which originally came from Kojima and has been cultured in the experimental garden of our institute. This is the same material which was investigated by HAGA ('39). The other is material collected from Usu in Hokkaido. In this plant, as in other *Trillium* species, a single shoot usually comes out of a corm, but twin or triplet shoots are rarely met with. The present observations were made about middle of May 1940.

Direction of Metamorphosis.

Material from our experimental garden shows 144 abnormals (84.3%) in the total 172 flowers, and that from Usu 396 abnormals (97.7%) in the total 405 flowers.

In the grand total 540 abnormal flowers, those in which inner parts are effected and petals did not show any change, are counted as 6 (1.1%), and those showing affected petals and normal inner parts are 117 (21.7%), and, lastly, those in which both parts of petals and inner organs are affected are 417 (77.2%). This suggests that the direction of metamorphosis is centripetal and that there is some correlation in the metamorphosis of petals and inner parts (Table 9).

Correlation in the metamorphosis between two flowers on twin shoots.

For a study on the correlation in twin shoots, material of Usu was used, and the data of correlation in the number of metamorphosed petals and of reduced stamens on each flower are given in Table 1. It may be said with safety that there is no correlation between two flowers on twin shoots. This is the reason why flowers on single, twin and triplet shoots were treated in the following accounts without making any distinction between them.

Flowers on single and twin shoots.

According to the data obtained by HAGA ('39), flowers on twin shoots show a frequency of metamorphosis twice as compared to those of single shoots. To make clear the frequency of metamorphosis in these flowers, petals were examined statistically as shown in Table 2. In material from our experimental garden, the frequency of metamorphosis in twin shoots is higher than that in single shoots, but when compared with the data of HAGA ('39), the difference is reduced in the present case and in material from Usu, single shoots show a higher frequency conversely. Concerning triplet shoots any definite statement cannot be made in such small data.

Table 1. Correlation in twin shoots.*

Y \ X	1	2	3	Total
1	—	—	3	3
2	—	—	10	10
3	4	13	53	70
Total	4	13	66	85

$M_x = 2.807 \pm 0.040$ $M_y = 2.867 \pm 0.042$ $r = -0.097 \pm 0.073$
$\sigma_x = 0.477 \pm 0.025$ $\sigma_y = 0.576 \pm 0.030$

* X and Y indicate the number of metamorphosed petals of each flower on twin shoots.

Y \ X	1	2	3	Total
1	2	2	3	7
2	1	5	5	11
3	5	8	24	37
Total	8	15	32	55

$M_x = 2.545 \pm 0.065$ $M_y = 2.436 \pm 0.066$ $r = 0.207 \pm 0.087$
$\sigma_x = 0.710 \pm 0.046$ $\sigma_y = 0.733 \pm 0.047$

* X and Y indicate the number of eliminated stamens of each flower on twin shoots.

It may be presumably said, however, that the tendency of metamorphosis in each flower is equal, having no relation to its developmental condition, that is, whether it grows on single, twin or triplet shoots. Tables 2–3 and 4 are made in a similar way as HAGA ('39). It is easily understandable by these tables that the frequency of metamorphosis is variable in different environmental conditions of each year.

Table 2. Frequency of the metamorphosis of petals.*

E.

Grouping		†0	1	2	3	Total	Abnormal flowers
1 shoots	Flowers	18	13	13	19	63	45
	%	28.6	20.6	20.6	30.2	99.9	71.4
2 shoots	Flowers	13	8	9	74	104	91
	%	12.5	7.7	8.7	71.2	100.1	78.5
3 shoots	Flowers	1	0	1	2	4	3
	%	25.0	0	25.0	50.0	100.0	75.0
In total	Flowers	32	21	23	95	171	139
	%	18.7	12.3	13.5	55,6	100.1	81.3

U.

Grouping		†0	1	2	3	Total	Abnormal flowers
1 shoots	Flowers	4	7	17	133	161	157
	%	2.5	4.3	10.6	82.6	100.0	97.5
2 shoots	Flowers	7	9	29	181	226	219
	%	3.1	4.0	12.8	80.1	100.0	96.9
3 shoots	Flowers	0	0	2	16	18	18
	%	0	0	11.1	88.9	100.0	100.0
In total	Flowers	11	16	48	330	405	394
	%	2.7	4.0	11.9	81.5	100,1	97.3

* E.: material from the experimental garden.
U.: material from Usu.
† number of metamorphosis per one flower.

Metamorphosis in petals.

Sepals are very stable and do not vary in their number and form. Petals always metamorphose in high frequency, but their basic number is constantly three. The grade of metamorphosis is continuous from the antherody to the extreme type, that is, staminody. Figure 4 shows a flower carrying a normal, an antheroid and a staminoid petal. Figures 1–3 represent flowers of lower metamorphoses. The entire petals of flowers which were extremely affected are shown in Figures 6–7 and 9–10.

Table 3. Frequency of various types of abnormal flowers.*

Type	(2P+1a)	(2P+1s)	(1P+2a)	(1P+1a+1s)	(1P+2s)	(3a)	(2a+1s)	(1a+2s)	(3s)	Total
E. Flowers obs.	14	7	18	2	3	19	26	20	30	139
U. Flowers obs.	14	2	26	19	3	25	36	58	211	394
Total	28	9	44	21	6	44	62	78	241	533

* P: petal, a: antheroid, s: staminoid.

In the case of metamorphosis of petals, various combinations of affected petals are possible (Table 3), and the data indicate that there is a clear difference in the tendency of metamorphosis between the two classes, one having at least one normal petal and the other entirely lacking petals. Namely, in the former, the frequency decreases as staminoids increase, while in the latter it increases as staminoids do. This tendency accords with the data of HAGA ('39). It seems that this plant has two opposing characters, one to produce normal petals and the other to change petals into stamens, and the frequency of staminoids increases as affected flowers increase, as will be seen in the comparison of this table to HAGA's data and those in material from the experimental garden to those in Usu material.

Table 4. Frequency of staminoids in the metamorphosed petals.

E.

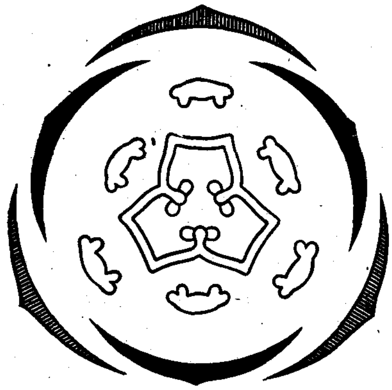
Number of metamorphosis	Flowers	Staminoids	Antheroids	% of staminoids
1	21	7	14	33.33
2	23	6	40	13.04
3	95	156	129	56.74
Total	139	169	183	48.01

U.

Number of metamorphosis	Flowers	Staminoids	Antheroids	% of staminoids
1	16	2	14	12.50
2	48	25	71	26.04
3	330	785	205	79.29
Total	394	812	290	73.68

Metamorphosis and elimination of stamens.

The metamorphosis of stamens is difficult to study, because their affected forms are carpeloids and there are many irregular forms at their



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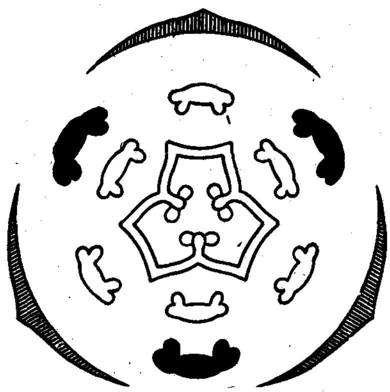

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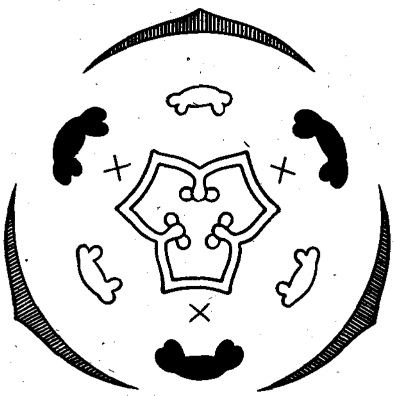

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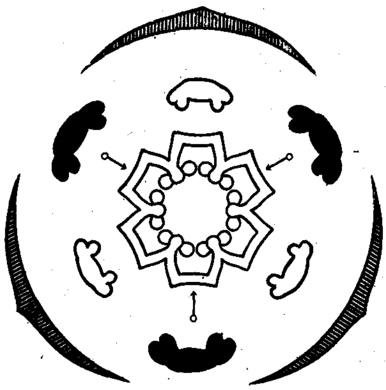

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Figs. 13–16. Flower diagrams of *T. amabile.* **13**, The normal flower, "*kamtschaticum* type". **14**, The balanced type. **15**, The one extreme type, "*Smallii* type". **16**, The other extreme type. The blackened stamen indicates "Staminoid".

Table 5. Frequency of eliminated stamens and of carpeloids.

Number of reducible stamens	Number of reduced stamens	No. of eliminated stamens %	684 77.2
1707	1018	No. of carpeloids %	334 32.8

adhesion to carpels, which mostly show obscure boundaries from the true carpels and often are not detectable as such.

In the six stamens (Fig. 13), three outer ones are stable, showing no variation in their number and form (Figs. 3, 6–7 and 9–10), but three inner ones decrease in their number and metamorphose with high frequency. Stamens changed into carpeloids are shown in Figures 3, 6, 10 and 16. The comparison of the strength of tendency of carpellody and of elimination is shown in Table 5; the latter arises twice as the former. Three carpels do not usually metamorphose, except varying in their number on rare occasions. Making no distinction of carpeloids from carpels, there are four classes with respect to their number, namely, 3, 4, 5 and 6. Table 6 shows a frequency of the number of carpels in the highest metamorphosed type which has three staminoids and three stamens. By combining variable numbers in stamens and carpels, 16 possible cases are expectable (Table 7).

Table 6. Frequency of various numbers of carpels in (3s) + (3S) type.

Carpel number	3	4	5	6	Total
E. No. of flowers	3	0	1	0	4
U. No. of flowers	53	77	14	2	146
Total %	56 37.3	77 51.3	15 10.0	2 1.3	150 99.9

Table 7. Frequency of various combinations of stamens and carpels.*

Combinations (S–C)	(6-3)	(6-4)	(6-5)	(6-6)	(5-3)	(5-4)	(5-5)	(5-6)	(4-3)	(4-4)	(4-5)	(4-6)	(3-3)	(3-4)	(3-5)	(3-6)	Total
E. Flowers obs.	90	0	0	0	12	25	0	0	4	7	7	0	10	7	4	2	168
U. Flowers obs.	75	8	0	0	14	23	2	0	6	43	13	0	82	113	20	3	402
Total %	165 28.9	8 1.4	0 0	0 0	26 4.6	48 8.4	2 0.4	0 0	10 1.8	50 8.8	20 3.5	0 0	92 16.1	120 21.1	24 4.2	5 0.9	570 100.1

* S: stamen, C: carpel.

Since stamens decrease in their number from six to three and carpels are constantly three, their total number must be from 6 to 9, but in fact the present writer met with those exceeding 9 which are out of this rule.

Table 8 shows the combination of numbers in the stigma and the carpel. It will be seen that frequencies of equally numbered variants such as 3–3, 4–4 etc. are at the maximum in each class. The results suggest that, as the number of carpels increases, the frequency of irregular combinations increases.

Table 8. Frequency of various combinations of carpels and stigmas.*

Combinations (C–Stig)	(3-3)	(3-4)	(3-5)	(3-6)	(4-3)	(4-4)	(4-5)	(4-6)	(5-3)	(5-4)	(5-5)	(5-6)	(6-3)	(6-4)	(6-5)	(6-6)	Total
E. Flowers obs.	117	1	0	0	19	18	0	0	2	5	3	0	0	1	1	0	167
U. Flowers obs.	170	2	0	0	34	137	12	0	1	16	17	1	0	0	2	1	391
Total	287	3	0	0	53	155	12	0	3	21	20	1	0	1	3	1	558
%	51.4	0.5	0	0	9.5	27.7	22.1	0	0.5	3.7	3.6	0.2	0	0.2	0.5	0.2	100.1

* C: carpel, Stig: stigma.

The correlation between staminody of petals and elimination of stamens is shown in Table 9. In each material from the experimental garden and from Usu, the correlation coefficient was calculated as 0.492±0.059 and

Table 9. Correlation in staminody and stamen diminution.*

E.

Y \ X	1	2	3	Total
1	13	—	—	13
2	4	3	—	7
3	18	14	22	54
Total	35	17	22	74

Mx = 1.824 ± 0.067 My = 2.554 ± 0.060 r = 0.492 ± 0.059
σx = 0.860 ± 0.048 σy = 0.774 ± 0.043

U.

Y \ X	1	2	3	Total
1	2	3	2	7
2	13	10	8	31
3	27	48	208	283
Total	42	61	218	321

Mx = 2.548 ± 0.027 My = 2.860 ± 0.015 r = 0.219 ± 0.036
σx = 0.714 ± 0.019 σy = 0.405 ± 0.011

* X indicates the number of eliminated stamens and Y the staminoids.

0.219±0.036 respectively, indicating a certain positive correlation.

Irregular variations.

As shown in Table 10, 54 (9.3%) among the total 577 flowers varied in irregular fashions which are out of the rule of metamorphosis just

Table 10. Frequency of irregularities.

Sepal	Petal	Stamen	Carpel	Stigma
* 1	1	4	23	43
†−1	-1	−1 → −2	+1 → −1	+2 → −3

* number of plants.
† variation of basic number.

stated. Among them, one unique type appeared which had 2 sepals, 2 petals, 4 stamens and 2 stigmata. Recently the present writer happened to observe only one plant of the same type in another species of *Trillium*, viz., *T. Tschonoskii*. Generally outer organs—sepals and petals—are very stable, while the inner organs—stamens, carpels and stigmata—are unstable in the order mentioned; in other words, the stability of floral organs is lessened centripetally.

Comment

The chromosome complement of the present species seems to indicate that it is a hexaploid ($n=15$) presumably raised from an apetalous species, *T. Smallii* ($n=10$) (Fig. 12), and a petalous species, *T. kamtschaticum* ($n=5$) (Fig. 8) (HAGA's unpublished data). The connection of this supposed origin of the present species with the metamorphosis of the floral organs is very interesting.

The characters of this plant, in which metamorphosis and variation on floral organs take place, are presumably considered as the following:

(A) Formation of normal petals,
(B) Changes of petals into stamens,
(C) Elimination of three inner stamens,
(D) Changes of three inner stamens into carpels,
(E) Changes in the basic number of each floral organ.

In these, (A) belongs to the character of *T. kamtschaticum* and (B) and (C) to those of *T. Smallii*. The so-called normal flower is of "*kamtschaticum* type" (Fig. 13) and that which extremely metamorphosed, having 3 staminoids, 3 stamens and 3 carpels, is of "*Smallii* type" (Fig. 15).

Figure 9 represents an extremely metamorphosed type of *T. amabile* which is not different in every respect from the flower of *T. Smallii* (Fig. 12). The variation curve of metamorphosed flowers with these two types as the extremes is *U*-shaped in both materials from our experimental garden and Usu. This means that the phenomenon of metamorphosis is always fluctuating between the "*kamtschaticum* type" and the "*Smallii* type". At the beginning of floral development, different environmental conditions seem to be responsible in different grades of tendency of metamorphosis. Probably the flower represented in Figure 7 (cf. Fig. 14) is of a balanced form between those two extremes.

From observation on 200 plants of *T. kamtschaticum* and 194 ones of *T. Smallii* growing in our experimental garden and suburbs of Sapporo, it was revealed that there exists a definite spacial relationship of carpels to sepals, as represented in Figures 13 and 15. A carpel of *T. Smallii* situates on the line passing through the center of the flower and a sepal; on the other hand, one of *T. kamtschaticum* situates between a sepal and the adjoining one, and therefore the position of the carpel rotates by 60° from the case in the former. This is a conspicuous character which distinguishes the former from the latter, and there is no exception.

These characters just mentioned manifest themselves in metamorphosed flowers of *T. amabile*. When flowers have either petals or antheroids or staminoids and three inner stamens remaining unaffected, the situation of the carpel is always of the "*kamtschaticum* type", and when they have 3 staminoids and are entirely lacking three inner stamens, its situation is always of the "*Smallii* type". Accordingly, the situation of carpels against 6 stamens (in extremely metamorphosed flowers 3 out of 6 stamens are staminoids) is not altered.

In *T. Smallii*, 6.2 per cent of abnormalities were recognized (namely, 11 flowers have 4 carpels and 4 stigmas and one has 2 carpels and 2 stigmas in the total 194 flowers), while in *T. kamtschaticum* there was no abnormality in the 200 flowers under observation. The unstability of the inner organs, as described above, might well be related to such a variable character of *T. Smallii*.

Summary

The flower of *Trillium amabile* consists of three sepals, three petals, three outer stamens, three inner stamens and an ovary which is composed of three carpels forming three pracentae and three stigmas. Petals and inner stamens of this plant frequently metamorphose into "stamens" and

"carpels" respectively. The grade of metamorphosis is, however, various; there exist many intermediate forms. The metamorphosis takes place from the outer organs to the inner ones, thus the direction of it being centripetal. There is no correlation in the metamorphosis between two flowers on twin shoot (Table 1). The occurrence of metamorphosis is approximately unaltered in frequency between flowers on single, twin and triplet shoots (Table 2).

Petals metamorphose into either "antheroids" or "staminoids" (cf. HAGA '39). The latter represent the extreme form of metamorphosed petals, the only distinction from the true stamens being in their broader filamental parts. "Antheroids" include all the intermediates between the true petal and the staminoid, bearing "anthers" in various sizes and various degrees of development on the petal margin.

Three sepals and three outer stamens are quite stable, showing no metamorphosis and variation in number (Figs. 14–16). On the contrary, three inner stamens frequently metamorphose into carpels, which may be complete or incomplete, or are eliminated completely or partially. When the elimination is partial there remains a rudimental filamental part lacking the anther proper (Fig. 5). Elimination of the inner stamens occur approximately twice as frequently as the metamorphosis into carpels (Table 5).

There is a considerable correlation between the metamorphosis of petals and the reduction in the number of inner stamens (Table 9). Except a few cases (Table 10), the basic number of each floral organ is very stable.

The phenomenon of the metamorphosis of this plant is connected with its nuclear organization, that it is a hexaploid ($n=15$) presumably raised from an apetalous species, *T. Smallii* ($n=10$) and a petalous species, *T. kamtschaticum* ($n=5$). *T. Smallii* forms stamens at the position of each petal and does not produce three inner stamens. In fact, the normal flower of this plant shows the "*kamtschaticum* type" and the extreme form of metamorphosis is of the "*Smallii* type" (Figs. 9 and 15) and, further, in the spacial relationship of carpels against sepals, the former corresponds to the "*kamtschaticum* type" and the latter to the "*Smallii* type", namely, the position of carpels against sepals shows a rotation by 60° in these two species.

Literature cited

HAGA, T. 1939. A Note on Staminody in *Trillium amabile* MIYABE et TATEWAKI. Jap. Jour. Genet. **15**: 235–240.