CYTOLOGICAL STUDIES OF THE GENUS *LINUM*, I.

By

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(With Two Plates)

INTRODUCTION.

The recent cytological knowledge in the plant kingdom ascertains that the numerical relation of chromosomes can exist among species of the same genus.

Genus *Linum*, to which the most important common flax belongs, involves large numbers of species, affording the interesting materials for cytological studies. There are several references on genetics and cytology of *Linaceae*. The first report on chromosome number of species belonging to *Linum* is the paper of TAMMES (1922). She pointed out, from experiments of REYNDERS, *Linum usitatissimum* L. (cultivated flax) and *L. angustifolium* Huds., which is considered as the original form of the former, as having equal number of chromosomes, i. e. 30 in the diploid.

Recently the author also published (1926) his preliminary report on chromosome number of *Linaceae*, and then MARTZENITZINA (1927), EMME and SCHEPELJEVA (1927), VILMORIN and SIMONET (1927) and INOUE (1929) also worked on the similar topics.

The author, however, had much interest to continue his cytological studies on the present genus, as these workers obtained results somewhat different from him. At the same time the author succeeded in getting a new hybrid between some perennial species of *Linum*. Some out of works hitherto done by him are described in the present paper.

MATERIALS AND METHODS.

Most of the materials were obtained from several Botanical Gardens of Europe and some came from the the Botanical Garden of Hokkaido Imperial University. All of them were grown in the Experimental Plot of the College of Agriculture.

For the count of the haploid chromosome numbers, the meiotic division of pollen mother cells were observed. Flower buds, having diameter of about 1m.m., were selected, their tops were cut off, but the caryxes not removed. They were preliminarily treated by the Carnoy's fluid and then fixed with FLEMMING's solution. For the observation of somatic chromosomes the young root tip fixed only by CARNOY's fluid

was used.

The paraffin work was carried on after the tentative schedule of CHAMBERLAIN. The microtome section was examined in various thickness, but usually the section of about $5\ \mu$ gave the most satisfactory result. For the staining the HEIDENHEIN's iron-alum haematoxylin method was exclusively used.

RESULTS.

The meiotic division of pollen mother cells was normal as far as the karyological conditions are concerned. The counts of chromosomes were usually performed in the metaphase and the anaphase. Each chromosome takes the spherical shape in both stages.

The somatic chromosomes which were observed in the root tip, were commonly characterized by a long rod, more or less bent in shape and each in almost equal length.

The number of the gametic and somatic chromosomes shows some variation and may be classified as follows:

Group I;those species having 9 chromosomes in the haploid.

Group II; " 15 " "

Group III; " 18 " "

Group IV; " 43(?) " "

Group I. To this group belong the following species;

a. <i>L. perenne</i> L.	(from Trieste)
b. <i>L. austriacum</i> L.	(" ")
c. <i>L. altaicum</i> Fisch.	(" Delft)
d. <i>L. hologynum</i> Reichb.	(" Lithuania)
e. <i>L. extraaxillare</i> Kit.	(" Switzerland)
f. <i>L. narbonense</i> L.	(from Amsterdam)
g. <i>L. sibiricum</i> DC.	(" Sutton)
h. <i>L. muelleri</i> Moris.	(" Edinburgh)
i. <i>L. lewisii</i> Pursh.	(" Tabore)

All of these species have perennial habit and flowers are colored in deep purplish blue, except *L. sibiricum*, which has two varieties, the white and the blue. Most of these species have the heterostyled flowers. Seeds are dark brown and very thin. Capsels are dehiscent in the ripened stage.

In the karyological observation 9 paired chromosomes were counted fairly in the diakinesis of the division. In this stage each element showed more or less rod shape but in the metaphase spherical. (Pl. VI Figs. 7—12).

Group II. In this group are involved the following species:

- a. *L. usitatissimum* L. (from Sapporo)
- b. *L. corymbiferum* Desf. (" Tabore)
- c. *L. americanum* L. (" ")
- d. *L. angustifolium* Huds. (" Holland)
- e. *L. flavum* L. (" Amsterdam)

These species have 15 chromosomes in the haploid and 30 in the diploid (Pl. VI Figs. 1—6). *L. usitatissimum* and *L. corymbiferum* are annual. *L. angustifolium* is described as biennial or perennial but it shows the annual habit in this locality.

The writer has reported in his preliminary paper (1926) that *L. angustifolium* may have 9 chromosomes in the haploid number. The plant previously examined by the writer, however, was not *L. angustifolium*. This error was caused by the mis-named seed which were sent from a foreign Botanical Garden.¹⁾

Group III. *L. alpinum* Jacq. is only one species of this group used by the writer. The morphological characters of this species is very similar to those of *L. perenne* and others, belonging to Group I, but cytologically a decided difference exists between them. The present species has twice as many chromosomes as these of the Group I, that is, exactly 18 in the haploid and 36 in the diploid (Pl. VI Figs. 5 & 6). SIMONET reported in his paper that the haploid number of this species is 9 and he wrote to the writer that the material examined by the latter might have been a Japanese tetraploid form. The writer intends to ascertain, whether or not his assumption is right, by a further investigation.

Group IV. *L. monogynum* Forst. was used as only one species of this group. This plant is also perennial and its morphological characters are somewhat different from others. Its pale purple colored stem is very long and slender, leaf is a little larger than others. Flowers are large and pale yellowish white.

In the karyological study of this species, various numbers of chromosomes were counted. The haploid number of 43 appeared quite frequently, while 86 was detected in somatic cells. As far as the present experiment is concerned, it may be stated that this species has 43 chromosomes at least in the haploid.

CHROMOSOME BEHAVIORS IN A SPECIES BASTARD OF *LINUM*.

GAERTNER (1849), TAMMES (1911, '13 and '15), LAIBACH (1925) BATESON (1916), CORRENS (1912) and BLARINGHEM (1923 and '26) made some informations on the spe-

¹⁾ The writer is much obliged to Miss. T. Tammes, who kindly sent him seeds of this species. The writer also offers his hearty thanks to Prof. A. W. HENRY, Alberta University, Canada, for seeds cordially sent him.

cies crosses of *Linum* from the standpoint of genetics, though no cytological meaning was considered.

In the summer of 1926 the writer examined the cross of *L. alpinum* $\times$ *L. perenne*. As above mentioned, these species are perennial plants and the chromosome numbers are just $18+9$ in the haploid. Some seeds were raised in the autumn of 1926, and the cytological investigation was carried on about them.

Fig. 13 (Pl. VII) shows the somatic metaphase in the young root tip, counting positively 27 chromosomes. This number is obviously the sum of the parental haploids, but as their size was almost same, it was quite difficult to distinguish chromosomes of the paternal plant from those of the maternal. A few of these hybrid plants bloomed in 1927, and more of them in 1928.

In the pollen mother cells of these F_1 plant, no abnormal figures were observed in the prophase and in the metaphase of the heterotypic division, but in the heterotypic anaphase some irregularities were detected. In the Figs. 14—16 (Pl. VII) we can see clearly that 9 bivalent chromosomes are massing at each pole after the division, while the other 9, presumably univalents, lagging on the spindle and moving to either pole at random in the progress of the division. In such way some variations of the chromosome numbers must occur in the heterotypic division, settling themselves at each pole. The examination of many preparations proved that various numbers of chromosomes were counted in the homeotypic metaphase and anaphase of the pollen mother cells. Figs. 17—20 (Pl. VII) show divisions to 13 and 14, 12 and 15 or 11 and 16 chromosomes in these stages.

Thus one may be able to surmise that in the gametic division of the F_1 plant the variation of the chromosome number may occur as follows:

F_1 plants were crossed *inter se* in both natural and artificial ways, and a few seeds (F_2) were obtained in the former case. On these seeds many cytological experiments were made and several numbers of somatic chromosomes were counted as follows

in the young root tip. (Pl. VII Figs. 22-27).

Plant number.	somatic chromosomes.
(P × A) No. 6	20
(P × A) No. 14	28
(P × A) A 8	34

The writer expects to continue the present studies in more detail.

DISCUSSION.

Many reports were published regarding the difference in the chromosome number among species of *Linum*. The first paper was made by TAMMES (1922). She insists that *L. usitatissimum* and *L. angustifolium* have 30 chromosomes in the somatic cells. MARTZENITZINA (1927) states in his paper that species of *Linum* can be grouped into 5 sections according to the number, dimension and shape of the chromosome. He counted chromosomes in the meristem of the rootlets or in the meristem of the stem; his results may be summarized as follows;

section	diploid number of chromosomes	species
I	18	<i>L. austriacum.</i> <i>L. tenuifolium.</i> <i>L. corymbiferum.</i> <i>L. punctatum.</i> <i>L. perenne.</i>
II	16	<i>L. grandiflorum.</i>
III	32	<i>L. usitatissimum.</i> <i>L. angustifolium.</i>
IV	30 (possibly 32)	<i>L. flatum.</i>
V	over 57	<i>L. catharticum.</i>

From these results he concludes that the genus *Linum* is karyologically not homogeneous and species belonging to this genus differ from each other not only in the number, but also in the size and shape of chromosome. And from the forgoing results he said that the cytological data agreed best with the arrangement of species in the synopsis of ASCHERSON and GRAEBNER (1914). For the diploid number of 32 in the third group he described as follows: The divergence between his data and those of REYNDERS (*L. usitatissimum* and *L. angustifolium*, $2x = 30$ chromosomes each) may be explained by an accidental segmentation or by the fact that REYNDERS treated flax races differing karyologically from his ones. The last mentioned explanation is made in view of the analogy with experiments in rye, in which KIHARA (1924), GOTOH (1924) and BELLING (1925) found 2 races differing in chromosomes of the somatic cell.

The writer also carefully observed the number of chromosomes in *L. usitatissimum* and *L. angustifolium* and always found that their chromosome numbers were $2x=30$ and $x=15$.

EMME and SCHEPELJEVA (1927) reported their studies on *L. usitatissimum* and especially on *L. usitatissimum* L. var. *crepitans*. They observed 2 cases; in one case they found 30 as the somatic chromosome number but in many others 32. Such a fact was already found by GOTOH (1924) in *Secale cereale* and by EMME (1927) in *Secale fragile*.

VILMORIN and SIMONET (1927) made the cytological works on the genus *Linum*, counting 8, 9, 10, 14 and 15 as haploid chromosome numbers in various species of *Linum*.

INOUE (1929) informed in his latest report that he observed 16 and 9 as haploid chromosome numbers of *L. usitatissimum* and *L. perenne* respectively, while he counted previously 15 as the haploid number of *L. usitatissimum*. Thus he assumes two forms in *L. usitatissimum* having 15 and 16 haploid numbers respectively.

So far as these studies are concerned, we find decided differences in chromosome numbers of species belonging to *Linum*, and also some divergence in resultt of these investigations. The writer's results are mostly consistent with the others', but in some cases are not. As to *L. usitatissimum* and *L. angustifolium*, observations of TAMMES, VILMORIN and SIMONET agree with the writer's. But MARTZENITZINA reports $2x=32$ in above species, EMME and SCHEPELJEVA describe two cases for *L. usitatissimum*, i.e. $x=15$ or 16, $2x=30$ or 32, and INOUE reports for *L. perenne* the same chromosome number as found by the writer, while for *L. usitatissimum* the same as reported by EMME and SCHEPELJEVA. From these investigations they conclude that the divergence of the chromosome number can exist in *L. usitatissimum* just as detected in rye, but thus far the writer has never found such a case. In *L. corymbiferum* MARTZENITZINA counts 18 as the diploid number, while the writer 15 in the haploid and 30 in the diploid. The writer doubts whether or not the material used by both workers are genetically the same. Further cytological investigations may be able to note more divergence of chromosome numbers in the genus *Linum*.

In the following table are indicated the results obtained by the writer and others.

Name of author Name of species	TAMMES	MARTZENITZINA	EMME AND SCHEPELJEVA		VILMORIN AND SIMONET	INOUE	KIKUCHI	
	2x	2x	x	2x	x	x	x	2x
<i>L. perenne</i>	—	18	—	—	9	9	9	18
<i>L. austriacum</i>	—	18	—	—	—	—	9	18
<i>L. altaicum</i>	—	—	—	—	—	—	9	18
<i>L. hologynum</i>	—	—	—	—	—	—	9	18
<i>L. extraaxillare</i>	—	—	—	—	—	—	9	18
<i>L. narbonense</i>	—	—	—	—	—	—	9	18
<i>L. sibiricum</i>	—	—	—	—	1	—	9	18
<i>L. muelleri</i>	—	—	—	—	—	—	9	18
<i>L. lewisii</i>	—	—	—	—	—	—	9	18
<i>L. salsoloides</i>	—	—	—	—	9	—	—	—
<i>L. strictum</i>	—	—	—	—	9	—	—	—
<i>L. tenuifolium</i>	—	18	—	—	9	—	—	—
<i>L. punctatum</i>	—	18	—	—	—	—	—	—
<i>L. maritimum</i>	—	—	—	—	10	—	—	—
<i>L. campanulatum</i>	—	—	—	—	14	—	—	—
<i>L. nervosum</i>	—	—	—	—	15	—	—	—
<i>L. flavum</i>	—	30	—	—	—	—	15	30
<i>L. americanum</i>	—	(possibly 32)	—	—	—	—	15	30
<i>L. corymbiferum</i>	—	18	—	—	—	—	15	30
<i>L. usitatissimum</i>	30	32	(15 16)	(30 32)	15	16	15	30
<i>L. angustifolium</i>	30	32	—	—	15	—	15	30
<i>L. alpinum</i>	—	—	—	—	9	—	18	36
<i>L. catharticum</i>	—	over 57	—	—	8	—	—	—
<i>L. grandiflorum</i>	—	16	—	—	8	—	—	—
<i>L. hirsutum</i>	—	—	—	—	8	—	—	—
<i>L. monogynum</i>	—	—	—	—	—	—	43(?)86(?)	

In many species hybrids appearances of the irregular behavior in the heterotypic division are described by several authors. ROSENBERG (1909) reported that in the hybrid between two species of *Drosera*, having 10 and 20 haploid chromosomes respectively, 10 bivalent and 10 univalent chromosomes were observed in the diakinesis. He also found the similar fact in a hybrid of *Hieracium auricula* ($x=9$) $\times$ *H. auran-tiacum* ($x=18$). In the hybrid of *Triticum polonicum* ($x=14$) $\times$ *T. spelta* ($x=21$) KIHARA (1919) detected 14 bivalent and 7 univalent chromosomes in the heterotypic metaphase. Moreover, GATES (1909) found the same behavior of chromosomes in the hybrid between two species of *Oenothera*, YASUI (1921) in *Papaver*, SAX (1922) in *Triticum*, TAECKHOLM (1920, 1922) in *Rosa* and ICHIJIMA (1926) in *Fragaria* hybrids.

In species hybrids in *Linum* many experiments also were made by several authors. KOELREUTER (1787) described on the hybrid of *L. usitatissimum* $\times$ *L. narbonense* and of the reciprocal crossing, but by CORRENS (1921) and LAIBACH (1925) it was proved that his hybrid was *L. usitatissimum* $\times$ *L. angustifolium*.

Later the crossing experiments of *L. usitatissimum* × *L. narbonense* were tried by TAMMES (1915), BATESON (1916), CORRENS (1921) and LAIBACH (1925), but none of them brought any result. GAERTNER (1848) tested to make crosses of *L. usitatissimum* with *L. maritimum*, *L. flavum* and *L. perenne*, but there was no result.

In crossing *L. usitatissimum* with *L. perenne*, *L. austriacum*, *L. grandiflorum* and *L. flavum*, TAMMES (1915, 1918) noticed the formation of slightly developed seeds, which failed to germinate. TAMMES (1911, 1913), LAIBACH (1925) and BLARINGHEM (1923, 1926) investigated genetically in the hybrid of *L. usitatissimum* × *L. angustifolium*.

This cross was very easily produced, and it is only one species hybrid hitherto known in the genus *Linum*.

GARGAS and SMITH (1915—16) examined vast numbers of crosses between *L. peirrense*, *austriacum*, *narbonense*, *monogynum*, *grandiflorum*, *flavum*, *arborescens* and *maritimum*. Out of these various crosses, however, only two of *L. monogynum* × *L. narbonense* and *L. monogynum* × *L. arborescens* gave some seeds. They stated that these

F₁ plants were closely related to the mother plant (*L. monogynum*), but further descriptions of their descendants are not yet published.

As far as the writer's memory goes, he has never seen any cytological paper regarding species hybrid in *Linum*. So he feels a great interest in continuing his studies to confirm how his hybrid and its descendants behave as regards the chromosome number, and if any of them can be bred true, it may bring a much more interesting result.

SUMMARY

The results obtained from the above mentioned investigations may be summarized as follows:

1. According to the chromosome number, species of *Linum* used by the writer may be classified into four groups having 9, 15, 18 and 43 (?) in haploid numbers respectively.

2. The difference in the size and shape of chromosome was not noted in both gametic and somatic cells.

3. *L. usitatissimum* did not reveal any variation in the chromosome number, showing always $x=15$ and $2x=20$

4. In the hybrid of *L. perenne* × *L. alpinum*, chromosome number in the somatic cell of F₁ is the sum of gametic ones of the parental plants, i. e. $9+18=27$.

5. In the heterotypic division of pollen mother cells of F₂ plant, there is seen the irregular chromosome behavior, where 9 lagging univalent chromosomes separate at random to each pole, and in the homeo-typic metaphase various numbers of chromosomes from 9 to 18 were counted.

6. In the karyological observation of F₂ plants, 20, 28 and 34 somatic chromosome numbers were detected in young root tip cells.

In conclusion the writer wishes to express his heartiest thanks to Mr. K. YOSHIDA, who carried out most of the laboratory technics. He is also greatly indebted to Prof K. AKEMINE and Mr. HIRATA for their valuable advices.

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Explanations of Plates

All figures were observed under ZEISS compensation ocular 18 and apochromatic objective 1,5mm. (1/12), and were drawn by the aid of ABBE's camera lucida.

- Fig. 1. 15 gametic chromosomes at the heterotypic metaphase in *L. usitatissimum*.
- Fig. 2. 30 somatic chromosomes of the same.
- Fig. 3. 15 gametic chromosomes at the heterotypic metaphase of *L. americanum*.
- Fig. 4. 30 somatic chromosomes of the same.
- Fig. 5. Homoeotypic metaphase of *L. alpinum*, showing 18 gametic chromosomes.
- Fig. 6. Root tip cell of the same, showing 36 somatic chromosomes.
- Fig. 7. 9 chromosomes at the homoeotypic metaphase in *L. perenne*.
- Fig. 8. 9 chromosomes at the homoeotypic metaphase in *L. sibiricum*.
- Fig. 9. Heterotypic metaphase of *L. austriacum*, showing 9 gametic chromosomes.
- Fig. 10. Root tip cell of *L. perenne*, showing 18 somatic chromosomes.
- Fig. 11. 18 somatic chromosomes in the root tip cell of *L. austriacum*.
- Fig. 12. 18 somatic chromosomes in the root tip cell of *L. sibiricum*.
- Fig. 13. 27 somatic chromosomes in the root tip cell of the hybrid *L. perenne* × *L. alpinum*.
- Fig. 14-16. The early anaphase of the heterotypic division in the pollen mother cell of the same hybrid, showing 9 bivalent chromosomes aggregating at the pole and 9 univalents, which lagged in the spindle, separating at random to each pole.
- Fig. 17. The late metaphase of the homoeotypic division in the pollen mother cell of the same hybrid, showing 12 chromosomes exactly.
- Fig. 18-20. Homoeotypic metaphases in pollen mother cells of the same hybrid, showing 12 and 15, 13 and 14, and 11 and 16 respectively.
- Fig. 21. The tetrad formation of the F₁ plant.
- Fig. 22-23. 34 somatic chromosomes in F₂ individual.
- Fig. 24-25. 23 " " " " "
- Fig. 26-27. 20 " " " " "

Linum 属の細胞學的研究 (第一報)

菊地武直夫

摘 要

Linum 属には多數の種(Species)を含で居るが、是等に就て細胞學的研究は他の植物に比較して最近に於て進められたもので、TAMMES (1922), KIKUCHI (1926), MARTZENITZINA (1927), EMME 及 SCHEPELJEVA (1927), VILMORIN 及 SIMONET (1927) 及 INOUE (1929) に依つて報告せられて居る。著者は1925年以來本研究を繼續し其の間に種間雜種に就ても興味ある實驗を進めつゝある。其の大略を摘録すれば、

1. MARTZENITZINA は彼の研究に用ひた *Linum* 属の種を染色體數の上から5群に分類した、即ちダイプロイド數に於て 16, 18, 30, 32 及 57 以上の各を有する諸群に分ち、而も此の分類は ASCHERSON 及 GRAEBNER の分類と相通する所あるを述べて居る。著者は其の研究材料を染色體のハプロイド數により次の如く分類した。

第一類 ($x=9$ を有するもの)	第二類 ($x=15$ を有するもの)	第三類 ($x=18$ を有するもの)	第四類 ($x=43(?)$ を有するもの)
<i>L. perenne</i>	<i>L. usitatissimum.</i>	<i>L. alpinum.</i>	<i>L. monogynum.</i>
<i>L. austriacum.</i>	<i>L. corymbiferum.</i>		
<i>L. altaicum.</i>	<i>L. americanum.</i>		
<i>L. hologynum.</i>	<i>L. angustifolium.</i>		
<i>L. extraaxillare</i>	<i>L. flavum.</i>		
<i>L. narbonense.</i>			
<i>L. sibiricum.</i>			
<i>L. muelleri.</i>			
<i>L. lewissii.</i>			

2. MARTZENITZINA は種により染色体の数、形状及大小を異にすると述べて居るが著者の研究では數的差異は明であるが他の差異は認め得ない。

3. *L. usitatissimum* 及 *L. angustifolium* に就ては多くの研究者により次の如く染色体數の異なるものを報告されて居る。

	<i>L. usitatissimum.</i>		<i>L. angustifolium.</i>	
	x	$2x$	x	$2x$
TAMMES		30		30
KIKUCHI	15	30	15	30
MARTZENITZINA		32		32
EMME 及 SCHEPTELJEVA	{ 15 16	{ 30 32		
VILMORIN 及 SIMONET	15		15	
INOUE	{ 15 16			

EMME 及 SCHEPTELJEVA と INOUE は *L. usitatissimum* に於て $x=15$ 及 $x=16$ の二種類ある事を述べて居るが、著者は此の種に於て15以外のハプロイド數は數へ得ず。

4. 従來 *Linum* 屬の種間雜種に就ては多くの研究者により報告せられてあるが、何も遺傳學的方面のみで細胞學的に記載せられたものはない。著者は1926年多年生なる *L. perenne* ($x=9$) と *L. alpinum* ($x=18$) との交配により得た雜種に就き研究し其の根端細胞に於て 27 の染色体を數へた。此の數は明に兩親のハプロイド數の和である。

5. 上記の雜種の F_1 に於ける花粉母細胞に異型核分裂に於て染色体の不規則なる行動を明に認めた。即ち同分裂の後期に於て 9 の二價染色体が兩極に進んだ後、赤道板附近に散在する單價染色体が任意な分離をなして兩極に進む結果兩極には 9 から 18 までの染色体を數へられる理で、著者の觀察に於ても 11 と 16, 12 と 15, 13 と 14 の三通りの分れ方が第二分裂の中期に於て認められた。此の類の現象は他の種間雜種に於ても見られた現象で、ここに新に一例を見出した理である。

6. 此の種種の F_2 に於て根端細胞に於ける染色体數を觀察し、20, 28 及 34 を讀み得た。之は F_2 個體の一部分を研究したのみで今後如何なる數が現はるか、又其等の何が固定するものかは更に研究の上報告する考である。

Fig. 1.

Fig. 5.

Fig. 7.

Fig. 2.

Fig. 6.

Fig. 3.

Fig. 10.

Fig. 8.

Fig. 11.

Fig. 9.

Fig. 12.

Fig. 4.

Fig. 13.

Fig. 14.

Fig. 15.

Fig. 17.

Fig. 16.

Fig. 18.

Fig. 19.

Fig. 22.

Fig. 21

Fig. 20.

Fig. 27.

Fig. 26.

Fig. 23.

Fig. 24.

Fig. 25.