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Chromosome Structure in *Lilium*

By

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With Plates XIX & XX and 9 Text-figures

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The present paper is a complementary paper to the previous one (KATO and IWATA, 1934) reporting the results of observation obtained with the acetocarmine smear method. The observation was confined, as in the case of the previous observation, in the stages from the metaphase of the first division to that of the second division in meiosis.

Materials and Methods

Pollen mother cells in *Lilium longiflorum* and *L. speciosum* were used as material. They were fixed with FLEMMING's stronger solution without acetic acid, diluted one-fourth with distilled water, or with BOUIN's solution, the fixation being made for about 24 hours in both cases. The anthers fixed with the former fixative were washed with running water for 24 hours and were then dehydrated with a series of graded alcohols beginning with 5 %, and those fixed with BOUIN's solution were directly passed through a series of graded alcohols from 30 % upwards without rinsing with water. Both materials were then imbedded in paraffin as usual. Sections were cut 12 micra thick and stained exclusively with HEIDENHAIN's iron alum hæmatoxylin.

Observation

Heterotype metaphase. Soon after the synizetic stage has passed, the nucleus increases in volume, and the threads in it become gradually contracted in length to form the distinctly individualized chromosomes in diakinesis. The chromosomes in this stage generally present an ill-defined mesh-like appearance. In some cases, however, in certain regions of the chromosomes a zig-zag or wavily corrugated aspect of chromatic threads can be observed in each chromatid as described by TAYLOR (1931), while in some other regions, where the thread is not zig-zag, but is more or less straightened, a minute spiral of very small gyres is observable in the thread (Fig. 1). The matrix substance of the chromosome seems to be much more abundant in the region where the thread is zig-zag than where it is straightened.

When the nuclear membrane disappears, the chromosomes are gathered towards the centre of the cell for a short time (Fig. 2), but soon become radially arranged on the equatorial plane with their points of spindle fibre insertion towards the centre (Fig. 3). Fig. 2 illustrates the spiral structure of chromosomes in the stage immediately after the nuclear membrane has disappeared. The chromosomes in metaphase in which the spiral structure is clearly visible are reproduced in Figs. 4 and 5. In these chromosomes the spiral threads are rather thin. The space between the turns of the chromatic spiral seems to be free from the matrix substance, but contrary to many authors, no figure showing a chromatic thread embedded in the rod-shaped matrix is observed. In Figs. 4 and 5 chiasmata are shown.

1 2 3 4

Text-figs. 1–4.
1 and 2. *L. speciosum.* Bivalent chromosomes in heterotype metaphase showing both homologues in the same direction of coiling. Both are of right handed twist.
3. The same. A bivalent chromosome in heterotype metaphase showing the homologues in different directions of coiling.
4. The same. A bivalent chromosome in heterotype metaphase showing the left handed twist of spirals in both upper and lower parts on the left hand side of a chiasma and the right handed twist in both parts on the right hand side.

A closer observation of metaphasic chromosomes shows that the direction of coiling differs not only between different chromosomes, but also between homologous chromosomes, or even different parts of the same chromosome. In the chromosomes (gemini) shown in Text-figs. 1 and 2 the direction of coiling is the same in both homologues, both being of the right handed twist, except for the regions of the chiasmata where the direction can scarcely be determined. In Text-fig. 2 the spirals have been greatly unravelled in the region near the insertion point. In Text-fig. 3 the direction of coiling is of the left handed twist in the homologue on the left hand side, whereas in the other on the right hand side it is of the right handed. In the bivalent shown in Text-fig. 4 both upper and lower parts on the left hand side of a chiasma are of the left handed twist, but again those on the right hand side are of the right handed. In other words, each univalent in this bivalent has a turning point at the chiasma at which the direction of coiling is reversed. At the region of the chiasma, the spirals are straightened out to a certain extent, and the chromatic threads seem to be generally thinner in this region than in the other where they are regularly coiled. The direction of coiling is moreover indefinite at this region of the chiasma, as shown in Text-fig. 4, the regular orientation of the turn being more or less displaced.

Heterotype anaphase. When the chromosomes begin to enter the anaphasic stage the diad nature of the univalents becomes evident. Strictly speaking, the stage at which this duality is first visible is different in different univalents or even in different parts of the same chromosome. An example is presented by the bivalent reproduced in Figs. 6 *a* and *b*. While in the upper univalent the duality is distinctly visible, it is obscure as yet in the lower. The chromatic spiral seen in this lower chromosome appears to be rather thick in comparison with the two spirals found in the upper one. This apparently greater thickness in the lower chromosome may perhaps be an optical illusion caused by two spirals in the act of separating. The direction of coiling of the two spirals in the upper chromosome seems to be different (Fig. 6 *b*). While in the present material the duality is discernible in the chromosomes in which the chromatic threads are coiled regularly, it is, according to Sax (1930), not visible in *Secale* before uncoiling. In anaphase, the chromosomes of the terminal attachment take the form of V's, while those of the median attachment are double V's. When the homologous chromosomes are pulled towards the poles, they are often subjected to elongation, the separation from each other being difficult. In case they are considerably elongated, the spiral is conspicuously drawn out (Fig. 7). When the chromosomes are once released from tension, the end chiasma between them being broken, the chromonema spirals contract again and revert to the more or less normal state of coiling (Fig. 8). The chromosomes in this state are seen fully furnished with the matrix substance. In the midway towards the poles the chromosomes again become elongated to a certain extent, the drawing-out of the chromonema spiral being especially conspicuous in the proximal region of the chromosomes (Figs. 9–16). In this region it is often clearly observed that the threads uncoiled from the spiral are not homogeneous threads but again spirals of a small diameter (the spirals of the lower order; Figs. 9, 10, 11, 12 and 13). The drawing-out of the spiral in the proximal region is a characteristic feature of the anaphasic chromosomes in *Lilium* (cf. SAX, 1930; TAYLOR, 1931). Since the drawing-out differs in degree in different chromosomes and in different stages, the number of spiral turns of the anaphasic chromosome varies (Figs. 8–17). The range of variation is from 2 to 7. The drawing-out of the spiral is not confined to the proximal region of the chromosome, but takes place in the other regions too, and not infrequently in even more than one region. In the chromosome shown in the middle of Fig. 14 and that on the left hand side of the upper group in Fig. 15 the spirals are drawn out in both proximal and distal regions, the middle region between them remaining intact. In the chromosome indicated by an arrow in Fig. 16 the spiral is drawn out in two regions in one of the arms (longitudinal halves), that is, in the proximal and near the distal, while in the other arm it is unravelled only in the proximal region. The region in which the spiral is drawn out may, therefore, be different in both arms of the same chromosome. In the extreme case the entire spiral is almost drawn out into a slender thread which presents the structure of a linear series of chromatic beads (Fig. 17).

The direction of coiling, and the number of turns, of the spirals of the greater diameter (the spiral of the higher order) observed in the anaphase are given in Tables I and II. In these tables the spiral of the right handed twist is denoted by the letter R_n and the spiral of the left handed twist by L_n, where n represents the number of turns of the spiral. R_n and L_n are written, like the numerator and the denominator, on different levels with a horizontal line between them if they represent different chromatids of a diad, and they are written on the same level if they represent different parts of the same chromatid. In the latter case the spiral is coiled in opposite directions with a turning point. This point is denoted in the formula by the mark +. In Table II the lengths of the chromosomes or chromosome arms are represented by the lengths of the horizontal lines, the point of spindle fibre insertion being marked by a point.

Table I

Chromosomes with terminal spindle fibre insertion

(These chromosomes are V-shaped in anaphase, the sister chromatids being widely separated)

Case	Direction of coiling and no. of turns	No. of chromosomes observed	No. of chromatids with turning point	Total no. of	
				Chromatids with turning point	Chromosomes observed
	$\frac{L_4}{L_4}$	20	—	—	
	$\frac{L_3}{L_4}$	6	—	—	
	$\frac{L_5}{L_5}$	5	—	—	
	$\frac{L_4}{L_5}$	5	—	—	
I	$\frac{L_3}{L_3}$	5	—	—	44
	$\frac{L_2}{L_2}$	1	—	—	
	$\frac{L_5}{L_6}$	1	—	—	
	$\frac{L_6}{L_6}$	1	—	—	
	$\frac{R_4}{R_4}$	24	—	—	
	$\frac{R_5}{R_5}$	9	—	—	
	$\frac{R_3}{R_3}$	6	—	—	
	$\frac{R_6}{R_6}$	3	—	—	
II	$\frac{R_4}{R_6}$	1	—	—	46
	$\frac{R_2}{R_3}$	1	—	—	
	$\frac{R_3}{R_4}$	1	—	—	
	$\frac{R_3}{R_5}$	1	—	—	

Table I (Continued)

Case	Direction of coiling and no. of turns	No. of chromosomes observed	No. of chromatids with turning point	Total no. of	
				Chromatids with turning point	Chromosomes observed
III	$\frac{R_6}{L_6}$	1	–	–	58
	$\frac{R_5}{L_5}$	13	–	–	
	$\frac{R_4}{L_5}$	4	–	–	
	$\frac{R_5}{L_4}$	4	–	–	
	$\frac{R_4}{L_4}$	28	–	–	
	$\frac{R_3}{L_4}$	1	–	–	
	$\frac{R_3}{L_3}$	5	–	–	
	$\frac{R_4}{L_3}$	1	–	–	
	$\frac{R_3}{L_2}$	1	–	–	
IV_1 (Symmetrical type)	$\frac{R_2+L_2}{R_1+L_1}$	1	2	10 . . . 10	5
	$\frac{R_{2\frac{1}{2}}+L_{2\frac{1}{2}}}{R_2+L_2}$	1	2		
	$\frac{R_{2\frac{1}{2}}+L_{2\frac{1}{2}}}{R_{2\frac{1}{2}}+L_{2\frac{1}{2}}}$	2	4		
	$\frac{R_{1\frac{1}{2}}+L_{1\frac{1}{2}}}{R_{1\frac{1}{2}}+L_{1\frac{1}{2}}}$	1	2		
IV_2 (Asymmetrical type)	$\frac{R_3}{R_2+L_2}$	2	2		
	$\frac{R_4}{R_2+L_2}$	1	1		
	$\frac{R_5}{R_{2\frac{1}{2}}+L_{2\frac{1}{2}}}$	4	4		
	$\frac{R_5}{R_2+L_2}$	2	2		
	$\frac{R_5}{R_3+L_3}$	2	2	22 . . . 22	
	$\frac{L_3}{R_1+L_1}$	1	1		
	$\frac{L_4}{R_{2\frac{1}{2}}+L_{2\frac{1}{2}}}$	1	1		
	$\frac{L_4}{R_2+L_2}$	5	5	31	31
	$\frac{L_5}{R_2+L_2}$	3	3		

Table I (Continued)

Case	Direction of coiling and no. of turns	No. of chromosomes observed	No. of chromatids with turning point	Total no. of: Chromatids with turning point	Total no. of: Chromosomes observed
IV_2 (Asymmetrical type)	$\frac{L_5}{R_{1\frac{1}{2}}+L_{1\frac{1}{2}}}$	1	1	9 (unequal type)	
	$\frac{R_2}{R_1+L_2}$	1	1		
	$\frac{R_3}{R_2+L_1}$	1	1		
	$\frac{R_4}{R_3+L_2}$	1	1		
	$\frac{R_4}{R_2+L_3}$	1	1		
	$\frac{R_2}{R_3+L_2}$	1	1		
	$\frac{L_3}{R_3+L_1}$	2	2		
	$\frac{L_4}{R_1+L_3}$	2	2		
IV_3	R_2+L_2*	3	3	6..6	6
	$R_{1\frac{1}{2}}+L_{1\frac{1}{2}}$*	3	3		
	R_x+L_x**	5	5	5	5
Total				52 38 (equal type)	195

* Determined in only one of the two chromatids
** No. of turns could not be determined

Table II

Chromosomes with subterminal spindle fibre insertion

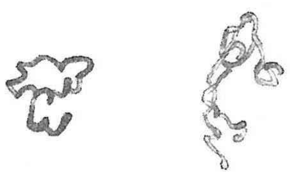
(These chromosomes are of the shape of a double V and have two long and two short arms)

Case	Direction of coiling and number of turns	Number of chromosomes observed	Total
I	$\frac{L_3}{L_2} \cdot \frac{L_2}{L_2}$	1	3
	$\frac{L_4}{L_4} \cdot \frac{L_3}{L_2}$	1	
	$\frac{L_3}{L_3} \cdot \frac{L_2}{L_2}$	1	
II	$\frac{L_4}{L_4} \cdot \frac{R_2}{R_2}$	1	1

Table II (Continued)

Case	Direction of coiling and number of turns	Number of chromosomes observed	Total
III	$\frac{L_3}{L_3} \cdot \frac{L_2}{R_2}$	1	1
IV	$\frac{R_3}{L_2} \cdot \frac{L_3}{R_2}$	1	1
V	$\frac{L_1+R_2}{R_2} \cdot \frac{L_3}{L_2}$	1	1
VI	$\frac{R_2+L_2}{R_4} \cdot \frac{R_3}{R_2}$	1	1
Total			8

While studying the direction of coiling it was noticed that in some cases where the spiral of the higher order is considerably uncoiled in the proximal part, so that the coiling of the lower order is more clearly observable in this part than in the distal where the spiral of the higher order remains coiled, the direction of the coiling of the former is generally the same as that of the latter (Figs. 10 and 11), though it is not always the case. The case where the direction of coiling is opposite in both spirals of the higher and the lower order is shown in Figs. 12 and 13.



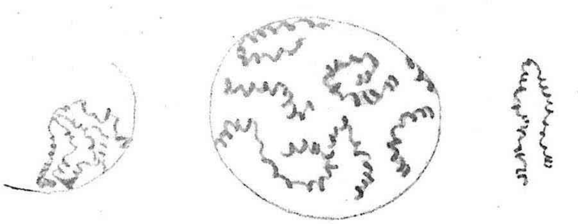
5 6

Text-figs. 5 and 6. *L. longiflorum.* Chromosomes in late heterotype telophase showing uncoiling of chromatic spirals of the higher order.

Telophase. When the chromosomes reach the poles, they are shortened in length, so that the turns of the spirals are brought closer and closer together (Fig. 18). This shortening of the chromosomes in telophase has been ascertained by LENOIR (1932) in the living state in *Lilium candidum.* The chromosomes are then packed together and the new nuclear membrane is formed (Fig. 19). The nucleus thus formed is first irregular in outline with protuberances formed of some isolated parts of chromosome arms (Fig. 20; TELEŻIŃSKI, 1931). The outline then becomes smooth. The nuclei are first semispherical, but later transformed into the spherical shape

(Fig. 21). The larger coiling of the chromonemata (the spiral of the higher order) becomes more and more irregular as the stage advances, usually unravelling to such an extent as to form loosely winding threads. Some chromosomes in this stage isolated from the others are shown in Text-figs. 5 and 6. The chromosomes in the nuclei in Fig. 21 seem to be composed of a row of chromatin beads which probably represent the turns of the spiral of the lower order. In the chromosomes in which the uncoiling of the spirals of the higher order has already taken place in the previous anaphase, no conspicuous changes are observable during these stages of telophase.

Interkinesis. The daughter nuclei which are found at the maximum distance from each other in the telophase come nearer with the advances in stage, and enter the interkinesis. In this stage the matrix of chromosomes is scarcely visible, but more or less regular spirals of the lower order come to sight which run sinuously throughout the nucleus (Fig. 22). In this nucleus anastomoses between the chromonemata are not observed.



7 8 9

Text-figs. 7–9.
7. *L. speciosum.* A chromosome in homotype prophase with median spindle fibre insertion showing spirals of the lower order.
8. *L. longiflorum.* A nucleus in homotype prophase.
9. *L. speciosum.* A chromosome in homotype metaphase showing the spiral of the small gyres.

Homotype prophase. When the nucleus enters the prophase, it becomes larger and larger in volume. A nucleus in this stage is shown in Fig. 23 (the lower nucleus). A chromosome in this stage with the median spindle fibre insertion is reproduced in Text-fig. 7. In this chromosome the spirals of the four arms are not the same in the regularity of coiling; in one of the arms on the right hand side the coiling is irregular while in the remaining others it is comparatively regular. In Text-fig. 8 it is seen that the direction of coiling is different not only in different chromosomes, but also in different parts of one chromosome. The nucleus immediately after the nuclear membrane has disappeared is reproduced in Fig. 24. One of the chromosomes indicated by an arrow shows that in some parts the spiral is regularly coiled, while in the others it is unravelled to a greater or less extent.

Homotype metaphase. Fig. 25 shows the chromosomes in the early metaphase in the homotype division. Drop-like bodies stained deeply with hæmatoxylin, or the rests of nucleoli, are visible in this figure. A drawing of a chromosome in this stage is reproduced in Text-fig. 9. As is shown in these figures, the chromosomes in this stage are rather thick and the spirals are more or less regularly coiled in comparison with those in the prophase. The chromosomes in the metaphase proper, are shown in Fig. 26. In this stage the chromosomes are thinner and the number of turns of their spirals is more numerous than in the heterotype metaphase. In some cases, a similar aspect to that of the double-coiled chromosomes in the heterotype metaphase is observed through a certain length of the chromosomes. This phenomenon suggests that the parts of the chromosomes presenting this aspect are doubly coiled as was very often actually observed in acetocarmine smear preparations (KATO and IWATA, 1934).

The chromosomes in anaphase and telophase are shown in Figs. 27 and 28 respectively. In these chromosomes the larger coiling is still more or less distinct.

Conclusion

In the *Lilium* plants observed, the fixed chromosomes in the heterotype metaphase appear to be clearly differentiated chromatic spirals, and no matrix substance is conspicuous between the turns of the spiral. In the anaphase the chromosomes or the chromatic spirals assume the shape of a V or that of a double V according to the position of insertion point of the spindle fibre. In this stage the spirals are, as a rule, drawn out in a greater or less degree, a characteristic feature in these plants. The drawing-out is generally conspicuous in the proximal region of the chromosomes, though it may take place in any other region of the chromosomes too. In the region where the spiral is drawn out it is often observed that the drawn out part is wavily corrugated. In the extreme case, the spirals are drawn out into chromatic threads each of which appears to be composed of a linear series of chromatic beads. In the previous investigation with the smear method (KATO and IWATA, 1934), it was observed that the spirals so drawn out present coils of small gyres. From this result of observation it may be said that the linear series of chromatic beads observed in the fixed material represents the spiral of the small gyres in the smear. We may then conclude that while the spirals of the larger gyres or the spirals of the higher order are clearly visible in both fixed and smear preparations, it is only when they are drawn out that the spirals of smaller gyres or the spirals of the lower order make their appearance in both preparations. The latter spirals usually appear, in fixed material, as solid threads when they regularly coil into the spirals of the higher order. A good illustration to this conclusion is found in his Fig. 25, Pl. 25 in SAX' paper (1930), in which the spirals of the small gyres are shown in the drawn out part of the larger spirals. That the spiral of the lower order comes to view when the spiral is free from coiling of the higher order is also shown in the interkinesis where the spirals of the lower order become more marked as the spirals of the higher order are lost from view.

The direction of coiling of the chromonemata is interesting. As shown in Table I, out of 195 cases observed, 90 are those where both arms (longitudinal halves or sister chromatids) are coiled in the same direction, of which 44 (22.6 %) are left-handed, and 46 (23.6 %) right handed; 58 (29.7 %) are those in which the two arms coil oppositely to each other; and 47 (=5+31+6+5; 24.1 %) are those where one of the two chromatids or both have a turning point at which the direction of coiling is reversed. As is seen in the same table 38 chromatids out of the 52 are those where the numbers of coils on both sides of the turning points are the same (equal type), 9 being those where they are different (unequal type), and the remaining 5 being those in which exact counting was hardly possible. This result of observation is comparable to the case of coiling in the plant tendril (KUWADA, 1933). The percentages given above in brackets show that the frequency of occurrence of these four cases is approximately the same. From these data we may perhaps conclude that each chromatid is independently coiled from the others. The free separation of the sister chromatids in the anaphase in the heterotype division shows that this is actually the case. If not, a certain entanglement between the chromatids would take place.

Summary

1. Pollen mother cells in *L. longiflorum* and *L. speciosum* were observed in fixed material.

2. The chromosomes in metaphase in the heterotype division show the double-coiled structure.

3. The longitudinal halves of the chromosomes are observed at early anaphase.

4. The drawing-out of the spirals of the higher order in the heterotype anaphase is a characteristic feature in these plants.

5. The drawing-out occurs usually in the proximal region of chromosomes, but in other regions as well.

6. The extent to which the drawing-out takes place is different in different chromosomes and even in the two sister halves of one chromosome.

7. In fixed material the spiral of the lower order is observable usually in the drawn-out part only, and not in the part regularly coiled into the spiral of the higher order.

8. In the extreme case, the chromosome in a late anaphase is found completely unravelled from the spiral of the higher order and appears to be of the single-coiled structure.

9. There is no regularity in the direction of coiling of the spiral. In the two sister chromatids the direction may be the same, both being (1) right handed or (2) left handed, or be (3) different from each other. The case (4) where it is different in one chromatid on both sides of a point which makes the turning point is also observed. These four cases are found almost in the same frequency.

10. In the double-coiled spiral the direction of coiling of the spiral of the lower order may sometimes be reversed to that of the spiral of the higher order, though the direction is more usually the same in both spirals.

11. When the chromosomes reach the poles they contract, and the drawn-out spirals in the anaphase are rendered regular in coiling again.

12. In the late telophase the spiral of the higher order begins to unravel to form an irregular mass of the spirals of the lower order which fill the cavity of the interkinetic nucleus.

13. In the homotype metaphase the chromosomes are slender in form and the turns of the spirals which they contain are much more numerous than those of the spirals of the higher order in heterotype metaphase chromosomes.

14. The sinuosity of the chromosomes or the residue of the turns of the spirals of the higher order is observed in the chromosomes in the homotype metaphase.

In conclusion the writer wishes to express his cordial thanks to Prof. Y. KUWADA for his suggestions and criticisms throughout the course of the investigation.

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Explanation of Plates

All the figures are microphotographs taken with ZEISS' apoch. imm. 2mm. and comp. oc. K. 12. Figs. 6*a*, 6*b*, 7, 15, 20, 22 and 23 are from the material fixed with BOUIN's solution, and all the others are from the material fixed with the modification of FLEMMING's stronger solution.

Fig. 1. *L. speciosum*. A nucleus in diakinesis. The chromosome indicated by an arrow shows both the spirals of the higher and the lower orders.

Fig. 2. Ditto. Chromosomes in early metaphase of the heterotype division.

Fig. 3. *L. longiflorum*. Heterotype metaphase in poler view showing the chromosomes in the equatorial plate.

Figs. 4 and 5. *L. speciosum*. Chromosomes in the heterotype metaphase.

Figs. 6*a* and *b*. Consecutive optical sections of the same chromosome. *L. longiflorum*. A bivalent chromosome in the heterotype metaphase. The longitudinal split is shown in the upper chromosome.

Fig. 7. Ditto. Chromosomes in heterotype anaphase showing the drawing-out of the spiral of the higher order.

Fig. 8. Ditto. Chromosomes in heterotype anaphase showing clear chromatic spirals.

Fig. 9. Ditto. Heterotype anaphase showing the spiral of the lower order in the region drawn-out from the spiral of the higher order.

Figs. 10 and 11. Ditto. Heterotype anaphase chromosomes showing the case where both spirals of the higher and the lower order are coiled in the same directions.

Figs. 12 and 13. Ditto. Heterotype anaphase chromosomes showing the case where both spirals of the higher and the lower order are coiled in different directions.

Figs. 14, 15, 16 and 17. Ditto. Chromosomes in the heterotype anaphase showing the drawing-out of the spirals of the higher order. In Figs. 15 and 17 chromosomes show a corrugated appearance in the regions where the spirals of the higher order are drawn-out entirely. A point at which the direction of coiling is reversed is shown in the chromosome indicated by an arrow in Fig. 16.

Figs. 18 and 19. Ditto. Telophase showing the contraction of the chromosomes (spirals).

Fig. 20. Ditto. Telophase chromosomes in poler view.

Fig. 21. Ditto. Nuclei in late telophase showing the uncoiling of the chromatic spirals of the higher order into the threads of corrugated or wavy appearance.

Fig. 22. Ditto. A nucleus in interkinesis. Fine spiral threads are seen in the slender chromosomes.

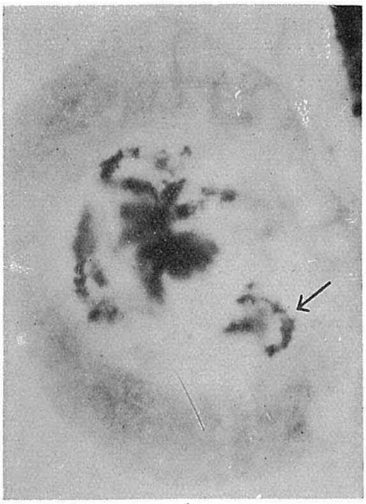
Fig. 23. Ditto. Early prophase of the homotype division showing the chromatic spirals of small gyres.

Fig. 24. *L. speciosum.* Prophase of the homotype division.

Fig. 25. Ditto. Chromosomes in the early metaphase of the homotype division showing the slender spirals of small gyres.

Fig. 26. Ditto. Chromosomes in the metaphase of the homotype division showing the spiral of small gyres.

Figs. 27 and 28. Ditto. Chromosomes in anaphase (Fig. 27) and telophase (Fig. 28) of the homotype division showing some indication of coiling of the higher order.



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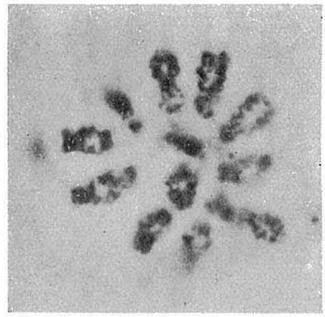

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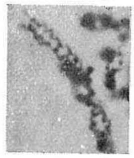

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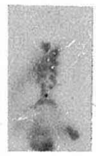

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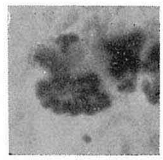

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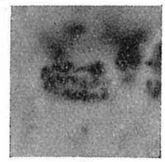

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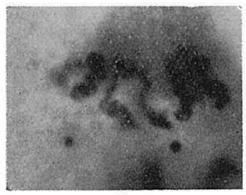

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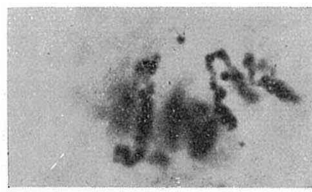

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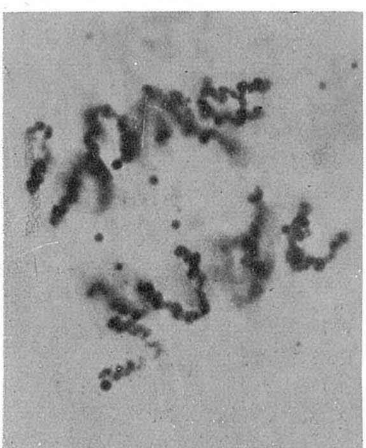

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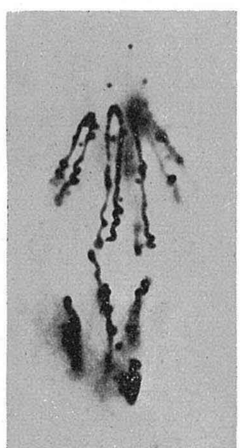

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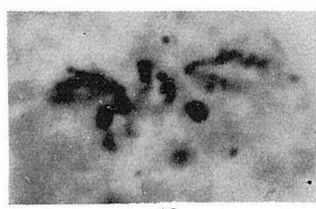

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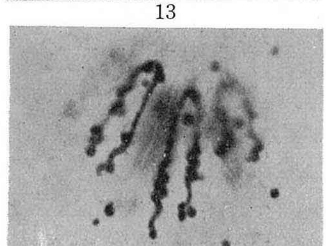

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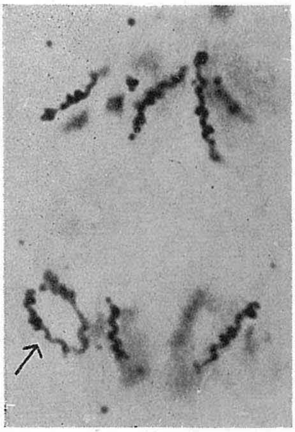

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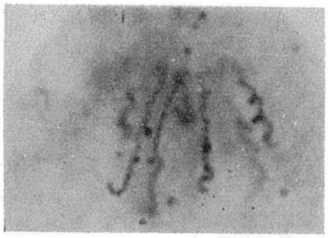

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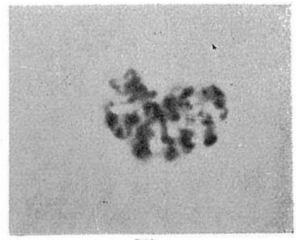

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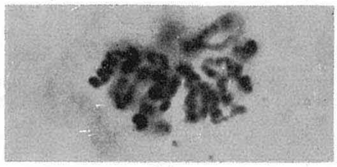

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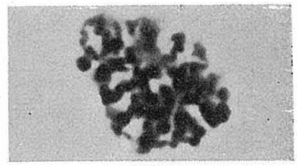

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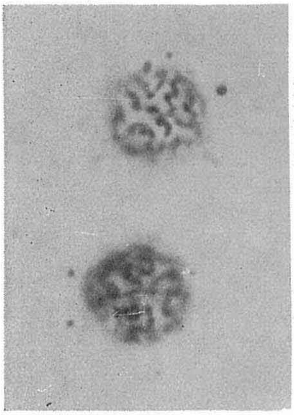

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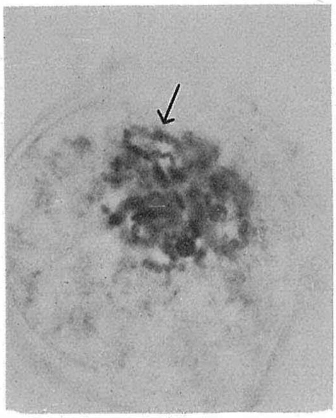

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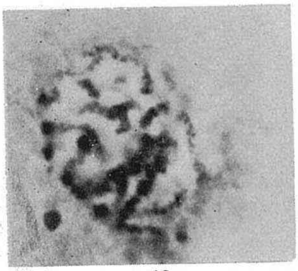

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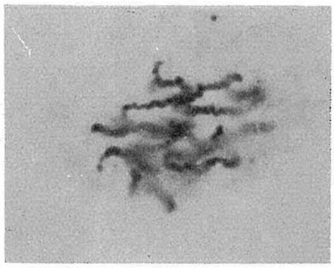

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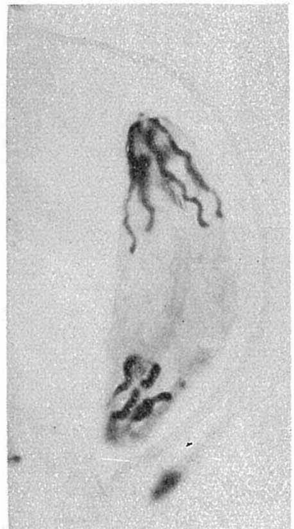

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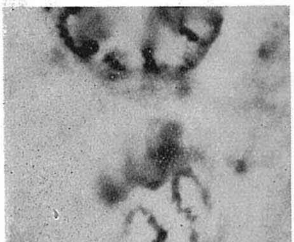

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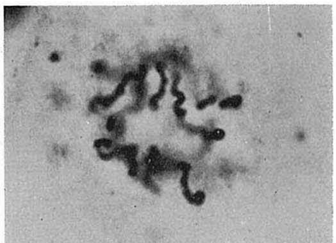

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