TITLE:

Spiral Structure of Chromosomes in Meiosis in Sagittaria Aginashi

AUTHOR(S):

Shinke, Namio

CITATION:

Shinke, Namio. Spiral Structure of Chromosomes in Meiosis in Sagittaria Aginashi. Memoirs of the College of Science, Kyoto Imperial University. Ser. B 1934, 9(5): 367-392

ISSUE DATE:

1934-03-30

URL:

http://hdl.handle.net/2433/257803

RIGHT:

京都大学学術情報リポジトリ
KURENAI 紅
Kyoto University Research Information Repository

Memoirs of the College of Science, Kyoto Imperial University, Series B,
Vol. IX, No. 5, Art. 11, 1934.

Spiral Structure of Chromosomes in Meiosis in *Sagittaria Aginashi*

By

Namio SHINKE

(Botanical Institute, Kyoto Imperial University)

With Plates XVII-XIX and 7 Text-figures

(Received Feb. 16. 1934)

The chromonema theory or the spiral theory of chromosome structure is becoming more and more generally accepted by investigators (cf. Teleżyński, 1931). According to this theory, the chromosome is composed of the chromatic spiral, or the chromonema, and the less chromatic ground substance or the matrix, the former component being assumed to be retained also in the interphase. We have a good many reports on the life cycle of the chromonemata in the case of the large somatic chromosomes, but only a few which deal with the meiotic chromosomes, especially those in the heterotype prophase. In the present investigation, with a view to contributing to the knowledge in this field of investigation, observation of the behaviour of chromonemata in the stages from the late telophase in the last premeiotic division to the metaphase in the first post-meiotic devision in pollen grains was undertaken, and the observations were made in *Sagittaria Aginashi* with special reference to the points: 1) the difference in shape and structure between chromosomes in the heterotype and the homotype division, and 2) the direction of the coiling of the chromonemata. Root-tips were also observed in order to make clear the morphology of each chromosome.

Method

Young flower buds were fixed with various fixing fluids such as Nawaschin's solution, Flemming's stronger solution, and its Bonn

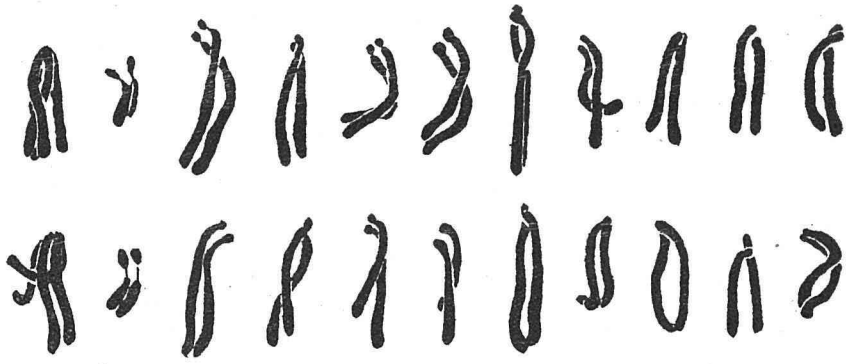
modification with or without preliminary treatment with CARNOY's fluid. Sections were cut 5–15 micra thick according to requirements, and stained with HEIDENHAIN's haematoxylin. Observations were also made with aceto-carmine preparations. Root-tips were fixed in the BONN modification of FLEMMING's solution, cut 10–15 micra thick, and stained with HEIDENHAIN's haematoxylin.

Observation

Morphological characteristics of the chromosomes

The somatic chromosomes in root-tip cells are far more slender than those in the division in pollen grains, and show more clearly their morphological characteristics than the latter, but it is rather difficult to count them correctly. According to TAYLOR (1925), the diploid number of chromosomes in *S. montevidensis* is probably 20 and according to NAWA (1928), the number is clearly 20 in *S. sagittifolia*, f. *sinensis*. In *S. Aginashi*, on the other hand, it is certainly 22 in root-tip cells, and is 11 in both heterotype and homotype divisions and in the post-meiotic division in pollen grains. A set of metaphasic chromosomes taken from a root-tip cell is given in Text-fig. 1, from which some idea about the morphology of the chromosomes may be obtained. As may readily be seen from this figure, these chromosomes can be roughly classified into four groups in respect to the size of the chromosome body and the position of the spindle fiber attachment point. The first group consists of a pair of the largest chromosomes with a middle constriction at which the spindle fiber is attached. This pair of chromosomes which were designated the M-chromosome in the previous paper (1929), present themselves as a V in the metaphase in the homotype as well as the post-meiotic divisions, and as an X–, 8– or other various shapes regarded as derivatives in the heterotype metaphase. The second group consists of a pair of rod-shaped chromosomes which are the shortest of all. The remaining nine pairs of chromosomes which are also rod-shaped but longer than those of the second group can be divided into two groups, the third and the fourth. In the third group the attachment constriction which is found near the proximal end is deep and clear, while it is obscure in the fourth. All the rod-shaped chromosomes belonging to these three groups take the shape of a hosizontal V,' a ring or various other modified shapes in the heterotype metaphase, while they are rod-shaped in the homotype as well as in the first post-meiotic division in pollen grains. In Text-figs. 2 and 3, polar views of the heterotype metaphase and the

homotype anaphase are shown respectively, and in Text-fig. 4 is shown a nuclear plate in the first post-meiotic division in the pollen grain.



Text-figs. 1. A complete set of metaphasic chromosomes from a root-tip cell.

Text-fig. 2. Heterotype metaphase in polar view showing the number and the shape of chromosomes. For clearness' sake arms in the lower level are omitted from drawing.

Text-fig. 3. One of the groups of anaphasic chromosomes in homotype division in polar view. As the chromosomes are viewed obliquely or from their end, their true length and shape are not to be seen from the figure.

Text-fig. 4. Polar view of a metaphasic plate of chromosomes in the first division in pollen grain. All the chromosomes are found lying strictly on one plane.

Behaviour of chromonemata in meiosis

Telophase in the premeiotic division. In order to make clear the life history of the chromosomes in the heterotype division, it is necessary to begin with the study of the telophase chromosomes in the last premeiotic division. It is, however, difficult to discriminate the last premeiotic telophase accurately from those in the preceding divisions. Figs. 3 and 4 are drawings from cells in telophase in the loculus in which most of the nuclei are uniformly in the late telophase or interphase. In flower buds which are younger than those from which these figures were drawn, the prevailing condition is that

the nuclei found in a loculus show every stage in mitosis. From this difference in the uniformity of stage it seems highly probable that the figures shown in Figs. 3 and 4 represent those in the last premeiotic division. In the nuclei in the early telophase, the chromosomes present no clear spiral structure, but show an unevenness of contour which is often so manifest that it suggests this structure of the chromosomes (Fig. 1). Here and there, delicate connecting threads are seen between adjacent chromosomes. In Fig. 2, a more advanced stage is shown. In the chromosome in the middle of this figure, an axial line which is less chromatic is seen. This probably represents the so-called longitudinal split in the telophase, taken as such by DIGBY (1910 and 1919), NOTHNAGEL (1916) and SARBADHIKARI (1924) in their studies of the premeiotic mitoses in some higher plants. In the other chromosomes in Fig. 2, chromatic threads running in an irregular zig-zag or spiral around the less chromatic axial portion of the chromosomes can be seen. The coiling into a spiral of the chromatic threads is more clearly shown in Fig. 3, it being especially clear in the chromosome on the left-hand side, in which the differentiation into the chromatic and non-chromatic parts is more distinct than in the one on the right. The anastomoses are found between the chromosomes. This structure of the telophase chromosome resembles that of those which BONNEVIE (1908 and 1911) observed in the sporogenous tissue as well as in root-tip cells in *Allium*. Fig. 4 shows a part of a nucleus in a slightly later stage. Often a broad satellite which is perhaps formed by union of two satellites in juxtaposition is found, a fact which seems favourable to the view of KAUFMANN (1926) that two chromonemata are contained in the chromosome in the premeiotic telophase.

Interphase immediately preceding the heterotype prophase. The interphasic nuclei just before the heterotype division, or the nuclei in the last premeiotic stage, can be easily distinguished from those of cells in the sporogenous tissue by the larger size of the cell and the uniformity in the stage of division of the cells contained in a single loculus.

A part of a nucleus in this last premeiotic interphase is reproduced in Fig. 5, in which a reticulated structure appears more manifest than in the nuclei in the late telophase mentioned above, the meshes being finer and more numerous. Each chromosome is generally hard to discriminate from the others, though in places zig-zag threads can be traced through a certain length. The network in this

stage is more irregular in its constitution than reported by KAUFMANN (1926) and SHARP (1929) in root-tip cells. In the present investigation the occurrence of the "Karyosomen" (LUNDEGÅRDH, 1910), the "chromatic beads" (DIGBY, 1910 and 1919) and the "chromomeres" (VEJDOVSKÝ, 1926-7) were not confirmed in all the interphasic nuclei in the premeiotic phase. The structure of the nucleus mentioned above is so far in accord with the view of BONNEVIE (1908 and 1911), KUWADA (1921 and 1926), KAUFMANN (1926), SHARP (1929), TELEŻYŃSKI (1931) and some others that the network is composed of chromonemata and their connectives. But no evidence to show that in the interphase two chromonemata are regularly interlaced in a chromosome, as reported by some of these authors in root-tip cells, and by KAUFMANN (1926) in the premeiotic mitosis, was obtained.

Early prophase in the heterotype division. When the heterotype prophase approaches, the nucleus becomes larger, and its internal anastomoses grow thinner in places. Fig. 6 represents a part of a nucleus in this stage. In this figure, the coiled state of the thread which is now thicker than in the preceding stage can be recognized again to a certain extent. There are often found some small chromatic granules, reminding one of the karyosomes, chromatic knots or other related structures, on the coiled or zig-zag threads. CHIPMAN (1925) has regarded these "chromatic knots" as simply spirally entangled portions of the chromatic threads.

The thinning of the connectives or the anastomoses goes so far that the coiled preleptotene threads become quite free from their neighbours (Fig. 7). A special observation was made to find whether these coiled threads are single or double, and the result obtained was that the threads are single. Sometimes, a certain length of the threads present the appearance of being double, but until further evidences are obtained it can hardly be decided whether this doubleness represents true doubleness due to the longitudinal splitting or not, because partial or localized doubleness may be caused by the rudiments of the anastomoses or the entanglement of a portion of the threads, either of which phenomena is often liable to be misinterpreted as two interlaced chromonemata.

The coiled aspect of the thread or the chromonema in this stage of prophase in the heterotype division resembles, to a remarkable extent, that of the late telophase in the preceding division as has been reported in the case of the somatic mitosis (KUWADA 1921, KAUFMANN 1926, SHARP 1929, BĚLAŘ 1929).

Then the coiled chromonemata begin to unravel, the process gradually proceeding (Fig. 8) until the delicate leptotene threads which run throughout the nucleus, filling it densely, are formed. A remarkable resemblance is recognized, as pointed out by BONNEVIE (1911) in *Allium*, between this process of the formation of the leptotene thread and that of the early prophasic threads or spiremes in the somatic mitosis.

A general view of a nucleus just before the synizetic contraction is shown in Fig. 9, in which both coiled and uncoiled threads are seen. Then the threads begin to become apart from the nuclear membrane clearly, and to show doubleness in places through a certain length (Fig. 10), although it can not be decidedly stated whether this doubleness is due to approximation in pairs or to longitudinal splitting of the leptotene threads; the behaviour in the later stages of these double threads or spiremes seems to show that it is due to the approximation of the homologous chromosomes in pairs (parasyndesis).

The inner structure of the leptotene threads is obscure, but the contour of the threads is not smooth. The so-called chromomeric structure of the threads, which has been regarded by SZAKIEN (1927) and SCHAEDE (1928) as an optical illusion was not observed in my material.

Late prophase in the heterotype division. In the open spireme, which follows the synizetic contraction the threads extend themselves more or less uniformly in the nucleus. An intermediate stage is shown in Fig. 11. Often two spiremes, each of which is clearly longitudinally double, run parallel through a certain length with a certain distance between them (Fig. 12), but there is no further evidence to show that a further approximation or, in other words, conjugation, takes place between them; that is to say, we have no positive reason to regard them as synaptic mates. The spiremes become gradually thicker and shorter, until the thick pachytene spiremes, the inner structure of which is generally obscure, are formed (Fig. 13). Not infrequently, however, they show the structure of a pile or a row of discs or rings (Figs. 14 and 15), which probably represents the "Chromatin Scheibe" of STRASBURGER (1888), the "chromatic flakes" of ALLEN (1905) or the "chromomeres" of BELLING (1928, a and b).

In well preserved preparations, however, the spiremes show no such internal structure as a pile of discs nor a row of chromomeres, but a spiral structure in which the threads are coiled into a spiral of short pitch (Fig. 16). In recent years, such a spiral structure of the

pachytene spireme has been ascertained by several authors, such as, for instance, BABCOCK and CLAUSEN (1929) in *Crepis*, SHINKE (1930) in *Amaryllis*, and SMITH (1932) in *Galtonia*. In the middle of Fig. 16, two coiled chromatic threads which must represent synaptic mates, as will be seen later, are found in the pachytene spireme, presenting the appearance of being interlaced.

In the diplotene stage, when the spireme is clearly double, being separated into the two component univalent threads (the synaptic mates) running parallel or twisted around each other, the spiral structure of the spireme becomes obscure again (Fig. 17), though sometimes the spiral aspect can be observed through a limited length (Fig. 18). Then follows the strepsitene stage where the twisting around of the component univalent threads is very marked (Fig. 19). In Fig. 20, it is shown that these threads are very unevenly thick, the unevenness being especially marked in the region near the points of intersection of them at which they are very thin. This fact seems to show that a greater coiling of the threads has taken place in the internodes than at the points of intersection. In the late strepsitene stage, the doubleness of the univalent thread due to the longitudinal fission becomes distinct through a certain limited length as a result of the partial separation of the halves (Fig. 21). The separation becomes first clear at the chasmata, as shown in a ring tetrad reproduced in Fig. 22. No evidence was obtained to support the finding of TAYLOR (1931) in *Gasteria* that in the bivalent chromosome there are four parallel straight strands with a clear space between them.

In diakinesis, the pair of the univalent threads becomes markedly condensed to form a geminus, this being accompanied by a decrease in the number of the chiasmata between the univalents.

When the nuclear membrane disappears, the chromosomes gather in the central region of the cell for a short time and are then arranged in a plane to form the equatorial plate (Text-fig. 2). In this stage, the tetrad nature of the gemini can be clearly observed, though the internal structure is generally still obscure.

It could not be determined in what manner the large spiral found in the ensuing metaphase and the stages following it is formed, whether by enlargement of the diameter of the spiral in the diplonema or by secondary coiling of this spiral into another with a larger diameter.

Meta- and anaphase in the heterotype division. In the metaphase, ten gemini which consist of the rod chromosomes assume the

shape of a ring, a V, or other modified forms derivable from these shapes, and take an orientation which is horizontal (the post-reductional type) or more or less inclined (Text-fig. 2). The remaining geminus consisting of the largest M-chromosomes is of the shape of an 8 or an X in horizontal orientation, or of shapes in which the 8 or the X is twisted in varying degree, so that the two rings of the 8 or the two pairs of arms of the X may be found on different planes variously inclined to each other; in the extreme case they are found on planes disposed perpendicularly to each other.

In this stage, the inner structure of the chromosome is obscure, the whole chromosome body being stained more or less diffusely. In the anaphase, separation of the chromosomes takes place without a hitch. The telomitic chromosomes take the shape of a single V, and the atelomitic M-chromosome that of a double V. In general, the elongation of the chromosomes which is often observed in this stage is not noticeable. When they approach towards the poles, they often show an uneven or nodulose contour. This may be regarded as indicating their internal spiral structure. Only rarely a structure of discs in a pile or a zig-zag structure is observed (Fig. 23). In aceto-carmine preparations, the chromosomes in metaphase and anaphase, especially those in the former, generally show the mesh or alveolar structure. In adequately prepared preparations, however, an apparently single, thick spiral with a short pitch is observed in each chromatid in anaphase, though it is not so clear as in the homotype division. In *Tradescantia*, KAUFMANN (1931) and NEBEL (1932, a) have stated that two chromonemata are found in each chromatid in the heterotype anaphase, but no case where the doubleness was clear was observed in *Sagittaria*.

Telophase in the heterotype division. A series of drawings is given in Figs. 24–32 to show the process of the chromosome transformation from late anaphase to interkinesis. When the chromosomes arrive at the poles, they become shorter and massive, their intense chromaticity remaining unaltered, being just as it was in the metaphase and early anaphase (Fig. 24). The contour of the chromosomes is rugged, and numerous lateral processes are found on the rugged surface (Fig. 25). In this stage, no indication of the spiral structure is observed, but in the chromosome body there is recognizable an inequality in the chromaticity which shows no definite pattern. The chromosomes become, then, released from their compact association at the early telophase and rather separated from one another. When

the interchromosomal space is distinct, and the nuclear membrane is visible, the karyolymph is reckoned to have made its first appearance. Then the chromosomes take on the appearance of being composed of a row of superimposed chromatic discs (Fig. 26). The nuclear membrane becomes more and more distinct, and a slight elongation of the chromosomes becomes perceptible. By and by, the differentiation into the chromatic and less chromatic portions becomes more pronounced, and the former comes to present the form of a zig-zag thread. In some cases, the chromatic substance is found mostly in the peripheral portion of the chromosomes, the inner portion being less stainable (Fig. 27) as has often been reported and drawn by several authors (cf. BONNEVIE 1908, SCHUSTOW, 1913). This seems to be due to the effect of fixation. The zig-zag thread takes later a more regular spiral form. A sequence of this transformation is shown in Figs. 28 29 and 31. In aceto-carmine preparations, the spiral threads in these stages are thicker than those mentioned above from paraffin sections, and numerous connectives are clearly observed between them. Not infrequently, a chromatic head or knob is found at the proximal end of the chromosome (Fig. 30). This body is stained deeply and makes a sharp contrast with the main part of the chromosome which is less stainable than the knob. This behaviour of the knob to the stain reminds one of the heteropycnosis known especially in sex-chromosomes in animals, and recently also found in chromosomes in certain *Bryophyta* (HEITZ 1928 and 1929, SHIMOTOMAI and KOYAMA 1932, TATSUNO 1933).

Interkinesis. In this plant, no reticulum stage is found in the interkinesis either in the permanent or the aceto-carmine preparations. In this stage, the matrix of the chromosome is quite hyaline, in sharp contrast with the strongly chromatic spiral threads (Figs. 32 and 58). Often there can be seen a longitudinal split at the apex of the chromatid. This probably suggests that the single-appearing spiral or chromonema is in reality double, a condition which shows that the longitudinal split for the ensuing division in the pollen grain has already occurred (Fig. 33). In this stage, the coiling of the chromonemata is so regular that the number of turns and the direction of coiling can be easily determined (Figs. 32 and 58). The coiled chromonemata are found in a polarised orientation as distinct as in the telophase (Fig. 58).

Prophase in the homotype division. When the homotype division approaches, the chromonemata are thickened gradually, this being ac-

companied by a partial straightening out at the proximal region of the chromosome, which gives rise to a slight elongation of the chromosome as a whole (Figs. 34 and 35). In Fig. 34, in which two pairs of sister chromosomes are drawn, the chromonema in the second chromosome from the right is seen to be double in the middle region, though such a doubleness is of unusual occurrence. Then the orientation of the chromosomes is rendered irregular, when the nuclear membrane disappears (Fig. 36).

As can be readily seen from the descriptions given above, neither the formation of the nuclear reticulum in the interkinesis nor the marked unravelling of the chromonemata in the prophase is observed in this plant, so that the chromosome in the late telophase in the heterotype division passes through the interkinesis without undergoing any special change in its shape and structure. Cases resembling this have been reported by TUAN (1931) in an abnormal microsporogenesis in *Gasteria* and by WILSON (1912) in some animals.

Meta- and anaphase in the homotype division. When the nuclear membrane disappears, the chromosomes tend to gather in the central region of the cell, and in the next moment, the points of the spindle fiber attachment become arranged on the equatorial plate, the free arms being subjected to haphazard orientations, mostly tending to stretch towards the poles (Fig. 37). In Fig. 37, various configurations in side view assumed by a pair of sister chromosomes in metaphase are shown. In this stage, the spiral threads are apparently thicker than in the interkinesis, the thickening of the threads being accompanied by a slight diminution in the number of turns of the spiral, as will be mentioned later with data. When the fixation is inadequate, the spiral is completely obscure and the chromosomes appear to be homogeneous rods. The "lateral process" and the "chromosome sheath," which LEE (1920 and 1924) has emphasized as of natural occurrence could not be confirmed in my preparations.

In the aceto-carmine preparations, the coiled chromonemata are so thick in the homotype metaphase that a marked difference can be noticed only at a glance between these and those of *Tradescantia reflexa*. While in *Tradescantia* the chromosomes in the heterotype division and those in the homotype division show a remarkable difference in shape and size (thickness), in *Sagittaria* no such remarkable difference can be found between them. They are nearly the same, and both resemble the heterotype chromosomes in *Tradescantia*. Careful examinations revealed that these thick spiral threads are not

of a homogeneous structure, but that the threads themselves are also spirals of the lower order, a complex structure which was first announced by FUJII (1926) in his study of chromosomes in pollen mother cells in *Tradescantia reflexa*. He has called the spiral of the higher order the "secondary" and that of the lower order the "primary." In Fig. 59, this doubly coiled aspect of the spiral is visible in the places indicated by the arrow. The diminution in the number of turns of the spiral and the increase in thickness of the spiral thread described above, may partly be due to the enlargement of the diameter of this primary spiral.

Not infrequently, chromosomes carrying certain evidence that the chromonemata are double were observed. In Figs. 37, b and 38, some such chromosomes are shown. They carry two satellite-like appendages at the proximal end. This doubleness of the satellite-like appendages suggests that the chromonemata in these chromosomes are longitudinally double, at least through a certain length.

In the anaphase, the sister chromosomes separate from each other first at the point of the spindle fiber attachment, and they migrate towards the spindle poles. Often, the proximal portion of the chromosomes is drawn out, so that the spiral chromonemata are uncoiled in this portion. As illustrated in Figs. 39 and 40, this portion of the chromosomes is thinner as compared with the distal part. When the chromosomes approach the poles, they become shorter and thicker (Figs. 41).

Telophase in the homotype division. The chromosomes at the poles lie closely together and are still shorter than those in the late anaphase, but soon become slightly elongated and separated from one another. Then coils of the secondary spiral are loosened, when it becomes more appropriate to substitute the term zig-zag for spiral. This stage is illustrated in Figs. 42–47.

In the telophase too, a satellite-like appendage is sometimes observed, connected to the proximal end of the chromosome with a fine thread (Fig. 43). An advanced stage is shown in Fig. 48. In this figure, the secondary spirals are rendered irregular. In part, they are markedly uncoiled. In the part where they remain in the coiled state, they often present the appearance of being composed of two interlaced threads. It was not determined whether this appearance indicates real duality of the chromonemata or not, but Fig. 44, in which two distinctly separated satellite-like appendages are seen at the proximal end of the chromosome, seems to indicate more affirmatively that the

chromonemata are double. The daughter nuclei formed are very small and compactly filled with chromonemata in the irregularly coiled state.

The doubleness of the chromonemata in the chromosome in the homotype division has been reported in *Gasteria* by TAYLOR (1931) and in *Galtonia* by SMITH (1932). According to these authors, two chromonemata are regularly interlaced through their whole length. In *Sagittaria* such an aspect as two chromonemata interlaced was only rarely observed.

Interphase between the meiotic and post-meiotic divisions. In Fig. 49 in which a thin section of an interphasic nucleus is reproduced, the spirals are found partly drawn out and partly remaining in their coiled form, though in this stage the connective threads between them, being fairly deeply stained, make it difficult to trace the chromatic threads which are very uneven in thickness throughout the whole length. This irregularity in the coiling and the unevenness in thickness of the chromatic threads seem to suggest that in this stage uncoiling takes place to a certain extent in both primary and secondary spirals as has been observed by KATÔ[1] in the interkinesis in *Tradescantia reflexa*. The general view of the nuclei resembles that of those in the last premeiotic interphase. It has not been determined whether in this case a further change goes on or not.

The first mitosis in pollen grains. In the early prophase, the connective threads are broken down, and individual spirals, the threads forming them being now thicker, become more and more clearly distinguishable from one another, they tending to assume a more regular spiral form (Figs. 50–52). In Fig. 51, each spiral can be clearly distinguished from the others, though there are still observable some remnants of the less chromatic threads connecting them. The form of the spiral resembles in appearance that of the late telophase in the homotype division, and hence, it seems highly probable that the spiral is the one formed by the reappearance of the double-coiled spiral in the homotype telophase. In Fig. 52, a more advanced stage is shown in which certain turns of the spiral appear to be double, though this doubleness is not so decisive as to give a clear answer to the question whether it represents a true longitudinal split of the chromonema or not. As can be seen from Figs. 53, 54 and 55, the spirals are then drawn out into spiremes which grow thicker as the former are straightened out, and each individual chromosome comes to stand out with

1) Not yet published.

great distinctness from the others. In Fig. 53, satellite-like appendages and constrictions are exhibited by some chromosomes, especially clearly by the one which is found on the upper side of the figure. The process mentioned above as taking place in the prophase, that is, the reappearance of the spiral followed by its being drawn out as a consequence of the thickening of the spiral thread, closely resembles that taking place in the prophase of the somatic mitosis in root-tip cells (SHARP 1920, KUWADA 1921, etc.), as well as in the homotype prophase in *Gasteria* studied by TAYLOR (1931), and in *Tradescantia* observed by KATÔ. The true longitudinal split becomes clearly observable first in the late prophase, where the term chromosomes is commonly used for shortened and thickened spiremes. In these chromosomes the internal structure is quite obscure (Fig. 56).

In the nuclear plate stage, the chromosomes which are much thicker than those found in division in root-tip cells in this plant are laid down strictly on the equatorial plate (Text-fig. 4). Sometimes, the satellite-like appendage is observed in some of the chromosomes in meta- and anaphase, but the structure of the chromosomes is quite obscure in these stages too.

Direction of coiling and number of turns of the chromonema spirals

As mentioned above, the direction of the coiling of the chromonema and the number of its turns can be clearly determined in the interkinesis. Some observations on these points were made with chromosomes in cells found in a single loculus. With the M-chromosome accurate observation was possible only in four cases. These chromosomes are reproduced in Fig. 57. In *a*, the coiling is right-handed in all the four arms of the chromosome; in *b*, it is left-handed in the two outside arms of the four, while in the inside two, it is hardly possible to determine whether it is right-handed or left-handed. In *c*, each of the four arms is drawn separated from the others. In the two arms on the left-hand side of the figure, the coiling is left-handed and in the third one it is right-handed, while in the fourth it is not quite clear whether it is left-handed or right-handed. In *d*, in which three arms of the four, of which the fourth was cut away by the microtome knife, are drawn separated from one another as in *c*; the two arms on the right-hand side of the figure are right-handed and the one on the left-hand side is left-handed.

In the case of the rod-shaped chromosomes, far more numerous

observations were possible than in the case of the M-chromosome. In 42.5% of 40 chromosomes observed, the coiling was left-handed in both sister chromatids (Fig. 32), and in 45% it was right-handed (Fig. 57, *e*). In the remaining 12.5%, the direction was opposite in both sister chromatids, it being right-handed in the one chromatid and left-handed in the other (Fig. 57, *f*). This result is in accordance with the result obtained by NEBEL (1932, b) in *Tradescantia*. Besides these cases, chromatids such as those shown in Fig. 57, *g*, in which the direction of the coiling is different in different parts of the chromatid, as has been reported by SAX (1930), TAYLOR (1931), ISHII (1931, a and b) and NEBEL (1932, b), were rarely observed. According to verbal information supplied by Mr. IWATA, this latter case is very frequently observed in the chromosomes in the heterotype meta- and anaphase in *Lilium longiflorum*.

In the anaphase in the homotype division, the frequency of occurrence of the right-handed, and left-handed spirals was approximately the same, being 47.7% and 52.3% respectively in 44 chromosomes observed.

The number of turns was counted in the interkinesis and the homotype anaphase. In the interkinesis, it was found that the number is the same, exactly or at least approximately, in the sister chromatids. The results obtained are given in Tables 1 and 2, respectively.

TABLE 1. (Interkinesis)

No. of turns.	3	4	5	6	7	8	Total
No. of chromatids observed.	0	14	27	27	12	0	80
Percentage.	0	17.5	33.8	33.8	15.0	0	100.1

TABLE 2. (Homotype anaphase)

No. of turns.	2	3	4	5	6	7	Total
No. of chromatids observed.	0	8	17	14	5	0	44
Percentage.	0	18.2	38.6	31.8	11.4	0	100.0

From these data, it can be seen that spirals with five or six turns are of most frequent occurrence in the interkinesis, and those with four or five in the homotype anaphase.

Chromonema behaviour in meiosis in some other higher plants

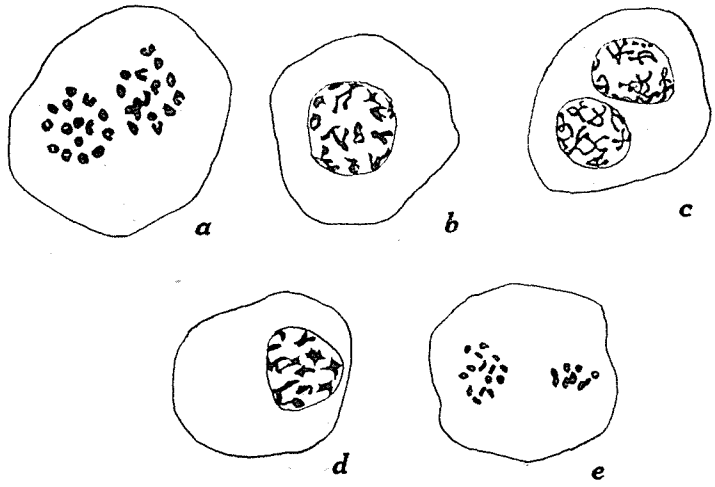
In the paper published in 1930, the writer pointed out that the chromonema spirals in the homotype division in *Sagittaria* differ very much in the thickness of the thread forming them from those found in the homotype division in *Tradescantia*, *Lilium*, and some other higher plants. For comparison with *Sagittaria*, it may not be out of place to give here brief descriptions of the behaviour of chromonemata in meiosis in *Lilium* and *Lythrum*, descriptions which are based on observations of aceto-carmine and permanent preparations.

Lilium tigrinum and L. longiflorum. In pollen mother cells in *Lilium*, the chromonema spirals found in the heterotype meta- and anaphase are markedly larger in diameter and smaller in the number of turns than those in the homotype division (SHINKE, 1930). As pointed out by KUWADA (1932, a) after inspection of the original photomicrograph which was reproduced in the previous paper Fig. 1, Pl. XVII (SHINKE, 1930), the chromosomes in the heterotype division in *Lilium tigrinum* are of the double-coiled structure (Fig. 60) like those of *Tradescantia reflexa* (cf. FUJII, 1926, KUWADA 1932, a and b, KUWADA and NAKAMURA 1933, KATÔ). Generally, the thick double-coiled spirals undergo no remarkable change in their coiling up to the early interkinesis, when the first appearance of uncoiling is recognizable (Figs. 61–63). When, however, there is a hitch in the separation toward the poles at the anaphase, which is largely connected with the presence of a chiasma, the thick spirals are drawn out to a greater or less extent, which often gives rise to the partial loss of the coiling aspect (Fig. 64). This behaviour of chromosomes in the heterotype meta- and anaphase has been illustrated by SAX (1930) in *Lilium*. According to the verbal information supplied by Messrs. KATÔ and IWATA, the drawing out of the spirals takes place sometimes so intensely that in the ana- and telophase there are found only slender chromosomes containing a fine ordinary single-coiled spiral of a smaller diameter within.

In the interkinesis, the spirals (secondary spirals) are drawn out and run sinuously (Figs. 63 and 65); the drawn out threads often present a fine spiral or zig-zag (primary spiral) aspect in places (Figs. 63 and 65). At the beginning of the homotype prophase, these threads recover their original spiral form in the telophase to a certain extent (Fig. 66), but are soon drawn out again, and slender chromosomes containing a regular spiral of a smaller diameter within are formed (SHINKE

1930, Fig. 13, Pl, XVII). The number of turns of the spiral in this stage is far greater than in the heterotype division (SHINKE 1930). According to the verbal information given by Messrs. KATÔ and IWATA, these chromosomes sometimes present a winding aspect. Chromosomes in the homotype anaphase presenting a somewhat similar winding aspect are reproduced in Fig. 67. Rarely, an indication of doubleness of the spiral in the homotype chromosome was observed.

Lythrum salicaria, var. vulgare, subvar. genuina. In this plant, metaphase chromosomes which are small and spherical show no internal structure in either heterotype or homotype divisions, as is usually the case with small chromosomes (SHINKE 1929 and 1930). In the



Text fig. 5. *Lythrum salicarta*, var. *vulgare*, subvar. *genuina*. *a*) Heterotype anaphase in polar view. *b*) A nucleus in late telophase in heterotype division with slender chromosomes. *c*) Two daughter nuclei in mid-interkinesis with chromosomes of the shape of a slender cross. *d*) Still later stage; Chromosomes are thicker than those in the mid-interkinesis. *e*) Showing spherical chromosomes in homotype metaphase.

anaphase in the heterotype division, the separated chromosomes are somewhat angular, the sister halves of the chromosomes having been recognizably separated from each other (Text-fig. 5, *a*). When the chromosomes reach the pole, they are gathered into a mass so tightly that it is hardly possible to distinguish individual ones. In the ensuing stage, the chromosomes are separated from one another again and they become more slender than in the preceding stages (Text-fig. 5, *b*). In the interkinesis, they assume the shape of a cross with slender arms (Text-fig. 5, *c*). This thinning of the chromosomes probably shows that the coiled chromonema in the preceding stages is drawn out in

this stages. When the homotype division approaches, the arms of the cross become shorter and thicker (Text-fig. 5, *d*), until the crosses are transformed into small spherical chromosomes in the equatorial plate (Text-fig. 5, *e*).

Conclusion

While in many plants, such as, for instance, *Tradescantia*, *Lilium*, *Gasteria*, *Fritillaria*, *Rhoeo* etc., the chromosomes in the homotype division have been reported to be far more slender than those in the heterotype division, presenting a close resemblance in shape to those in the somatic mitosis, they have been stated in some other plants, to differ both in shape and thickness only very slightly from those in the heterotype division (cf. WILSON, 1925, p. 532). It has also been reported that in some of the plants of the former group such as *Tradescantia*, *Lilium*, *Rhoeo* etc., the spirals are much finer and the number of their turns is greater in the homotype division than in the heterotype division (FUJII 1926, KUWADA 1927 and 1932, a and b, SHINKE 1930), while in an abnormal type of *Gasteria* which belongs to the latter group, TUAN (1931) has found no such differences in the spiral between the heterotype and homotype divisions.

The peculiar shape of the chromosomes in the heterotype division has been interpreted by FUJII (1926) as due to the peculiar type of coiling of the chromonemata in this division. He found that in the heterotype division in *Tradescantia reflexa* the chromonemata are doubly coiled, that is, that the thick spiral found in the chromosomes is formed by the coiling of a finer spiral. In the other divisions, the spiral is the ordinary single-coiled one, and hence the chromosomes are longer and thinner than those in the heterotype mitosis. FUJII has called the spiral of the smaller diameter in the heterotype division, the "primary" and that of the larger diameter, i. e., the spiral formed of the primary spiral the "secondary." This double-coiled structure of the chromosomes in the heterotype division in *Tradescantia reflexa* was confirmed by KUWADA and NAKAMURA (1933), KUWADA (1932, a). According to KUWADA (1932 a and b), a coiling takes place in the early prophase of the homotype mitosis to form a new spiral which replaces the old double-coiled spiral, it being drawn out as a result of the new coiling. This spiral newly formed is the single-coiled one, and therefore, it resembles the primary spiral in the heterotype mitosis. The results obtained by KATÔ from observation of fixed material are

in accord with the view of KUWADA. Dealing with *Tradescantia reflexa*, NEBEL (1932, a) has also expressed the view that the chromonemata which he takes as having been uncoiled from their "meiotic spirals" in the interkinesis are thrown again into the formation of new "secondary" or "somatic spirals" with small gyres, though he is, unlike FUJII and KUWADA, of the opinion that the coiling is single both in the heterotype and homotype divisions.

The results of observation of the chromosomes in *Lilium* which were reported in the previous paper (SHINKE 1930) and those mentioned above in the present paper are also in accord with the case of *Tradescantia reflexa* in regard to the chromosome structure. They may be given in a summarized form as follows:

1) The chromosomes in the heterotype metaphase are shorter and thicker than those in the homotype anaphase (SHINKE 1930, Figs. 1, 2, 11 and 13, Pl, XVII).

2) A single spiral is recognizable in a single chromatid in the heterotype anaphase (SHINKE 1930, Figs. 2 and 6, Pl. XVII).

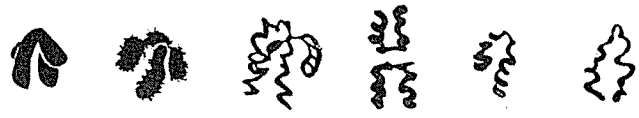
3) These spirals generally appear as ordinary single-coiled spirals, but not infrequently it can be clearly seen that they are double-coiled ones (Fig. 60).

4) In the homotype meta- and anaphase, the chromosomes which are now slender are of the single-coiled structure (SHINKE 1930, Figs. 11 and 13, Pl. XVII).

No evidence was found in *Lilium* which was in accord with the view of NEBEL (1932, a) that the coiling is single both in the heterotype and homotype divisions. The case of the normal meiosis in *Gasteria* reported by TAYLOR (1931) shows a close resemblance to those mentioned above in the case of *Lilium*, though TAYLOR has said nothing about the doubly-coiled structure of the chromosomes.

In another type, which is represented by *Lythrum*, *Sagittaria*, the abnormal type of *Gasteria* and some other plants, the shape of the chromosomes in the heterotype division hardly differs, or only slightly, from that of those in the homotype division. In this type there are some subordinate types. One of the subtypes is represented by *Lythrum*, in which the unravelling of the chromonema spirals seems to take place in the interkinesis (Text-fig. 5). The chromosome shape peculiar to the heterotype division comes to sight again in the homotype division probably by restoration of the spiral in the first division. The shape of the chromosomes is similar, therefore, in both hetero-

type and homotype divisions, as has been frequently reported in plants with small chromosomes (cf. DAVIS 1910, KUWADA 1911). Somewhat similar cases have been reported by SMITH (1932) in *Galtonia* and by MAEDA (1928) in *Lathyrus*, from which plants the authors have drawn spiral threads that are similar in the heterotype and the homotype divisions.



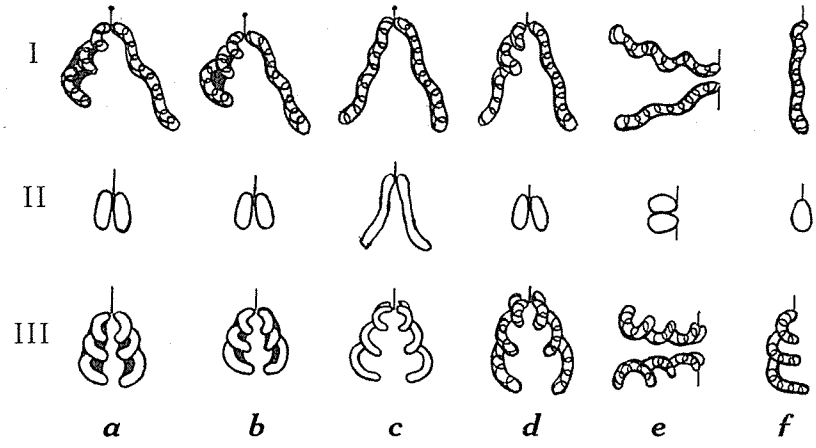
Text-fig. 6. *Sagittaria Aginashi*. Chromosomes with median spindle fiber attachment in different stages in meiosis. *a*) anaphase; *b*) telophase in heterotype division; *c*) interkinesis; *d*) metaphase; *e*) anaphase; *f*) telophase in homotype division.

In the second subtype which is represented by *Sagittaria*, the unravelling of the meiotic spirals does not take place in the interkinesis to such a great extent as in the cases mentioned above, but the spirals rather remain without showing any fundamental change in the coiling. In *Sagittaria*, there is only a slight difference in shape between the chromatids in the heterotype and the homotype division (Text-fig. 6). The threads which coil into a spiral are not simple, smooth threads in the homotype division as they are in the case of *Tradescantia* and *Lilium*, but present a zig-zag or spiral appearance. This fact seems to indicate that the short massive form of the chromosomes in the homotype division of this plant is due to their doubly-coiled structure, as has been maintained by FUJII (1926) in the case of the massive form of the chromosomes in the heterotype division of *Tradescantia reflexa* in which the chromonemata are doubly-coiled.

The case found by TUAN (1931) in the abnormal meiosis in *Gasteria* differs from the case of *Sagittaria* mentioned above in the point that in the former the interkinesis and homotype prophase stages, are completely omitted, neither the formation of the nuclear membrane nor the unravelling of the chromonemata taking place in any stage at all between the heterotype and the homotype division.

In Text-fig. 7, three different kinds of the behaviour of the chromonemata in the heterotype and homotype divisions represented by *Lilium*, *Lythrum* and *Sagittaria* are schematically shown. As will be readily seen from Text-fig. 7, there are remarkable differences

among *Lilium*, *Lythrum* and *Sagittaria* in the behaviour of the chromonema during the interkinesis and the homotype prophase, which have an important bearing upon the determination of the structure, and consequently, of the shape of the chromosome in the homotype metaphase and anaphase. The two extreme examples found by TAYLOR (1931) and TUAN (1931) in the normal and abnormal cases of *Gasteria*



Text-fig. 7. Diagrams showing the behaviour of a telomitic chromosome at successive stages in meiosis in:

I) *Lilium longiflorum* and *L. tigrinum*,
II) *Lythrum salicaria*, var. *vulgare*, subvar. *genuina*,
III) *Sagittaria Aginashi*.

a) anaphase; *b*) telophase in heterotype division; *c*) interkinesis; *d*) prophase; *e*) metaphase; *f*) anaphase in homotype division.

seem to suggest that a certain environmental change may cause the change in the behaviour of the chromonema in the interkinesis, which gives rise to the alteration of the structure, and accordingly the shape of the chromosomes in the homotype division (cf. DARLINGTON 1932, p. 113).

Before concluding, it may be added that in *Sagittaria* the chromonema can, in fixed material, be clearly observed in the interkinesis and the interphase, and it is obscure in the late prophase, metaphase and anaphase in the heterotype and the first post-meiotic mitoses, while in the homotype mitosis it is very distinct throughout all stages, as will be seen from the following table (Table 3).

TABLE 3.

Stage	Appearance of Chromonema
Premeiotic telophase	Zig-zag.
Interphase	Partly straightened.
Heterotype preleptotene	Coiled or spiral.
leptotene	Straightened.
zygotene	Straightened.
pachytene	Straightened, but spiral is often clear within spireme.
diplotene	Straightened; spiral is generally obscure.
strepsitene	Generally obscure.
diakinesis	Generally obscure.
metaphase	Obscure.
anaphase	Obscure; rarely discs.
telophase	Zig-zag or spiral.
Interkinesis	Very distinct spiral.
Homotype prophase	Very distinct spiral, but thick.
metaphase	Very distinct spiral, but thick.
anaphase	Very distinct spiral, but thick.
telophase	Spiral or zig-zag; very distinct.
Interphase	Partly straightened.
Post-meiotic early prophase.	Spiral or coiled.
mid-prophase	Straightened; inner structure is obscure.
late-prophase	Straightened; inner structure is obscure.
metaphase	Obscure.
anaphase	Obscure.

Summary

1) Important results obtained from *Sagittaria Aginashi* may be summarised as follows:

a) In the last premeiotic interphase, the nuclear network is composed of the chromonemata which are partly straightened out and the anastomoses which connect them.

b) The pachytene spireme consists of the fine spiral thread and the matrix.

c) The doubleness of the fine nuclear threads observed in the early prophase in the heterotype division is regarded as due not to

the longitudinal division of the univalent chromosome, but to the approximation of two univalents (parasyndesis).

d) In the metaphase in the heterotype mitosis, there are tetrads of a ring or a V shape in horizontal orientation (post-reductional type) among others.

e) The chromosomes in the telophase in the heterotype division pass through the interkinesis with a slight change in structure and shape.

f) In the interkinesis, the directions of coiling of the chromonemata in the sister chromatids are generally the same, while they are not infrequently opposite.

g) Some evidences of the doubleness of the chromonema were obtained in chromosomes in the interkinesis and chromosomes in the homotype division.

h) In the chromosomes in the homotype metaphase which are as massive in shape like those in the heterotype metaphase, certain clear evidence of the double-coiled nature of the chromonemata was obtained,—a sort of coiling in which the ordinary spiral of the chromonema (the primary spiral) coils again to form a large secondary spiral.

2) The behaviour of the chromonema during the interkinesis and the homotype prophase in *Sagittaria* was compared with that observed in *Lilium* and *Lythrum*, and it was shown that there are remarkable differences among them.

In conclusion, the writer wishes to acknowledge Prof. Y. KUWADA's kind guidance and encouragement throughout the present investigation.

Literature Cited

ALLEN, C. E. (1905) Nuclear division in the pollen mother-cells of *Lilium canadense*. Ann. Bot. Vol. 19.

BARCOCK, E. B. and CLAUSEN, J. (1929) Meiosis in two species and three hybrids of *Crepis* and its bearing on taxonomic relationship. Univ. California Publ. Agricul. Sci. Vol. 2.

BĚLAŘ, K. (1929). Beiträge zur Kausalanalyse der Mitose. III. Untersuchungen an den Staubfaden, Haarzellen und Blattmeristemzellen von *Tradescantia virginica*. Ztschr. Zellf. Vol. 10.

BELLING, J. (1928, a) A working hypothesis for segmental interchange between homologous chromosomes in flowering plants. Univ. California Publ. Bot. Vol. 14.

—— (1928, b) The ultimate chromomeres of *Lilium* and *Aloë* with regard to the numbers of genes. Ibid. Vol. 14.

BONNEVIE, K. (1908) Chromosomenstudien. I. Chromosomen von *Ascaris*, *Allium* und *Amphiuma*. Arch. Zellf. Vol. 1.

—— (1911) Chromosomenstudien. III. Chromatinreifung in *Allium cepa* (♂). Ibid. Vol. 9.

CHIPMAN, R. H. (1925) A study of synizesis and synapsis in *Lilium superbum*. Amer. Jour. Bot. Vol. 12.

DARLINGTON, C. E. (1932) Recent advances in cytology. London.

DAVIS, B. M. (1910) The reduction division of *Oenothera biennis*. Ann. Bot. Vol. 24.

DIGBY, L. (1910) Nuclear divisions of *Galtonia candicans*. Ibid. Vol. 24.

—— (1919) On the archesporial and meiotic mitoses of *Osmunda*. Ibid. Vol. 33.

FUJII, K. (1926) The recent progress in cytology, and methods of its investigation (Japanese). Rep. Japan. Assoc. Adv. Sci. Vol. 2.

HEITZ, E. (1928) Der bilaterale Bau der Geschlechtschromosomen und Autosomen bei *Pellia Fabbroniana, P. epiphylla* und einigen anderen Jungermanniaceen, Planta. Vol. 5.

—— (1929) Heterochromatin, Chromocentren, Chromomeren. Ber. d. Deutsch. Bot. Gess. Vol. 47.

ISHII, T. (1931, a) On the structure of chromosomes (Preliminary note). (Japanese). Japan. Jour. Genet. Vol. 7.

—— (1931, b) Sensyokutai no Rasen no Hôkô ni tuite. (On the direction of turns of the spiral of the chromosome. (Japanese). Bot. Mag. (Tokyo). Vol. 45.

KAUFMANN, B. P. (1926) Chromosome structure and its relation to the chromosome cycle. I. Somatic mitosis in *Tradescantia pilosa*. Amer. Jour. Bot. Vol. 13.

—— (1931) Chromonemata in somatic and meiotic mitoses. Amer. Nat. Vol. 65.

KUWADA, Y. (1911) Maiosis in the pollen mother cells of *Zea Mays* L. Bot. Mag. (Tokyo). Vol. 25.

—— (1921) On the so-called longitudinal split of chromosomes in the telophase. (Preliminary note). Ibid. Vol. 35.

—— (1926) On the structure of the anaphasic chromosomes in the somatic mitosis in *Vicia Faba*, with special reference to the so-called longitudinal split of chromosomes in the telophase. Mem. Coll. Sci., Kyoto. Imp. Univ. Ser. B. Vol. 2.

—— (1927) On the spiral structure of chromosomes. Bot. Mag. (Tokyo) Vol. 41.

—— (1932, a) The double coiled spiral structure of chromosomes. Ibid. Vol. 46.

—— (1932, b) Sensyokutai no Seikatsukwan. (The life-history of chromosome). (Japanese). Kagaku. Vol. 2.

KUWADA, Y. and T. NAKAMURA, (1933) Behaviour of Chromonema in Mitosis. I. Observation of pollen mother cells in *Tradescantia reflexa*. Mem. Coll. Sci., Kyoto Imp. Univ. Ser. B. Vol. 9.

LEE, A. B. (1920) The structure of certain chromosomes and the mechanism of their division. Quart. Jour. Microsc. Sci. Vol. 65.

—— (1924) The chromosomes of *Paris quadrifolia* and the mechanism of their division. Ibid. Vol. 69.

LUNDEGÅRDH, H. (1910) Über Kernteilung in den Wurzelspitzen von *Allium cepa* und *Vicia faba*. Svensk. Bot. Tidsk. Vol. 4.

MAEDA, T. (1928) The spiral structure of chromosomes in the sweet-pea (*Lathyrus odoratus*, L.). Bot. Mag. (Tokyo). Vol. 42.

NAWA, N. (1928) Some cytological observations in *Tricyrtis, Sagittaria* and *Lilium*. Ibid. Vol. 41.

NEBEL, B. R. (1932, a) Chromosome structure in *Tradescantiae*. I. Methods and Morphology. Ztschr. Zellf. Vol. 16.

—— (1932, b) Chromosome structure in *Tradescantiae*. II. The direction of coiling of the chromonema in *Tradescantia reflexa* Raf., *T. virginiana* L., *Zebrina pendula* Schnizl. and *Rhoeo discolor* Hance. Ibid. Vol. 16.

NOTHNAGEL, M. (1916) Reduction divisions in the pollen mother cells of *Allium tricoccum*. Bot. Gaz. Vol. 61.

SARBADHIKARI, P. C. (1924) Cytology of *Osmunda* and *Doodia*. I. On the somatic and meiotic mitoses of *Doodia*. Ann. Bot. Vol. 38.

SAX, K (1930) Chromosome structure and the mechanism of crossing over. Jour. Arnold Arbor. Vol. 11.

SCHAEDE, R. (1928) Vergleichende Untersuchungen über Cytoplasm, Kern und Kernteilung im lebenden und im fixierten Zustand. Protoplasma, Vol. 3.

SCHUSTOW, L. von, (1913) Über Kernteilung in der Wurzelspitze von *Allium cepa*. Arch. Zellf. Vol. 11.

SHARP, L. W. (1920). Somatic chromosomes in *Tradescantia*. Amer. Jour. Bot. Vol. 8.

—— (1929) Structure of large somatic chromosomes. Bot. Gaz. Vol. 88.

SHIMOTOMAI, N and Y. KOYAMA (1932) Geschlechtschromosomen bei *Pogonatum inflexum* Lindb. und Chromosomenzahlen bei einigen anderen Laubmoosen. (Japanese) Bot. Mag. (Tokyo) Vol. 46.

SHINKE, N. (1929) Chromosome arrangement. IV. The meiotic divisions in pollen mother cells of *Sagittaria Aginashi*, Makino, and *Lythrum salicaria*, L. var. *vulgare*, D. C., subvar. *genuina*, Koehne. Mem. Coll. Sci., Kyoto Imp. Univ. Ser. B. Vol. 4.

—— (1930) On the spiral structure of chromosomes in some higher plants. Ibid. Vol. 5.

SMITH, F. H. (1932) The structure of the somatic and meiotic chromosomes of *Galtonia candicans*. Cellule Vol. 41.

STRASBURGER, E. (1888) Histologische Beiträge. I. Ueber Kern- und Zelltheilung im Pflanzenreiche. Jena.

SZAKIEN, B. (1927) La formation des chromosomes hétérotypiques dans l'*Osmunda regalis*. Cellule Vol. 37.

TATSUNO, S. (1933) Geschlechtschromosomen bei einigen Lebermoosen. I. (Japanese) Bot. Mag. (Tokyo). Vol. 47.

TAYLOR, W. R. (1925) Chromosome constrictions as distinguishing characteristics in plants. Amer. Jour. Bot. Vol. 12.

—— (1931) Chromosome studies on *Gasteria*. III. Chromosome structure during microsporogenesis and the postmeiotic mitosis. Ibid. Vol. 18.

TELEŻYŃSKI, T. (1931) Cycle évolutif du chromosome somatique. II. Observations sur le matériel fixé (racines d'*Haemanthus Katharinae* Back.) Acta Soc. Bot. Polon. Vol. 8.

TUAN, H. C. (1931) Unusual aspects of meiotic and postmeiotic chromosomes of *Gasteria*. Bot, Gaz. Vol. 92.

VEJDOVSKÝ, F. (1926-27) Structure and development of the living matter. Prague.

WILSON, E. B. (1912) Studies on chromosomes. VIII. Observations on the maturation phenomena in certain hemiptera and other forms, with considerations on synapsis and reduction. Jour. Exper. Zool. Vol. 13.

—— (1925) The cell in development and heredity. III. ed. New York.

Explanation of Plates

All the figures except Figs. 58-67 have been drawn with the aid on an ABBE's camera lucida using LEITZ achrom. homog. imm. obj. 1/12 and ZEISS comp. oc. 18. Fig. 58 is the photomicrograph from a permanent preparation taken with ZEISS apochr. imm. obj. 2mm. and comp. oc. 12. Figs. 59 und 60 are those from aceto-carmine preparations taken with the same obj. 2mm. and comp. oc. 18, and Figs. 61-67 are those from chloral-carmine preparations taken using comp. oc. 15×, instead of the comp. oc. 18.

Figs. 1-59 .....*Sagittaria Aginashi*.

Fig. 1. Chromosomes in early telophase in premeiotic mitosis, some showing a certain indication of their zig-zag structure.

Fig. 2. The same in a slightly later stage, the so-called longitudinal split is seen in the middle chromosome.

Fig. 3. Chromosomes in late telophase showing chromonemata distinctly. Several connecting threads or anastomoses are seen between the chromonemata of neighbouring chromosomes.

Fig. 4. A later stage. In this stage the spiral form of chromonemata is more pronounced.

Fig. 5. Nuclear reticulum in interphase.

Fig. 6. Very early prophase in heterotype division. Anastomoses between neighbouring chromonemata are considerably broken down, distinguishment of individual chromonemata being rendered easier.

Fig. 7. Preleptotene threads, of which spiral or zig-zag aspect is still conspicuous.

Fig. 8. Do. Unravelling is taking place.

Fig. 9. The whole view of a nucleus just before synizesis. In this nucleus the coiled aspect of the threads is still visible in places.

Fig. 10. Later stage showing the process of side-by-side pairing of the threads.

Fig. 11. A later synizesis showing pairing of two delicate threads.

Fig. 12. Showing apparent parallelism of two thick spiremes which consist of two delicate threads each.

Fig. 13. Nucleus in late pachytene stage.

Fig. 14. A part of a pachytene spireme presenting a structure of a row of discs or rings, or some other modified structures.

Fig. 15. The same, showing the structure of a row of chromatic discs.

Fig. 16. The same. Showing spiral aspect in places.

Fig. 17. A late diplotene stage. Two longitudinal halves are found twisted about each other.

Fig. 18. Early diplotene spireme with numerous lateral processes.

Fig. 19. Strepsitene stage.

Fig. 20. Typical chromosomes in strepsitene stage.

Fig. 21. A V-shaped tetrad in early diakinesis showing spiral structure.

Fig. 22. A ring chromosome tetrad in the same stage with longitudinal fission.

Fig. 23. An anaphasic chromosome in which the presence of chromonema spiral is indicated.

Fig. 24. A diad chromosome at pole in late anaphase.

Fig. 25. A couple of the same in a still later stage, showing somewhat irregular distribution of chromatic substance.

Fig. 26–31. Successive stages in telophase.

Fig. 26. A diad chromosome in early telophase with lateral processes.

Fig. 27. A couple of diads in the same stage showing peripheral deposition of chromatic substance.

Fig. 28. A diad chromosome in the mid-telophase.

Fig. 29. A couple of the same in later mid-telophase.

Fig. 30. A diad in the same stage with a chromatic knot at proximal end of each chromatid.

Fig. 31. Diad chromosomes in late telophase showing a marked decrease in stainability of the matrix substance.

Fig. 32. Chromosomes in interkinesis. Note highly achromatic state of matrix and regularity in coiling of chromonemata.

Fig. 33. A chromosome in late telophase or interkinesis showing the doubleness of its chromonema at upper end.

Fig. 34. Chromosomes in early prophase in homotype division.

Fig. 35. The same in a slightly later stage. The chromonemata are thicker than those in interkinesis.

Fig. 36. The same in late prophase. Note that the regular polar orientation (or relative position) of chromatids in the preceding stage is much disturbed.

Fig. 37, *a-d*. Showing various configurations of dividing chromosomes in the homotype division.

Fig. 38. A II-metaphasic chromosome with two satellites.

Fig. 39. II-anaphasic chromosomes showing their thick chromonemata and a more or less increased chromaticity of matrix.

Fig. 40. The same near the pole.

Fig. 41. Chromosomes in late anaphase becoming shorter.

Fig. 42. Chromosomes in telophase with chromonema spirals being unravelled into zig-zag appearance.

Fig. 43. Chromonema in telophase with a satellite.

Fig. 44. Chromonema in the same stage showing its doubleness.

Fig. 45. Chromonemata in mid-telophase showing the unravelling of the spirals more distinctly.

Fig. 46. A still later stage.

Fig. 47. Late telophase.

Fig. 48. A thin section of a nucleus in the final stage of telophase.

Fig. 49. Nucleus in interphase between homotype division and the first division in pollen grain. Delicate zig-zag threads are visible in places.

Fig. 50. Early prophase in the first division in pollen grain. Thick chromonemata are seen.

Fig. 51. More advanced stage. Fine connecting threads between chromonemata are disappearing.

Fig. 52. Later stage. Individual chromonemata are distinct, the connecting threads having been broken down.

Fig. 53. Chromosomes in mid-prophase.

Fig. 54. The same in later stage. Chromosomes are thicker and shorter.

Fig. 55. The same in still later stage.

Fig. 56. The same in late prophase. Longitudinal split of chromosomes is now becoming evident.

Fig. 57. *a-g*, Chromonema spirals in interkinesis. *a*, *b*, *c* and *d* are the M-chromosomes and *e*, *f* and *g* are rod-shaped chromosomes.

Fig. 58. Nuclei in interkinesis.

Fig. 59. Chromosomes in II-metaphase showing the double-coiled structure.

Figs. 60—67.....*Lilium*.

Fig. 60. *L. tigrinum*. Chromosomes of the double coiled structure in metaphase in heterotype division taken from a preparation in which a press was given on the cover glass to make the internal structure clearer.

Fig. 61. *L. longiflorum*. Chromosomes in anaphase in heterotype division in side view.

Fig. 62. *L. cordatum*? The same in later stage.

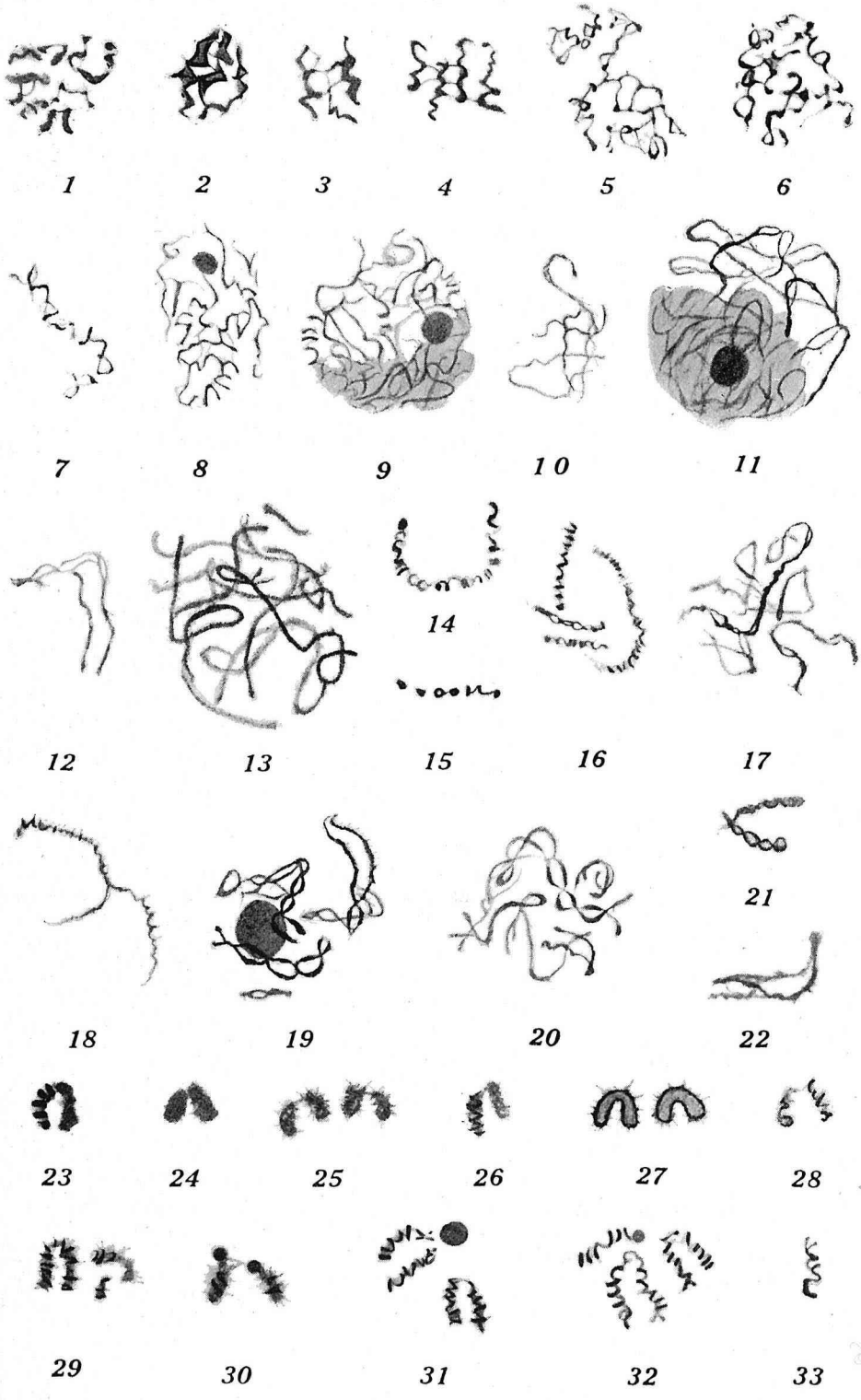
Fig. 63. *L. longiflorum*. Interkinesis, showing unravelling of chromonemata.

Fig. 64. *L. longiflorum*. Chromosomes in anaphase in heterotype division showing chromonemata partly drawn out from their coiling.

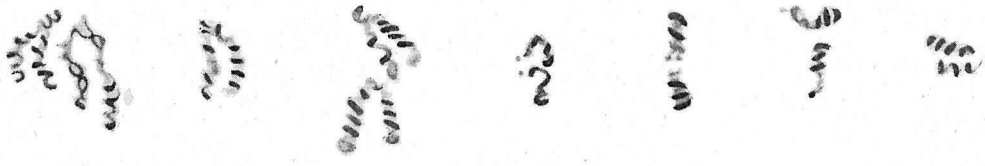
Fig. 65. *L. longiflorum*. Interkinesis.

Fig. 66. *L. longiflorum*. Prophase in homotype division.

Fig. 67. *L. longiflorum*. Chromosomes in anaphase in homotype division.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

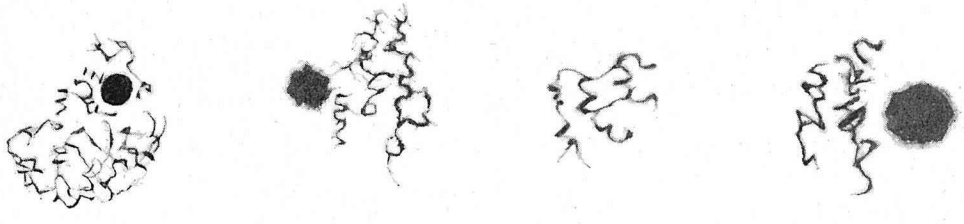
N. Shinke



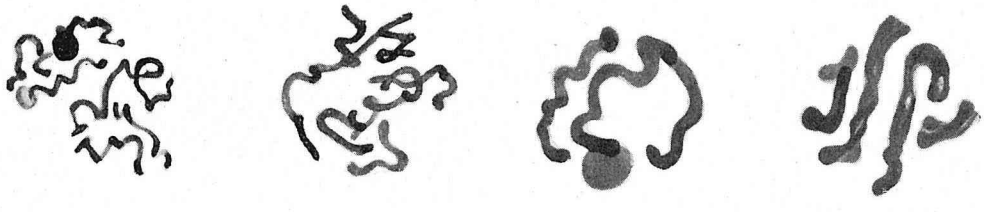
34 35 36 37 a b c d

38 39 40 41 42

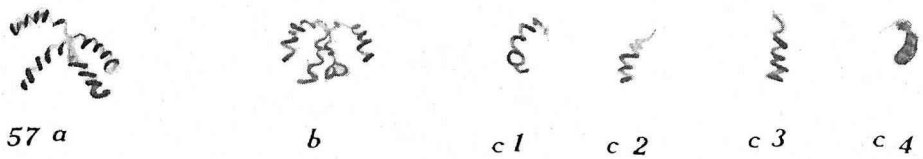
43 44 45 46 47 48



49 50 51 52

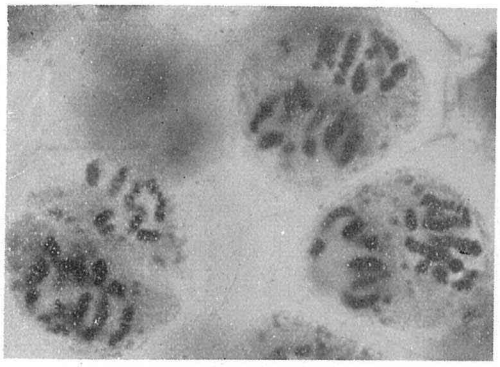


53 54 55 56

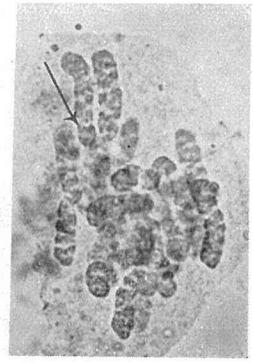


57 a b c 1 c 2 c 3 c 4

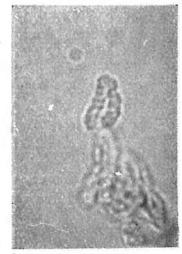
d 1 d 2 d 3 e f g



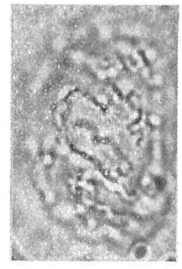
58



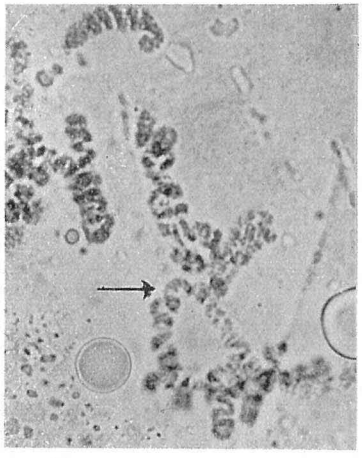
59



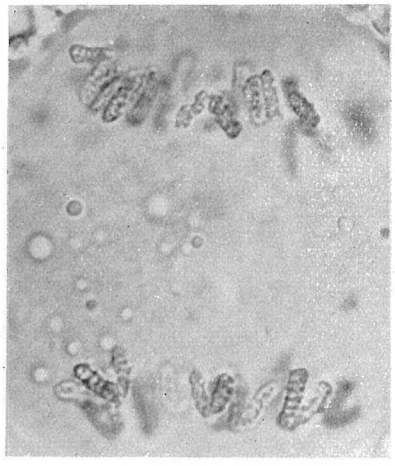
61



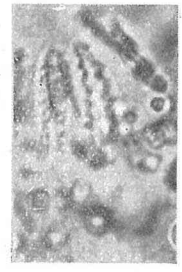
63



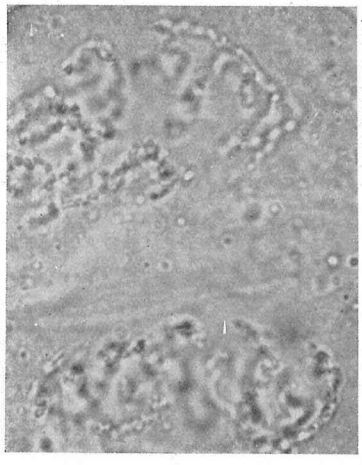
60



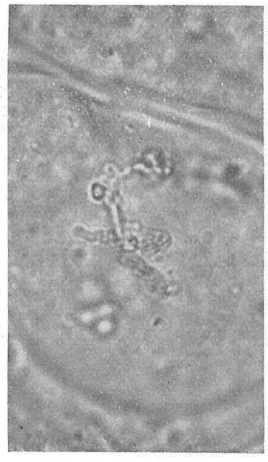
62



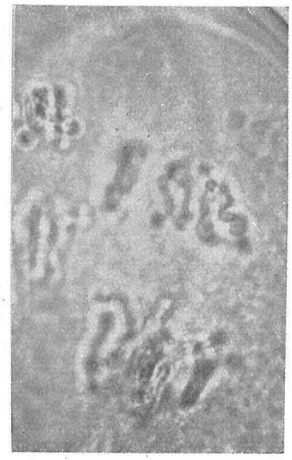
64



65



66



67

N. Shinke