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v. 1924. The Rhododendrons of Hupeh, pp. 84-107; A new species of *Reevesia*, pp. 233-235.

vi. 1925. The Rhododendrons of eastern China, the Bonin and Liukiu Islands and of Formosa, pp. 156-186; *Rhododendron chrysocalyx* Lévl. & Vaniot, pp. 200-201.

vii. 1926. The Taxads and Conifers of Yunnan, pp. 37-68; *Thuja orientalis* Linnaeus, pp. 71-74; *Gymnospermae* [of New Caledonia], pp. 76-85.

viii. 1927. *Juniperus procera* Hochst., pp. 1-2; An enumeration of the ligneous plants of Anhwei, by Alfred Rehder and Ernest H. Wilson, pp. 150-199; 238-240.

ix. 1928. Enumeration of the ligneous plants collected by J. F. Rock on the Arnold Arboretum expedition to northwestern China and northeastern Tibet, by Alfred Rehder and Ernest H. Wilson, pp. 4-27; 37-125; *Podocarpus falcata* R. Br., pp. 143-144.

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The ragweed or hay fever plant. (Not yet published.)

A NEW ARUNDINARIA FROM CHINA

AIMÉE CAMUS

Arundinaria Fangiana, nov. subsp.

Culmi 0.30 m. alti, fistulosi, ramulis ad nodos fasciculatis. Folia chartacea, lanceolata, basi rotundata, in petiolum brevem attenuata, apice longe acuminata, 3–5 cm. longa, 0.4–0.7 cm. lata, glabra, margine scabra, nervis secundariis utrinque 3, venulis transversis conspicuis; vaginae elongatae, striatae, glabrae, superne truncatae, fimbriatae; ligulae truncatae. Panicula foliata, paucispiculata; pedicelli 1–1.7 cm. longi, glabri, tenues; spiculae 2–2.5 cm. longae, 6-florae, subglabra; glumae steriles contiguae, prima 0.5–2 mm. longa, ovata, acuminata; secunda 3–7 mm. longa, subulata, margine scabra; rachillae internodium 1 mm. longum, sericeum; gluma fertilis inferior ovato-lanceolata, apice cuspidata, 1.2–1.4 cm. longa, superne pilosula, 7-nervia nervis conspicuis, scabris. Palea 7–8 mm. longa, apice bicuspidata, subnervia, carinis ciliatis; rachillae internodia 4–6 mm. longa, sericea, superne dilatata; stamina 3; stylus longus; stigmata 2, elongata, plumosa. Caryopsis oblonga, superne attenuata, 6 mm. longa, sulcata, glabra.

SZECHUAN: Mt. Omei, alt. 3000–3300 m., *W. P. Fang*, no. 3002, August 15, 1920.

The leaves here described are those of flowering branches; those of sterile branches are probably much larger.

In the lower flower the fertile glume is 1.2–1.4 cm. long, in the second flower 0.8–1 cm.; the length decreases gradually toward the upper part of the spikelet.

In its general characters *A. Fangiana* approaches closely *A. racemosa* Munro to which, I believe, it should be attached as a subspecies. *Arundinaria racemosa* grows in the Northeast Himalayas, Nepal and Sikkim, at about the same altitude and differs from the Szechuan plant in the two glumes being very distant from each other and much smaller (2–3.5 cm. long), often less long cuspidate, in the internode of the rhachilla being much longer between the upper sterile glume and the first flower, often exceeding 2 mm., and finally in the often less long-cuspidate fertile glumes exceeding the palea not so much.

In *A. racemosa* the shape and size of the sterile glumes are very variable, but in all specimens which I have seen in the Paris Herbarium and in those of the Kew Herbarium the empty glumes are more distant and the upper glume is farther removed from the lower flower than in *A. Fangiana*. This character of the lengthening of the lower internodes of the rachilla seems constant.

I wish to thank Dr. Hill, Director of the Royal Botanic Gardens at Kew, for his kindness in having had compared the Chinese plant collected by Fang with the numerous specimens of *A. racemosa* in the Kew Herbarium.

MUSÉUM D'HISTOIRE NATURELLE,
PARIS.

CHROMOSOME STRUCTURE AND THE MECHANISM OF CROSSING OVER

KARL SAX

Plates 25 and 26

THE correlation between the chromosome mechanism and the genetic behavior of hybrids is now so completely established that the chromosome theory of heredity is no longer questioned. There are, however, several important genetic facts which have no adequate cytological explanation. The cytological problems of greatest importance in connection with the chromosome theory of heredity are the maintenance of the linear order of the genes and the mechanism of crossing over.

The present study of meiotic chromosomes was undertaken primarily to determine the significance of spiral chromonemata. It was found that the coiling of the chromonemata is not a mechanism essential for the preservation of the linear order of the genes, as has been suggested by several investigators, but is due to a difference in the rate of contraction of the chromosome and the chromonema at certain stages of meiosis.

The organization of the chromatids in the chromosomes of *Secale* and *Lilium* was so different from that commonly found in Orthopteran chromosomes that a comparative study was made of the chromatids in certain plants and animals. The chromosome behavior is fundamentally the same in the plant and animal species, but in the plant chromosomes there is a much closer association of the paired chromatids, which at metaphase appear as a single coiled chromonema.

This work has led to a cytological interpretation of crossing over which seems to be in accord with all genetic requirements.

MATERIALS AND METHODS

The figures on which the present study is based were from smear preparations of *Secale cereale* and *Lilium regale*. Pollen mother cells were smeared on a dry slide, fixed in Navaschin's solution, and stained with crystal violet iodine. Smears of the spermatocytes of the grasshopper, *Melanoplus femur rubrum*, were also studied.

In *Secale* it was difficult to get satisfactory figures of diplotene and early diakinesis stages. If the pollen mother cells were smeared thin enough for critical study, the cell walls were usually ruptured and the

chromatin was irregularly distributed among neighboring cells. Even in late diakinesis and metaphase the chromosomes may pass from one p. m. c. to another or be lost entirely, where the cells are subjected to too much pressure.

Throughout this paper the term chiasma will be used to mean the point where an exchange of partners occurs between the paired chromatids, and does not mean that a break has occurred as the original use of the term by Janssens would imply (Diagram 2).

Sister chromatids are those derived from a longitudinal splitting of one of the parental chromosomes. The association of homologous chromatids means that one chromatid from one parental chromosome is associated with a chromatid from the other homologous chromosome.

CHROMOSOME STRUCTURE IN SECALE

In the smear preparations it was not easy to get intact cells smeared sufficiently thin at the earlier stages of meiosis. The occasional critical figures obtained show that at pachytene there is an apparently split thread with pairs of chromomeres much like those pictured in *Lilium* by Belling (1928). Since the chromosomes appear to be double throughout most of their length at this stage, it is probable that they are longitudinally four-parted as Belling has described in *Lilium*.

At early diplotene the chromatids open out at various points forming the nodes and internodes so commonly seen in Orthopteran chromosomes. In *Secale* it was not possible to see the individual chromatids, but it is probable that the nodes and internodes represent exchange of partners among the chromatids. Possibly some of the apparent association between chromosomes may be due to twisting, but if so the twisting is slight as there is little evidence of it at later stages. There may be as many as four or five possible points of contact in a single chromosome at early diplotene as shown in figure 1.

The chromosomes shorten and thicken until at early diakinesis they appear as shown in figure 2, which represents three chromosomes from a single cell showing the typical structure at this stage. The loops have opened more fully and there are three or four points of contact which probably represent points where the chromatids exchange partners, although the relations of the chromatids at the chiasmata cannot be observed. There is no evidence of twisting of the chromosomes around each other in smear preparations, but in sectioned material such figures often show an apparent strepsinema condition. No internal structure of the chromosomes could be seen at this stage.

At late diakinesis the chromosomes have shortened and thickened further and the association between members of a bivalent is approximately the same as it is at metaphase. A typical chromosome at diakinesis is shown in figure 3. At this stage the chromosomes are usually attached only at the ends, although occasionally an additional median

attachment is evident. Occasionally there is an apparent separation of chromatids for a short distance at one end of the chromosome.

The seven haploid chromosomes of *Secale* vary somewhat in the location of spindle fiber attachment which results in various types of metaphase associations. The points of fiber attachment range from subterminal to median and are apparently constant for each chromosome. At early metaphase most, or often all, of the chromosomes are ring shaped, but at slightly later stages there may be as many as four pairs of chromosomes which are in contact at only one end. The seven pairs of chromosomes at metaphase are shown in figure 7, and are so arranged that the details of each one can be shown, which would not be possible if drawn in their natural positions. In all chromosomes there is a coiled chromonema, but no evidence of its dual nature except at the ends of certain chromosomes. Often one end appears to be in contact with no indication of a chiasma or exchange of partners among chromatids, while the other end shows the association between the homologous chromatids. In most cases where the spiral chromonemata could be followed, they appear to coil in opposite directions in the two homologues at metaphase, which means that when the homologues are side by side the coiling is in the same direction. Each homologue also has approximately the same number of coils. In some cases the chromonema seems to reverse its direction of coiling near one end.

The chromosome with the subterminal attachment is easiest to follow in respect to chromonema coiling. This chromosome at early metaphase is shown in figure 4. The coiling here is more uniform than is usual. At this stage the chromonema is finer and more coiled than at the later stages. In this figure, there are about six coils in each homologue. The points of attachment show no evidence of a previous chiasma or exchange of partners among chromatids.

More typical examples are shown in figures 5 and 6. In these chromosomes the coiling is not so uniform and apparent breaks occur in the chromonemata at about the points of the spindle fiber attachment.

In the early metaphase it is often difficult to differentiate the chromonema from the less chromatic portion of the chromosome. In these figures only the chromonemata are pictured, except in figure 16 where they are shown surrounded by the lighter staining constituent of the chromosomes. The less chromatic material extends to, but not beyond, the coiled chromonema which suggests that the coiled chromonema is limited by a definite sheath or pellicle. At the lower end of the chromosome represented in figure 6, the chromonema appears extended and free from any matrix as if the pellicle had broken at the end and released part of the coiled chromonema. Outside of the chromosome, whether it shows coiled chromonema or is homogeneous, there is a hyaline area which gives the impression that there is a limiting membrane at some distance from the chromatic material, but this appearance may be an optical illusion.

Only occasionally is there evidence of an unterminalized chiasma at metaphase. Figures 8 and 9 show exchanges of partners among the chromatids but there is no evidence that there is any fundamental difference between these chromosomes and those shown in figure 10, or in the last chromosome of figure 7. In figure 10 the exchange of partners simply forms a cross as the chromatids are pulled apart and there is no apparent crossing of chromatids.

At the later stages when some of the chromosomes are about to divide, the chromonemata become less coiled and appear more or less corrugated rather than spiral. In figures 10 and 12 the number of turns is reduced to two or three compared with five or six at the early stages. Meanwhile the length of the chromosomes is about the same, although the chromonemata appear to be somewhat thicker.

The separation of the chromatids in each chromonema appears to occur very rapidly and appears only after the chromonema is straightened out. The chromosome represented in figure 13 shows a separation of chromatids through about half the length of each homologue. Occasionally one homologue is split while the other is still slightly coiled and apparently undivided (Figure 14). The point of the spindle fiber attachment is especially clear in this figure. When the chromatids are entirely split in both homologues the chromosome appears much like those frequently found in most Orthoptera. A typical tetrad is shown in figure 15. The homologous chromatids are parallel and show no evidence of coiling at this stage.

When the chromosomes divide and pass to the poles, most of them are in the form of double V's held together only at the point of the spindle fiber attachment. These anaphase chromosomes seldom showed any internal structure in my preparations although occasionally some indication of a spiral chromonema could be observed (Figure 16). In this figure only one chromatid of each daughter chromosome is shown.

As the homologues reach the poles the split chromosomes elongate and the two members of each daughter chromosome separate widely except at the point of fiber attachment (Figure 17). When the nuclear wall is formed the chromosomes appear as long, more or less twisted, chromonemata held together by a still thinner constriction. The fiber constriction involves an appreciable portion of the two chromonemata. There is no true resting stage between the first and second meiotic division. Often the nuclei appear to contain an indefinite spireme stage, but it is always possible to identify some of the chromosomes and doubtless all of them retain their earlier association throughout this stage.

At the second division the chromosomes are shortened and the pairs of chromosomes lie parallel and more or less at right angles to the axis of the spindle fibers. No spiral chromonemata were observed during the second divisions, but it is quite possible that they exist. Although in the interphase the chromosomes are held together only at the point of spindle

fiber attachment, they show evidence of an attraction throughout their length at second metaphase and various degrees of association as the chromosomes are pulled apart (Figure 19). It is evident that at the second reduction division the chromosomes are not held together by the fiber attachment alone.

CHROMOSOME STRUCTURE IN *LILIUM*

The behavior of the chromosomes in the meiotic divisions of *Lilium* has been described by many investigators and only the more critical stages will be considered here.

As the four-parted chromosome reaches the diplotene stage and the chromatids open out, the chromonemata can be seen to be associated at a number of points. Most of these points probably represent points of exchange of partners among chromatids, although the individual chromatids could not be identified in my preparations at this stage (Figure 20). As the chromosomes shorten and are oriented on the first metaphase plate they show a reduction in the number of points of attachment. At this time there is an average of about two points of attachment for each chromosome. The orientation of the nodes and internodes is much like that found in the multiple ring chromosomes of certain Orthoptera. The looped internodes are usually more or less at right angles to each other. Such a chromosome with three nodes is shown in figure 21. The chromonemata are not clearly differentiated from the less chromatic substance in the chromosome at this stage, but do show evidence of a coiled structure. This coiled chromonema appears to be single at the earlier stages, but its double nature is indicated by the separation of the chromatids during the division of the chromosomes.

The chromosome represented by figure 22 has only two nodes and a comparatively long section of the chromonema between the fiber attachment end and the first node. If a chiasma has been partially terminalized prior to this stage, there should be some evidence of the dual nature of the chromonema at some point, which is not the case.

The nodes in *Lilium* are apparently points of exchange of partners among the four chromatids. The relation of the chromatids is shown in figure 23 where the chromatids are pulled out showing the chiasma. One of the paired chromosomes shows the separation of the chromatids. The other may be split, but in most cases the two daughter chromosomes lie in different planes more or less at right angles to each other so that the double nature of both chromosomes is not evident until the chromatids are widely separated.

The chromatids often vary in their rate of separation. One pair of chromatids may be completely pulled apart while the other is still coiled at the distal end (Figure 24). In these cases, one chromatid may be almost straight between the point of fiber attachment and the point where the chromatids are coiled together at their ends. The other

chromatids, which are separated at the distal ends and are not under tension, begin to form spirals or corrugations. This behavior is especially clear in figure 25, where two chromatids have separated and contracted into a more or less coiled structure while the other two chromatids are still associated and are relatively straight. Often all four chromatids are straightened out forming a distorted diamond-shaped tetrad. When the division is completed the chromatids of the daughter chromosomes contract and show more or less coiling as shown in figure 26. They are associated only at the point of spindle fiber attachment. Only chromosomes with a terminal fiber attachment are shown, although two of the twelve *Lilium* chromosomes have a sub-terminal attachment.

CHROMOSOME STRUCTURE IN MELANOPLUS

The spermatocyte chromosomes of *Melanoplus* are so similar to those described in other Orthoptera that a detailed description of them is unnecessary. The individual chromatids can be followed at all stages from diplotene to the end of the meiotic division. The chromatids are seldom so closely paired that they appear as a single chromonema. The chromatids shorten as the chromosome shortens between diplotene and metaphase so that during this period there is no coiling of the chromonema.

DISCUSSION

COILED CHROMONEMATA

The spiral structure of the chromonema was first described in 1880 by Baranetzky in *Tradescantia*. Since that time the spiral chromonemata of meiotic chromosomes have received little attention until recent years, although they were described in *Ascaris* and *Lilium* by Bonnevie (1908), and Vejdovsky (1912).

Coiled chromonemata in meiotic chromosomes have been described in *Tradescantia* by Sands (1923), Kaufmann (1926), Kuwada and Sugimoto (1926), Kuwada and Sakamura (1927), Sakamura (1927), and Clausen (1929). They have also been described in *Podophyllum* by Kaufmann (1926), in *Secale*, *Vicia*, *Fritillaria*, and *Lilium* by Sakamura (1927), in *Lathyrus* by Maeda (1928), in *Hosta* by Inariyana (1928), in *Lilium* by Belling (1928), in *Crepis* by Babcock and Clausen (1929), and in *Matthiola*, *Polemonium*, *Allium* and *Lathyrus* by Clausen (1929). The writer has also observed spiral chromonemata in *Pinus*, *Sambucus*, and *Triticum*.

According to Kuwada (1927), the coiled chromonemata in *Tradescantia* chromosomes at meiosis are double with the two chromatids so arranged that the two spirals can be easily separated without uncoiling. In most genera there is little evidence of the double nature of the chromonemata until late metaphase or early anaphase.

Spiral chromonemata have been described in a considerable number of representative genera and as the smear technique and proper differential staining comes into more general use, it is probable that most plant

genera will be found to have spiral chromonemata, at least in certain stages of meiosis. The fact that these structures are found in living cells and are so consistent in their form in a given genus, indicates that they are not artifacts produced by fixation. No doubt they are coagulated by fixation and may be greatly altered by certain reagents, but their definite organization and behavior must mean that the spiral chromonemata actually exist in the living chromosomes.

The behavior of the chromonemata, especially in *Lilium*, suggests that they possess the properties of a stiff elastic gel. When the coiled chromonema is stretched out at anaphase, it appears to contract and coil as soon as the tension is released when the chromatids finally separate (Figure 25). The contraction is not rapid since all stages of contraction can be observed in pollen mother cells from a single anther, but the behavior does suggest some elasticity of the chromonema.

In the earlier stages in both *Secale* and *Lilium*, the chromonemata lie in a matrix of lighter staining chromatic material, but when the chromatids are separated and elongated only the chromatids are differentiated from the cytoplasm. When the chromosomes shorten as they pass to the poles the less chromatic matrix is again visible (Figures 16 and 26). At a later stage when the daughter nuclei are organized, the *Secale* chromosomes again seem to consist of only the paired chromonemata (Figure 18). Bridges (Alexander 1928) suggests that the chromosome consists of a pellicle containing a chromonema of stiff gel coiled in a more fluid matrix. Such a chromosome sheath is described by Clausen (1929). A sheath, or limiting membrane, seems essential to account for the structures observed in the chromosomes.

THE SIGNIFICANCE OF SPIRAL CHROMONEMATA

According to Belling (1928), the chromonema of *Lilium* can contract to one-third of its original length before the chromomeres come in contact with each other. But the metaphase chromosome is only about one-tenth as long as the original chromonema at pachytene. Thus, in order to maintain the linear arrangement of the chromomeres a coiling or "zig-zagging" is necessary at the later stages of contraction. The approximation of the chromomeres and the corrugation of the chromosomes are sufficient to account for all of the contraction observed according to Belling.

A similar explanation of chromosome coiling has been presented by Bridges (Alexander 1928) based on the description of chromosomes of *Ascaris* by Bonnevie (1908) and Vejdovsky (1912, 1926). Bridges assumes that the genes are in contact at all stages and that the gene string does not change its actual length by stretching or contraction except to a subordinate degree. The contraction of the chromosome would of course necessitate a coiling or looping of the chromonema which contains the gene string, if the linear arrangement of the genes is to be

maintained. Bridges accepts Kuwada's (1927) interpretation of the method of coiling. According to this interpretation the two chromatids of the chromonema coil in such a manner that for each turn of the spiral there is a twist of the two threads about each other in the reverse direction. Such a relation of the chromatids is essentially the same as a corrugation of two threads in only one plane. Such an arrangement of the chromatids permits free separation even though they may appear to be united in a single coil. This type of coiling would occur if the two chromatids are held fixed at the ends as the coiling occurs. Bridges assumes that coiling is caused by the contraction of the pellicle forcing the more or less elastic chromonema into a coil within the pellicle. The coiled condition is supposed to persist through metaphase and subsequent stages as pictured by Kuwada (1927) and Vejdovsky (1926).

In *Secale* there is evidence that coiling of the chromonema is caused by the contraction of the chromosome without any shortening of the chromonema. The chromosomes at metaphase are about one-third as long as they are at early diplotene while the chromonemata are about the same length at both stages (Compare Figures 1 and 4). At later stages, however, there is a shortening of the chromonemata while the chromosome length remains essentially unchanged. The spirals become fewer (Figures 12, 13, 14) and finally the chromatids appear as parallel rods (Figure 15). During the period from early metaphase to the stage where the chromosome shows its tetrad structure, the chromonema contract until they are about one-third as long as they were at early metaphase or early diplotene. Obviously, the coiling of the chromonemata is not a mechanism essential for the preservation of the linear arrangement of the genes.

In *Lilium*, the chromosomes at metaphase are about one-half as long as they are at diplotene. This shortening is associated with a coiling of the chromonemata which probably do not change their length to any great extent during this period. The length of the chromonemata at metaphase is about three times the length of the chromosomes which would mean that coiling begins when the chromonemata have decreased to about one-third of their original length, as Belling has found.

In *Lilium* the coiled chromonemata are found at all stages of the first meiotic division except for a short time when the chromatids are stretched out just before the final separation of the chromosomes. During metaphase the chromatids do contract somewhat but not more than one-half of their original length at diakinesis. When free from tension the chromatids are always coiled or corrugated at the first meiotic division.

The chromosomes of grasshoppers show approximately the same amount of contraction as found in *Secale* between diplotene and metaphase. There is, however, no coiling of the chromonema and the chromatids are easily identified as separate units through the various stages. At diakinesis and at metaphase of the meiotic divisions the chromatids

are so oriented in most cases that they are as free to separate as if they were parallel rods. In early prophase there is some evidence of a coiled structure but in the later stages the shortening of the chromosomes is accompanied by a corresponding shortening of the chromonemata.

A comparison of the behavior of the chromosomes in *Secale*, *Lilium* and Orthopteran species indicates that the coiling of the chromonema is due to the difference between the rate of contraction of the chromosome and the chromonema. In grasshoppers the chromonema shortens as the chromosome contracts; in *Secale* the chromosome shortens rapidly in the prophase while the chromonema is practically unchanged in length, but at metaphase the chromosome is unchanged while the chromonema shortens; and in *Lilium* the chromonema shortens somewhat, but is always longer than the chromosome except when it is stretched out at early anaphase. Possibly the rate of division has something to do with these differences. In the two species of plants the stages from diplotene to late diakinesis are not easily obtained but in grasshoppers these stages are the most common. A rapid contraction of the chromosome might prevent the corresponding change in the chromonema while a relatively slow change in chromosome length and organization would permit the chromonema to accommodate itself to this change.

If the spiral chromonema is the result of a contraction of the chromatids held in a relatively fixed position, then they would be free to separate while still coiled as Kuwada describes for *Tradescantia*. In *Secale*, however, the paired chromatids do not separate while coiled and in *Lilium* the paired chromatids separate only when pulled apart at time of division of homologous chromosomes. In *Lilium* the chromonema between the spindle fibre attachments and the first chiasma, is usually straightened out before any split appears. Occasionally the distal ends of the chromonema separate while still coiled, but in most cases the chromatids appear to be closely associated and pull apart only under considerable tension. However, the coiling must be primarily of the type described by Kuwada, which is essentially the same as a corrugation in one plane, or the chromatids would be so entangled that they could not be pulled apart at metaphase. It is probable, however, that some twisting of the chromatids occurs so that they are not easily separated while coiled.

CHROMATID ASSOCIATION

In both plants and animals the most critical studies indicate that the meiotic chromosomes consist of four chromatids at diplotene. In some animals the four chromatids can be followed through the prophase stages and "tetrads" are commonly observed at diakinesis and at metaphase. Even in the more complicated ring formations in the Orthoptera the four chromatids can be identified.

In most plants, however, the tetrad nature of the chromosome cannot be seen until late metaphase when the homologous chromosomes are



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