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The Spiral Structure of Chromosomes in the Meiotic Divisions of *Podisma* (Orthoptera)¹⁾

By

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(With Plate III and 4 Textfigures)

Nowadays, the chromonema theory of chromosome structure, that the chromosome is differentiated in its inner structure into the chromatic filament or chromonema, which coils in spiral manner, and the achromatic ground substance or matrix surrounding the former, prevails over all other hypotheses and seems to meet, at the same time, both the cytological and the genetic requirements. The works prosecuted vigorously on this line of study by plant cytologists in late years, have offered a great many data from the plant cells, sufficient to permit one to accept this conception of chromosome structure. As to the animal kingdom, however, one can scarcely find any references in which the corresponding feature of chromosome is chiefly dealt with except some classical papers²⁾ and some fragmental descriptions.³⁾ Following the suggestion of Prof. Oguma, that, were the spiral structure common to the chromosomes in general, it should widely be observable in the animal chromosomes as well as in the plant under favourable circumstances at least, the present author commenced this study to learn how far the findings in plant cells may be applicable to animal cells. While working with the smear method applying the fixative to the slide, the author fortunately discovered definite figures of chromonemata showing a clear coiling in the meiotic chromosomes of *Podisma* and *Stauroderus* (Orthoptera),

1) Contribution No. 100 from the Zoological Institute, Faculty of Science, Hokkaido Imperial University, Sapporo.

2) Janssens ('01), Bonnevie ('08), Vejdvsky ('11-'12), etc.

3) Kaufmann ('31 b) in the somatic chromosomes of *Drosophila*, de Winiwarter ('31) in the heterochromosome of *Tettigonia* (Orthoptera), Iriki ('32) in the sex-chromosome of *Hyla* (Amphibia), Sinoto and Yuasa ('35) in the salivary chromosomes of *Lycoria* (*Sciara*) and *Drosophila*, each noted the spiral structure of chromosomes.

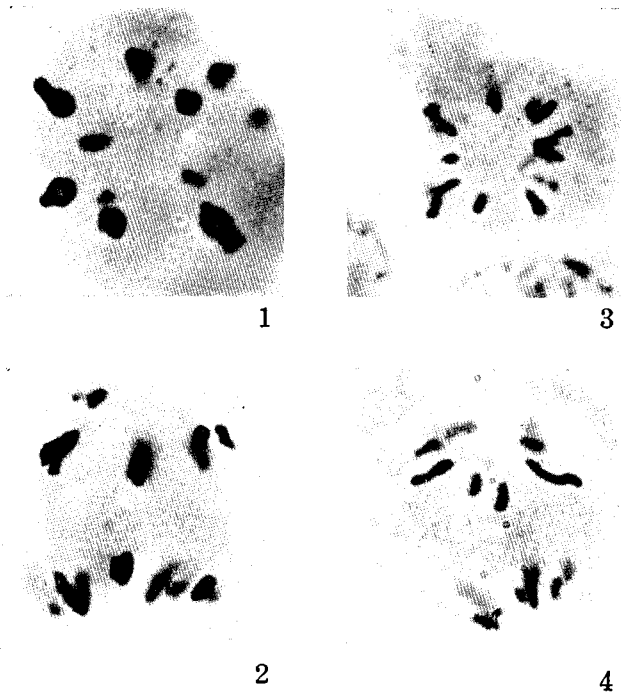
which hardly differ in essential point from those hitherto observed in plant cells. A description of the former, *Podisma*, only will be presented in the present paper.

The author wishes to offer his sincerest thanks to Prof. Kan Oguma for his kind conduct of this problem. Further, the author is greatly indebted to Prof. Hajime Matsuura of the Botanical Institute, who has given important advices and also to Mr. Tiharu Sutô, especially for kindness on the side of technique.

General morphology of chromosomes in *Podisma* and technique

Of animal groups the orthopteran insects, especially those belonging to the Acridiidae, seem to offer advantageous material for such a karyological study as the present one, due to the following facts; the large size of chromosomes, the relatively low number of chromosomes, the clear morphological features of individual chromosomes, and ease in securing desirable dividing figures. Two species of the common grasshoppers from the suburbs of Sapporo, *Podisma sapporoense* and *P. mikado*, were first adopted as the material in the present study, and the observations were mainly based on the former species, owing to preponderance of number in field. Both species show no essential differences in the configuration of chromosomes, except in number; the diploid number is 23, or 11 autosome pairs and one heterochromosome, in *P. sapporoense*, while in *P. mikado* 21, that is, 10 autosome pairs and one heterochromosome. All the chromosomes belong to the telomitic kind in the fiber attachment, showing a typical appearance of the *Hippiscus*-type after McClung ('14). Corresponding to the size difference of diploid group of chromosomes there result, after conjugation, various kinds of tetrads in the primary spermatocyte; in general, ring-shaped tetrads, compound and single, of larger size are observed lying horizontally in the periphery of the equatorial plate of metaphase, surrounding smaller tetrads with cross- or rod-shapes. An example of the tetrads in typical arrangement at the primary spermatocyte metaphase is shown in Textfig. 1. In the anaphase, the tetrads separate into two equal V-shaped dyads, each of which is composed of two chromatids (monads) joined at one end where the spindle fibers attach (Textfig. 2). The heterochromosome fails to divide in this division and

goes to one pole expressing a dyad nature. At the secondary spermatocyte metaphase, the dyads again appear like V-shaped ones, as anaphasic chromosomes in the preceding division, but the constituent two rod-shaped chromatids (monads) open at their distal end along



Textfigs. 1-4. Photomicrographs. 1400 \times .

1, polar view of primary spermatocyte chromosomes in metaphase (*Podisma mikado*). 2, lateral view of the same in anaphase (*P. sapporoense*). 3, polar view of secondary spermatocyte chromosomes in metaphase (*P. sapporoense*). 4, lateral view of the same in anaphase (*P. mikado*).

the long axis of the spindle, while the proximal end is still in close contact (Textfig. 3). In the ensuing division they are all divided into single rod-shaped chromatids (monads); thus the meiotic divisions are completed (Textfig. 4).

The investigation started with observation of fresh material, the germ cells mounted with the body fluid.¹⁾ It was proved, however, that fresh material was not suitable for such a study, since in such unstained preparations the chromonema substance was hardly distinguished from the matrix unless some stains were applied (Figs. 23 and 24). In the smear preparation of fresh material using the aceto-carmine method, the chromosomes show somewhat better differentiation between composing substances, chromatic and achromatic, as compared with the former, though they swell up abnormally, representing distortion in various grades. In this case, the larger the chromosome is, the more conspicuous is its structural differentiation. Sometimes, discontinuous bars can be seen within the chromosome showing a vacuolated appearance (Fig. 25). Such a configuration as fragmental bars may be due to some artifact influenced by fixative, since in favourable cases, some number of bars can be traced continuously, though not regularly, by moving the micro-screw from one to the other, as if they constitute a continuously coiled thread. In the sectioned and stained material details of inner structure were almost entirely lost, as the chromosomes represent a homogeneous appearance without showing any kind of internal differentiation.²⁾ The desirable slides for the investigation of the chromonema structure were only obtained from smear preparations applying the fixative to the slide, after the improved method of Matsuura ('35). General procedure is as below: the cells from testicular follicles were smeared on the glass slides, previously coated with egg albumen. The smears were then covered with the fixing fluid applied with a medicine dropper. Of the fixatives employed, Flemming's strong solution proved to be satisfactory. Fixation for 2 or 3 minutes seems to be sufficient; the slides were then rinsed in water and directly stained with gentian-violet according to Newton's method. After being dehydrated by gradatory alcohols, the slides were mounted in Canada balsam. Thus the preparations were completed in less than one half hour. All the observations in the present study were based on only those slides, in which the chromonemata are deeply stained and ex-

1) Studies of Bělař ('29), Lucas and Stark ('31) and Baumgartner and Payne ('31) who worked with the fresh material of certain grasshoppers, each with improved methods, seem not to be extended to the internal precise structure of chromosomes.

2) Recently Shimakura ('35) has worked this field with much detail.

hibit a definite form as thick and coiled threads embedded within the matrix.

Observations

1. *The primary spermatocyte chromosomes*

In the satisfactorily differentiated preparations, the chromonema structure is clearly observable in the metaphasic chromosomes. The chromonemata appear as deeply stained, thick and coiled threads which are optically differentiated from the matrical substance within the chromosomes. Figs. 1 to 9 show various kinds of tetrads found in the equatorial plate of the primary spermatocyte meta-anaphase, in each of which the spiral nature is absolutely clear except at some points where chiasmata may probably have been formed (Figs. 1 to 4, ring-tetrads; Fig. 5, double ring-tetrad; Figs. 6 and 7, cross-tetrads; Figs. 8 and 9, rod-tetrads). In some cases the gyres of the spirals run closely in the chromosomes, consequently the whole chromosome appears as if composed of a pile of discs. The matrical substance coating the spiral is considerably thick and thus the chromosome takes, as a whole, an appearance of vesicle in which the spiral is enclosed.

The chromonemata forming the spirals generally seem to be single, but in some cases where the spiral is uncoiled its double nature is recognizable. For instance, as shown in Figs. 11, 12 and 13, at the so-called chromosome bridge—the connecting part of two associated chromosomes—or at the chiasma region where the spirals are straightened out to some extent, the threads infrequently seem to be double (see the portions indicated by arrows in the figures). This fact is sufficient to indicate that the apparently single spirals in the metaphase are in reality double. In other words, the thick spiral in the metaphasic chromosome (tetrad) consists of two thinner coiled threads which are close in contact and tightly combined with each other into a seemingly single spiral. For this reason, at the metaphase, four chromonemata which corresponded probably to the composing four chromatids of a tetrad, are not independently discernible in every tetrad. This, however, first becomes manifest when the dyads composing a tetrad separate into longitudinal halves (chromatids) in the late metaphase and in the anaphase. These conditions seem to be practically similar to the findings obtained from certain

plants such as *Tradescantia* (Kuwada and Nakamura '33, Kato '35), *Lilium* (Kato and Iwata '35), and *Trillium* (Matsuura '35), etc. And, so far as based on the present author's preparations, no case has been found which is favourable to the view of Shimakura ('35), who worked with the fresh material of some grasshoppers, that four chromonemata corresponding to each component chromatids are visible in the chromosomes at metaphase.

The double-coiled or spiral-within-spiral structure of the chromosome first announced by Fujii ('27) in *Tradescantia*, was confirmed by Kuwada and Nakamura ('33) after detailed investigation with the same plant, and later the same structure has been found by several authors to occur in various plants (Shinke '34, Kato '35, Kato and Iwata '35, Iwata '35, Matsuura '35, Sax '35). While working with the present material the author came across a certain evidence which suggests the occurrence of the double-coiled structure just mentioned: Though, in the deeply stained preparations, the chromonemata forming the metaphasic spirals generally appear to be of homogeneous solid structure, in some cases where the texture of chromonema becomes loosened by unravelling of spirals, frequently in the late metaphase, a complicated structure is visible which seems to show that the chromonemata forming the spirals are not a simple solid thread in structure but are spirals within which one more spiral with small gyres is to be found. As seen in Fig. 13, for example, about the regions indicated by arrows, where the spirals of large gyres are drawn out and the paired nature of chromonema becomes striking, the threads represent a spiral structure of small gyres. Thus the chromosomes in the primary spermatocyte possess the double-coiled structure: i.e., the spirals of large gyres (the secondary spirals according to Fujii '27) are constituted of spirals of small gyres with a short diameter (the primary spirals).

When the chromosomes enter the anaphase four chromatids composing a tetrad become apparent, every two constituting a dyad (sister chromatids) assuming a V-shape, joined at one end where the spindle fibers attach. In the course of the anaphasic migration, the chromatids are elongated to a considerable extent, due probably to the fact that the spirals of large gyres become unravelled (Figs. 14 and 15). The part where such drawing out of the spirals occurs is wavily corrugated. In the extreme case, the spirals are quite drawn out into threads without apparent coiling. In this case the texture of the

chromonema seems to become loose and presents a rugged appearance on the surface, suggesting an internal spiral structure. It is in this stage that fine coils which represent the spirals of small gyres occasionally make their appearance in the drawn-out part of the large spirals (see Figs. 19 and 20).

When the chromosomes migrate toward the poles, they still keep their radial arrangement with a vacant space at the centre. As is in Fig. 16, in this stage the spirals of large gyres, which were previously drawn out, recover their coiling nature again, though the turns of the spirals are much fewer than those in the metaphase, as was shown to have occurred in *Lilium* (Iwata '35). Further behavior of chromonemata through the late telophase and the interkinesis is left for future study.

2. *The secondary spermatocyte chromosomes*

At the metaphase of the second division the chromosomes or the dyads appear in the form of V's, as two composing rod-shaped chromatids remain in close at the apex, to which the spindle fibers attach, taking a radial arrangement with this apex towards the centre. The chromonema spirals in these chromosomes seem to be rather slender as compared with those in the primary spermatocyte metaphase and contain a greater number of turns than the latter. In Fig. 17, three V-shaped chromosomes are shown, in every arm of the V's the spiral structure of such fashion being clearly recognizable. In some cases, the relic turns of a large spiral irregularly coiled are visible in the chromosomes. Considered from such coiling aspect it seems to the author that the chromonema spirals in the metaphasic chromosomes of this division may be in nature homologous to those of the telophase of the previous division. Kato and Iwata ('35) have noted a similar kind of structure in the corresponding stage of some *Lilium* plants. Any decided statement however, should be made after completion of research on the behaviour of chromonemata during the interkinesis which is unknown at present.

In the ensuing division V-shaped dyads separate into two telomitic, sister chromatids or monads, which enter the spermatid nuclei later. The spiral structure can be traced further on up to anaphase and telophase. In the telophase, as seen in Fig. 18, the chromosomes are found completely unravelled from the relic spirals

of large gyres and appear to be slender in form containing rather a regular and fine spiral of small gyres within.

3. *The doubleness of chromonemata within the chromatid ('monad')*

In preparations well differentiated certain figures were found which lead to the conclusion that the chromatids ('monads') forming the meiotic chromosome contain paired chromonema spirals in each. Figs. 19 and 20 show the anaphasic complexes of the primary spermatocyte, in which the chromosomes (dyads) assume, without exception, a V-shape, composed of two telomitic chromatids (monads) coming in contact at their inner ends. In these figures, it is shown by some of the chromosomes, particularly by those indicated by arrows, that every arm of the V's contains double chromonema spirals, probably of small gyres, which run parallel to but independently from each other. Strictly speaking, therefore, there exist actually a pair of the ordinary single-coiled chromonemata in every chromatid ('monad'), accordingly a single dyad is constructed from four chromonemata as its fundamental structure. At the following metaphase of the secondary spermatocyte, however, such structure in a dyad is markedly altered, due probably to the fact that the turns of spirals become so intimately applied with one another, as if two chromonemata were fused together into one as illustrated in Fig. 17; while in some cases, where the spirals are unravelled, the structure of the chromonema is clearly found in a condition favourable for ascertainment of its original double nature. Further, this structure was again encountered in some anaphasic chromosomes of the second division, when the spirals become unravelled. Fig. 21 represents such an example, in which a monad in act of separation, indicated by an arrow, is differentiated into two parallel, thinner chromonema spirals.

From the above observed fact it is naturally to be concluded that one tetrad is constituted of eight chromonemata. Fortunately one has such an example, Fig. 22, as may serve to corroborate the above view to a great extent. This figure is the lateral aspect of a tetrad, probably one of the rod-tetrads of larger size, in the early anaphase of the first division. Four independent telomitic chromatids are in combination in the configuration \diamond , with its long axis parallel to that of

the spindle. This tetrad later separates into two identical sister V-shaped dyads as already illustrated in Textfig. 2. In each of the sister dyads of this tetrad, especially in that of the lower part, there are strikingly discernible two thin spiral chromonemata which run parallel without twisting with each other. The dyad being composed of two distinct arms or monads, hence an entire tetrad is provided with eight chromonemata.

Here, taking this into consideration, some mention should be made of the structure of the heterochromosome which corresponds to a dyad in nature without a synaptic mate. If a chromatid actually contains two chromonemata, there should be then observed four chromonemata in one heterochromosome. Fig. 10 shows the heterochromosome at the metaphase of the primary spermatocyte. The spiral configuration of this chromosome observed in the figure seems to suggest that the threads forming the spirals are more than two in number. Detailed observations now in progress will be described in another paper.

Still in plants, it is only a few species in which this structure of chromatid is taken into account. The findings of Kaufmann ('31 a) and Nebel ('32) in *Tradescantia* indicate that four chromonemata were observed in a dyad in the heterotypic anaphase. Recently Kuwada ('35) has noted a similar structure in the late prophase in the pollen mother cells in *Trillium*, prepared by Iwata, his collaborator. In connection with this structure, the somatic chromosomes should naturally be brought under consideration. According to Kaufmann ('26 a, b), Sharp ('29), Nebel ('32), Geitler ('35) and some others, it seems to be agreed that two chromonemata act as a structural unit in the somatic chromosomes, though there are some controversies among them with regard to the arrangement of the chromonemata within the chromosome. From this consideration it may be quite natural to expect that a similar structure is also present in the meiotic chromatids.

Summary

The spiral structure of chromosomes was studied in the meiotic chromosomes of the grasshoppers, *Podisma sapporoense* and *P. mikado* (Acridiidae), with smear preparations applying the fixative to the slide. The chromonemata appear as deeply stained and coiled

threads which are optically differentiated from the matrical substance within the chromosomes. The chromosomes of the primary spermatocyte were ascertained to be of double-coiled structure.

Evidence is presented that each chromatid contains two chromonemata; hence four chromonemata exist in a dyad and eight in a tetrad.

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Explanation of Plate III

All figures are photomicrographs taken with the aid of a Leitz MAKAM camera, with the lens combination of a Zeiss apochr. obj. 2 mm and Leitz periplan ocs. 10 × and 15 ×. Figs. 10 to 15 and Figs. 20 to 22 are enlarged from the original negatives taken with a Zeiss 2 mm and a Leitz periplan 10 ×, to the magnifications indicated in each.

All the photos, except Figs. 23 to 25, were made from smear preparations fixed with Flemming's strong solution and stained by Newton's gentian-violet method.

Figs. 1-9. Various kinds of tetrads seen in the primary spermatocyte metaphase. Figs. 1 to 4 are ring-tetrads in polar or slightly oblique view. Fig. 5 is a compound ring-tetrad in oblique view. Figs. 6 and 7 are cross-tetrads in act of separation, lateral view. Figs. 8 and 9 are rod-tetrads in lateral view. 1400 ×.

Fig. 10. Heterochromosome in the primary spermatocyte metaphase, lateral view. 2800 ×.

Figs. 11–12. Lateral views of rod-tetrads in the primary spermatocyte metaphase. Fig. 11 is an enlargement from Fig. 8 and Fig. 12 from Fig. 9. At the portions indicated by arrows, the double nature is recognizable in the threads forming the spirals. 3500 \times .

Fig. 13. Tetrads in the primary spermatocyte metaphase, showing the double-coiled structure. At the portions indicated by arrows where the pairedness of chromonema is visible, the threads represent spirals of small gyres. 1800 \times .

Figs. 14–15. Two successive stages in the anaphase of the primary spermatocyte. The spirals of large gyres are drawn out in every chromatid. 1500 \times .

Fig. 16. Telophase group of chromosomes in the primary spermatocyte, slightly oblique view. 1400 \times .

Fig. 17. Metaphase group of chromosomes in the secondary spermatocyte, lateral view (three V-shaped dyads are shown). 1400 \times .

Fig. 18. Telophase group of chromosomes in the secondary spermatocyte, oblique view. Rod-shaped monads are arranged radially surrounding the pole. 1400 \times .

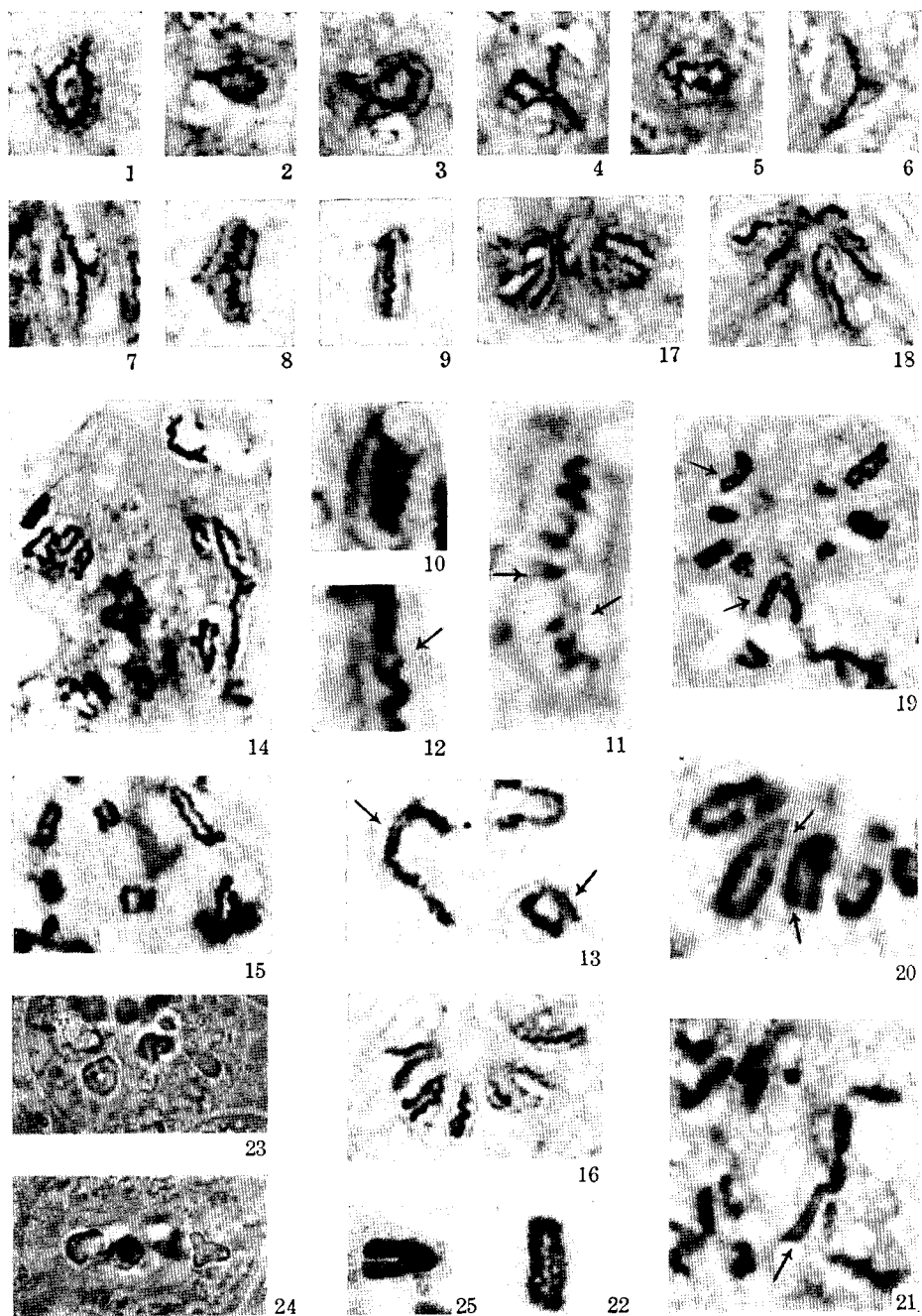
Figs. 19–20. Anaphase groups of chromosomes in the primary spermatocyte. In some chromosomes, especially those indicated by arrows, two thinner spiral chromonemata running parallel in each arm of the V's are discernible. Fig. 19, polar view, 1400 \times . Fig. 20, slightly oblique view, 2000 \times .

Fig. 21. Lateral view of the secondary spermatocyte anaphase. A monad indicated by an arrow, shows a clear inner differentiation into two parallel, thin chromonema spirals. 2000 \times .

Fig. 22. A tetrad in the early anaphase stage of the primary spermatocyte, lateral aspect, consisting of four telomitic chromatids (monads) in combination like a configuration \diamond . In every chromatid, two parallel chromonemata are visible, hence eight chromonemata are countable in this tetrad. 1500 \times .

Figs. 23–24. Metaphasic chromosomes of the primary spermatocyte in the living state, taken from the preparations mounted the germ cells with the body fluid. Fig. 23 is the polar view of the equatorial plate; a ring-tetrad is seen at the lower left side. Fig. 24 is the lateral aspect of the metaphase spindle. 900 \times .

Fig. 25. An anaphasic chromosome of the primary spermatocyte (a dyad). From the acetocarmine preparation. 1400 \times .



S. Makino photo.

S. Makino: Spiral structure of chromosomes in Podisma