Chromosome Structure in Tradescantiae IV
The history of the chromonemata in mitosis of
***Tradescantia reflexa* Raf.**

By

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Introduction

The history of chromonemata in mitosis of plants with large chromosomes as described by KAUFMANN (1931 and earlier) and SHARP (1929) has been corroborated by HEDAYETULLAH (1931), PERRY (1932), TELEZYNSKI (1930 and 1931) and others. These workers agree, in general, that in every chromosome at anaphase there are two chromonemata which are entangled. At interphase these chromonemata form a reticulum by anastomoses.—According to HEDAYETULLAH (l.c.) the achromatic materials only anastomose.—In early prophase two chromonemata are seen for every chromatic tract. Four chromonemata are observed immediately previous to metaphase, or slightly earlier. Visible reduplication is therefore claimed to have taken place in prophase. An anaphasic entanglement of chromonemata is generally described which disentangles at interphase. Some authors however describe disentanglement during late prophase.

DARLINGTON (1932) turns the wheel of experience backwards some two score years and considers the anaphase chromosome single and the metaphase chromosome double, the split occurring very early in prophase, thus rendering the chromonemata duplicate thruout prophase.

NEBEL (1932, pp. 275–278) stated that the telophase chromosome is tetrapartite, visible reduplication of chromonemata occurring at this stage. No anastomoses at any stage of the cycle were recorded. No entangling or disentangling of chromonemata were observed. The four chromonemata were reported to become oriented into their meta-

phase condition during prophase thus introducing only slight changes in length, thickness and orientation of chromonemata thruout the cycle of mitosis.

Further details elaborating the previous findings will be given in the present paper. The technique employed bridges the viewpoints derived from classical paraffin preparations and those derived from preparations of fresh material mounted in liquid media without dehydration.

Material and Methods

Root tips of *Tradescantia reflexa* were taken from pots and placed in a 0.1 per cent solution of commercial ammonium hydroxide¹⁾ for five minutes, then transferred to a 0.01 molar solution of thorium nitrate and finally fixed in 10 parts of solution A plus 3 parts of solution B, A being 2.5 per cent osmic acid dissolved in a one per cent solution of platinum chloride, B a one per cent aqueous solution of chromic acid. All solutions were held at room temperature (20°C.). The material remained in the fixative for 24 hours and was then imbedded in paraffin thru alcohol and xylol in the usual way; each step was taken at 1 hour intervals and the material left in 40 per cent alcohol overnight. Sections were cut 7 and 10 μ in thickness and stained with crystal violet after NEWTON.

Camera lucida drawings were made to the scale of 1:2620 and free-hand drawings of details to a slightly larger scale. I endeavored to draw photographically from a single optical section, drawing several focal levels only with great reservation. NEBEL (1932) explained in detail why the representation of several adjoining focal planes in a drawing may lead to erroneous results when complicated rhythmical patterns are involved, especially when their size only slightly exceeds the wave length of light. Microscopical images of chromonemata cannot be interpreted without the knowledge of optical phenomena in model spirals made of translucent material. Painstaking drawings without this knowledge lead to images which are optically correct but physical misapprehensions, even when relatively good fixations are at hand (cf. HEDAYETULLAH l.c. and KOERPERICH 1931). For this reason the physical interpretation of the optical impression is presented separately in this paper (cf. figs. 7 with 10, 8 with 11, etc.).

1) NH_4OH has been employed also by KUWADA (1932) in making preparations of meiosis.

Emphasis should also be placed upon the hydrogen ion concentration under which material is killed and fixed. According to STRUGGER (1932) pretreatment with slightly alkaline media would cause matrical materials to be preserved in position and in their natural PH. By classical methods of acid fixation matrical materials are not only fixed by flocculation (disorderly) but their electrical charge is at the same time shifted towards the negative side to such an extent that they will freely take basic stains by which they are not colored in their living state. The chromonema, in the author's view, is a long cylindrical body (the coiling may be neglected in this connection) with a neutral or slightly negative charge on the surface and an increasingly positive charge towards the axis. Acid fixation changes the charge of the outer layers and precipitates these "en masse" (adjoining matrices of chromonemata coalesce). Acid fixation dislocates the central region of the chromonema as a consequence of the disorderly flocculation taking place in the surface layers.

It is believed that the pretreatments used have an effect upon the living cell similar to that described by NEBEL (1932) for desiccation and initiation of autolysis when making smear preparations. Under the influence of the pretreatments the living protoplasm becomes reversibly coagulated, forming "vital artefacts." Perhaps also in the case of prolonged pretreatment the protoplasm is slowly salted out "in loco." These "vital" or "supravital artefacts" are then conserved by the heavy metal action which allows them to be carried thru desiccation and infiltration without far-going changes. Dehydration tends to increase the havoc done by acid fixatives whereas it deals less roughly with the pretreated type of preparations. KAUFMANN, SHARP, and TELEZYNSKI l.c. have appreciated these phenomena, while the work of HEDAYETULLAH, HSU-SIANG (1932). KOERPERICH, and PERRY l.c. has been impaired by the lack of proper pretreatments.

Terminology

Resting stage is considered synonymous with *interphase*. *Early prophase*, the spireme stage of the early investigators, follows and is marked, in the material to be described, by the duplicity of the chromatic tracts. Then follows *spiral prophase* when the gyres show their largest diameters; this merges into *late prophase*.

"Primary" and "secondary sister chromonemata" are used in the following way: If a chromonema divides or multiplies forming two

identical daughter chromonemata, these are considered primary sisters. If each one of the resultant chromonemata divide again each member of a pair of grand daughter chromonemata are considered "secondary sisters." If the four secondary sisters pair up again it is tacitly assumed that this occurs in directly reversed order primary sisters uniting after secondary sisters have joined.

Observations

Preliminary statement

The history of the chromonemata in mitosis of *T. reflexa* is briefly as follows: Two chromonemata are visible in every *anaphase* chromosome. These are spirally coiled and the two coils are shoved into one another.

In late *telophase*—when the areas of the chromosomes within the nucleus may still be discerned and when occasionally ends of chromosomes still protrude from the margin of the newly forming nucleus—*four* chromonemata are visible within every chromosome. They are oriented as four spirals running in four columns parallel to one another and only slightly shoved into one another. At this stage the chromaticity of the chromonemata is low and each chromonema is surrounded by a relatively thick coating of matrical material which does not take much basic stain after mildly acid fixation.

In *resting* stage *four* chromonemata are present for every chromosome. The gyres of the spirals are similar to those of telophase but the individual members of the group of four chromonemata are no longer strictly parallel to one another. Probably they are held together only at the insertion region. The individual spirals become pliable thus allowing the nucleus to become spherical in volume and causing the telophasic chromosome tracts to disappear. Occasionally two chromonemata may be seen running parallel to one another for some distance. At this stage the chromaticity of the chromonemata is low and each chromonema is surrounded uniformly by a relatively thick coating of matrical material as in late telophase. There is very little if any free karyolymph filling the interstices of the tightly packed chromonemata.¹⁾

1) The increase in size of the nucleus at this stage is believed to be due to imbibitional phenomena affecting the matrices of the chromonemata primarily. The source of the materials imbibed may be the spindle, cf. SHARP l.c.

During *early prophase* the secondary sister chromonemata pair tightly forming two spirals closely shoved into one another. At this stage the chromaticity of the chromonemata increases and they lose much of their matrical coating. Free karyolymph separates the paired chromonemata. If the chromatic tracts at this stage are counted, twice as many chromatic tracts as chromosomes at metaphase are found to be present. Taking a as the number of chromatic tracts, at early prophase we have $a = 4n$, but every chromatic tract contains only half the number of chromonemata of a chromosome, i.e. 2 instead of 4. At this stage the chromonemata show tightly twisted gyres of small diameter. Pairs of paired chromonemata are probably still joined at the insertion region.

During later prophase, which leads to the *spiral prophase* described in the literature, pairs of pairs of chromonemata pair to form a group of *four parallel* spirals finally. The gyres of the spirals of the earlier prophase increase in diameter and the chromonemata regain some of their matrical coating which they lost previously. An ample quantity of karyolymph separates the areas of the future chromosomes. Chromatic tracts are now present in the somatic number and the chromosomes of the following metaphase are essentially established. Primary and secondary sister chromonemata may be spaced at almost equal distances but usually secondary sister chromonemata are spaced much more closely than primary sister chromonemata. Occasionally secondary sisters seem to fuse, at least optically, thus giving the appearance of only two spirals being present. The orientation of the chromonemata is not strictly parallel thruout the length of a future chromosome and the chromonemata are relatively thin where they are single.

The late prophase leads to the final formation of *metaphase* chromosomes. The spiral chromonemata become more strictly parallel thruout the length of the chromosome. The matrical coatings of the chromonemata increase considerably in thickness. Secondary sister chromonemata are shoved closely together, the two spirals in each half chromosome thus appearing almost as one. Half chromosomes finally lie parallel thruout their length and usually in the same plane relative to the main axis of the chromosome.

Description

This account is illustrated by eighteen drawings. Figs. 1-5 are camera lucida drawings 1:2620, fig. 6 is a scheme of cross-sections of chromosomes at various stages. Figs. 7 to 18 are drawings and interpretations of pieces of chromosomes at various stages, the interpretation being placed immediately below the original drawing. As regards the nature of the drawings cf. p. 2.

At *anaphase* (figs. 7 and 10) two coils are visible in each chromosome going to the pole. They are shown as optical sections in fig. 7 and as interpreted in fig. 10. The orientation of the two coils is such that they will separate without entangling which is due to the fact that they are independent parallel coils shoved into one another. The type of fixation used renders the chromonemata at this stage as thin threads imbedded in a common matrix. Why this image is considered partially an artifact has been explained elsewhere (NEBEL 1932, pp. 255-257 and 268).

Late *telophase* is illustrated by figs. 1 and 8 and interpreted by fig. 11. For this stage, fig. 70 of NEBEL (1932) should also be compared giving a different type of image of the same stage and the same underlying facts. The three horizontal rows of four dark specks in fig. 8 are considered the optical sections of four coiled chromonemata. The connecting pieces between the visible parts of the gyres are invisible and cannot be focused upon because all light coming from the condenser of the microscope is affected by the lower and the partly superimposed upper gyres of the spirals in such a way as to give an almost immovable series of light and dark bands regardless of the focus (cf. NEBEL 1932, text figs. 22 and 28, pp. 269-271). It must be remembered that the chromaticity of the chromonemata at this stage is low and somewhat diffuse. Dark bands (in the present case violet bands, since crystal violet was used) appear only at periodic distances on the course of the spirals just as the dark bands in fig. 22 of NEBEL (1932) would be blue and not grey if blue glass had been used. Where the chromonemata are massed (see fig. 1 towards the right) a reticulum appears to be present due to optical laws of refraction from superimposed lens systems (cf. NEBEL 1932, text figs. 25 to 27). Actually no anastomoses of adjacent chromonemata are believed to be present for living material and well prepared fixations.

Figs. 1-5. Camera lucida drawings of optical sections. ca. $\times 2620$. 1, telophase; 2, resting stage; 3, early prophase; 4, spiral prophase; 5, late prophase.
 Fig. 6. Diagram showing orientation of chromonemata in cross section; M = metaphase, A = anaphase, T = telophase, R = resting stage, PE = early prophase, PL = late prophase.

Telophase gradually merges into the *resting stage* (fig. 2). The figure was drawn from a nucleus in which the chromonemata towards the center were underlying a second nucleolus removed by the knife, thus rendering the chromonematic tracts especially clear and undisturbed by uncontrolled refraction from other coils. A pair of chromonemata marked $\sim$ appears to extend from the center of fig. 2 towards six o'clock, and another less clearly towards eight o'clock. It is believed that the chromonemata are individually surrounded by matrical coatings and imbedded only in a sparse amount of continuous karyolymph. This fact is rather hard to bring out in a drawing but appears much more evident from photomicrographs (cf. NEBEL 1932, figs. 25 and 62). It seems that the chromonemata become more flexible in position during the resting stage wherefore the nucleus becomes spherical. Parallel association of chromonemata is rare and it is suggested that the four chromonemata of a chromosome are held together only at the insertion region.

Early prophase (figs. 3, 9 and 12) is marked by the appearance of many tracts of high chromaticity which now are set off against a clear background of karyolymph. This is the first time in the mitotic

Figs. 7, 8, 9. Free hand drawings of optical sections. $\times 5000$. 7, end of an anaphase chromosome; 8, end of telophase chromosome (the one shown also in fig. 1); 9, end of half a chromosome in early prophase.

Figs. 10, 11, 12. Physical interpretation of optical images in figs. 7, 8, and 9 respectively.

Figs. 13, 14, 15. Free hand drawings of optical sections. ca. $\times 5000$. 13, end of a chromosome in spiral prophase; 14, end of a chromosome in late prophase; 15, end of a chromosome in metaphase.

Figs. 16, 17, 18. Physical interpretation of optical images in figs. 13, 14 and 15 respectively.

cycle that this constituent appears definitely. The chromatic tracts can, upon close examination at favorable points in the sections, be resolved into two closely-paired coiled chromonemata of high chromaticity (fig. 9 and interpretation fig. 12). The chromonemata have at this stage only thin matrical coatings. Fig. 3 is a rough drawing of this stage. The fixation is a long way from perfect: most of the paired chromonemata have coalesced into cylindrical bodies showing the actual chromonemata badly distorted and their matrical coatings partly fused. However, it is clear that the chromatic tracts lie in pairs. One pair is shown in cross section just above the grey nucleolus in fig. 3 and another pair in side view just to the right towards 1 o'clock from the grey nucleolus. This condition is really the second step of the very earliest prophase and leads to

the *spiral prophase* which is roughly sketched in fig. 4 and the details of which are given and interpreted in figs. 13 and 16. In this stage pairs of pairs are paired into one unit, the final chromosome of the ensuing metaphase. It is admitted that the interpretation of this stage (fig. 16) is only one of several possible modes of arrangement of chromonemata. It is considered the mode which is finally reached by all chromonemata of *T. reflexa* in prophase and it is obviously correct for the chromosome shown immediately below the nucleolus of fig. 4. But slightly to the right there is visible a fragment of a chromosome (towards 5 o'clock from the nucleolus, close to its margin) in which there appears only a single or possibly a double chromonema fused into one which is thrown into a wide gyre. Apparently the chromonemata at this stage have not all attained the same stage of development and orientation. Secondary sister chromonemata may visually at least, be fused into one chromonema and primary sisters may then appear closely shoved into one another and the "pair" coiled widely, a single gyre thus transgressing the entire breadth of the future chromosome. Probably the secondary pairing of chromonemata in mitosis i.e. the pairing of pairs is inacted as follows: Secondary sister chromonemata have paired in early prophase. Secondary sisters then temporarily stretch and fuse, at least visually,¹⁾ forming one chromonema. Primary sister

1) There is evidence that stretching of closely parallel chromonemata at anaphase of meiosis—leads to their visual union into one; reversely shortening and thickening would lead to visual duplication.

chromonemata then approach one another coiled in wide gyres stretching and thinning out still more. The coils are shoved into one another completely—this giving the most common aspect of spiral prophase. As soon as this re-pairing of primary sisters has taken place primary sisters separate slightly, the gyres becoming less wide and the coils proper becoming thicker—i.e. the chromonemata shortening and thickening, and secondary sisters re-emerge from their temporary visual fusion. This process does not take place simultaneously thruout the length of a single chromosome let alone thruout the length of all chromosomes in the nucleus thus giving rise to variable images.

Figs. 5, 14 and 17 finally give the development of the chromosome in *late prophase* leading to *metaphase* (figs. 15 and 18). Actually during late prophase the changes described for the spiral prophase merely become completed. At the same time the metaphase chromonemata attain their maximum thickness with regard to their matrical envelopes. This is possibly of theoretical importance (see discussion). At metaphase there are visibly four chromonemata composing one chromosome, two and two being paired closely. The presence of matrices common to more than one chromonema is considered an artefact as pointed out previously.

The mutual orientation of the chromonemata is diagrammatically illustrated in fig. 6 showing schematic cross-sections of chromosomes or groups of chromonemata. Four chromonemata at metaphase (above M in fig. 6) are shown oriented in a single plane. Two chromonemata are drawn for anaphase (A) these separate in early telophase (T) and simultaneously divide forming four chromonemata, the basic number thus being re-established. Four chromonemata are present in resting stage (R) without definite orientation except for their assumed union in the insertion region. In early prophase (Pe) secondary sister chromonemata are paired. In spiral prophase (Pl) pairs of pairs are united into the orientation leading to metaphase.

Discussion

The author's observation that chromonemata carry their individual matrices has been set forth in detail in the first paper of the series (l.c.). It may be added that this viewpoint has decided advantages in terms of electrochemistry and cell kinetics. Every chromonema with a core charged positively holds its own matrix

which has a negative or at least a lesser positive charge. Multiplication of the core leads to immediate repulsion of the two resulting units. The matrix will be split because each core will have the same electrical attraction.

The account of chromonemata seems to bring up the question of chromomeres within chromonemata especially since HEDAYETULLAH writes (l.c. p. 369) "one can conclude that the chromomeric or chromonemic structure of the chromatic thread is the different structure of the same thing under different conditions and at different stages." It is not permissible to confuse chromomeres with the periodic bands or dots arising from the refraction pattern of a spiral. HEDAYETULLAH and PERRY (l.c.) succumb to this error.

Chromonemata have been considered by NEBEL (l.c.) to be cylindrical bodies with a chromatic core which is of variable chromaticity along the longitudinal axis. The visible chromatic swellings may be termed chromomeres. In the *Tradescantia* evident chromomeres are rare and relatively small during mitosis.¹⁾

It has been voiced by BĚLAŘ and SHIWAGO (see NEBEL 1932) and adopted by TELEZYNSKI (1930) that the chromatic specks of interphase are optical sections of spirals. This interpretation should be made use of more freely for other stages of the chromosome cycle.

The mode of reduplication of spirals and their successive separation has been discussed on p. 277 and 278 of the first paper of the series. No unravelling is required if the spirals (or the gene thread in their core) divide at all points in any *one* plane parallel to the longitudinal axis of the chromosome. There seems no logical objection to this, especially since the material of a chromosome thru latest prophase and prometaphase is very definitely laterally polarised—giving the appearance of a flat ribbon. Metaphase may well have just this orienting influence upon the molecules of the reduplicating

1) I am willing to adopt for true chromomeres the definition of HEITZ (HEITZ, E.: Die Herkunft der Chromocentren III. *Planta* 18. 571–636. 1932). He terms "chromomeric chromocentres" parts of the chromonemata which show increased chromaticity. As has been pointed out by HEITZ *these* "chromocentres" should not be confused with the chromatic parts of the insertion regions which have been very apparent in my preparations and which survive the resting stage in full visibility. These have been described earlier by GREGOIRE (GREGOIRE, V.: *Euchromocentres et chromosomes dans les vegetaux*. Acad. Roy. Belg. 17, 12 1932). In passing it may be said that HEITZ (l.c. 1932) refers to the *quadri*-partite chromomeres of telophase, (cf. HEITZ's fig. 5) thus confirming my own observations.

gene thread.¹⁾ For these reasons it is believed that the reduplication of the gene thread proper takes place at prometaphase or metaphase.

This brings us to the point of the obvious lag between observed reduplication and actual multiplication of the gene thread proper. According to GOWEN and GAY (1933) the maximum size of a "physical gene" should be set at 10^{-18} c.c. so that the physical gene would have to increase by at least 20 diameters or 20^3 in mass to become visible. It is possible to imagine that this increase in size could be accomplished between prometaphase and the succeeding telophase, if we remember that what we see of the chromonema is only the thick coating of the gene thread which may consist of less highly specific proteins and may envelope the new gene thread almost instantaneously after its formation. Similar reactions if not explained electrochemically are familiar experiences in enzyme chemistry. Our case would require an increase in mass from 1 to 8000 in approximately 10 minutes which represents a reaction of relatively low speed. If again we consider the matrix bound to the gene thread by electrical charges there is still more reason to look at the kinetic side of reduplication as a rapid process. At present telophase is considered the earliest stage at which the reduplication of chromonemata can be *observed*, while the invisible preparation for this visible condition is *believed* to come about at the preceding *prometaphase* and *metaphase*.

The mechanical consequences of the observations presented above greatly simplify the process of nuclear division. A priori it seems doubtful that the nucleus which may be considered a highly efficient and smoothly operating unit should waste energy disentangling large parts of itself which immediately re-entangle, since it has easier means of achieving the same result without this waste. (cf. EINSTEIN: Der Herr Gott ist raffiniert aber böse ist er nicht).

1) Added during proof:

SMITH (SMITH, F. H. 1932: The structure of the somatic and meiotic chromosomes of *Galtonia candicans*, La Cellule XLI, 3: 243-263), describes the multiplication of chromonemata in much the same way as MARTENS (l.c. NEBEL 1932) has done earlier. "Bilateral repartition of the substance of the chromosome" may be taken as the grossly morphological phenomenon accompanying the process postulated above. MARTENS' and the authors mode of reduplication make use of the lateral polarisation of chromatic materials, but MARTENS and SMITH do not appear to have considered an orderly molecular reduplication of the physical units forming the gene string as a basis of their observations.

Genetical complications likewise do not seem to arise since the findings but confirm the postulated continuity of the chromosome. The numerical basis of DARLINGTON's theory of meiosis (the number of threads) appears still further removed from the facts. This may modify the hypothesis somewhat but in which way cannot be predicted until a thoro study of the history of chromonemata in premeiotic interphase and prophase is at hand. The behavior of *chromatids*¹⁾ is not influenced by the presented analysis of their constituents. It appears likely that chromatids may be found to contain 2 chromonemata in every case but that these pairs of chromonemata will continue to be considered the ultimate partly autonomous units of chromosomes.

Summary

The history of chromonemata in mitosis of *T. reflexa* is briefly summarized on pp. 4-5. As the chromosomes spread out in telophase four chromonemata become visible instead of the two of anaphase. They pass thru interphase without anastomosing and without much dislocation; occasionally at resting stage pairs of chromonemata may be observed, their members running parallel for some distance but mostly the chromonemata run in single paths. Early prophase shows 4n chromatic tracts in each of which two chromonemata are paired, the spirals being shoved into one another closely. In spiral prophase pairs of pairs of chromonemata are arranged into a group of four and the metaphase chromosome is thus essentially established. Later prophase involves only an increase in quantity and change in PH of the matrical coatings of the chromonemata, and lateral polarization of the materials of the chromosome which is believed to be essential for the reproduction of the (invisible) gene thread. At no stage in mitosis do chromonemata entangle.

Discrepancies between the observations presented above and those of other authors is laid to two main reasons: acid fixation without proper pretreatment and the difficulty of interpreting refraction images.

The author is indebted to Dr. L. W. SHARP and Dr. C. L. HUSKINS for suggestions and criticism.

1) I would like to extend this term to designate half chromosomes in mitosis and meiosis.

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