Idiograms, Nucleoli, and Satellites of Certain Ranunculaceae

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IDIOGRAMS, NUCLEOLI, AND SATELLITES OF CERTAIN RANUNCULACEAE

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A study of an idiogram of a plant possessing satellites inevitably brings the investigator in contact with the problem of what becomes of the satellites during the stages of nuclear division other than metaphase and during the resting period. While a complete answer is still beyond our knowledge, since we do not know exactly what becomes of the chromosomes themselves during the resting stage of the nucleus, some very interesting data are gradually accumulating which suggest the existence of a close relationship between the nucleoli and chromosomes, and apparently between nucleoli and satellites. For the purpose of comparison of the behavior of the nucleoli, and the relation of the latter to the chromosomes and the satellites, somatic mitoses were studied of the plants possessing entirely different idiograms but belonging to the same family.

Anemonella thalictroides (L.) Spach. was selected to represent the karyotype with very short and small chromosomes; *Isopyrum biternatum* (Raf.) T. & G., that with slightly longer chromosomes; *Ranunculus abortivus* L. as an example of long and slender chromosomes; and *Ranunculus Chius* DC. as an example of long and thick chromosomes.[1]

The plants mentioned possess true and very well developed satellites.

TERMINOLOGY

In describing the idiogram of a plant the easiest way to refer to individual morphologically distinguishable chromosomes is by indicating them by certain accepted letters. This is the common practice at the present time. The letters of the beginning of the alphabet are often used by the investigators. In most cases the chromosomes are arranged by their size and the largest pair is indicated by the letter *A*. The writer also used this method in her earlier publications (Sorokin 1927, *a*, *b*) for the designation of the individual chromosomes and for the purpose of convenient reference to the particular pair in the text. To indicate the morphological distinctions of the chromosomes belonging to different species of *Muscari*, *Bellevalia*, and *Ornithogalum* Delaunay (1926) used entirely different sets of symbols for

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[1] All the plants investigated except *Ranunculus Chius* are found growing wild in Minnesota. The seeds of *R. Chius* were obtained from Nikita State Botanical Garden, Crimea, U. S. S. R., for which the writer wishes to acknowledge her indebtedness to the administration of this garden.

each genus, employing both letters and Roman figures. This method, however, is not very satisfactory and does not permit a comparison of the individual chromosomes of different plants. Such a comparison as indicated by the work of Sveshnikova (1927) could be of great importance in many cases. It seems, therefore, that a more or less uniform terminology for designation of certain types of chromosomes is highly desirable. This, indeed, has been proposed by Heitz (1925–1926). The chromosomes are referred to as symmetrical and asymmetrical, the first group including the chromosomes with equal arms, and the second those with unequal arms. The length of the arms is expressed symbolically by the letters *L* and *K*, and the approximate difference in length of the arms of chromosomes is indicated by the series of combinations of the capitalized and non capitalized letters *L* and *K*.

The terms symmetrical and asymmetrical, while expressing quite satisfactorily a purely morphological conception of the chromosomes with two equal arms and those with two unequal arms, contradict the genetic conception, since genetically the two arms of the equal-armed chromosomes are not symmetrical. The above terminology does not give place either to strictly rod-shaped chromosomes or to the chromosomes of irregular shape. Besides, the terms symmetrical and asymmetrical have been proposed by S. Nawaschin (1912, 1915) for indication of the races of plants which have satellites of equal and unequal size. Therefore, the use of identical terms for the designation of entirely different conceptions in the karyotype should be avoided, since similar use may often cause misunderstanding.

A large number of plants seems to possess four principal types of somatic chromosomes: (1) with two arms of equal length, (2) with two arms of unequal length, (3) rod-shaped with a knob, (4) rod-shaped with a satellite. Such are, for example, the groups given by M. Nawaschin (1926) for *Crepis*. The four groups of chromosomes given by Sveshnikova (1927) for the genus *Vicia* are similar. In classifying the chromosomes in these four groups, however, Sveshnikova includes in her first group both equal-armed and those of the unequal-armed in which the short arm is longer than half the length of the long arm.

It seems that the terms *monobrachial* [2] and *dibrachial* describe the types of chromosomes somewhat more clearly than the term symmetrical and asymmetrical. The term monobrachial refers to chromosomes with one arm, either strictly rod-shaped, rod-shaped with a knob and a satellite, or *S*-shaped and arch-shaped. The chromosomes which possess two arms could be designated by the term dibrachial. Furthermore, dibrachial chromosomes could be divided into *isobrachial* chromosomes, with arms of equal length, and *heterobrachial* ones, with arms of unequal length. As to the symbolic expression of the individual chromosomes the easiest way perhaps is to refer to them by certain accepted letters of the alphabet, and particu-

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[2] The writer is indebted to Dr. F. K. Butters for the suggestion of these terms.

larly by the letters which at the same time describe the shape of the chromosomes. Such letters have been long in use in plant and animal cytology.

In his text on cytology, Wilson (1925, p. 123–133) refers to *V*-shaped and *J*-shaped chromosomes. It is therefore advisable to retain these letters for symbolic indication of the specific shape. The isobrachial chromosomes therefore, could be designated by the letter *V*. The differences in size of the *V*-shaped chromosomes could be indicated by employing the capitalized and non-capitalized letters and, if desirable to indicate slight differences in the larger *V*-shaped chromosomes, to designate the corresponding pair by numbers. And finally, actual measurement of the length of the arms could be made. The heterobrachial chromosomes could be indicated by the letter *J*. The same finer distinctions could be drawn between the individual pairs as indicated for the *V*-shaped chromosomes. The monobrachial chromosomes could be conventionally indicated by the letter *I* and the satellite indicated by an apostrophe. Thus *I'* will indicate a rod-shaped chromosome with a satellite.

Because this method uses symbols which at the same time indicate the shape of the chromosomes, it is simple and does not require much guessing in choosing the set of letters which is better to use to designate the chromosomal formula of the plant. Accordingly the *S*-shaped and the *U*-shaped chromosomes, while belonging first to the monobrachial and second to the isobrachial type, could be designated by the corresponding letters.

With the progress of the study of the morphology of the chromosomes, new types of chromosomes are described. In a paper by Kuzmina (1927) the somatic chromosomes of *Beta vulgaris* appear to be of an entirely different type, representing some little arches and semicircles. While such chromosomes would generally belong to the monobrachial type their symbolic expressions would have to be purely conventional.

RANUNCULUS ABORTIVUS L.

The idiogram of *Ranunculus abortivus* is characterized by the presence of mono-, iso-, and heterobrachial chromosomes. The *V*-chromosomes are represented by three sizes, two pairs of large chromosomes almost equal in size, one pair of slightly smaller, and one pair of small chromosomes. The *J*-chromosomes are represented by three pairs each differing in size from another. The *I* chromosomes have satellites of equal size. The formula of the somatic chromosomes of *R. abortivus* is $2(3V + v + 3J + I')$. An equatorial plate stage of *R. abortivus* is represented in figure 1, Plate XXXVII, and the components of each pair are given in figure 2. Langlet (1927) also reports 16 somatic chromosomes for *R. abortivus*. However, no figure or description of the individual chromosomes is given by this author.

The behavior of the satellites during the metaphase and the anaphase stage of *R. abortivus* could be followed easily. They divide and become distributed together with the *I* chromosomes to the daughter nuclei.

Although granules of the size of satellites are oftentimes visible in close proximity to the nucleoli during the telophase stage, their identity with satellites could not be definitely proved. The behavior of the nucleoli and their relation to the chromosomes are more definite. After the chromosomes have reached the opposite poles during the telophase stage, they remain clumped together and do not show such distinct alveolation as is typical for many other long chromosomes. Later, four or three distinct chromatic aggregations are always visible, two of them being larger in size and having distinct outlines of the nucleoli, the other two aggregates being smaller and connected with the larger by means of threads. With the progress of reconstruction of the daughter nuclei, the smaller aggregates decrease in size, while the larger ones enlarge somewhat and assume the shape of nucleoli. This is illustrated in figures 3 and 4 of Plate XXXVII. The upper and the lower nuclei of figure 3 represent two daughter nuclei and are drawn from the same section at different foci. Similarly the right and the left nuclei of figure 4 are daughter nuclei in the stage of reconstruction, the outlines of the cell wall being represented only in one of the daughter cells in each figure. The chromatic aggregates in figure 3 show irregular outlines and protrusions; those of figure 4 are more regular. Numerous mitochondria are visible in the cytoplasm in the preparations fixed by chromic-acid-formalin according to Němec. These stain somewhat bluish with good Heidenhain's haematoxylin, and are well differentiated from the small granules of chromatin material.

Further stages of the nuclear reconstruction are represented in figures 6 and 7. The nucleoli appear still more regular. In figure 8 an interkinesis stage is reached. The smaller chromatic aggregates have disappeared and two nucleoli have attained their typical shape and dimensions. Numerous mitochondria are visible at the upper focus of the section of the cell. It is interesting to note here that the nucleoli do not show any clear area about them. In all the material investigated, with the possible exception of one case, two nucleoli could be found during the stage of the reconstruction of the daughter nuclei and the early interkinesis. The case in which the above condition was not quite so evident is represented in figure 5, Plate XXXVII. It is possible that two nucleoli are present also in each of the daughter nuclei, and due to the fact that they are superimposed one upon the other they appear as one. During the late interkinesis the two nucleoli fuse and at this stage the clear area begins to appear about the fused nucleolus as in figure 9. This area expands later on and the nuclei merge into prophase. The fused nucleolus always shows two small chromatic bodies attached to it. Although it is at first very difficult to observe these bodies on the deeply stained nucleoli, they could be detected easily on every nucleolus after a careful examination by focusing up and down. The bodies are distinctly shown in the nucleoli in figures 10, 11, 12, 13, 15, 16, and 17, and are always of a uniform size. In figures 10, 11, and 12, the bodies project clearly against the clear area formed about the nucleolus. Because of the absence of other dark staining chromatic granules in the nuclei of *R. abortivus* at this stage, these bodies could not be confused with or taken for something else. Their uniform shape and their constant presence on the nucleoli suggest that they are constant components of the cell. Whether these bodies represent the satellites of the chromosomes, as has been suggested by Nawaschin, or some other nucleolosome is rather difficult to say. Their size corresponds to that of the satellites as the latter appear during the metaphase. Due to the comparatively small size of the nuclei of this plant, no figures were seen which would suggest the picking up by the chromosomes of the satellites from the nucleolus as has been described by Nawaschin (1927) for some similar structures in *Galtonia* and by his pupils in certain other plants.

As the nuclei progress further into the prophase stage the clear area about the nucleolus increases and at the same time the reticulum condenses and forms distinct threads. These threads stain very faintly during all the early prophase stages and begin to stain dark only very late in the prophase. The fused nucleolus increases in size during the early prophase and later assumes an amoeboid or irregular shape. Protrusions from its surface are often observed, the latter being oftentimes connected with the threads, as for example is illustrated in figure 13, Plate XXXVII. Only exceedingly rarely were two nucleoli seen in the nuclei in the advanced stage of the prophase, as is illustrated in figure 19.

ANEMONELLA THALICTROIDES (L.) SPACH.

The chromosomes of *Anemonella thalictroides* are very slender and small. They belong to the monobrachial type. There are 12 I chromosomes and two I' chromosomes with satellites, the somatic formula being $2(6I + I')$. An equatorial plate stage of *A. thalictroides* is represented in figure 20, Plate XXXVIII. The satellites of the I' chromosomes are extremely small and therefore it is difficult to follow their behavior during the resting stage of the nucleus as well as during all stages of nuclear division but metaphase.

After the chromosomes have reached the poles during the telophase stage they assume a circular arrangement. From two to four larger chromatin groups begin to be prominent in each of the circles of the telophasic daughter chromosomes. This is illustrated in figure 21. The two daughter nuclei were drawn at different foci, the cell wall and cytoplasm being pictured only in the cell to the left. As the reconstruction of the nuclei proceeds further the chromatin aggregates become more prominent and show delicate connecting threads between them. This is shown in figure 22. In figure 24, smaller aggregates fuse into two nucleoli, the delicate anastomosing threads which are connected with the nucleoli still being visible. In figure 26 the nucleoli become larger and assume a more regular shape. At this stage small chromatic bodies are seen to be in connection with the nucleoli by very delicate threads and the anastomosing threads have disappeared. The nuclei represented in figures 24 and 26 are the daughter nuclei at different foci. Similar are the nuclei figured in 23 and 25. These latter are still further advanced in the reconstruction process. In the nucleus shown in figure 23 a fusion of the two nucleoli is taking place. The fused nucleolus in figure 27 shows two chromatic nucleolosomes, one being attached to the nucleolus by a delicate thread. No other dark-staining chromatic granules are found in the nucleus. During this stage of the prophase the chromosomes begin to appear. They originate as faintly stained bodies at the periphery of the nucleus. A late prophase stage is represented in figure 28. The chromosomes are formed and show a close connection with the nucleolus, which becomes faintly stained and shows vacuoles inside. Some of the chromosomes are located closely about the nucleolus, others being connected with it by delicate threads.

ISOPYRUM BITERNATUM (RAF.) T. & G.

The idiogram of *Isopyrum biternatum* is characterised by the presence of mono-, iso-, and heterobrachial chromosomes. Exceedingly small size makes the study of the individual chromosomes rather difficult. The presence of the satellites, however, could be established. These are of equal size. A metaphase stage of *I. biternatum* in which 14 chromosomes could be distinguished is represented in figure 29, Plate XXXVIII. The outstanding feature of the somatic equatorial plate stage of this plant is that the chromosomes are arranged in pairs. While the paired arrangement of the chromosomes has been found by Nawaschin (1926) to occur in *Crepis tectorum* as a mere chance, in *I. biternatum*, as far as the material studied permits one to make definite conclusions, the paired arrangement of the somatic chromosomes is a general rule. This, as will be seen later, is apparently a result of the occurrence of somatic diakinesis in this plant.

The chromosomes during the early telophase move towards the poles as more or less distinct units; a clumping into separated aggregates occurs considerably later. During the telophases the cells of the larger portion of the root tip did not show any chromatic bodies in the cytoplasm of the type of extruded nucleoli. In the exceedingly large cells which are found adjacent to the dermatogen, dark-stained globules are found in the cytoplasm during the telophase as well as during all other stages of division. Such globules are represented during the telophase stage in figure 30, and during the interkinesis in figure 33. The absence of similar bodies from the cells of the larger portion of the root, the exceedingly large number and size of these bodies, and their occurrence at different stages of division, not only during the telophase, suggests that these bodies are not extruded nucleoli. In a recent paper by Guilliermond (1929) bodies somewhat similar in appearance to those described in the present study are represented. These bodies are found in the vacuoles and according to Guilliermond represent globules of vacuolar precipitates. The first stages of the reconstruction of the daughter nuclei are somewhat similar to the corresponding stages in *Anemonella thalictroides*. A clumping of the chromatin material into separate aggregates could be also observed in *I. biternatum*. This is represented in figure 31, Plate XXXVIII. The chromatin aggregates are connected by delicate threads. Further on two nucleoli become distinctly evident in each of the daughter nuclei. These fuse during the late interkinesis (figure 32). The fused nucleolus always shows the presence of two nucleolosomes on its surface (figure 34). The chromosomes appear first as faint bodies at the periphery on the nucleus (figure 35). They become denser after being in close contact with the nucleolus (figure 36). Finally a stage is reached which could be interpreted as one immediately preceding a somatic diakinesis. Fourteen distinctly paired chromosomes are seen to be arranged in a spiral in figure 37. The first and second pair, if counted from the free end of the spiral, have parallel chromosomes. In the third pair the chromosomes are disjointed. The fourth pair forms a cross. The components of the fifth and the sixth pair are more or less parallel. The chromosomes of the seventh pair are superimposed on the surface of the very faintly stained nucleolus, which at that time has decreased considerably in size. The spiral arrangement of the chromosomes is also evident in figure 38, although the individual pairs are not so distinct. The nucleolus in this case is seen to be connected with one pair of the chromosomes in the lower portion of the spiral. "Somatic diakinesis" is represented in figures 39 and 40, and the chromosomes are shown to be arranged in pairs. This arrangement of chromosomes suggests the typical diakinesis stage of the meiosis. One pair of chromosomes seems to be distinctly disjointed, while the remaining six pairs are more or less close together. Kuhn (1928) has described in the somatic mitosis of *Thalictrum* spp. a stage which he called "somatic diakinesis." This stage resembles the diakinesis stage of the heterotypic division and follows immediately the formation of the chromosomes from the chromatic centers at the periphery of the nucleus.

RANUNCULUS CHIUS DC.

The idiogram of *Ranunculus Chius* is characterized by large and thick chromosomes, fourteen in number. The chromosomes belong to the mono- and dibrachial types. One pair bears comparatively large satellites. The exact somatic formula was not established due to lack of material.

The equatorial-plate stage is represented in figures 41 and 42. In figure 41 only one chromosome bearing a satellite is visible. In figure 42 both of the satellite-bearing chromosomes are apparent. Chromosomes with the satellites are represented still better in figure 43. From this figure it is possible to draw a conclusion as to the comparative size of the two equal satellites and as to that of the satellite-bearing chromosomes.

During the metaphase and anaphase stages the satellites divide and become distributed with their chromosomes to the daughter nuclei. The behavior of the satellites during the telophase stage could not be followed. In the interkinesis and the early prophase the nucleolosomes which appear on the surface of the nucleoli are of exactly the same shape, size, and staining ability as the satellites of the *I'* chromosomes. The behavior of the nucleoli in *Ranunculus Chius* differs considerably from the three other plants studied. Neither was evidence found which suggested that two nucleoli appear in the reconstructed daughter nuclei, nor was there observed a fusion of the two nucleoli.

In the early prophase a large nucleolus, stained a light gray, always shows the presence of two dark-stained bodies of uniform size situated either directly on its surface, or attached to it by delicate threads. This is represented in figure 44. At a similar stage the nucleolus is beginning to be surrounded by the clear area, and in the forming reticulum no other dark-staining granules of the size of the nucleolosomes could be observed. A slightly later stage is pictured in figure 45. The reticulum has formed denser threads, the nucleolus stains a light gray and shows the two black bodies. In figure 46 a still later stage of the prophase is pictured. The figure is drawn at different foci to indicate that the forming chromosomes and the nucleolosome are found at different levels and are not connected. A somewhat later stage is represented in figure 47. These two pictures represent the same nucleus at different foci. In the figure at the right the nucleolus is shown with the nucleolosomes; in that at the left the two chromosomes hide the nucleolosomes. One of the chromosomes shows a constriction. In the material studied pictures were often observed which showed one nucleolosome on the nucleolus, and next to it one chromosome with the satellite which is exactly of the same size as the nucleolosome (figure 48).

DISCUSSION

The idiograms described in the present paper show that the plants studied belong to the symmetrical race in the sense of S. Nawaschin, (1912, 1915, 1927), and that the *I'* chromosomes possess satellites of equal size. In *Anemonella thalictroides* the chromosomes and the satellites were so small as to make studies of the sizes of the structures mentioned extremely difficult. However, there seems to be no marked difference in the size of the satellites of this plant. In the metaphase stage the satellites were found on the proximal end of the chromosome *I'*.

During the anaphase stage the split satellites were distributed to the corresponding poles together with the daughter chromosomes *I'*. During the telophase stage the satellites became indistinguishable from the rest of the chromatin. Such a condition existed until interkinesis when the two nucleoli fused to form one large nucleolus. At that stage and later during the prophase the fused nucleoli always exhibited the presence of two nucleolosomes on their surface. Although there is apparently no fusion of the nucleoli in *Ranunculus Chius* during the interkinesis or the early prophase, since only one nucleolus is formed in each of the reconstructed daughter nuclei of the meristematic region, the nucleolosomes were very distinct on the nucleolus during the resting stage and the prophase.

Two nucleolosomes were seen on the surface of the nucleoli in the resting nuclei and in those in the prophase stage in *Ranunculus acris* by Sorokin (1924) and Senjaninova (1926). Both authors interpreted these as true satellites. During the prophase stage the presence of two nucleolosomes on the surface of the nucleolus has been reported by many authors (S. Nawaschin, 1927; M. Nawaschin, 1925; Baranov, 1926; Kuhn, 1928). Nawaschin's school interprets the nucleolosomes as true satellites which are picked up from the nucleolus later in the prophase by the delicate threads extended from the two chromosomes. Haase-Bessell (1928), however, considers the chromatin granules found in the resting nuclei on the surface of nucleoli not to be true satellites but the products of the transformation of the nucleolar material, namely chromatin. These granules can be absorbed by the satellites. The satellite itself is interpreted as a differentiated part of the chromosome, an organelle for the absorption of chromatin. Although nucleolosomes were observed by Kuhn (1928) during the prophases of the somatic mitosis on the surface of nucleoli in certain species of *Thalictrum*, no definite opinion is expressed by him regarding the nature of these structures.

In studying the karyotypes of different varieties of *Hyacinthus orientalis* which have chromosomes with permanent secondary constrictions, de Mol (1927) found correlation between the number of chromosomes with constrictions and the number of the nucleoli. Moreover, in cases in which the secondary constriction of the long chromosomes was lacking the nucleoli were seen to be attached to the long chromosomes. De Mol also observed satellites in *Hyacinthus orientalis*, or rather "pseudo-satellites," as he correctly remarked. These were regarded as nucleolar globules which are not taken in by the chromosome body. De Mol made a clear distinction between true satellites and the "pseudo-satellites" of *Hyacinthus*.

The writer of this paper is engaged at the present time in the studies of the karyotypes of certain varieties of *Pisum sativum*, in which the true satellites are apparently lacking. There seem to exist two or more distinctly different kinds of karyotypes, one with the chromosomes possessing true satellites which are attached by delicate threads to the proximal end of the metaphasic chromosomes, and another type with pseudo-satellites attached to the distal end of the chromosomes. It is likely that the two structures mentioned are homologous in their functions.

In a recent paper Delaunay (1929) also makes a distinction between the different types of satellites saying: "Es ist eine ganz andere Frage, ob die *großen Tarabanten* dieselben Eigenschaften besitzen wie die *kleinen*. Augenscheinlich nicht, und zwar zeigen die Untersuchungen, daß die *besonderen Eigenschaften* der kleinen Tarabanten, welche sich sichtbar dadurch außern, dass sie schon in frühen Prophasen als *einzelne* Körperchen auf den Nucleolen sitzen, erst dann von ihnen erworben werden, wenn sie einen bedeutenden Reduktionsgrad erreicht haben."

Returning to the interpretation of the satellites of the present investigation, it appears quite probable that the nuceolosomes seen at different stages of the nuclear division and at the resting stage in *Ranunculus Chius* represent the satellites of the metaphasic chromosomes. Their constant appearance, size, and shape, identical with the satellites, and the presence of the pictures showing the picking up of the satellite by the chromosome, make the author agree with Nawaschin's interpretation of the nucleolosomes. Other plants studied, owing to the comparatively small size of the chromosomes and the satellites, do not permit such definite conclusions to be made. However, the probability is great that the nucleolosomes in these plants are also satellites.

Various authors differ considerably in their interpretation of the nature and behavior of the satellites. There seems to exist much less disagreement in the opinion of a large number of writers regarding the relation of the nucleolus to the chromosomes. The adherents to the transformation theory are gradually increasing. Some of the recent literature is discussed in a paper by Haase-Bessell (1928).

De Mol (1927) is of the opinion that "there probably exists a genetically determined relationship between nucleoli and chromosomes." Kater (1928), on the basis of a series of investigations, comes to the conclusion that the "so-called plasmosomes always arise as a karyosome, as a product of parts of chromosomes and rapidly loose their basophilic character, becoming true nucleoli." In the oöcyte of *Cambarus* the nucleolus is considered to be merely a giant net-knot of the reticulum.

The behavior of the nucleoli during the telophase stage of *Anemonella thalictroides*, *Isopyrum biternatum*, and *Ranunculus abortivus* is somewhat similar. The telophasic chromosomes become resolved into chromatin aggregates and a delicate reticulum. The chromatin aggregates which are connected with the reticulum by threads soon form two nucleoli which fuse into one later during the interkinesis. Schaede (1928) observed two nucleoli to be constantly present during the telophase stage in a number of plants. These fused later and one nucleolus was found in the resting nuclei. Schaede thinks, however, that the fusion of the nucleoli is of no significance since he regards the whole nucleolus merely as a vacuole.

In the light of the present investigation the fusion of the nucleoli during the interkinesis seems to be of great importance. It assembles in one mass all of that portion of chromatin matter which became stored in the nucleoli and did not resolve into the reticulum of the resting nucleus. The above facilitates more even distribution of this chromatin to the faint reticulum of the following prophase stage.

Suggestive as to the rôle of the nucleolus as a contributor to chromosome formation during the prophase is its behavior in a plant exhibiting somatic diakinesis, such as was found in *Isopyrum biternatum*, in which the nucleolus showed great activity during the prophase stage and was constantly connected by threads with the forming chromosomes. Later the chromosomes formed pairs arranged in a spiral and the remainder of a very faintly-stained nucleolus was seen between the two chromosomes of the last pair. This pair was not the one which contained the chromosomes provided with satellites. Therefore if in *Isopyrum biternatum* the nucleolosomes of the prophase stage represent satellites, the latter must have been picked up from the nucleolus by the corresponding chromosomes before the close association of the nucleolus with the last pair of the spiral was established.

SUMMARY

1. The idiogram of *Ranunculus abortivus* is characterized by the presence of mono-, iso-, and heterobrachial chromosomes. The *I'* chromosomes have satellites which are equal in size. The idiogram of *Anemonella thalictroides* shows the presence of only monobrachial chromosomes, two of which have satellites, also of equal size. In the idiogram of *Isopyrum biternatum* the chromosomes are of mono- and dibrachial type. The satellites are very small. In *Ranunculus Chius* the chromosomes are of the three types, and the satellites are large and are equal in size.

2. In *R. abortivus*, *A. thalictroides*, and *I. biternatum*, during the telophase stage the chromosomes resolve into a faint reticulum and dark chromatic aggregates. The larger aggregates gradually assume the shape of two nucleoli, while the smaller aggregates disappear, either becoming resolved into the reticulum, or fusing with the larger aggregates. The nucleoli, therefore, contain at least part of the actual chromatin material of the chromosomes.

3. The fusion of the two nucleoli into one is a common feature of late interkinesis of the three plants mentioned.

4. The fused nucleolus of each of these species and the single nucleolus of *Ranunculus Chius* all show the presence of nucleolosomes on the surface. These stain dark and are clearly distinguishable during the resting stage and the prophase.

5. In *Ranunculus Chius* the identity of the nucleolosomes with the satellites could be established. In the other plants studied this identity is probable.

6. In *Isopyrum biternatum* was observed a "somatic diakinesis" and paired arrangement of the chromosomes during the metaphase stage.

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EXPLANATION OF PLATES

All figures were drawn with the aid of an Abbe camera lucida, with Zeiss apochromatic objective 3 mm., 1.30 N. A., compensating ocular 12.

PLATE XXXVII

The figures represent stages of somatic nuclear divisions in *Ranunculus abortivus.* Material was fixed in chromic acid formalin according to Němec, and stained in Heidenhain's iron haematoxylin.

FIG. 1. Metaphase stage showing 16 chromosomes.

FIG. 2. Size and shape of the individual chromosomes.

FIG. 3. Telophase stage. The upper and the lower nuclei represent the two daughter nuclei drawn from the same section at different foci. Four chromatin aggregates are seen in each nucleus.

FIG. 4. Slightly later stage than one in figure 3. The larger chromatin aggregates assuming the shape and size typical for the nucleoli. The right and the left nuclei are the daughter nuclei of the same section at different foci.

FIG. 5. Stage as in figure 4. A rare case in which only one nucleolus is present during the telophase stage.

FIG. 6. Stage somewhat similar to one in figure 4.

FIG. 7. Later stage of nuclear reconstruction. Two nucleoli are present in each of the daughter nuclei.

FIG. 8. Interkinesis. Two nucleoli do not show the presence of a clear area about them. Mitochondria are abundant.

FIG. 9. Late interkinesis. Fusion of the two nucleoli.

FIG. 10. Early prophase. Nucleolus is surrounded by a clear area.

FIG. 11. The area about the nucleolus has increased. Two nucleolosomes are clearly distinguishable on the surface of the nucleolus.

FIG. 12. Stage similar to one in figure 11.

FIG. 13. Dark-stained protrusions are visible in contact with the nucleolus.

FIG. 14. The nucleolus has become amoeboid.

FIG. 15. Later stage of prophase.

FIG. 16. Two nucleolosomes are distinctly seen on the nucleolus.

FIG. 17. Nucleolus during the prophase stage.

FIG. 18. Stage as in figure 17.

FIG. 19. Rare case of prophase containing two nucleoli.

PLATE XXXVIII

FIGS. 20–28. Stages of somatic mitosis in *Anemonella thalictroides*. Material was fixed in Nawaschin's modification of Flemming's solution and stained in Heidenhain's iron haematoxylin.

FIG. 20. Metaphase stage with 14 chromosomes.

FIG. 21. Telophase stage.

FIG. 22. Late telophase stage. Four chromatic aggregates are easily distinguishable in each of the daughter nuclei.

FIG. 23. Interkinesis, a fusion of two nucleoli.

FIG. 24. Fusion of the chromatic aggregates into two nucleoli.

FIG. 25. Interkinesis.

FIG. 26. Two nucleoli of a nucleus during the interkinesis.

FIG. 27. Prophase stage. Chromosomes appear as faintly stained bodies at the periphery of the nucleus.

FIG. 28. Chromosomes become dark stained. Close connection with the nucleolus is still apparent.

FIGS. 29–40. Stages of somatic mitosis in *Isopyrum biternatum*. Material was fixed in chromic acid formalin according to Němec, and stained in Heidenhain's iron haematoxylin.

FIG. 29. Metaphase stage showing paired arrangement of the 14 chromosomes.

FIG. 30. Telophase stage. The chromosomes have reached the poles. Vacuolar precipitates are seen in the vacuoles in the cytoplasm.

FIG. 31. Later stage of telophase. The chromosomes resolve into chromatin aggregates and the reticulum.

FIG. 32. Fusion of two nucleoli.

FIG. 33. Early prophase stage. The fused nucleolus shows the presence of a clear area about it. Vacuolar precipitates are seen in the vacuoles in the cytoplasm.

FIG. 34. The fused nucleolus shows the presence of two nucleolosomes on its surface.

FIG. 35. Early prophase.

FIG. 36. Later stage of prophase. The nucleolus is shown to be connected with some chromosomes.

FIG. 37. Stage preceding the "somatic diakinesis." The chromosomes are arranged in pairs in a spiral. The chromosomes of the pair in the center are situated on the surface of the nucleolus.

FIG. 38. Stage similar to that in figure 37.

FIG. 39. Stage of "somatic diakinesis." The chromosomes are arranged in pairs.

FIG. 40. "Somatic diakinesis." Certain of the chromosome pairs form crosses, in other pairs the chromosomes are parallel.

FIGS. 41–48. Stages of somatic mitosis in *Ranunculus Chius.* Material was fixed in Nawaschin's modification of Flemming's solution and stained in Heidenhain's iron haematoxylin.

FIG. 41. Metaphase showing 14 chromosomes.

FIG. 42. Metaphase showing two chromosomes bearing satellites of equal size.

FIG. 43. Two satellite-bearing chromosomes.

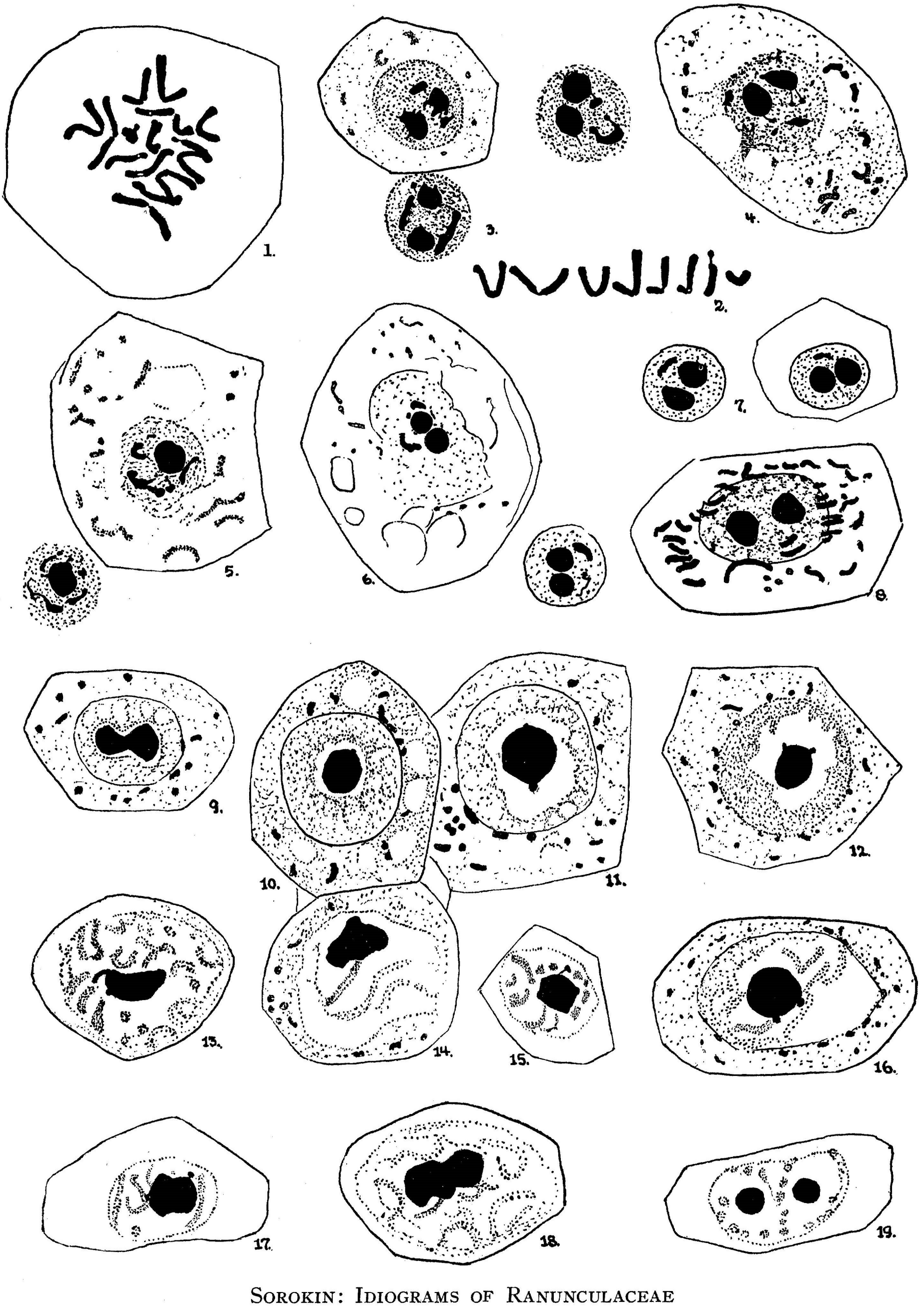
FIG. 44. Prophase stage showing a faintly stained nucleolus with two dark stained nucleolosomes.

FIG. 45. Somewhat later stage. Two nucleolosomes are equal in size.

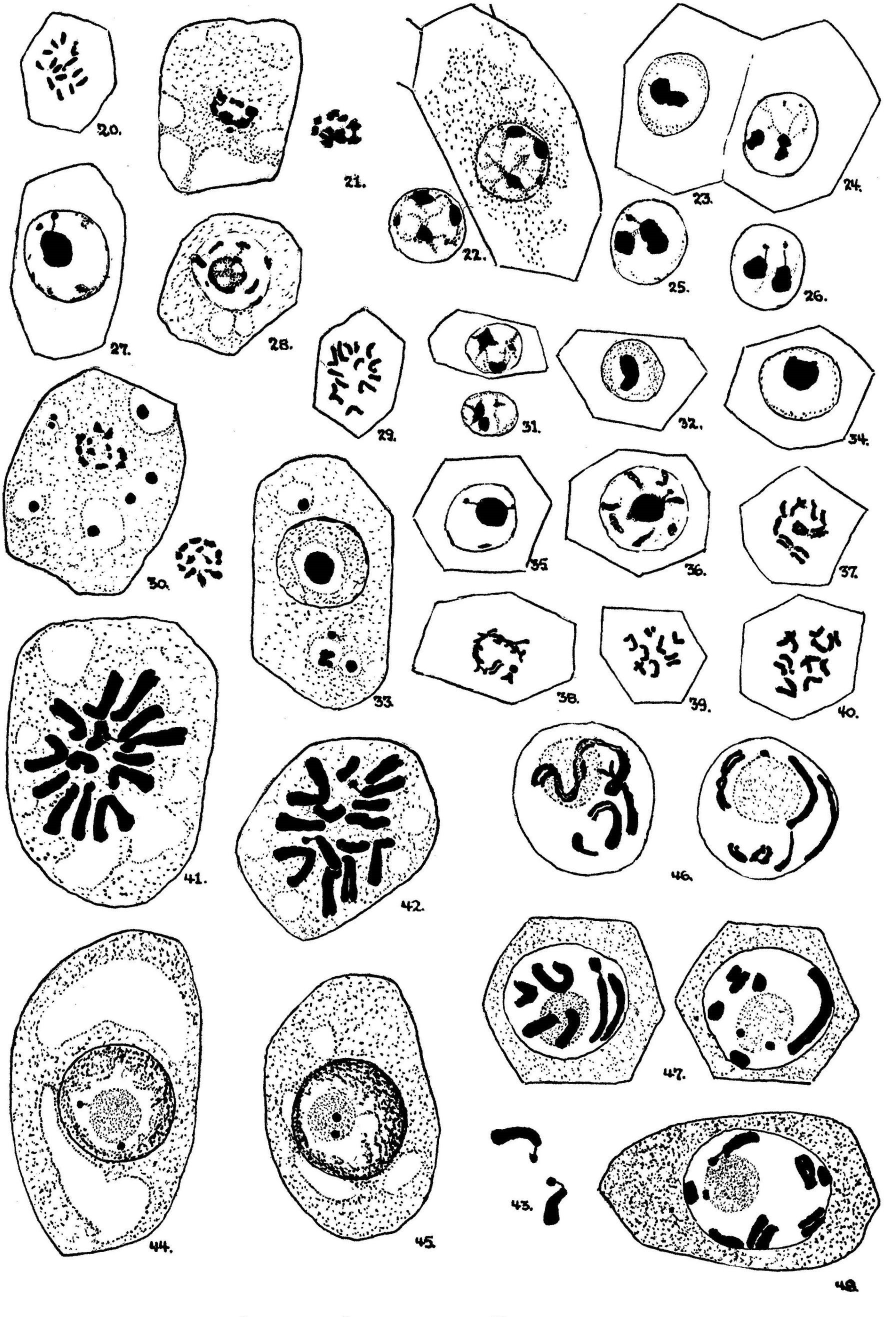
FIG. 46. The same nucleus is pictured at different depths of focus. In the figure at the right one nucleolosome is apparent.

FIG. 47. Nucleus as in figure 46, a somewhat later stage. Two nucleolosomes are distinct on the nucleolus.

FIG. 48. Late prophase. One of the nucleolsomes is on the nucleolus, the other is attached to the slender thread extended from the chromosome.



SOROKIN: IDIOGRAMS OF RANUNCULACEAE



Sorokin: Idiograms of Ranunculaceae