Meiosis in *Rumex*. II. The origin and behavior of the so-called sex-chromosomes in *Rumex*

By
Henry Wilhelm Jensen

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Even to those who are but casually familiar with cytological disputes, the telosynaptic-parasynaptic quarrel cannot be unknown. It, a question still more fundamental to cytological doctrine has already enlisted its champions and gives promise of offering a spectacle not altogether happy but nevertheless necessary for scientific progress. We must again call into question whether there exists such a thing as synapsis at all. Why? Because such matters as sex-chromosomes, crossing-over, etc. hang preeminently on the assumption that meiotic synapsis takes place. It is fitting that an essay which pretends to deal with the cytological basis of sex-determination should logically begin with a consideration of the pertinent assumptions. In the particular instance of this article the author feels that he must approach the theory of synapsis because, if the reader agrees with the first section of this paper, he need not bother with the second half; the arguments would be superfluous. On the other hand, if the reader turns the first half, the evidence gained from a far different approach might serve to convince him as to the validity of the author's opinion on the so-called sex-chromosomes in *Rumex*.

Our present conception of sex-chromosomes demands that the chromosomes or portions of chromosomes which were contributed by the parents must retain their individuality throughout the ontogeny of their offspring so that they may be segregated at meiosis to the progeny. One may ask if there is any evidence which might nullify the logic of this assumption. One possible source of information might be found in the origin of the meiotic chromosomes. After studying the history of the meiotic spore in *Rumex*, *Rheum*, *Fagopyrum*, and *Calycanthus*, the author finds that *Rheum* provides the most graphic illustration of what seems to take place in all four genera. The chromosomes are larger in *Rheum* than in the other genera, and so are the nuclei; the chromosomes are less dense and tannin more easily removed. Let us therefore begin with the first appearance of a spore which the author was able to discover in the microsporogenous tissue of *Rheum rhaponticum*.

As the cells in the sporogenous tissue begin their meiotic history, the nucleus possesses a single nucleolus and an evenly dis-

tributed weft of twisting spireme. These strands which always seem to pass across the exposed hemisphere of the nucleus are so fine that little more may be said of them. Their number and termination are quite without definition. However, as the history of the spireme progresses, the spireme collapses to one portion of the nucleus where still less can be seen of the minute details. When the synizetic contraction is concluded and the spireme begins to loosen, the strands are much more dense and contain certain sections which appear thicker than the general dimension. When the spireme has again filled the confines of the nucleus, during which it condenses so that it takes a deeper stain and increases in thickness, a condition similar to figure 37 is revealed. One may first notice that the spirem is double, the halves loosely twisted about each other, and that the spireme is essentially continuous. That is to say, there is but one spireme. One may also notice that the future meiotic chromosomes exist as thickened portions of the spireme, (n-22) and that each chromosome is represented by two halves, which may either lie parallel or twist about each other. From this stage, pachytene, to the heterotypic metaphase there is a gradual increase in the thickness of the chromosomes and a decrease in the length of the spireme and its segments. The strepsitene, figure 38, still finds the chromosomes linked in a continuous spireme, but the halves are quite closely coiled around each other so that the duality is no longer generally visible, except in the regions of the chromosomes. During diakinesis, or what approaches that stage, the contraction of the spireme and growth of the chromosomes continues until the nuclear wall disintegrates, such as is shown in figure 39. As in *Rumex*, the meiotic chromosomes of *Rheum* are mostly telosynaptoid in appearance at the heterotypic metaphase, figure 40, and yet, the halves of the meiotic chromosomes originate side by side in the spireme. How, then, is the change accomplished? Though the author had already built his text figure 1 on his observations on *Rumex*, the situation is still easier to demonstrate in *Rheum*. One may see in figure 39 that several of the "pairs" have opened out so that the chromosome halves no longer appear as crooked rods, but rather as V's, joined thusly. Evidently, the contraction of the spireme aids in pulling the chromosomes into V's...., one must remember that they are still linked in one continuous spireme. The diagram in text figure 1 will explain the actual shifting and collapsing of the chromosomes better than words. As a result of this folding, the chromosome halves, as they migrate toward the heterotypic anaphase poles and as they manifest the longitudinal split which anticipates the homeotypic division, figure 45, show all stages between a simple member and those "tetrads" which have

figured in Darlington's (1) "double nondisjunction" and other's work on *Rhoeo* and *Tradescantia*. These findings confirm Jeffrey's (5) opinion that the facts warrant a simpler explanation than that which some investigators have tried to promulgate. Similarly, in the heterotypic metaphase, figure 40, many of the chromosomes remain linked into zig-zagging strings of what might be construed, with an incomplete knowledge of events, as a chain of simple "univalents" which alternately depart for opposite poles. However, as previous remarks have pointed out, this is not the case. A study of the meiotic spireme in *Rheum* leads one to believe that said spireme is continuous in origin and essentially so in development, and that the meiotic chromosomes originate in a parasynaptoid position.

If there is any pairing in *Rheum*, it must occur between two strings of 22 members each and must take place before or during synizesis. The author finds it hard to conceive of such an act taking place with necessary exactness and at the same time involving two such extensive strings coiled and twisted into the usual synizetic tangle. Though the author remains open on the matter, a longitudinal splitting of a single spireme into two equal portions appeals to his sense of logic with greater merit than does the synaptic theory which is currently held valid. Then too, such an origin of the "univalents" would be in accord with the frequent anticipation of the homeotypic division as evidenced by the apparent duality of the chromosomes in the heterotypic anaphase. Such phenomena, if of granted similarity, suggest that meiotic and mitotic divisions cannot be discriminated upon or the basis of their mechanism. Through the evidence in support of this contention (diploid parthenogenesis, haploids, etc.) is legion and perhaps even more convincing than the above demonstration, the author must leave this section of the argument with the statement that he is of the opinion that the meiotic spireme in *Rheum* is fundamentally continuous and that the meiotic chromosome originate by a longitudinal split of a spireme which has become segmented into the haploid number of members.

We turn back to the genus *Rumex*. Though not microscopically so favourable, the several species investigated reveal the same conditions as manifested in *Rheum rhaponticum*, and without a detailed repetition, they are worthy of comment.

When activity is first discernable, the prophase in microsporogenesis in *Rumex crispus* appears as shown in figure 1. Many fine, irregular strands traverse the nucleus. These strands later collapse, or contract into the stage known as synizesis, from which they again meander, but with the very evident change that they are now present as a continuous and double spireme. See figure 2. As the chromatin

becomes concentrated into chromosomes after the pachytene stage, figure 3, the duality of the spireme is frequently obscured. Nevertheless, early diakinesis, figure 4, will sometimes show places in the

Text-fig. 1. The parasynapto-telospireme shift of the chromosomes in the spireme of *Rumex crispus* during diakinesis. Equally true of other species of *Rumex* and *Rheum rhaponticum*. A, B, C, and D are respective stages in the shift drawn from preparations. A', B', C', and D' are diagrammatical interpretations of the drawings immediately above them. The process as outlined from A to D, or A' to D', demonstrates how the shifting of the chromosome attachment to the continuous spireme accomplishes an end-to-end relation of the originally parasynapto-toid members. By the time the chromosomes initiate the metaphase all evidence of the folds is frequently lost.

spireme, particularly between halves of chromosomes, where the original doubleness is still visible. It should be noted, that the chromosomes are of the haploid number and are still contained in a continuous spireme. There is certainly no opportunity for pairing after synizesis and yet the chromosomes are present in the reduced number, 30. The continuity of the spireme is also shown in *R. crispus* $\times$ *obtusifolius*, figure 7, *R. Patientia*, figure 9, and *R. Britanica*, figure 8.

A complete history of the spireme in *Rumex acetosella* is shown in figure 10 to 17. This species has yielded sex-chromosomes according to Meurman(13) and Kihara (8) . . . , and yet, a glance at

the above mentioned figures reveals that the spireme is practically continuous from synizesis to metaphase and that the chromosomes appear in the haploid number despite this barrier to pairing. The same is true in *R. Acetosa*, as shown in figure 22 to 26. In the author's opinion, the proceeding discussion has demonstrated that the meiotic chromosomes in *Rumex* and *Rheum rhaponticum* do not undergo an act of pairing and yet appear in the haploid number. It is felt that the difference between meiosis and mitosis is one of number and not of mechanics. If this be granted, the individuality of the paternal and maternal chromosomes in *Rumex Acetosa*, for example, must have been lost at some stage in the ontogeny of a single plant. This must logically follow, because if the meiotic chromosomes, which are composed of two members, do not arise by a pairing, then a splitting process seems to be the only alternative. Under such circumstances sex-chromosomes, as we now think of them, could hardly survive, because they demand a clear-cut retention of their identity

from cell to cell and from generation to generation. Since this cannot be the case in *Rumex Acetosa* and *R. acetosella*, the author concludes that the description of sex-chromosomes in these species is not warranted.

For those who are not persuaded by the foregoing argument, let us turn to a study of the actual behavior of the described sex-chromosomes in the dioecious species of *Rumex*.

Because the author's observations differ with those of previous investigators, it is felt that clarity will be enhanced by postponing references and comparisons with previous work to a section of discussion.

Most of the literature pertaining to this subject has already been reviewed in the author's previous article. Since the author has described the so-called sex-determining apparatus in part in said article and since it is a part of nearly all modern books on cytology, repetition is deemed unnecessary.

Figure 26 is a section of a P.M.C. of *R. Acetosa* in a late stage of diakinesis, with a tripartite chromosome lying in the lower portion of the nucleus. This tripartite chromosome is the sex-determining mechanism which Kihara and Ono(10) described in 1923. Due to the matted nature of the diakinetid figure, this complex is frequently obscured. As the meiotic chromosomes arrange themselves in a somewhat irregular metaphase plate, a typical metaphase stage is generally lacking, the tripartite chromosome takes a position in the plane of the spindle. In the majority of cases, when it was visible, the early anaphase found the tripartite chromosome stretched out on the spindle as shown in figure 27. Occasionally, it was bent into the shape of a U. As the anaphase progressed, figure 28, the complex frequently lay stretched across the face of the spindle. Occasionally, the tripartite chromosome gave evidence of a constriction around the central and larger member of the complex. This state culminated in a few cases in a strand of four members stretched from one heterotypic anaphase pole to the other, figure 29. In fact, such a procedure suggests that the tripartite chromosome is essentially a tetrapartite association. If it were only tripartite and meiosis was performed with regularity, one should be able to observe only 6 autosomes and 2Y's (terminal pieces) at one pole and 6 autosomes and one X (central member) at the other . . . , that is, a 7-8 distribution. Such a count of anaphase groups was frequently confirmed. On the other hand, if the tripartite string may also behave as a string of four members, one might reasonably expect to find a few 8-8 counts. Figure 31 and 36 are drawings of anaphase groups within the same P.M.C.; eight chromosomes are plainly visible in each case. How-

ever, not only counts of 7-8 and 8-8 were observed, but distributions of 6-9 and 7-9 as well. Evidently the so-called determining mechanism is at times rather frivolous, and after the standards of good sex-chromosomes, possesses a conduct subject to some reproach. With such an irregular behavior, the author feels that these meiotic phenomena must have some origin and interpretation other than a sex-determining apparatus. The foregoing events in *R. Acetosa* bear certain similarities to conditions found in the hybrids between species of the *Lapathum* section of the genus *Rumex*, Jensen(6). One may question the legitimacy of comparing phenomena in one species with those in another. . . , yet, there are grounds for such an action.

In a previous article on polyploidy in *Rumex*, Jensen(6), the author demonstrates that there are certain cytological phenomena which are diagnostic of hybrids or plants of hybrid ancestry. Lagging meiotic chromosomes, presence of "univalents" and "bivalents", extrusion of chromatin, polycary, polyspory, strings of chromosomes, abnormal modes of string separation, sterility, etc. are listed as peculiar to *Rumex* hybrids and not to their parents. The first question which now arises is, does *R. Acetosa* possess any of these diagnostic hybrid characteristics.

Figure 30 shows a number of lagging chromosomes on the heterotypic anaphase spindle of a P.M.C. of *R. Acetosa*. Such conditions were of frequent occurrence. Thus, too, some of the pollen was sterile, and, as previously described, an unequal and variable distribution of the chromosomes takes place during the heterotypic division. Such phenomena suggest that *R. Acetosa* has had a hybrid ancestry. . . , but more evidence may be gained from the articles of other investigators. Kihara and Yamamoto(12) observed the lagging and extrusion of chromatin from the first and second divisions in a 17 chromosome male plant. Takenaka(20) states that the first division of triploid intersexes is very irregular, the second is omitted. It appears that a polycaric condition arises from the first division. On the other hand, Ono(16) states that the two divisions are present and that only four spores are formed, but that these soon abort. He also observed P.M.C.'s appearing with the diploid number of chromosomes at meiosis, similar to the conditions in diploid parthenogenesis which Ernst(2), Winge(21), and Stebbins(18) consider to be caused by the hybridization. Though there still is much evidence which could be quoted, let us pass on with the observation, compiled from the many Japanese investigators, that a species so full of meiotic irregularity which gives rise to 14, 15, 16, 17, 20, 21, 22, and 29 as diploid numbers can scarcely avoid being classed with

those plants which possess a hybrid past. The next logical step would be to compare the meiotic activity of *R. Acetosa* with that of *Rumex crispus* $\times$ *obtusifolius* in an effort to learn just what may be expected of plants with a hybrid background. In the author's previous paper, Jensen(6), he pointed out that there appeared from time to time in *R. crispus* $\times$ *obtusifolius* strings of two to four bivalents, chromosomes which had failed to separate out from the spireme, and that these strings reveal a variable history. They may separate into individual chromosomes during the late anaphase or the separation may be suppressed so that the terminal halves of these telosynaptoid chains may appear to effect a separation with a random distribution of the segments. When one compares such a peculiar behavior in a known hybrid with the occasional tetrapartite evolution of the tripartite chromosomes in *R. Acetosa*, the two phenomena become basically the same. It is the author's opinion that previous hybridization has induced a suppression of the normal mode of separation of a pair of so-called bivalents, that such a view is logical because parallel phenomena exist in known hybrids of the same genus, and, since it has been demonstrated that the mechanism commonly behaves contrary to its reputation, that the tripartite chromosomes in *R. Acetosa* consequently have little to do with the determination of sex.

The matter is still more open when it comes to *Rumex acetosella*. Figure 42 is a photograph of five specimens of *R. acetosella* collected from a patch of a few feet in diameter. One should notice the marked variation in the character of the leaves. . . . , they vary from narrowed to auriculate to three cleft. Such diversity of shapes suggests that this species is in a state of flux; and the cytology of meiosis confirms this view.

The heterotypic metaphases are so irregular that one can hardly determine what occurs most often. However, the large number of chromosomes ($n=22$) may be considered as one reason why the tripartite chromosomes were not commonly seen. It did seem to the author that in particularly favorable cases that the so-called sex-chromosomes were not always present. When they were, the tripartite complex occupied a position, as Meurman(13) described it, parallel to the axis of the spindle, as in figure 18. During the early anaphase, figure 19 (incidentally, this is about as regular a figure as could be found), the tripartite association strings out much as in the author's description of events in *R. Acetosa*. An effort was made to follow the conduct of the chromosomes through the anaphase, but their mass prevented anything definite from materializing. As to anaphase counts; they were tried but because of the peculiar

mass tendency and the lagging of chromosomes on the spindle, the author does not feel free to be dogmatic. It appeared that there was a variation from 17 to 23 in the groups counted. Meurman(13) records distributions of 21-21, 20-21, and 18-20. The point is that there is not a predictable regularity in the distribution of the chromosomes. However, this is not the most serious difficulty. Not only does one tripartite chromosome appear at the heterotypic metaphase, but one may observe several, figure 18, and every gradation from an apparently tripartite to tetrapartite condition. Kihara(9) suggested some relation between the four piece strings and shorten chains of these members...., the above observations confirm this idea.

Figure 17 demonstrates a few of the many phenomena which may arise from a tardy and variable break-up of the spireme. The shorter strings frequently develop into anaphase bridges, figure 20, some of which appear to be of a tripartite nature. From one to three such bridges were observed in at least a third of the P.M.C.'s in some anther-sacs. This meiotic phenomenon is also indicative of a hybrid ancestry; *Rumex crispus* $\times$ *obtusifolius*, Jensen(6); *Hemerocallis fulva*, Juel(7). The presence of a varying number of strings of meiotic chromosomes in *R. acetosella* is also of significance since Håkansson(4) found that the presence of strings was quite marked in his *Godetia Whitneyi* $\times$ *amoena* hybrids while they seldom occurred in the parents. Müntzing(14, 15) obtained similar results with his *Galeopsis* hybrids. Therefore, such features as lagging chromosomes, strings, variable distributions of the meiotic chromosomes, anaphase bridges and extreme variation in the form of the foliage strongly indicate a hybrid ancestry for *R. acetosella*. Here again, as for *R. Acetosa*, it must be pointed out that the cytological phenomena observed in *R. acetosella* are duplicated in *Rumex crispus* $\times$ *obtusifolius*. The author feels that the facts suggest a more natural interpretation and by no means uphold the view that there are sex-chromosomes in *R. acetosella*.

Some investigators may feel that the author has slighted the consistency with which the female plants of *R. acetosella* and *R. Acetosa* appear to maintain the same chromosome number. It is true that all reports to date set the female plants of *R. Acetosa* at 14 and *R. acetosella* at 42 (the males at 41, 42, and 43, Kihara(9)). Yet, this uniformity is not in itself convincing because Täckholm(19) found that in *Rosa canina* all the univalents divided during the heterotypic anaphase of microsporogenesis, while they consistently failed to divide in megasporogenesis. Therefore, a consistent difference between male and female behavior in the same species is neither

peculiar to dioecious species nor indicative of a sex-determining characters.

Sex-chromosomes have been ascribed to several other species of the *Acetosa* section, for a list and references see Gaiser (3), or the author's previous paper, but from what can be gained from figures and descriptions of the respective authors, the conditions in these species are strikingly similar to those in *R. Acetosa*.

The fact that Roth (17) determined the haploid number of *R. acetosella* as sixteen may be worthy of a remark in passing. All investigations since then have placed it at twenty one or two. However, Roth's determination was made before 1906 while the next work on the species, as far as the author is aware, came in 1925. The author has demonstrated how variable in cytology and habit *R. acetosella* is today. May it not be true that we have before us a specific example of how relative data can be when it concerns the march of events in the trek of evolution? Probably, sixteen was the correct number for *R. acetosella* in 1906.

Tripartite chromosomes, which may subsequently effect an unequal chromosome complement in the daughter nuclei, are by no means peculiar to the dioecious species of *Rumex*. *R. pallidus* Bigel., an hermaphroditic species of the *Eulapathum* section possesses an odd meiosis. Sometimes the conduct of the chromosomes is graphically regular. Yet, occasionally the eight haploid chromosomes (figure 35) may separate into halves during diakinesis, figure 32. Not alone the heterotypic division, but the homeotypic may occur prematurely so that odd distribution ratios result. Such ratios as 8-8, 8-7, 9-7, and 6-9 were observed. Of course, the sizes of the daughter chromosomes vary accordingly . . . , whether they be a product of a first or a second division. If, as in figure 33, the halves of a meiotic (haploid) chromosome begin to separate and then one of the halves in turn begins to divide, a tripartite chromosome appears to be present. On the other hand, two chromosomes which have failed to segment out of the spireme may divide, and in the process assume a tripartite appearance, as in figure 34. Thus, the bare occurrence of a tripartite association among the meiotic chromosomes need not necessarily cast any sexed reflection on the complex.

To conclude the evidence, the author wishes to cite the case of *Rheum rhaponticum*. In at least half of the P.M.C.'s a half of one of the 22 haploid chromosomes is left in the cytoplasm after the daughter nuclei of the first division have been formed, figure 43. This fragment may either slowly disintegrate or persist through the homeotypic division to form a nucleus of its own, figure 44. This stray chromosome frequently splits into two or more fragments.

Now, this peculiar phenomenon results in an unequal distribution of the chromosomes, 22-21, as may be determined by counting in figure 43. The pollen of this species of *Rheum* is to a large degree imperfect, figure 46. Were it not for the unfortunate fact that the plant is hermaphroditic, some claims, resembling some of those made on the zoological side, might try to establish another case of sex-chromosomes. Let it be understood that the author in no wise precludes the existence of sex-chromosomes, but, he is convinced that we must scrutinize with increasing care all possible evidence before we admit every reported case of sex-chromosomes to the realm of fact.

Summary

1. A study of the meiotic spireme in *Rheum* and *Rumex* reveals that the spireme is essentially continuous throughout its tangible history, through diakinesis, and that the meiotic chromosomes originate by a longitudinal splitting of the spireme out of which the haploid number of chromosomes becomes segmented. Pairing does not take place in these genera because it cannot.

2. Because the above conclusion necessitates a fusion of maternally and paternally contributed chromosomes before meiosis, thus destroying the individuality of the chromosomes, sex-chromosomes cannot exist in *Rumex*.

3. From another angle, the so-called sex-chromosomes in *R. Acetosa* and *R. acetosella* are regarded as having little to do with the determination of sex, because....,

4. The described apparatus does not exhibit a uniform behavior, but rather one of irregularity.

5. The tripartite chromosomes reveal themselves to be essentially tetrapartite; a string of four elements the inner of which frequently fuse and behave as one entity.

6. Tripartite chromosomes also exist and perform an unequal distribution of the meiotic chromosomes in *R. pallidus*, but this species is hermaphroditic.

7. The dioecious species in question exhibit various cytological phenomena which indicate that they are of hybrid origin.

8. The meiotic phenomena in the dioecious species are duplicated to a large extent in the hybrid *R. crispus* $\times$ *obtusifolius*.

9. The so-called sex-chromosomes in *Rumex* are therefore nothing more than an abnormality resulting from previous hybridization of the species.

10. A peculiar cytological condition present in *Rheum rhabonticum* is used to demonstrate that a condition ascribed to sex-

determination in some unisexual organisms may also exist in hermaphroditic species and thereby annul the logical existence of such sex-chromosomes.

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Description of Plates

All figures are of microsporogenesis and, unless otherwise stated, $\times 730$.

Plate 2

- Fig. 1. *Rumex crispus*, early prophase.
- Fig. 2. Prophase, as a portion of the spireme emerges from synizesis.
- Fig. 3. Pachytene stage; note continuous spireme.
- Fig. 4. Late strepsitene, or early diakinesis.
- Fig. 5. Diakinesis.
- Fig. 6. Late diakinesis.
- Fig. 7. *R. crispus* $\times$ *obtusifolius*, diakinesis, showing chromosomes still largely held in a spireme.
- Fig. 8. *R. Britannica*, diakinesis, presence of strings.
- Fig. 9. *R. Patientia*, prophase just before synizesis.
- Fig. 10. *R. acetosella*, P.M.C. nucleus in "resting" condition.
- Fig. 11. Early prophase of the same.
- Fig. 12. Synizesis.
- Fig. 13. Strepsitene stage showing continuous, dual, spireme.
- Fig. 14. Pachytene, where duality is again largely concealed.
- Fig. 15. Stage between above and early diakinesis.
- Fig. 16. Diakinesis, chromosomes double and in strings (irregular segmentation of the spireme).
- Fig. 17. Heterotypic metaphase showing the presence of strings in various stages of partition.
- Fig. 18. Another metaphase showing a tripartite chromosome at the left and striking amount of lagging and irregularity.
- Fig. 19. A rather regular early anaphase with tripartite chromosome.
- Fig. 20. Heterotypic anaphase with bridges.
- Fig. 21. Polar view of heterotypic metaphase, 21 chromosomes.

Plate 3

- Fig. 22. *R. Acetosa*, early anaphase.
- Fig. 23. Synizesis of the same.
- Fig. 24. Expansion of spireme following synizesis.
- Fig. 25. Pachytene stage; still some evidence of duality in spireme.
- Fig. 26. Portion of nucleus in diakinesis; showing a tripartite chromosome in a segment of the spireme.
- Fig. 27. Early anaphase; first division.
- Fig. 28. Heterotypic anaphase.
- Fig. 29. Late anaphase revealing a tetrapartite chromosome.
- Fig. 30. Anaphase showing lagging chromosomes.
- Fig. 31. and fig. 36. Polar views of anaphase groups within the same cell..., each with eight chromosomes.
- Fig. 32. *R. pallidus*, a type of diakinesis in which the "bivalents" have started to fragment.
- Fig. 33. Early heterotypic anaphase of same showing tripartite chromosomes.
- Fig. 34. Heterotypic metaphase showing irregularities.
- Fig. 35. Eight haploid chromosomes seen in polar view during the heterotypic metaphase.
- Fig. 36. See fig. 31.
- Fig. 37. *Rheum rhaponticum*, pachytene stage with double continuous spireme and young chromosomes.
- Fig. 38. Strepsitene.
- Fig. 39. "Diakinesis"... , twisted halves of chromosomes still held in continuous spireme; a few members beginning to open into V's.
- Fig. 40. Metaphase with spireme still persisting.
- Fig. 41. Heterotypic anaphase with bridge and laggards.
- Fig. 42. *Rumex acetosella*, leaf character divergence, $\times 1/5$.
- Fig. 43. *Rheum rhaponticum*, end of first division, one chromosome eliminated from daughter nuclei.
- Fig. 44. Polycaric condition at the end of meiosis.
- Fig. 45. Polar view of heterotypic anaphase group showing all varieties of "tetrad" formation.
- Fig. 46. Typical microspores; many are imperfect or abortive, $\times 330$.

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