Meiosis in an F₁ Hybrid Between a Turkish Wild Beet (Beta Vulgaris, ssp. Maritima) and Beta Procumbens

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Introduction

Hybrids between *Beta vulgaris* L. and species of the section *Patellares* Tr. are usually lethal and die in the seedling stage. Viable hybrids are very rare. The first hybrids to survive, obtained by Gaskill (9) from Swiss chard *(B. vulgaris)* X *B. webbiana* Moq. (hereafter referred to as "the webbiana hybrids") and the first hybrids obtained by Oldemeyer (24), were completely sterile. Coe's lethal hybrids (3), preserved by grafting, were also sterile, but Johnson (13) succeeded in obtaining some seed by grafting similar lethal hybrids.

One viable semi-fertile hybrid plant was obtained by Stewart (35), but its backcross progeny survived only until the second generation. Another viable semi-fertile plant obtained by Oldemeyer and Brewbaker (25) from crosses of a Turkish wild beet *(B. vulgaris)* X *B. procumbens* Chr. Sm. (hereafter referred to as "the procumbens hybrid") produced backcross progeny for several generations.

The purpose of hybridization of *B. vulgaris* with nematode-resistant wild beets is for the introduction of resistance to the sugar beet nematode *(Heterodera schachtii* Schmidt).

Meiosis was studied in two hybrid matings: the sterile "webbiana hybrids" (Swiss chard X *B. webbiana*) (33) and the semi-fertile "procumbens hybrid" (Turkish wild beet X *B. procumbens*). Both F₁ hybrids arose from hybridization of two diploid species and contained 18 chromosomes (9 chromosomes from *B. vulgaris* and 9 from *B. webbiana* or *B. procumbens*, respectively). Meiosis was studied to reveal the causes of sterility or partial fertility in these hybrids, as well as the possibility of association of chromosomes from different species in these remote F₁ hybrids. Chromosome association and crossing-over are important for the transmission of genes responsible for nematode resistance.

Materials and Methods

Floral axes of the F₁ hybrid plant (Turkish wild beet X *B. procumbens*) were fixed in chrom-aceto-formol, dehydrated, em-

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bedded in paraffin and sectioned. Slides were stained by iron hematoxylin. Camera lucida drawings and photomicrographs are presented.

Experimental Results

Chromosome Pairing

Chromosomes of *B. vulgaris* associated to some extent with chromosomes of *B. procumbens*. The number of bivalents varied in different cells from 0 to 5. (Figures 1, 2). The grade of pairing in the semi-fertile hybrid (Turkish wild beet X *B. procumbens*) was but a little higher than in the sterile "webbiana hybrids." The majority of pollen mother cells (P.M.C) in the "procumbens hybrid" contained four bivalents instead of three as in the "webbiana hybrids" (Table 1). The chiasma frequency per P.M.C. was estimated at 3.04 for the sterile "webbiana hybrid" and at 3.6 for the semi-fertile "procumbens hybrid," but there were more bivalents with interstitial chiasmata in the "procumbens hybrid" that could provide for interchanges of longer sections of chromosomes. In some cases it was possible to observe the intercrosses of two chromatids in the bivalent.

Table 1.—Distribution of Bivalents in P.M.C. of an F_1 Hybrid (Turkish Wild Beet X *B. procumbens*).

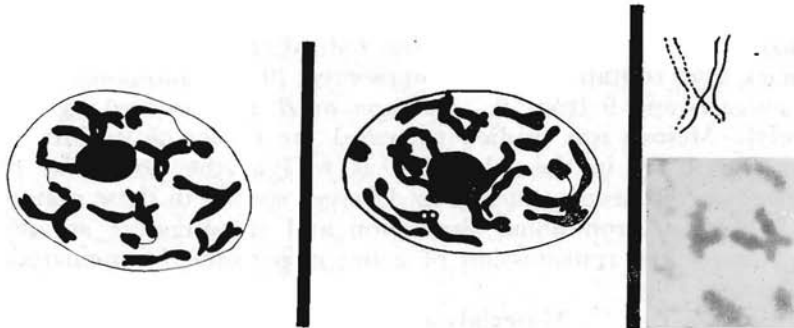| Number of bivalents	0	1	2	3	4	5	Total
Number of P.M.C.	3	3	5	17	22	3	53
Percent of P.M.C. with corresponding number of bivalents	5.7	5.7	9.4	32.0	41.5	5.7	

Figure 1. (left)—Diakinetic nucleus with 4_{11} and 10_1; three univalents with attenuated constriction area X 3100. Figure 2. (center)—Diakinetic nucleus with 5_1, and 7_1 plus 2 fragments; one univalent with attenuated constriction X 3100. Figure 3. (right)—Bivalent with intercrossed chromatids X 3100.

This observation indicates that crossing over really occurred between chromosomes of the different species (Figure 3).

Chromosome Breakage

In the prophases of meioses breakage of chromosomes was observed. The pattern of chromosome breakage was similar to that caused by radiation, chemical treatment, or to that which occurs spontaneously. Breakage of chromosomes may occur at any stage including the resting stage. The breaks can be distributed at random or localized at special areas. Ford (7) observed a random distribution of chromosome breaks in *Vicia faba* after treatment by mustard gas and Tjio (36) after treatment by pyrogallol. Special sensitive regions of chromosomes have been indicated by other authors. Koller (17) found in *Tradescantia* that the centromere and the adjacent region were susceptible. Jackson and Barber (12) indicated that the most sensitive region in *Tradescantia* was near terminal regions of chromosome arms, the centromere regions were less susceptible and the mid-arm regions were resistant. Rees and Thompson (28) found in an inbred line of rye that the breakage was localized mainly towards the ends of the chromosomes, agreeing with the distribution of chiasmata. The controversies in the localization of breaks observed in different experiments and in different plants were elucidated by the recent investigations of Lane (18), Haque (11) and Sparrow (34) who showed that physiological conditions of the cell and nucleus interaction with the type of treatment produce different sensitivity in different parts of the chromosomes.

In the hybrid studied the breaks were located at the centromere region. Some chromosomes at diakinesis showed a very pronounced attenuated constriction area which resembled a thin thread. One to three chromosomes in some nuclei exhibited such elongated constriction. Figures 1 and 2 show several chromosomes in the nuclei, the arms of which are connected by the thin thread only. The same appearance was observed in meiosis of F_1 "webbiana hybrids" (33). In these hybrids the chromosomes with attenuated constrictions were observed only occasionally, while in the hybrid with *B. procumbens* such chromosomes appeared with comparatively high frequency.

The fragmentation occurred by transversal breakage of the thin thread. The breakage was always symmetrical; it affected both chromatids at the same points and occurred always in the region adjacent to the centromere or through the centromere itself. The breakage of the chromosomes in the "procumbens hybrid" belonged to the chromosome type (B"), not to the

chromatid type, because the break occurred through the centromere region which is not divided at prometaphase and the break affected both chromatids symmetrically.

The same type of fragmentation was observed in several plants after treatment by narcotics. Kihlman and Levan (16) and Tjio (36) observed it in *Vicia faba*, Ostergren (26) and Levan and Tjio (20) in *Allium cepa*. Spontaneous breakage of chromosomes was described by Levan and Lotfy (19) in *Vicia faba*, by Muntzing (22) in rye, by Muntzing and Nygren (23) in *Poa alpina*, by Darlington (4) in *Tradescantia*, by Darlington and Wylie (6) in *Narcissus* and by Hair (10) in *Agropyron*.

Not only the univalents but sometimes the broken bivalents could be observed at prometaphase. In Figure 4 a bivalent with terminal chiasma is shown. One partner of the bivalent is fragmented at the constriction area and the fragment (one broken arm) is located at the opposite side of the bivalent.
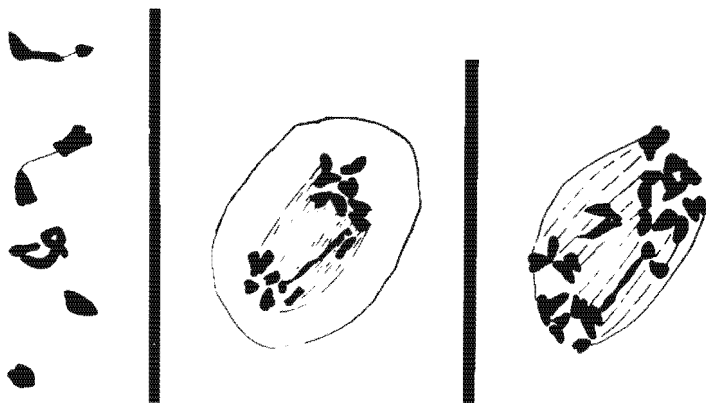

Figure 4. (left)—Fragmentation of chromosomes; 2 chromosomes with attenuated constriction, 1 univalent and 1 bivalent fragmented X 3100. . Figure 5. (center)—A dicentric bridge at anaphase X 3100. Figure 6. (right)— A bridge and a lagging bivalent (non-disjunction) at anaphase X 3100.

Some fragments were eliminated, but others reunited immediately. In several cells at the first anaphase the bridges which were formed by the chromatids of telocentrics united by their distal ends were observed (Figures 5, 6). These dicentric bridges were thin, stretched on the spindle and pulled out by their centromeres. The point of the reunion of the chromatids was always noticeable and attenuated like a constriction because of the resistance offered by the bridge to the anaphase pulling.

Acentric fragments were rarely observed. Sometimes partly eliminated small fragments were revealed in the plasm outside of the nuclei. It is most probable that the acentrics were not

located on the spindle area but were pushed out to the periphery of the nuclei toward the nuclear membrane. After the disappearance of the membrane, the acentrics were thrown out into plasm and eliminated immediately. It is less probable that the sister reunion in the acentrics made them indistinguishable from the lagging univalents, or the attraction to the ends of other chromosomes made them invisible.

In one cell the "trivalent" bridge (probably tricentric C_3) was observed (Figure 7). The bridge was formed by three united chromatids, at least one of which belonged to another fragment (non-sister reunion). One of the three fragments reached the anaphatic group of chromosomes, the others remained on the spindle. The same kind of chromatid reunion was observed by Ostergren (26) in *Allium cepa* after coumarin treatment.
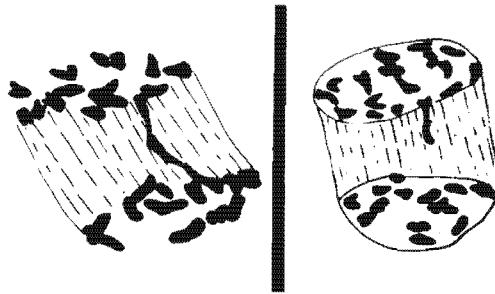

Figure 7. (left)—A "trivalent" bridge at anaphase X 3100. Figure 8. (right)—A lagging iso-chromosome X 3100.

Sometimes the iso-chromosomes with two arms of equal size connected by a constriction (centromere) were found moving on the spindle at the first anaphase. Figure 8 shows a belated iso-chromosome almost reaching the telophatic group of chromosomes at the time the nucleus had already been formed. Its lagging position close to the polar group of chromosomes may be caused either by the incompleteness of its centromere and insufficient poleward attraction or by the delay in the division of the telocentric from which it arose. The functional capacity of an iso-chromosome will depend on the number of centromeric chromomeres which the telocentric received after misdivision. If the break occurred through the central region of the centromere, the sister reunion within this region will give rise to the functional iso-chromosome (5).

There is no doubt that the unstable telocentrics could be formed with comparatively high frequency in the type of breakage observed, and they may lead, according to Sanchez-Monge (32), to the formation of iso-chromosomes with functional centro-

meres. Such iso-chromosomes could reach the poles and be included in the daughter nuclei. There is no doubt that when the breaks are localized at the centromere region more iso-chromosomes are formed than are observed. Not all iso-chromosomes, even with complete and functional centromeres, will reach the poles; some of them will be delayed because of the delay in division of some telocentrics and the formation and orientation of iso-chromosomes or because of different hazards. But just such iso-chromosomes, lagging or moving on the spindle at the late anaphase, have more chances to be detected than the iso-chromosomes which moved together with other chromosomes and were included in the nuclei.

The percentage of cells at diakinesis containing chromosomes with attenuated constrictions was relatively high. From 270 cells 120 cells, or 44.4 percent, contained fragments or chromosomes with very thin fiber-like constrictions, but the number of cells with fragments and bridges at the first anaphase equaled only 10 percent. From 280 cells at this stage the bridges and fragmented chromosomes were found in 28 cells. It can be assumed that 10 percent of the cells exhibited broken chromosomes at the first meiotic division. Obviously not all the chromosomes which showed attenuated constriction at diakinesis were later fragmented. Actually the chromosomes with an attenuated constriction region were observed sometimes at the first metaphase. But the constriction area, although distinctly separating the two arms of the chromosomes, was not so attenuated as at diakinesis (Figure 9). Probably the metaphatic contraction shortened the elongated constriction area in some chromosomes and enabled them to pass through metaphase and anaphase without breakage.

It is also probable that some of the broken chromosomes were not detected at anaphase because of their restitution in the original way, but in such cases the elongated centromere area had to be contracted anyway.

The fragmentation of the bridges was not observed. The majority of bridges remained on the spindle after the telophase nuclei were formed. The telophase bridges connecting the resting nuclei were revealed in several cells (Figure 10). Although some lagging fragments were observed on the spindle at the first anaphase, the others which succeeded in reaching the poles were included in the microspores and gave rise to structural aberrations.

In the second division the broken chromosomes were rarely observed. In such cases one of two daughter nuclei exhibited at the second anaphase a bridge sometimes accompanied by two

little acentric chromatids (Figure 11). The breakage might occur in this case at the interphase. The attenuated constrictions were indeed observed in some interkinetic nuclei.

Breakage of chromosomes was observed in some interspecific and interlinear hybrids. Bernstrom (2) observed inverted bridges in the interlinear hybrids of *Lamium amplexicaule*. Ribbands (29) described the breakage of chromosomes and the formation of inversion and translocation bridges in *Lilium* X *testaceum*.

Usually the chromosome breakage in interspecific hybrids is caused by translocations or by inversions followed by crossing over between inverted and non-inverted segments of chromosomes. As a result inversion and translocation bridges are formed. In the hybrid Turkish wild beet X *B. procumbens* the breakage of chromosomes was spontaneous and similar to that caused by chemicals or radiation. The disturbance of genetic balance and of the cell metabolism may be a possible explanation of this process.
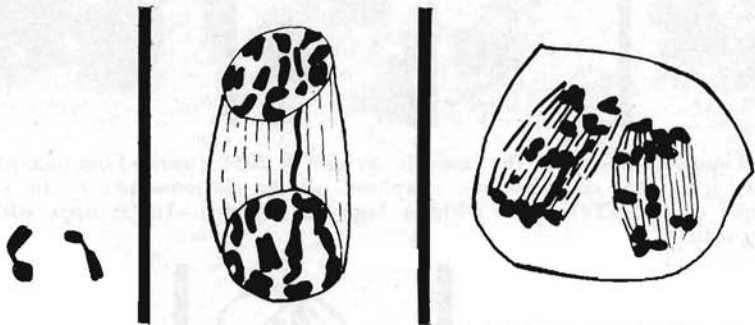

Figure 9. (left)—Chromosomes with shortened constriction at prometaphase X 3100. Figure 10. (center)—A telophatic bridge X 3100. Figure 11. (right)—Second anaphase; bridge and 2 acentrics in one nucleus X 3100.

First Meiotic Division

At metaphase all chromosomes were arranged in the equatorial plate. The bivalents as well as the univalents were distributed at random. Univalents often occupied the central part of the plate while the bivalents showed a tendency to lie at the periphery. Congression of the chromosomes was fair.

It is very characteristic of the "procumbens hybrid" that the first meiotic division in this hybrid is rather regular. In many cells the bivalents divided and their partners proceeded to the respective poles. Several univalents divided in the first division too. In some P.M.C. all the univalents divided in the first division. Division of some univalents in the first division was observed by von Rosenberg (30) in different species of *Hieracium*, by Mather (21) in the triploid wheat hybrids, by Kihara and

Nishiyama (15) in the hybrids *Triticum palonicum* X *Haynaldia villosa,* by Akerman and Hagberg (1) in oats hybrids, by Gaewski (8) in some *Geum* hybrids, by Savitsky (33) in the "webbiana hybrids." But in the hybrid Turkish wild beet X *B. procumbens* the division of univalents showed a higher manifestation.

The chromosomes in this hybrid were not scattered over the spindle, but in many cells they reached the poles simultaneously. The univalents which divided at the same time as the bivalents reached the poles together with them (Figures 12a, b, c, d).

On the other hand, the pictures of disturbances usual for interspecific hybrids were observed in other P.M.C. (Figures 13a, b). In some cells non-disjunction and lagging of bivalents were observed at the anaphase and at interkinesis (Figures 5
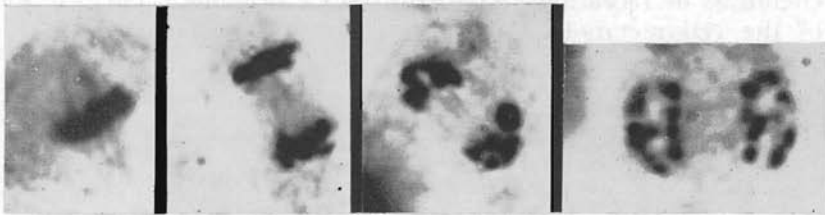

Figure 12.—Regular first meiotic division X 2034; (left)—First metaphase, side view. (left center)—Late anaphase, all the chromosomes at the poles. (right center)—Telophase without laggards. (right)—Interkinesis without laggards.
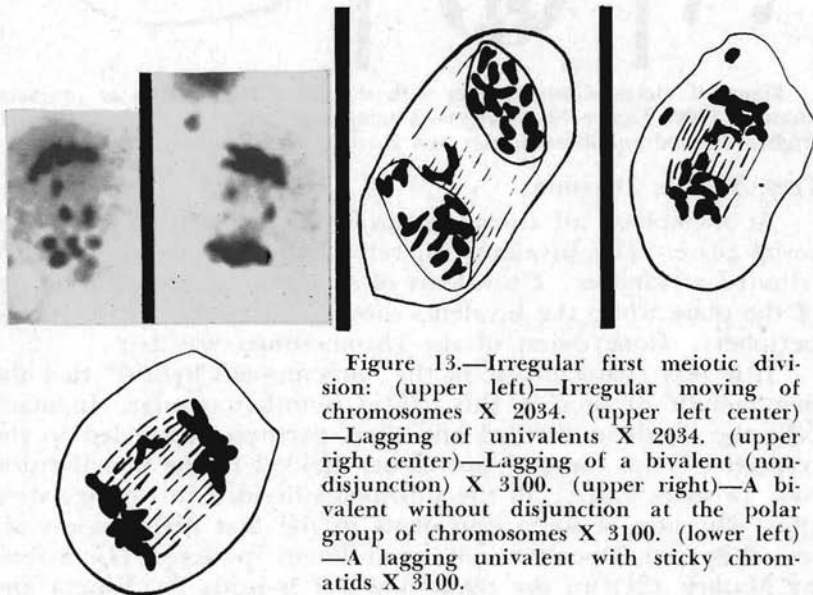

Figure 13.—Irregular first meiotic division: (upper left)—Irregular moving of chromosomes X 2034. (upper left center) —Lagging of univalents X 2034. (upper right center)—Lagging of a bivalent (non-disjunction) X 3100. (upper right)—A bivalent without disjunction at the polar group of chromosomes X 3100. (lower left) —A lagging univalent with sticky chromatids X 3100.

and 13c). Sometimes the bivalents (without disjunction) reached the polar group of chromosomes and might be included in the nucleus (Figure 13d). Some univalents in which the separation of chromatids was delayed remained on the spindle while other chromosomes reached the poles. Their centromeres divided, but the chromatids were stuck together in the region close to their distal ends (Figure 13e). Some of the univalents passed to the poles undivided.

Laggards and chromosomes thrown out into plasm were observed in the first division in only 18 percent of the P.M.C. Eighty-two percent of the cells did not contain lagging chromosomes. This confirms also the regularity of the first meiotic division.

Table 2.—Number of Chromosomes in P.M.C. after the First Meiotic Division in an F₁ Hybrid (Turkish Wild Beet X *B. procumbens*).

Number of chromosomes in P.M.C.	23	24	25	26	27	28	29	30	31	32	33	34	35	36	Total
Number of P.M.C. containing corresponding chromosome number	5	3	0	5	2	6	2	4	1	2	2	1	0	4	37

The number of chromosomes in P.M.C. at the first anaphase and at interkinesis varied from 23 to 36 (Table 2). In the majority of cells 23 to 30 chromosomes were observed instead of the 18 chromosomes which are normally expected in a diploid at this stage. This means that there were 5 to 18 chromosomes in excess. These excess chromosomes were derived from univalents which divided in the first division.

Because of successful division and distribution of univalents, the interkinetic nuclei contained a high number of chromosomes (Table 3). Instead of 9 chromosomes in a diploid plant they contained 10 to 18 chromosomes. The majority of nuclei had

Table 3.—Number of Chromosomes in the Interkinetic Nuclei of an F₁ Hybrid (Turkish Wild Beet X *B. procumbens*).

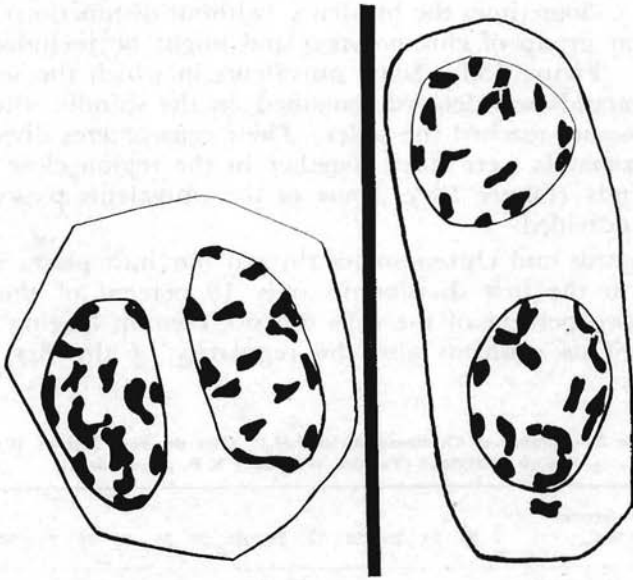| Number of chromosomes in the interkinetic nuclei	10	11	12	13	14	15	16	17	18	Total
Number of nuclei containing corresponding chromosome number	5	3	11	11	15	7	8	5	8	73

Figure 14. (left)—Interkinetic nuclei with 14:14 distribution X 3100. Figure 15. (right)—Interkinesis, 15:15 distribution: one nucleus with 15, another with 14 chromosomes and 1 chromosome in plasm. Derived from division of all chromosomes in the nucleus containing 3_{11} plus 12, X 3100.

12, 13 and 14 chromosomes. In some P.M.C. the distribution of chromosomes between two interkinetic nuclei was equal, for instance, 12:12, 13:13, 14:14 18:18 (Figures 14, 15). In the 14:14 distribution the 4 bivalents and all 10 univalents proceeded to the respective poles regularly. A distribution of 13:13 could occur when there was 3_{11} and 12_1 in the P.M.C. The 3 bivalents and 8 univalents divided and proceeded to the opposite poles. Of the remaining 4 univalents 2 moved undivided to 1 pole and 2 to another. The P.M.C. with the same number of bivalents, 3, and univalents, 12, could give rise to interkinetic nuclei with a 12:12 distribution in a case when from 12_1 only 6 divided and proceeded to the opposite poles and from the remaining 6_1, 3 undivided univalents reached one pole and 3 others reached another pole. Different numbers of chromosomes in interkinetic nuclei showing equal distribution are conditioned by different numbers of bivalents and different numbers of divided univalents in corresponding P.M.C. The lagging chromosomes and the unequal distribution of undivided univalents will change, of course, this equal distribution and interkinetic nuclei will occur with 12:13, 12:15 and other chromosome distributions.

Some P.M.C. contained at interkinesis 2 nuclei with 18 chromosomes in each (Figure 16a, b, c). Such nuclei arose in
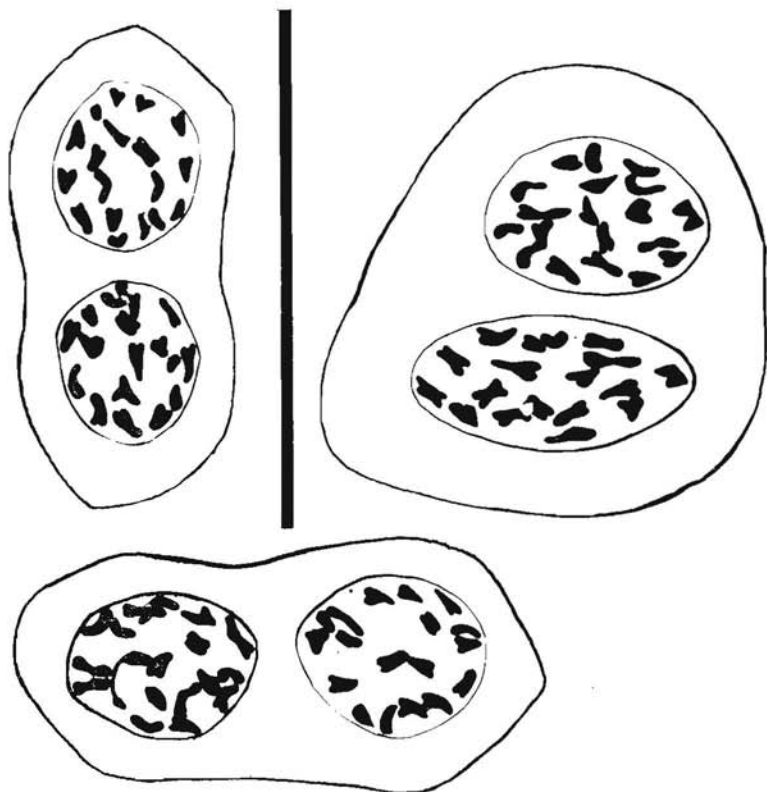
Figure 16.—a (upper left), b (upper right), c (lower left). P.M.C. containing 2 restitutional nuclei with 18:18 distribution at interkinesis X 3100.

the asynaptic P.M.C. with 18 univalents all of which divided and their chromatids proceeded to the opposite poles. Although the chromosomes in such nuclei showed split ends as usual at interkinesis, most of them did not undergo the second division. Occasionally the cells with one large restitutional nucleus containing 18 chromosomes were also observed at diakinesis (Figure 17).

Second Meiotic Division

In the second metaphase and anaphase a few chromosomes divided. The division and separation of the chromosomes were irregular, the chromosomes were scattered over the spindle and did not reach the poles at the same time (Figure 18). More lagging chromosomes were observed in the second division than in the first. In the tetrad stage only 17.5 percent of the cells did not contain chromosomes lagging in the cytoplasm.
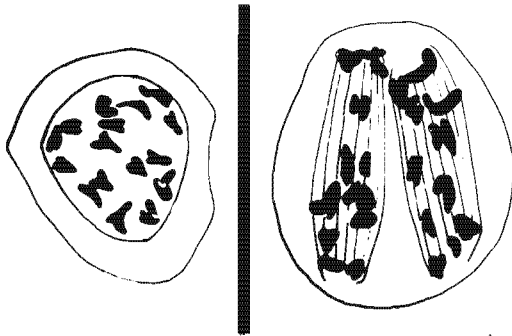
Figure 17. (left)—P.M.C. containing restitutional nucleus with 18 chromosomes at interkinesis X 3100. Figure 18. (right)—Second anaphase; irregular moving of chromosomes X 3100.

The number of chromosomes in P.M.C. at the second anaphase and in the tetrad stage varied from 27 to 42 (Table 4). The majority of cells contained 33 to 36 chromosomes. If we compare the number of chromosomes in P.M.C. after the first division (where the number of chromosomes in the cells did not exceed 36) with the number of chromosomes after the second division, it is obvious that in the second division most of the chromosomes which divided were partners of bivalents and the univalents which did not divide in the first division. Only a few univalents divided the second time.

The number of chromosomes after two divisions cannot exceed the somatic number of chromosomes unless some chromosomes divide equationally the second time. In the hybrid studied some P.M.C. at the tetrad stage contained 41 and 42 chromosomes providing that some univalents divided again in the second division.

The number of chromosomes in the nuclei at the tetrad stage varied from 1 to 20 (Table 5). In the majority of nuclei the number of chromosomes was lower than 9, but some nuclei carried a haploid, 9, and a diploid, 18, number of chromosomes.

In the tetrad stage in some locules of anthers normal tetrads with 4 nuclei prevailed; some P.M.C. contained 5 nuclei (pentads). In other locules most P.M.C. consisted of hexads or contained 7 or 8 nuclei. Rarely did the number of nuclei reach 10. The size of nuclei varied greatly depending on the number of chromosomes. In many sections of locules 1 to 3 dyads and sometimes a triad could be observed (Figure 19). The nuclei in dyads usually contained 9, 12, 13, 14, 15 and 16 chromosomes, i.e., the number of chromosomes typical of the interkinetic nuclei. This chromosome number indicates that in some P.M.C. the

Table 4.—Number of Chromosomes in P.M.C. after the Second Meiotic Division in an F₁ Hybrid (Turkish Wild Beet × B. procumbens).

Number of chromosomes in P.M.C.	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	Total
Number of P.M.C. containing corresponding chromosome number	2	3	3	2	2	3	7	5	6	1	2	1	1	1	2	1	44

Table 5.—Number of Chromosomes in the Nuclei at the Tetrad Stage in an F₁ Hybrid (Turkish Wild Beet × B. procumbens).

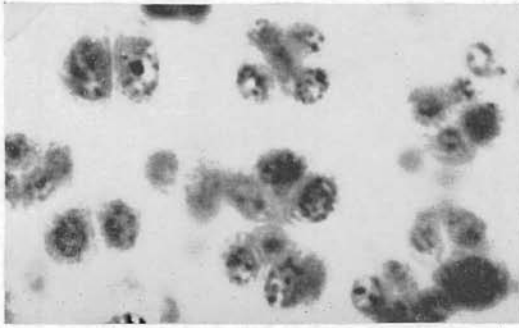| Number of chromosomes in the nuclei at the tetrad stage	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total
Number of nuclei with corresponding chromosome number	4	20	9	14	15	20	28	23	13	8	6	7	6	2	2	2	2	5	2	2	185

Figure 19.—Locule of anther containing dyads, tetrads, pentads, etc. X 1079.

second division did not take place. The same appearance which was highly expressed in the "webbiana hybrids" is only slightly expressed in the "procumbens hybrid." In some dyads the nuclei contained higher chromosome numbers.

What gametes of F_1 hybrids were really viable can indicate the number of chromosomes in the first backcross progeny (F_1 X 2n *B. vulgaris*). All first backcross hybrids were triploids or aneuploids approaching to triploids. They contained 26, 27, 28 and 30 chromosomes. Most of the hybrids were triploids with 27 chromosomes. They arose from asynaptic restitutional nuclei with 18 chromosomes. The plants with 26, 28 and 30 chromosomes arose from gametes which carried 17, 19 and 21 chromosomes, correspondingly.

The gametes with 17 chromosomes could arise from an asynaptic cell in which 17 of 18 univalents divided and proceeded to the respective poles and 1 univalent moved to either pole undivided, or if 2 undivided univalents proceeded to 2 different poles. Gametes with 17 chromosomes could originate also from the cells with 1 bivalent if the partners of the bivalent and the chromatids of 16 divided univalents proceeded to different poles or in the case of non-disjustion when 1 bivalent reached one pole undivided while 16 univalents divided and proceeded to different poles.

The origin of gametes carrying 19 and 21 chromosomes can be explained only by the assumption that the second division started in some of the restitutional nuclei, but this division was not complete (because of the incompleteness of the spindle) and after a certain number of univalents divided the whole set of chromosomes was included in one nucleus. In cases where gametes carried 19 chromosomes, 1 chromosome of 18 had to divided the second time. In cases of 21 chromosomes, 3 of 18 chromosomes in the restitutional nucleus divided the second time.
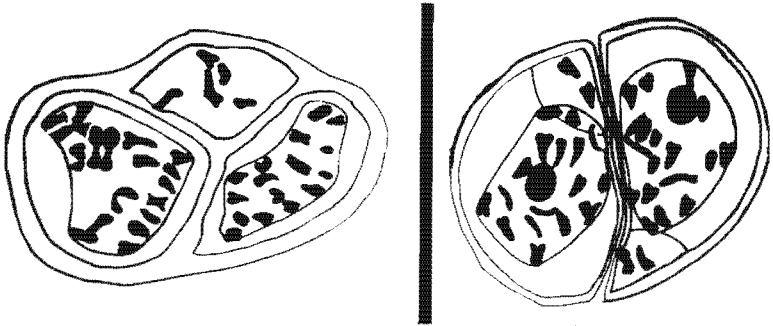
Figure 20. (left)—A triad with 20 chromosomes in one nucleus, 16 chromosomes in another and 5 chromosomes in plasm, derived from second incomplete division in both restitutional nuclei X 3100. Figure 21. (right)—A dyad containing 18 chromosomes in each nucleus and 4 chromosomes in plasm, derived from incomplete second division in both restitutional nuclei X 3100.

In the locules of anthers at the tetrad stage one could observe dyads or triads, the nuclei of which contained 19, 20 and 21 chromosomes. Figure 20 represents a triad with 20 chromosomes in one nucleus, 16 in another and 5 chromosomes thrown in the plasm which formed a little cell without formation of a nucleus. This triad arose from interkinetic P.M.C. containing 2 restitutional nuclei with 18 chromosomes in each. In the first nuclei 2 chromosomes divided the second time, but because of incompleteness of the second meiotic division they remained in the same nucleus. In the second nucleus 3 chromosomes divided a second time giving rise to 21 chromosomes from which 16 remained in the nucleus and 5 were thrown in the plasm. In Figure 21 a dyad is shown in which the second division started in both restitutional nuclei. In both nuclei 2 chromosomes divided the second time giving rise to 20 chromosomes from which 2 were thrown into plasm and formed little cells in both components of the dyad. Both restitutional nuclei contained 18 chromosomes as before, but in 1 nuclei among 18 chromosomes 4, and in another 2, thin chromosomes could be observed. These thin chromosomes certainly represent the chromatids derived after the second division of univalents. The chromosomes thrown into cytoplasm were not the chromosomes which underwent the second division. The division of a chromosome and its orientation and movement on the spindle and, consequently, the possibility of being eliminated in the plasm are independent processes. The division of a chromosome is an autonomous process stipulated by the division of the chromonema and of the centromere, while the movement on the spindle is conditioned by the

orientation of centromeric chromomeres of its centromere. Consequently, the gametes with 18 chromosomes which arose from restitutional nuclei will not always carry 9 chromosomes of *B. vulgaris* and 9 chromosomes from wild species. Their chromosome set may include some homologous chromosomes of either species.

In this way all the offspring of F_1 plants were obtained from gametes which arose from the asynaptic restitutional nuclei.

Conclusion and Discussion

The somewhat higher degree of chromosome pairing and higher chiasma frequency in the semi-fertile hybrid Turkish wild beet X *B. procumbens*, as compared with the sterile "webbiana hybrids," could not be responsible for the higher fertility.

The semi-fertility of the hybrid with *B. procumbens* was due to a rare and important pecularity—the formation of restitutional nuclei because of the regular division and distribution of univalents.

Formation of restitutional nuclei was described by von Rosenberg (30, 31) for *Hieracium laevigatum*, *H. lacerum* and *H. boreale*, and by Karpechenko (14) for *Raphano-brassica* hybrids. Restitutional nuclei were formed in *Hieracium* species: (a) when the nucleus entered interkinesis directly from diakinesis without formation of the spindle and (b) because of variation of "semi-heterotypic division" when the spindle disappeared after the univalents were distributed between the poles and the whole set of chromosomes was surrounded by the nuclear membrane.

In *Raphano-brassica* hybrids obtained by Karpechenko restitutional nuclei were formed because the incomplete development of the spindle prevented distribution of the univalents between poles at anaphase and the whole set of chromosomes was included in one nucleus.

The hybrids between the Turkish wild beet and *B. procumbens* revealed a new way by which restitutional nuclei may be formed, namely, by the regular division in an asynaptic P.M.C. of all the univalents during the first meiotic division.

The best explanation of the way by which the univalent may divide in the first meiotic division was given by Ostergren (27). According to his hypothesis the poleward factor -a may change the one-sided localization of centromeric chromomeres in the centromere of the univalent into the opposite one. Polarization of the centromeres leads to auto-orientation of the univalent and sufficient poleward attraction pulls the daughter chromatids

connected only by the interior zone of the centromere to the opposite poles.

Only diploid gametes containing a complete haploid set of chromosomes of both species involved in hybridization or the gametes with the number of chromosomes approaching to it were viable. Haploid gametes with 9 chromosomes were not viable because of the composition of their chromosome set. They contained variable numbers of chromosomes from both species, but this number was always much lower than the haploid number of either species, for instance, 4 chromosomes from one species and 5 chromosomes from another. Therefore, their physiological activity was limited.

Hybrids derived from two diploid species were unable to survive on the diploid base. To produce progeny the hybrids themselves increased the number of chromosomes and shifted to a higher ploidy level.

The origin of the first-backcross generation from the restitutional gametes leads to an important conclusion that in spite of the possibility of crossing over between associated chromosomes of different species and transmission of genes which provide for nematode resistance from wild species to the chromosomes of *B. vulgaris*, the progeny of the F_1 plant carried the chromosomes of wild beets, but not the chromosomes with segmental interchanges. This does not mean, of course, that the segmental interchanges between the chromosomes of different species may not occur in the next hybrid generation.

To overcome the barrier of sterility in interspecific hybrids between *B. vulgaris* and species of section *Patellares* it might be desirable to obtain hybrids on a higher ploidy level.

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