

# CYTOLOGICAL AND GENETIC STUDIES ON FRAGARIA

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## INTRODUCTION<sup>1</sup>

The eleven species and twelve cultivated varieties of the genus *Fragaria* which were included in this investigation may be divided into five different groups:

Group 1.—The European type, represented typically by the species *F. vesca* which is the most common wild species in Europe and is also widely distributed over NORTH AMERICA and western South America.

*Fragaria vesca* L.

*F. americana* Britton.

<sup>1</sup> Several genetic investigations on the genus *Fragaria* were started at the BUSSEY INSTITUTION in 1921 with material furnished by Mr. G. M. DARROW of the UNITED STATES DEPARTMENT OF AGRICULTURE. Mr. DARROW has very kindly visited the laboratory several times, has identified and checked the living material, and has made many suggestions of great value during the progress of the work.

In 1924, Mr. K. ICHIJIMA undertook to make a cytological examination of all of the pure species and of the most interesting hybrids then on hand. This study he finished in the spring of 1925, but was unable to make a detailed report at that time because of a long illness. In the winter of 1925-1926, however, the present paper was written, and left to the undersigned to edit.

In the meantime, a paper entitled "Chromosomes and their significance in strawberry classification," by Dr. A. E. LONGLEY, was published in the *Journal of Agricultural Research* 32: 559-568, issued March 15, 1926. The data reported here corroborate many of Dr. LONGLEY's results and furnish certain additional facts. Both papers gain in value from having been written simultaneously and independently.

E. M. EAST

*F. californica* Cham. & Schlecht.

*F. mexicana* Schlecht.

*F. Helli* Holz.

*F. bracteata* Heller.

Group 2.—The Haut-bois type, represented by *F. elatior*, indigenous to Europe.

*Fragaria elatior* Ehrh.

Group 3.—The American type, represented typically by the species *F. virginiana* which is very widely distributed in North America.

*Fragaria virginiana* Duchesne.

*F. glauca* Rydb.

Group 4.—The Chilean type, indigenous to the Pacific Coast of North and South America and represented by the species *F. chiloensis*.

*Fragaria chiloensis* Duchesne.

*F. cuneifolia* Nutt? from Oregon.

Group 5.—Certain cultivated varieties of a type often described as *F. grandiflora* in the Taxonomy of the genus.

Varieties used:

William Belt	La Pearl	Ettersburg
Champion Early	Clark's Seedling	Gardners
New York	Doctor Burrell	Progressive
	Chesapeake	Success

In addition to the above, the following hybrids were examined:

F<sub>1</sub> hybrids between the species—

*F. vesca* ♀ × *F. Helli* ♂

*F. vesca* ♀ × *F. americana* ♂

*F. Helli* ♀ × *F. americana* ♂

*F. bracteata* ♀ × *F. Helli* ♂ . . . . (type a)

*F. bracteata* ♀ × *F. Helli* ♂ . . . . (type b)

*F. glauca* ♀ × *F. virginiana* ♂

*F. bracteata* ♀ × *F. virginiana* ♂

*F. mexicana* ♀ × *F. virginiana* ♂

*F. bracteata* ♀ × *F. glauca* ♂

*F. americana* ♀ × *F. glauca* ♂

*F. grandiflora* var. *Dunlap* ♀ × *F. platypetala* ♂

RYDBERG's (1912) descriptions have been followed in making up the above list. The species which he designates as *F. Helli*, however, is merely a pink-flowered variety of *F. vesca*.

## METHODS

Maturation divisions occur very early in *Fragaria* flowers, and the chromosomes are very minute. For these reasons it was necessary to modify the cytological methods ordinarily in use in several particulars.

Flower buds were collected when about 1 mm in diameter, the calyx stripped off and fixed for 12 hours. For somatic chromosome counts, very young, thick root-tips from newly produced runners were found to be the most suitable material. As fixatives, Flemming's medium solution and chrom-acetic acid were found to be unsatisfactory. Bouin's solution as modified by ALLEN (1916) gave much better results, except in the hybrid between *F. bracteata* and *F. Helleri*, where straight Bouin's solution was used.

The material was washed 5 hours in water and then moved up through the alcohols. It was found necessary to transfer slowly to xylol, keeping the material 4 hours each in various percentages beginning with 15 percent.

The paraffine blocks cut very satisfactorily and the material examined unstained was not shrunken. But if care was not taken in staining, shrinkage was quite marked.

The best method of staining was found to be the use of 4 percent iron-alum as a mordant for only 2 hours, followed by transfer to haematoxylin for 3 hours. No destaining was necessary.

## CHROMOSOME DETAILS

a. *Chromosomes in Group 1—the European type*

All of the six species of this group which were investigated have 7 pairs of chromosomes in the pollen mother cells. No irregular behavior of the chromosomes in the course of the heterotypic division was observed. In the earliest stage the pollen mother cells are closely packed in the anther cavity. As the meiotic division proceeds the cells gradually begin to separate from one another. After the synapsis there is generally a distinct spireme stage in which the double thread-like nature can clearly be seen; but no second contraction has been observed. At early diakinesis the paired chromosomes are often unequal in size (figure 1), but gradually contract into a uniform size in the later stage. At this stage the 7 pairs of chromosomes can be seen clearly (figure 2). When the paired chromosomes become almost spherical the nucleolus and nuclear membrane disappear. The chromosomes then gather toward the center and arrange themselves on the equatorial plate. It is here at the metaphase and at the late anaphase that the chromosomes can be most readily counted (figures

3, 4). After the telophase and the subsequent resting stage the cells begin the homeotypic division which is carried out in the regular manner (figure 5), the resulting tetrads being quite normal. The 14 somatic chromosomes are seen clearly and may be counted readily at the metaphase of the root-tip cell (figure 6). The somatic chromosomes appear in a characteristic figure and are all separated from one another in well fixed preparations.

b. *Chromosomes in Group 2—The Haut-bois type*

In the single species, *F. elatior*, belonging to this group, the gametic number of chromosomes in the pollen mother cell is 21. Figure 7 shows the chromosomes in the heterotypic metaphase. There is no irregular behavior of the chromosomes during the whole process of maturation which indicates the stability of the species cytologically.

c. *Chromosomes in Group 3—The American type*

Two species of this type were investigated, *F. virginiana* and *F. glauca*. Both of them possess 28 chromosomes as the gametic number. Owing to the minute size of the pollen mother cell it is quite difficult to count the chromosomes when such large numbers are present. After a number of experiments it was found that counts could best be made in the late diakinesis of the heterotypic division (figure 8). The somatic chromosomes are closely and irregularly packed in the small root-tip cells. The somatic number of chromosomes could not be determined definitely although it appears to be approximately 56.

d. *Chromosomes in Group 4—The Chilean type*

*F. chiloensis* and *F. cuneifolia* both show 28 chromosomes as the gametic number. The behavior of the chromosomes is quite regular throughout both the heterotypic and the homeotypic divisions. No abnormalities in chromosomal behavior were found (figures 9, 10).

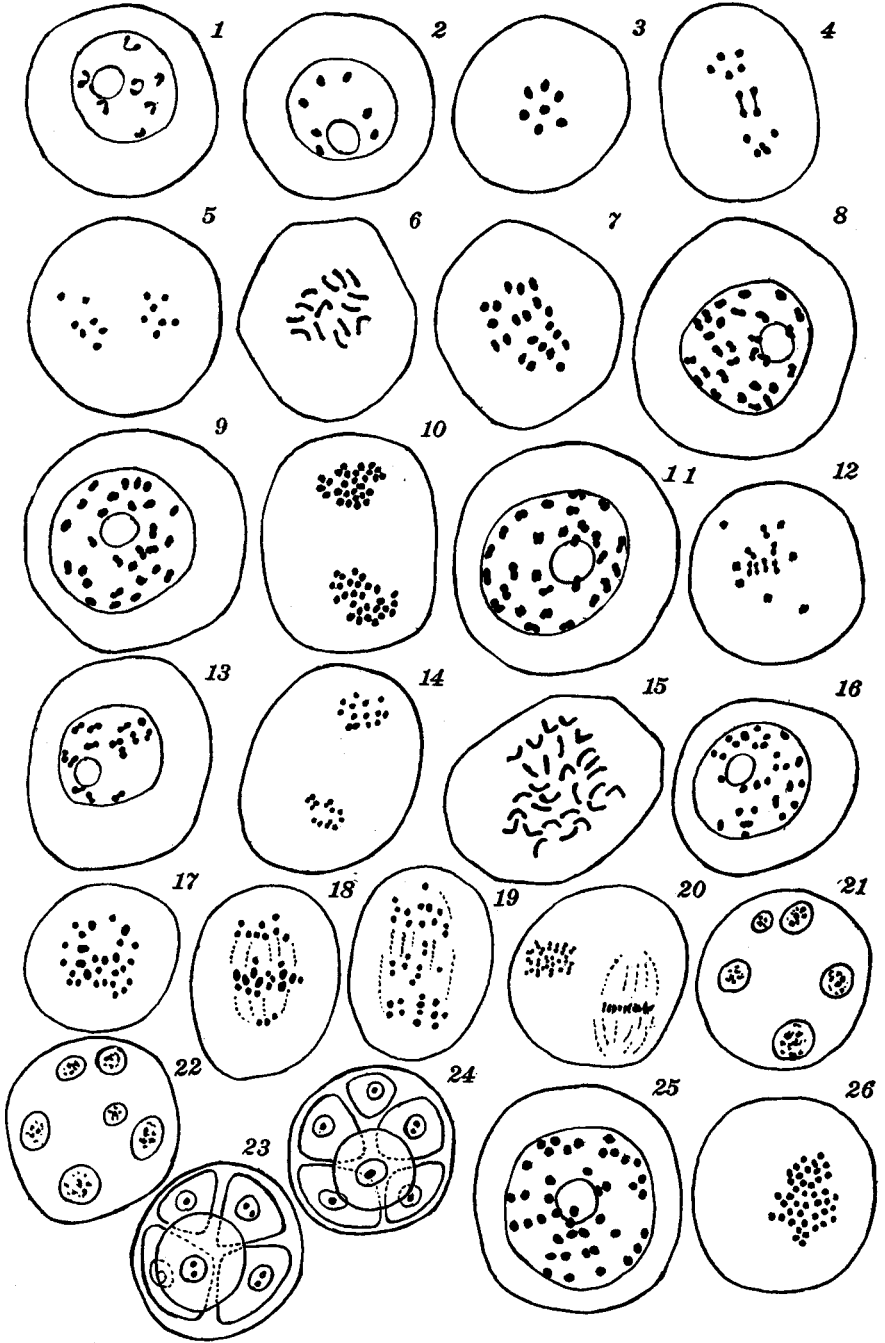
e. *Chromosomes in Group 5—The Cultivated variety type*

Twenty-eight pairs of chromosomes were in found the pollen mother cells of each of these varieties. Abundant pollen grains are produced and the process of reduction appears to be regular. There is little difference in the chromosome behavior between this type and the American type, both of which have the same number of the chromosomes (figure 11).

## PLATE I

- FIGURE 1.—The 7 paired chromosomes at diakinesis in *Fragaria vesca* var.  
FIGURE 2.—A later stage of the same.  
FIGURE 3.—Metaphase of heterotypic division.  
FIGURE 4.—Late anaphase.  
FIGURE 5.—Metaphase of homeotypic division.  
FIGURE 6.—Metaphase of division in the root-tip cell (14 somatic chromosomes).  
FIGURE 7.—Metaphase showing 21 pairs of chromosomes (*F. elatior*).  
FIGURE 8.—Diakinesis showing 28 paired chromosomes (*F. virginiana*).  
FIGURE 9.—The same stage in *F. chiloensis*.  
FIGURE 10.—Homeotypic metaphase of the same.  
FIGURE 11.—Diakinesis showing 28 paired chromosomes (a cultivated variety).  
FIGURE 12.—Metaphase of the F<sub>1</sub> hybrid of *F. bracteata* × *F. Helli*, showing two different groups of chromosomes.  
FIGURE 13.—Diakinesis of the same (14 paired chromosomes).  
FIGURE 14.—Homeotypic metaphase of the same (14 chromosomes).  
FIGURE 15.—Root-tip cell of the F<sub>2</sub> plant of *F. bracteata* × *F. Helli*, showing 28 somatic chromosomes.  
FIGURE 16.—Diakinesis of reduction division of F<sub>1</sub> of *F. bracteata* × *F. virginiana* showing 7 bivalents and approximately 21 univalents.  
FIGURE 17.—Metaphase of the same.  
FIGURE 18.—Early metaphase of the same,—univalents lagging behind.  
FIGURE 19.—Late anaphase of the same.  
FIGURE 20.—Homeotypic metaphase of the same.  
FIGURES 21–24.—Abnormal tetrad formations of the F<sub>1</sub> of *F. bracteata* × *F. virginiana*.  
FIGURE 25.—Diakinesis in *Duchesnea indica*.  
FIGURE 26.—Metaphase of the same.

Plate I



f. *Chromosomes in F<sub>1</sub> hybrids*

F<sub>1</sub> hybrids between species of the European type, such as *F. vesca* × *F. Helleri*, *F. vesca* × *F. americana*, *F. Helleri* × *F. americana*, and *F. bracteata* × *F. Helleri* possess 7 pairs of chromosomes. Ordinarily there is no irregular behavior of the chromosomes, but an interesting exception has been found in the F<sub>1</sub> of one such cross. An individual in one of the populations of F<sub>1</sub> hybrids between *F. bracteata* × *F. Helleri* was found showing 14 pairs of chromosomes (figure 13) in the diakinesis of the pollen mother cell. Presumably the 7 chromosomes contributed by the bracteata parent and the 7 chromosomes contributed by the *Helleri* parent had doubled during some abortive attempt at cell division. Figure 12 shows one group of 7 chromosome pairs in the heterotypic metaphase which is easily distinguishable from a second group of 7 chromosome pairs. In the homeotypic division 14 chromosomes as a haploid number may be counted clearly (figure 14). The behavior of the gametic chromosomes seems to be normal. The F<sub>2</sub> hybrids obtained by selfing this plant showed 28 chromosomes in root-tip preparations (figure 15). The writer has not been able to investigate conditions in the pollen mother cells of the F<sub>2</sub> plants.

In F<sub>1</sub> hybrids between the species of the American type, for example *F. glauca* × *F. virginiana*, no abnormal chromosome behavior was observed. But hybrids between species of the different types, for example American type ( $x=28$ ) × European type ( $x=7$ ), which can be obtained only with difficulty, show many irregularities. Among a population of F<sub>1</sub> hybrids between *F. bracteata* × *F. virginiana* some individuals were found having 28 chromosomes in the heterotypic metaphase, of which 7, presumably bivalents, appear to be larger than the other 21 (figure 17). In the early metaphase there are approximately 28 chromosomes of which 7 bivalents are on the equatorial plate, while 21 univalents are found on the spindle (figure 18). Figure 19 shows 7 bivalents which, having divided, are pushing toward the poles, while the 21 univalents are lagging in their approach to the poles. It is obvious that each of the bivalents divides before moving to the poles, but the univalents pass at random to either pole without dividing. Owing to the minute size of the chromosomes, it is quite difficult to count the number of the bivalents and univalents in the heterotypic division. In figures 21–24 one may observe clearly the irregularity of the tetrad formation, a consequence to be expected from the previous behavior of the chromosomes. This irregularity of tetrad formation supplies the cytological basis of the practically complete sterility of these hybrids.

## DISCUSSION

a. *Polyploidy in Fragaria species*

The foregoing investigation gives us another case of possible polyploidy in plant species. If the basic haploid chromosome number is taken to be 7, various *Fragaria* species may be interpreted as diploid, tetraploid, hexaploid and octaploid forms, that is, as forms having 7, 14, 21 and 28 pairs of chromosomes. Furthermore, *Duchesnea indica*, which once was classified as a species of *Fragaria* is found to have 42 pairs of chromosomes; and since it may be crossed with *Fragaria vesca*, it may possibly be regarded as a dodecaploid *Fragaria* (figures 25, 26).

The occurrence of chromosomes in a progressive arithmetical series has been found in several other genera. In *Chrysanthemum* TAHARA (1915, 1921) found species with haploid chromosome numbers 9, 18, 27, 36 and 45. In *Viola*, according to MIYAJI (1913) and MARCHAL (1920), there are species with 6, 10, 12, 24 and 36 haploid chromosomes. In *Hieracium* ROSENBERG (1917) found somatic numbers 18, 27, 36 and 54. In *Crepis* there are species with 6, 8, 10, 16, 18, 24 and 42 somatic chromosomes (ROSENBERG 1918, 1920). In *Triticum* SAKAMURA (1918, 1920) and SAX (1921, 1922) state that one species has 7 chromosome pairs, four species have 14 pairs, and three species have 21 pairs. In *Campanula* MARCHAL (1920) found 17, 34 and 51 haploid numbers. In *Rubus* LONGLEY (1924) found 7, 14 and 21 chromosome pairs. TÄCKHOLM (1920, 1922) and BLACKBURN and HARRISON (1921), investigating the genus *Rosa*, have established the most remarkable series with forms having 14, 21, 28, 35, 42 and 56 somatic chromosomes.

The European type of *Fragaria* which has the haploid chromosome number 7 may perhaps be regarded as the most primitive species of the genus. This species not only possesses the lowest chromosome number, but also its morphological characters appear to be the most primitive when compared with those of *F. elatior*, *F. virginiana*, and *F. chiloensis* which more closely resemble the horticultural varieties having higher chromosome numbers and more complex morphological characters. Furthermore the species of the European type are hermaphroditic, while certain species of the American type and of the Chilean type are partially dioecious.

No wild species were found possessing 14 pairs of chromosomes. Evidence of tetraploidy in *Fragaria*, therefore, rests upon a single case obtained in the cross between *F. bracteata* ( $x=7$ ) and *F. Helleri* ( $x=7$ ). The ordinary  $F_1$  plants obtained from this cross were intermediate



## PLATE II

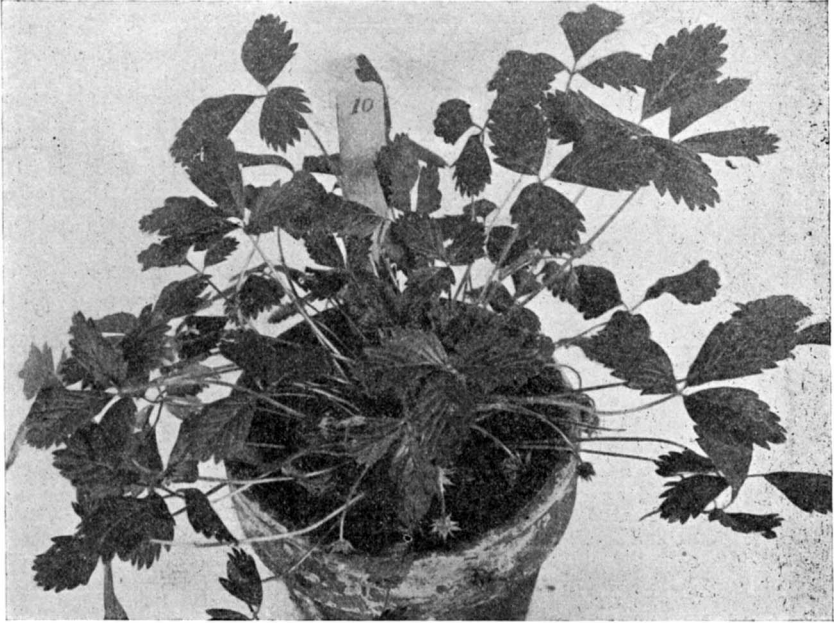


FIGURE A.—*F. bracteata*. A species of the European type.

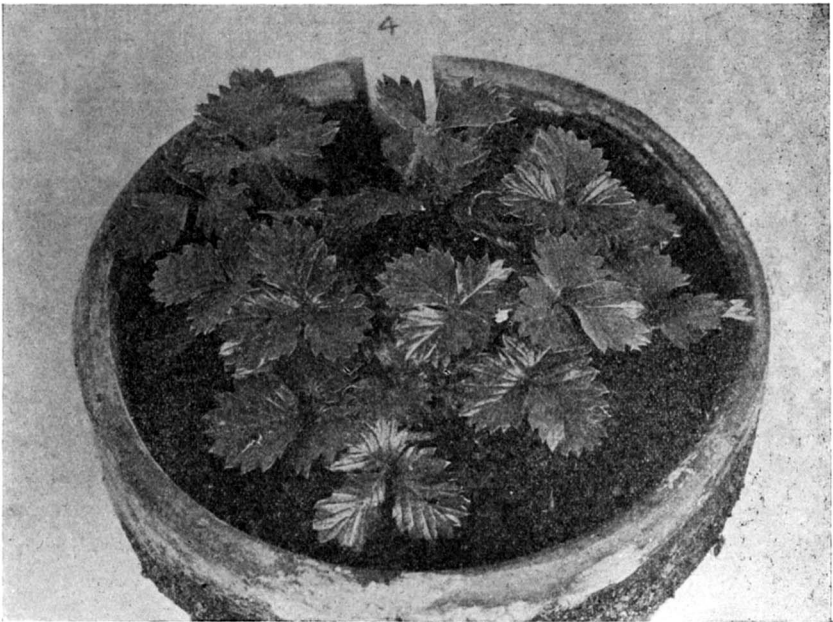


FIGURE B.—Hybrid, type b, of *F. bracteata* × *F. Helleri*.

## PLATE III



FIGURE A.—*F. virginiana*, a typical American type.



FIGURE B.—Hybrid of *F. bracteata* × *F. virginiana*.

between the parents except for flower color, the pink flower characteristic of *F. Helleri* being dominant. Nine of these ordinary hybrids (type a) were investigated cytologically and were found to have 7 pairs of chromosomes. The behavior at reduction was normal. The exceptional individual had 14 pairs of chromosomes, and instead of segregating and recombining the characteristics of the parental species as did the ordinary  $F_2$  populations, it produced a uniform population of a new type. The leaves were larger, thicker and more crenate than either of the parents. The petals also were thicker and the pollen grains were decidedly larger than in the forms from which it arose (Plate 2, A and B). The root-tip cells of seven individuals were examined, and in each case 28 chromosomes were found. These plants may therefore be considered to be representatives of a new species.

Several other cases of plant tetraploidy which occurred under observation have been reported. *Oenothera gigas*, a mutant form of *O. Lamarckiana*, is a well known case (LUTZ 1907). In *Primula* DIGBY (1912) found a tetraploid form with 36 somatic chromosomes, and in *Datura* a tetraploid form has been found which has 48 somatic chromosomes instead of the 24 of the original species (BLAKESLEE, BELLING and FARNHAM 1920). In *Nicotiana*, CLAUSEN and GOODSPEED (1925) produced a true-breeding hybrid between *glutinosa* ( $x=12$ ) and *tabacum* ( $x=24$ ) which possessed 36 pairs of chromosomes.

#### b. *Species hybrids*

In the  $F_1$  hybrids of *F. bracteata* ( $x=7$ ) $\times$ *F. virginiana* ( $x=28$ ), as previously stated, there are 7 bivalents and 21 univalents in the heterotypic spindle. In the reduction division the bivalents divide normally while the univalents pass at random, without dividing, to either pole. The behavior of these chromosomes in the second division has not been clearly observed. But the subsequent tetrad formation seems to be much disturbed, because the majority of the pollen mother cells form three, five or six daughter nuclei instead of the normal four, none of which are able to become normal mature pollen grains. The irregularities of the chromosome behavior show the cytological basis of the sterility of the hybrid. This view has been borne out in several other species hybrids (See Plate 3, A and B).

Similar chromosomal irregularities in the heterotypic division of hybrids have been investigated in many other species. In *Drosera* ROSENBERG (1909) has investigated a hybrid between a species with 10 haploid and a species with 20 haploid chromosomes which shows

10 bivalent and 10 univalent chromosomes at diakinesis. GATES (1909) found the chromosome number of the  $F_1$  of certain *Oenothera* crosses to be 20 or 21, the sum of the gametic number of the parents. In an  $F_1$  hybrid of *Hieracium auricula* ( $x=9$ ) $\times$ *H. aurantiacum* ( $x=18$ ), 9 bivalents and 8 or 9 univalents were found in the reduction division (ROSENBERG 1917). In *Triticum* KIHARA (1919) described 14 bivalents and 7 univalents in the heterotypic prophase of the  $F_1$  hybrid *T. polonicum* ( $x=14$ ) $\times$ *T. spelta* ( $x=21$ ). YASUI (1921) found a similar chromosome behavior in *Papaver* hybrids. TÄCKHOLM (1920, 1922) found that species of the Canina section in *Rosa* have usually 7 bivalents with 14, 21 or 28 univalents in the reduction division. SAX (1922) reports that in the  $F_1$  of *Triticum monococcum* ( $x=7$ ) $\times$ *T. turgidum* ( $x=14$ ), there are 7 bivalents and 7 univalents in the heterotypic division; and the  $F_1$  of the Emmer group ( $x=14$ ) $\times$ the Vulgare group ( $x=21$ ) shows 14 bivalents with 7 univalents in the first meiotic division, resulting in microspores having from 14 to 21 chromosomes.

## SUMMARY

1. The *Fragaria* species investigated may be divided according to their chromosome number into four groups having 7, 14, 21, and 28 chromosomes respectively.

2.  $F_1$  hybrids between different representatives of the American type have 28 gametic chromosomes.

3.  $F_1$  hybrids between different representatives of the European type have 7 gametic chromosomes, with the exception of the following case.

4. The cross of *F. bracteata* $\times$ *F. Helli* produced, in one case, a tetraploid form, having 14 gametic chromosomes, of which 7 are contributed by one parent and 7 by the other parent. The  $F_2$  plants which were obtained by selfing this tetraploid form have 28 somatic chromosomes in the root-tip cells, and possess distinct morphological characteristics which have not been observed in any other species. The type may be regarded as a new species.

5. In the  $F_1$  hybrid of *F. bracteata* $\times$ *F. virginiana* 7 bivalents and approximately 21 univalents were found. The bivalents divide normally, but the univalents pass at random to either pole without dividing. The tetrad formation seems to be greatly disturbed, consequently there are no normal mature pollen grains found.

6. *Duchesnea indica* is found to have 42 gametic chromosomes; and judging from possibility of crossing with *F. vesca*, it may possibly be considered to be a dodecaploid form of *Fragaria*.

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All drawings were made with the aid of the camera lucida. All figures were drawn from single sections. The lenses used were a 1.5-mm. Zeiss apochromatic objective and a No. 10 compensating ocular.