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In a preliminary note (Hollingshead, 1928) the occurrence of two haploid plants of *Crepis capillaris* ($n = 3$) was reported, in populations of *C. capillaris—C. tectorum* F_1 hybrids. In the course of the same experiment three other similar haploids were found. Shortly after the writer found the first two haploids, Dr. M. Navashin, working in the same laboratory, found a similar one in the progeny of a *C. capillaris—C. neglecta* F_1 hybrid which had been open-pollinated (unpublished data). Unfortunately it died at the rosette stage. The same summer another *C. capillaris* haploid was found by Mr. C. W. Haney of the laboratory staff in a population resulting from crossing *C. capillaris* and *C. setosa,* and its haploid nature was established by the writer. Four of the writer's five haploids reached maturity and these with the one obtained by Mr. Haney furnished material for meiotic as well as mitotic studies. Observations were also made on the morphology and fertility of these haploids. The results of the studies differ in certain aspects from observations on haploid plants of other genera hitherto reported by various writers.

Acknowledgments

Most of the investigation was carried out while the writer was research assistant to Professor E. B. Babcock, and her indebtedness to him for providing the opportunity of pursuing the study and for his continuous interest and helpful advice is gratefully acknowledged. Thanks are also due Mr. C. W. Haney for permission to include in the study the haploid found by him.

OCCURRENCE AND APPEARANCE OF THE HAPLOID PLANTS

The haploids developed from apparently normal achenes produced on heads of *C. capillaris* which had been emasculated and pollinated with pollen of another *Crepis* species, as described by Hollingshead (1930*b*). Five of them appeared in populations of *capillaris-tectorum* hybrids totaling over three thousand plants in an experiment extending over two years, and the sixth arose from one of two achenes produced on a *C. capillaris* head pollinated with pollen of *C. setosa*. Both *tectorum* and *setosa* have four pairs of chromosomes.

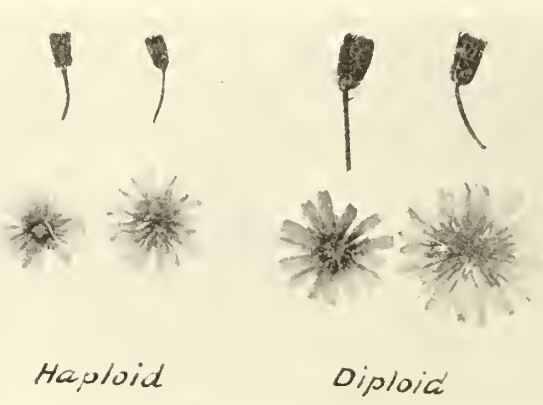

Fig. 1. Buds and heads from haploid and diploid *Crepis capillaris* plants. Natural size.

Attention was drawn to the haploids first determined by their appearance and by the fact that one of them was a viable plant in a population of hybrids which were dying at the cotyledon stage (Hollingshead 1930*b*). The rosettes, even at an early stage, were smaller, more compact, and flatter than normal ones. The leaves were smaller and the margins were less deeply indented, as shown in plates 6*a* and *b*. Chromosome counts from root tips established their haploid nature, and the other haploids were then picked out by their similar appearance, or in one case by flower size and sterility.

In habit and leaf shape, the mature plants resembled reduced diploids with fewer leaves. The branches tended to be slender and

usually the first branch emerged from the side of the crown rather than from the apex, as normally occurs. Plates 7 and 8 show mature diploid and haploid plants.

The haploid flower buds and heads were smaller than diploid ones (fig. 1). In a few instances only short rudimentary anther tubes were developed. The pollen was not pushed out of the anther tube by the elongating pistil at maturity as normally occurs, consequently the usual way of obtaining pollen for examination—dusting an albumen-coated slide with an opened flower head—failed on this account with haploid heads. It was necessary to remove the anther tubes and slit them open to free the pollen. The grains thus obtained were scant in number and the proportion of normally developed ones varied noticeably from floret to floret but it was always very small. The abnormal ones were small and faintly, or not at all, stained with aceto-carmine.

In the preliminary report it was stated that diploid areas were found in the roots of the haploid plants and the possibility was mentioned that parts of the plants above ground would be diploid and give rise to fertile branches. This possibility was realized. The first haploid to mature (28H.149–8) produced, early in its maturity, a tall branch bearing larger heads (pl. 8) and abundant pollen and, later, numerous achenes. Examination of the pollen mother cells (PMC's) revealed the diploid chromosome complex (below). It was presumed that the branch was wholly diploid until a haploid head appeared on it. The branch was possibly a diploid-haploid periclinal chimera, which would account for its larger size and the diploid nature of the reproductive organs. By a reorganization of tissue the haploid head could have been produced. This supposition is supported by the writer's impression (no measurements were made) that heads on a branch which appeared later were noticeably larger than those on the supposed chimeral branch. This later branch which arose from the same region of the crown produced only large heads with abundant pollen and more numerous achenes per head and was most probably wholly diploid.

Another haploid (29.036–9) produced three branches from one side of the crown, two of which had only diploid heads and the other had diploid, haploid, and chimeral diploid-haploid heads. This plant, grown in the unfavorable winter season, was attacked by mealy bugs and died before any achenes could be produced on the diploid heads. Two other haploid plants (28H.88–8 and 28H.54–19) produced chi-

meral diploid-haploid heads. Figure 2 shows haploid and diploid heads from plant 28H.149–8 and a chimeral head from 28H.88–8. Plant 28X.20–2 showed no evidence of diploidy above ground. Plant 28H.50–46 died before maturity. The classification of heads as diploid or haploid after the first large heads were shown to be diploid, with respect to PMC's at least, was made on size alone. No achenes were produced on any of the haploid heads nor did reciprocal crosses

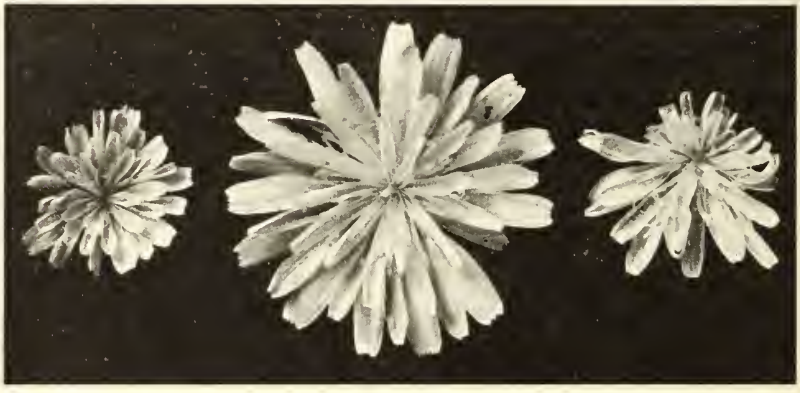

Fig. 2. Haploid and diploid heads from one haploid *Crepis capillaris* plant (28H.149–8) and a chimeral head from another (28H.88–8). Twice natural size.

with normal *C. capillaris* give any achenes. Possibly more extensive trials would have resulted in success, for there was, as noted above, a small amount of apparently good pollen. However, 130 well formed achenes were obtained from the chimeral(?) and diploid branches of plant 28H.149–8 which had been protected by a cage. The nature of *Crepis* pollen practically ensures selfing under such circumstances.

Since the diploid tissue arose from haploid, the pairs of chromosomes should be identical (barring mutation), and the progeny would be expected to be uniformly homozygous. In accord with expectation, the progeny were very uniform.

CYTOLOGICAL METHODS

Root tips were fixed in Navashin's chromacetic-formalin, flower buds in the same solution preceded by treatment for several minutes with Carnoy's solution and imbedding followed in the usual manner. Other flower buds were fixed in Carnoy's solution alone, run into 70 per cent alcohol and there kept until ready for use, and examined in aceto-carmine (technique, Hollingshead 1930*a*). Both methods gave good pictures of meiotic chromosomes but the latter caused more cyto-

plasmic shrinkage. PMC's from the paraffin material were smaller than those in aceto-carmine as shown by the figures. Haidenhain's haematoxylin was used for both root tips and PMC's and iodine-gentian-violet, too, proved to be a useful PMC stain. When the latter was used it was found better to lengthen the time in the stain to an hour or so. Otherwise J. Clausen's schedule (Babcock and Clausen, 1929) was followed.

The drawings were made with the help of a camera lucida using a Zeiss 90X apochromatic 1.3 objective and a 20X compensating eyepiece giving a magnification of approximately 3000 and were reduced one-third in reproduction. Except where otherwise stated they are from aceto-carmine material.

CYTOLOGICAL OBSERVATIONS

Diploid and haploid chromosome complexes from root tips are shown in figure 3. One member of each pair of chromosomes can be readily distinguished in the haploid complex. They behave normally in division. Similar complexes were observed in the walls of the ovaries of the haploid plants. The possibility that the chromosomes in haploids are smaller than those in diploids was mentioned in the preliminary note (1928). Further observations on this point were unconvincing.

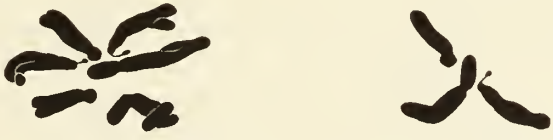

Fig. 3. Somatic metaphases from root tips of diploid and haploid *Crepis capillaris* plants.

As stated above, diploid cells and even wholly diploid root tips were found in the haploid plants. The number of root tips examined from each plant, the number in which some diploid metaphases were found, and the number in which only diploid metaphases were seen, is given in table 1. Of the 110 root tips of all plants examined, 28 showed at least one diploid metaphase in otherwise haploid tissue, and in 42 root tips only diploid metaphases were seen. Since the number of diploid metaphases observed in a single root tip varied from one to many, it is probable that some of the roots in which only haploid metaphases were seen actually had some diploid cells at a stage other

than metaphase. The diploid metaphases were usually to be found in one particular area in each of a series of many sections, but occasionally they were found in two such portions of the root tip. In some cases the diploid portion included all of the different root tissues. No divisions were seen which showed how the doubling of the chromosomes took place. Diploid cells were generally considerably larger than haploid ones. One instance of a group of tetraploid cells in an otherwise diploid root tip, and another of a wholly tetraploid root tip were observed.

TABLE 1

The Frequency of Diploidy in Root Tips of Haploid Plants

Plant Number	Number of root tips examined	Number with diploid and haploid metaphases	Number with only diploid metaphases
29.036-9	17	8	0
28H.50-46	14	2	8*
28H.54-19	19	3	6
28H.149-8	24	10	2
28H.88-8	36	5	26
Total	110	28	42

*One tip contained a group of tetraploid cells.

The meiotic material studied has included only stages from diaphase to tetrad formation. The writer is not unmindful of the value of a study of the prophases of these plants with three chromosomes but lack of time has prevented her from undertaking it.

Meiotic divisions of diploid *C. capillaris* were described in a recent paper (Hollingshead, 1930*a*). A single diploid metaphase (fig. 4*a*) is shown here for comparison with the haploid. Bivalents vary considerably in shape from cell to cell, but it is usually easy to distinguish them from univalents, which were shown to occur rather frequently in some plants of this species.

The outstanding feature of the meiotic behavior of the haploid plants is its variability and irregularity. As was expected, three single chromosomes appear at diaphase (fig. 4*b*) contracting as this stage proceeds, to more or less spherical bodies (fig. 4*c*), often to be distinguished from the nucleolus only by their darker staining capacity.

The disappearance of the nuclear membrane is usually closely followed by that of the nucleolus, and the chromosomes lie free in the cytoplasm. Spindle fibers appear, but only in extremely rare cases is a metaphase plate formed. Chance appears to determine the distribution of the three chromosomes which commonly move to the

Fig. 4. *a*, diploid *Crepis capillaris*, 1M with three bivalents; *b–f*, haploid, heterotypic division; *b*, early diaphase, *c*, late diaphase, paraffin material, *d–f*, illustrating random segregation of univalents.

poles without division, still retaining their spherical shape (fig. 4, *d–f*). One occasionally lies outside the spindle and may fail to reach either pole.

In many cases, however, division of the chromosomes occurs, still without the formation of a metaphase plate. This division may be initiated, as shown by the elongation and constriction of the chromosome, and rarely is even completed at late diaphase (fig. 5*a*). As this

and later figures show, division of the chromosomes within a cell does not always proceed synchronously. Usually, however, the division begins later, and the chromosomes in the shape of attached twin spheres pass irregularly to the poles (fig. 5, *b*, *c*) or one may be left out of the spindle and fail to reach a pole, giving rise to three iso-

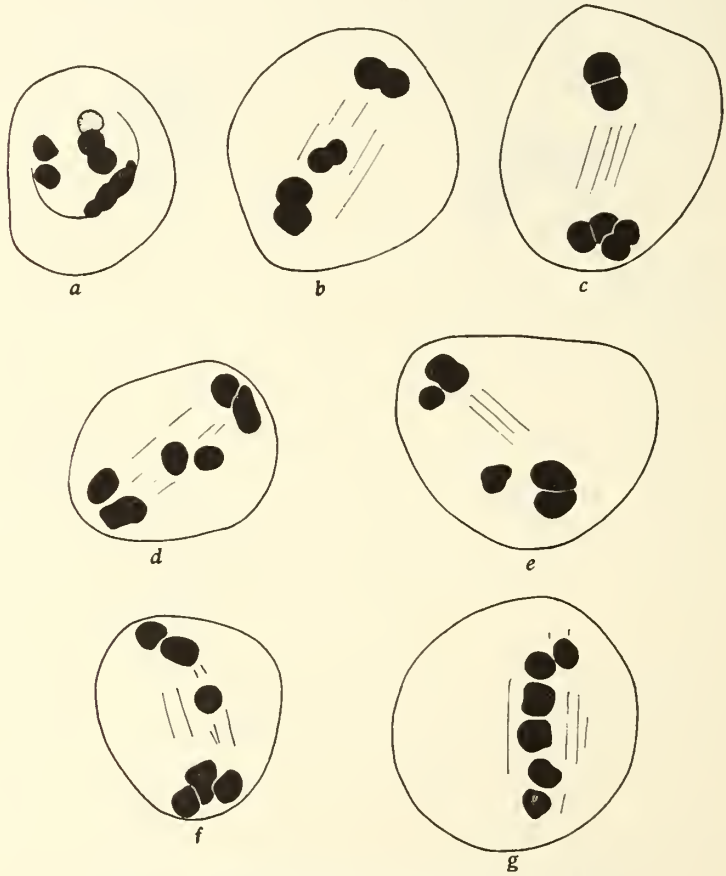

Fig. 5. Univalent division in haploid *Crepis capillaris*.
a, late diaphase, *b–g*, 1M or 1A.

lated, partly divided chromosomes at late anaphase. Complete division of some or all of the chromosomes frequently occurs, but only in a small proportion of cases do the daughter halves separate far or pass to different poles (fig. 5, *d–g*) ; usually they remain close together and are incorporated in the same nucleus. The positions assumed by these combinations of divided and undivided chromosomes are so many and varied that it is impossible to illustrate them all. Figure 5, *d* and *g*, shows cells in which each chromosome has completed its

division, but the daughter halves have remained close together. Figure 5*e* shows one undivided, one almost divided, and one completely divided chromosome whose halves are well separated. Quite commonly, whole or half-chromosomes fail to reach either pole. These processes give rise to telophase nuclei varying greatly in chromosome number and constitution.

As implied above, the three chromosomes rarely do line up on a metaphase plate and divide normally (fig. 6 *a*, *b*). In shape they are

Fig. 6. Haploid *Crepis capillaris*. *a*, *b*, division and separation of three univalents; *c*, three bivalents at 1 M.

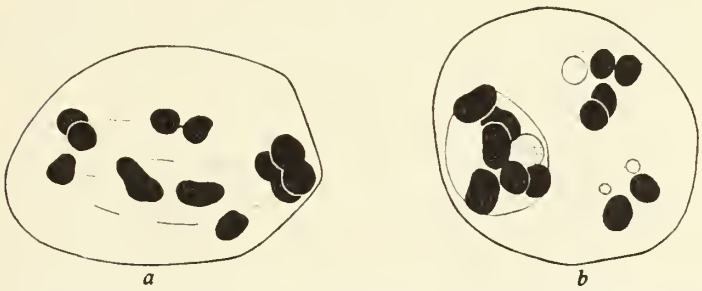

Fig. 7. Haploid *Crepis capillaris*. *a*, anaphase with eight single and two partly divided chromosomes; *b*, early telophase with twelve chromosomes.

typical dividing heterotypic univalents (cf. fig. 13*c*). In one slide, too, a few cells with three normal bivalents (fig. 6*c*) were seen. These probably arose from diploid cells in the lineage of the PMC's and normal meiotic behavior would presumably ensue. These two processes would be expected to give rise to gametes of normal chromosome constitution.

Several cells were observed with more than six chromosomes. One such is shown in figure 7*a*, where eight more or less spherical and two elongated constricted chromosomes are to be seen. Most of the chromosomes are in pairs and have evidently just finished dividing, and the two large ones are undergoing division. Counting the two divid-

ing chromosomes as four, the total of twelve suggests two successive divisions of three, or a single division of six univalents, the cause of either of which is obscure. A later stage—very early telophase—resulting from such a complex, is shown in figure 7*b*. Twelve chromosomes in groups of various numbers are to be seen and nucleoli and nuclear membranes are being differentiated. Other cells with twelve chromosomes in two or three groups at telophase were also observed.

One instance of two metaphase plates in a single PMC, each containing three bivalents, was observed (fig. 8). No explanation of this unusual occurrence is ventured.

The number and constitution of telophase nuclei are readily studied at this stage, for contrary to the normal behavior in this

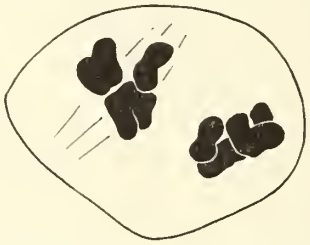

Fig. 8. Haploid *Crepis capillaris*. A cell containing two 1M plates each consisting of three bivalents.

genus, in most cases the chromosomes are clearly outlined and often can be distinguished from each other by their relative sizes in the telophase nuclei. Occasionally, however, a group of telophases is observed in which the chromosome outlines are not clear and the reforming nuclei resemble masses of chromatin. Telophase usually begins with the appearance of a clear area in the cytoplasm surrounding a clearly outlined chromosome or group of such chromosomes. An instance of an interesting and rare stage, the appearance of a faint nucleolus near each group of chromosomes before the appearance of the nuclear membrane, was observed, and is shown in figure 9*a*. Occasionally the nuclear membrane is formed around a chromosome or group of chromosomes without including a nucleolus. The telophase chromosomes elongate and commonly total six in number (fig. 9, *b–f*). Chromosomes whose divisions have been initiated but which have not divided on the spindle, complete their division at telophase within the nuclear membrane. It has not been ascertained whether chromosomes which showed no sign of division on the spindle divide at telophase, but it is possible that they do so, for among the many

telophase cells observed in which chromosomes could be distinguished, all had more than three and most had six chromosomes. A few instances of more than six chromosomes at this stage were observed (one with eight is shown in figure 9*g*). This could have arisen from non-disjunction in a previous division although no evidence of such an occurrence was seen in somatic cells. Telophase cells with twelve chromosomes have already been discussed.

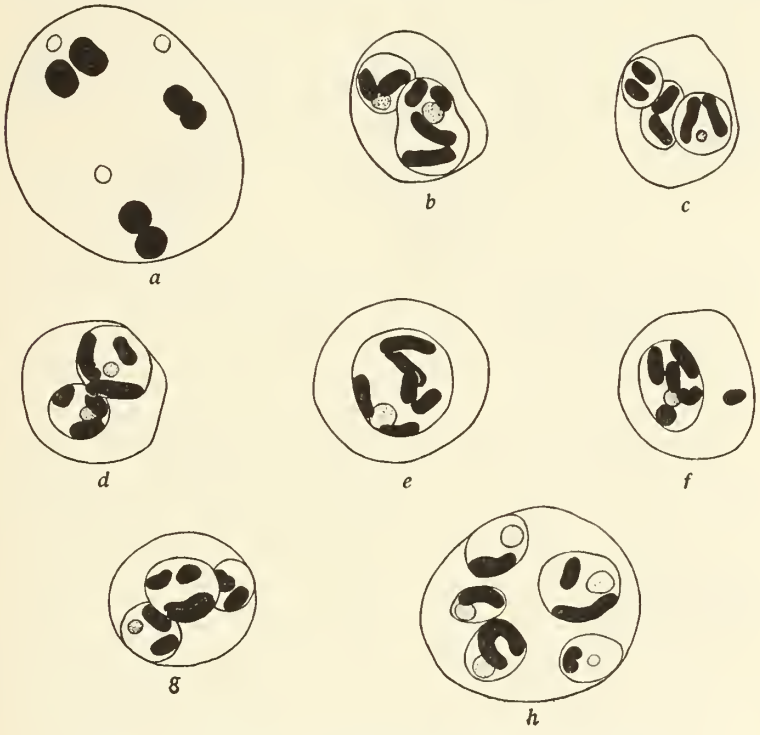

Fig. 9. Haploid *Crepis capillaris;* heterotypic telophases; *b–g,* paraffin material.

The previous distribution of the chromosomes determines the number and constitution of the telophase nuclei. The number observed varied from one (fig. 9*e*) to five (fig. 9*h*), two (fig. 9 *b, d*), and three (fig. 9*c*) being most common. Since chromosomes complete their division at this stage they commonly occur in pairs (fig. 9, *b–e*). However, an unpaired chromosome in a nucleus, the result of separation of daughter halves to different poles at anaphase, is to be seen occasionally (fig. 9*d*). These figures illustrate some of the many varied telophase combinations observed.

The telophase chromosomes continue to elongate (fig. 10, *a*, *b*) and the nucleus gradually passes into a typical interphase condition. Before this change is completed, furrowing begins to take place (fig. 10*c*) thus initiating microspore formation. No second meiotic divisions have ever been seen and the nature of the young microspore groups which are commonly diads and triads instead of tetrads, supports the conclusion that ordinarily no homeotypic division occurs.

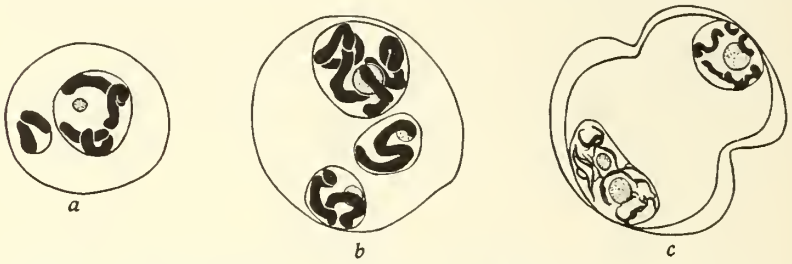

Fig. 10. Haploid *Crepis capillaris*. *a*, *b*, elongating chromosomes at 1T; *c*, furrowing. *a*, paraffin material.

TABLE 2

The Frequency of Tetrads, Triads, Etc., in Haploid Plants

Plant No.	Tetrad	Triad	Diad	Monad
28H.149-8	8	23	52	5
28H.54-19	10	15	69	5
28X20-2	1	19	74	2
Total	19	57	195	12

Table 2 shows the frequency with which tetrads, triads, diads, and monads were observed in smears from three buds. Diads are most frequent, triads are fairly common, monads, and tetrads are infrequent and only one instance of a pentad (in another smear) was seen. Young microspores frequently contain two nuclei. As would be expected from the variation in chromosome number in telophase nuclei, the young microspores in most groups are very different in size. Indeed many of the microspore groups called tetrads or triads would be better described as triads or diads with one or two microcytes. Diad cells are usually markedly different in size. Figure 11 illustrates a few of the many kinds of microspore groups observed.

It is obvious that very few of the microspores will contain a normal haploid chromosome complex. Diads, usually the result of nonreduction, are here commonly the result of a suppression of the homeotypic division and contain chromosome complexes varying widely in

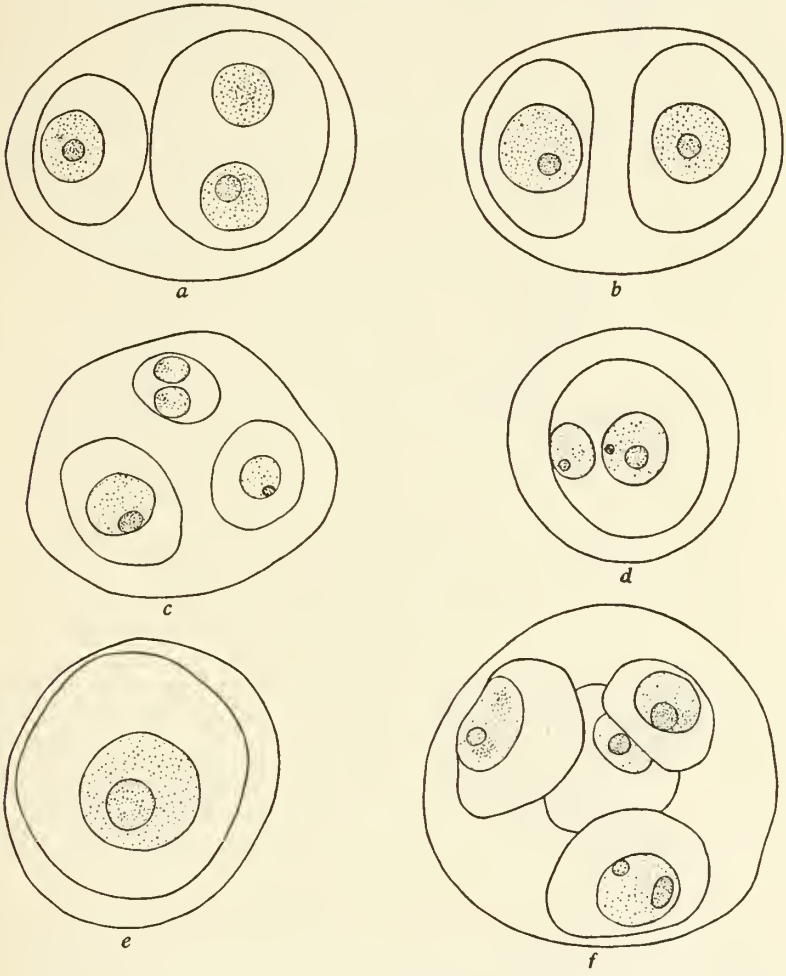

Fig. 11. Haploid *Crepis capillaris.* Representative microspore groups.

number and constitution. The diad which presumably results from division of all the chromosomes, and the tetrad which presumably arises from a diploid PMC, are probably the only ones which produce normal haploid gametes. As noted above, normal pollen grains were very rare. The monad presumably contains the diploid chromosome complex and would be expected to give rise to a diploid pollen grain.

MEIOSIS IN DIPLOID TISSUE OF A HAPLOID

Several buds of the chimeral(?) branch on plant 28H.149–8 which bore large heads were fixed and, as stated above, showed the diploid chromosome complex (fig. 12*a*). The members of each of the three pairs of chromosomes were presumably completely homologous (barring mutation), yet a high degree of non-conjunction occurred. Figure 12, *b–d*, shows first metaphases illustrating non-conjunction of one, two, and three pairs respectively. This failure to pair could be seen in late diaphase as illustrated in figure 13, *a, b,* which shows two and

TABLE 3

THE FREQUENCY OF FIRST METAPHASES WITH VARIOUS COMBINATIONS OF BIVALENTS AND UNIVALENTS IN THE DIPLOID PMC'S FROM BUDS ON A CHIMERAL(?) BRANCH OF THE HAPLOID PLANT 28H.149–8

3″	2″-4′	1″-4′	6′
42	51	22	6
43	48	19	2

six unpaired chromosomes respectively. Table 3 shows the frequency of first metaphase cells with three, two, one, and no bivalents respectively in two different buds. The amount of non-conjunction is comparable with that found in certain diploid plants of the *capillaris* X strain (Hollingshead, 1930*b*) which is the strain from which this haploid was derived.

The univalents either segregated without division or divided (fig. 13*c*), but no particular study of the later stages in microspore formation was undertaken except to note the frequent occurrence of micronuclei and microcytes in the tetrads. It is obvious that gametes with abnormal chromosome constitution would be formed frequently, and that these gave rise in some cases to inviable pollen grains, is indicated by the one pollen count made which showed 173 small and unstained grains in a total of 580, or nearly 30 per cent bad pollen. As stated above, the progeny of the branch from which these buds were obtained and that from a later diploid one, were normal and remarkably uniform. Probably no abnormal gametes functioned.

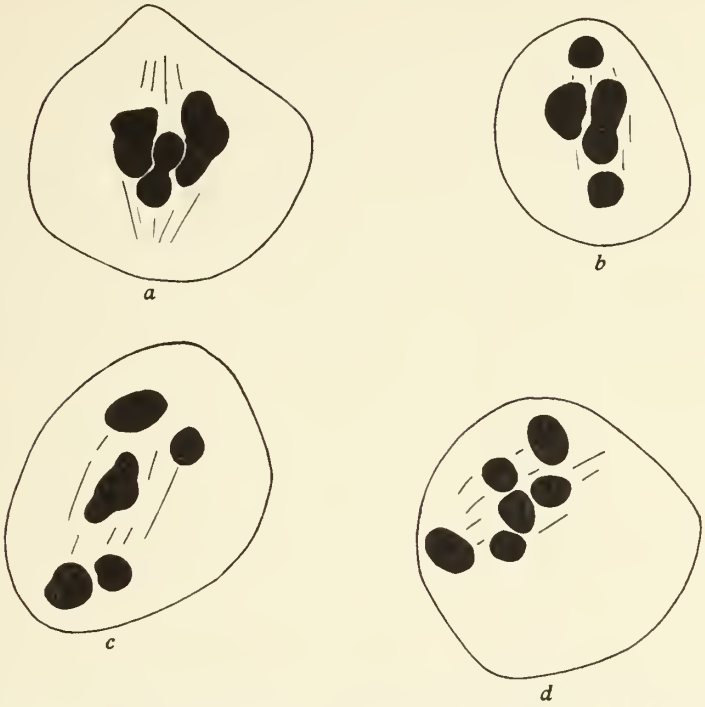

Fig. 12. 1 M in diploid tissue of haploid *Crepis capillaris*. *a*, normal, *b–d*, non-conjunction in one, two, and three pairs.

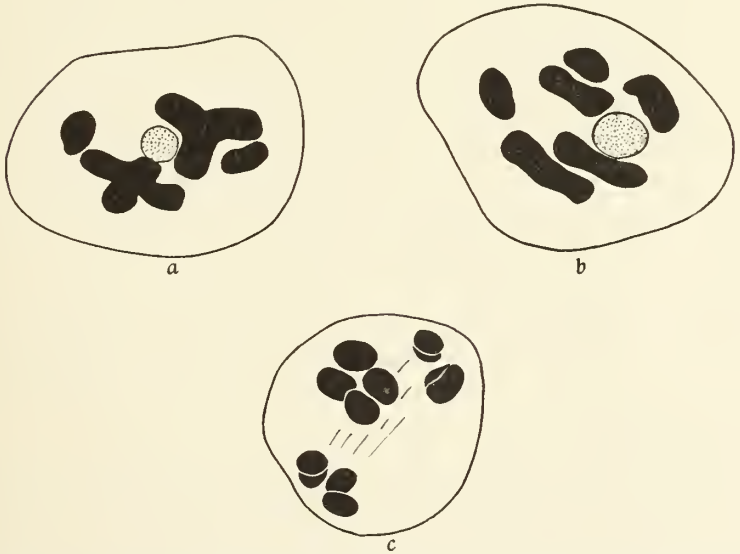

Fig. 13. Diploid tissue of haploid *Crepis capillaris*. *a*, *b*, non-conjunction of one and three pairs at diaphase; *c*, division of two univalents at heterotypic anaphase.

DISCUSSION

The list of reported instances of haploid sporophytes in Angiosperms includes at the time of writing *Datura stramonium, Nicotiana tabacum, N. glutinosa, N. Langsdorffii, Triticum compactum, Matthiola incana* (a disomic haploid), *Solanum nigrum, S. lycopersicum, Oenothera franciscana, O. rubricalyx, O. Hookeri, O. argillicola,* and *Crepis capillaris.* It has not yet been possible to secure a paper by Khristov (1930) on "A haploid tobacco plant." Some of the papers dealing with these haploids are specifically referred to below while others are cited only in the bibliography. As the literature on haploid plants has been reviewed recently in detail by Gates and Goodwin (1930) this discussion will be confined to a consideration of points in which the *Crepis* haploids resemble or differ from others previously described.

With the exception of haploid plants of *Nicotiana tabacum* (Clausen and Lammerts, 1929) and of *N. Langsdorffii* (Kostoff, 1929) each of which developed from a sperm nucleus thus becoming the first authentic cases of haploid merogony in higher plants, the origin of most of the haploids has been attributed to the development of unfertilized egg cells. The *Crepis* haploids doubtless arose in this same way. Foreign pollen in most cases, but cold in the case of some *Datura* haploids, probably acted as a stimulus for development, but in others, where the haploids arose in pure-line cultures (*Nicotiana glutinosa* and *Oenothera franciscana*), no stimulating factor is known. In the last two cases it is conceivable but less probable, that sperm nuclei developed into haploid plants. In the preliminary note it was stated that cold weather prevailed at the time of origin of the first two *Crepis* haploids, and it was suggested that this circumstance might have been a contributing factor in their origin. The occurrence of later haploids which developed under varying weather conditions seems to eliminate cold as a stimulating factor, and leaves the foreign pollen of *C. tectorum* and *C. setosa* as the probable stimulus to development.

As in *Crepis,* the haploid nature of a plant having been once established, it is usually possible to identify others of the same species by their similar morphology. They are frequently described as reduced replicas of diploids differing sometimes in minor characters, e.g.,

details of leaf shape in *Nicotiana tabacum* and *Oenothera franciscana* and flower color in *Nicotiana glutinosa.* However, considerable variation in degree of resemblance to diploids occurs, for the *Triticum* haploid could be distinguished from diploids only by its sterility, and the *Oenothera rubricalyx* haploid was described as being very much dwarfed. *Crepis* haploids were smaller than diploid plants and differed noticeably from them in other characters, particularly in leaf shape. In sterility the *Crepis* haploids resemble those of other genera, which were highly or completely sterile.

Diploid somatic cells have been found in haploid *Nicotiana* plants (Ruttle, 1928, Kostoff, 1929), and in the *Solanum* haploid (Lindstrom, 1929), and cells with apparently fusing nuclei were seen in somatic tissue of the *Triticum compactum* haploid (Gaines and Aase, 1926). The fusion of daughter nuclei not separated by a cell wall has been the most popular suggested explanation for the doubling of chromosomes in somatic cells. Why this doubling should occur much more frequently in haploid than in diploid tissue, as shown by Gaines and Aase (1926) in *Triticum,* by Ruttle (1928) in *Nicotiana,* and by the present work on *Crepis* haploids is unknown, but there undoubtedly exists in these haploids a distinct tendency toward diploidy.

Ruttle and Lindstrom sought in vain for diploid branches on their many *S. lycospersicum* and *N. tabacum* haploid cuttings, but one of the original *Datura* haploids propagated by cuttings, produced a branch characterized by a small proportion of aborted pollen grains and large capsules (Davenport, 1927). Dr. A. D. Bergner has kindly given further unpublished data in this connection. That this branch was diploid was shown by a chromosome count of both PMC's and root tip cells, cuttings from the branch having been rooted in sand. Dr. Bergner has also investigated a haploid-diploid periclinal chimeral branch of this *Datura* haploid plant which had diploid root tips and haploid PMC's. The diploid and chimeral branches or heads on the *Crepis* haploids indicated that doubling of chromosomes in the parts above ground took place rather frequently.

In meiotic behavior, the *Crepis* haploids differ in several respects from most others hitherto described. They are the most variable in behavior and exhibit hitherto unreported features in the occasional division of univalent chromosomes at diaphase, and the omission of the homeotypic division. Initiation and completion of univalent division at diaphase, while not described hitherto in haploids, has been

observed in *Crepis capillaris-C. aspera* F_1 hybrids with seven unpaired chromosomes (Navashin, 1927). The division of some of the univalents at first anaphase while others were segregating undivided, is another feature in which the *Crepis* haploids resemble Navashin's *capillaris-aspera* hybrids. Among haploids *Nicotiana tabacum* (Chipman and Goodspeed, 1927) and *Matthiola incana* (Lesley and Frost, 1928) exhibit this behavior. The failure of halves of divided univalents to separate to opposite poles has been observed in some hybrids with many univalents, as in wheat-rye hybrids (Thompson, 1926), and this was observed in *Triticum compactum* and *Nicotiana tabacum* haploids by Gaines and Aase (1926), and Clausen and Lammerts (1929). Blakeslee, Morrison and Avery (1927) have shown that *Datura* haploid plants throw a markedly higher percentage of trisomics than do diploids. They attribute it to a possible non-disjunction in pre- or post-meiotic divisions but it might be that it is the result of the failure of a pair of univalent halves to disjoin in meiosis.

In lack of pairing and in prevalence of random segregation of univalents at the first division, the *Crepis* haploids resemble most of the others described. Of all haploids only *Solanum nigrum* is known to exhibit true pairing (Jorgensen, 1928) and it was only in the *Matthiola* haploid that the usual mode of behavior was a division of all the univalents following the formation of a regular plate at first metaphase.

The occurrence of divided chromosomes at heterotypic telophase after the formation of a nuclear membrane, is the normal condition in many plants. In normal *Crepis capillaris*, however, after the formation of the nuclear membrane the individual chromosomes cannot usually be distinguished. In the haploid plants telophases in which paired and single chromosomes lay distinct and clear within the nuclear membrane were the more striking by their contrast with telophases in normal plants of this species. This stage, here interpreted as heterotypic telophase, bears a marked resemblance to that described as homeotypic prophase in *C. capillaris-aspera* hybrids by Navashin. In these plants, as in the haploids, halves of chromosomes which had divided and had separated during the first anaphase lay singly, while chromosomes which had segregated without division, had divided and lay in pairs within the nuclear membranes.

Considerable attention has been paid to the question whether this stage in the haploids could be homeotypic prophase and the possibility should not be overlooked completely. According to the latter inter-

pretation the occasional groups of nuclei which appear to form directly from anaphase chromosomes as their outlines grow increasingly indistinct might be considered typical telophases. The others, in which the chromosomes are clearly seen, would be homeotypic prophases. There were no homeotypic metaphases, so, according to this interpretation, the prophase nuclei would pass immediately into the interphase condition again and furrowing ensue. Although no positive evidence has been secured to disprove this interpretation, because of the simpler nature of the process, and the evidence from the seriation of stages within anther locules, the writer decidedly favors the interpretation given in the description of meiotic behavior. It should be noted however, that evidence from seriation of stages must be accepted with some reservation, for while all the PMC's in one locule are usually at about the same stage occasionally groups of cells at very different stages may lie in the same locule. Even if homeotypic divisions are initiated, however, and proceed to prophases they are really omitted for no further separation of chromosome halves takes place and the nuclei resulting from the heterotypic division persist unchanged.

There is no obvious cause for this omission of the homeotypic division. It has been shown that the chromosomes at heterotypic telophase are usually divided and apparently ready for the next division. Furrowing takes place, however, and young microspores are formed forthwith. This gives rise, as pointed out earlier, to a preponderance of diads, whose chromosome constitution, contrary to the general rule, is far from that of a haploid complex. In the *Nicotiana Langsdorffii* haploid the homeotypic metaphase was sometimes omitted (Kostoff, 1929). The chromosomes often spread out over the entire spindle at the heterotypic division and underwent interkinesis together. After such an interkinesis sometimes the chromosomes did not become organized into a normal equatorial plate. They divided, however, and formed a monad.

The small amount of apparently good pollen and the sterility of these haploid plants are easily understood in the light of their meiotic behavior. Division and separation of all the univalents to different nuclei, or the occurrence and normal behavior of three bivalents (processes which would probably give rise to gametes with the haploid chromosome complex), were rare occurrences. Even the few apparently normal male gametes had little chance of effecting fertilization for, as was pointed out, pollen was not extruded from the anther tubes as in normal florets. Possibly seeds could have been obtained

with more extensive hand pollination but it was not thought worth while to prolong these attempts.

The relatively large amount of non-conjunction in diploid tissue of a haploid plant is of great theoretical interest. Meiotic pairing is usually assumed to be evidence of chromosome homology, and when it frequently fails to take place the chromosomes are often considered to be weakly homologous. It is well known of course that occasionally two chromosomes which normally pair, fail to do so, but in this instance we have frequent non-conjunction between completely homologous chromosomes. This is clear evidence that complete homology alone does not necessarily result in bivalent formation. Diploid plants of this strain of *C. capillaris* frequently exhibit non-conjunction (Hollingshead, 1930*a*) in varying amounts. It is clear now that this is not necessarily due to heterozygosity. Possibly further studies on this strain might throw some light on what other factors are involved in the non-conjunction of chromosomes in a normal diploid complex.

SUMMARY

Five *C. capillaris* haploid plants were found in populations of *C. capillaris-tectorum* F_1 hybrids numbering over three thousand plants. A sixth haploid was one of two plants resulting from a *C. capillaris-C. setosa* cross. They doubtless resulted from the parthenogenetic development of *capillaris* egg cells.

The haploids resembled reduced diploids but differed noticeably from diploids in leaf shape and habit of growth.

Root tips usually showed the haploid chromosome complex of three individually different chromosomes but parts of some root tips in each haploid were diploid and some root tips were wholly diploid. A few parts of most of the plants above ground were also diploid, giving rise to diploid and chimeral heads and branches.

The haploid portions of the plants were sterile, but achenes were obtained from diploid parts of one haploid plant. The progeny, presumably completely homozygous, were remarkably uniform in appearance.

In meiotic behavior (PMC's) the haploids were irregular and variable. They resembled other haploids previously described in the occurrence of a random segregation of univalents at the heterotypic

division, and of a rare division of all univalents followed by separation of the daughter halves to different poles, or "non-reduction." New or unusual features were (1) the occasional division of univalents at diaphase, (2) the frequent division of univalents but the inclusion of most pairs of daughter halves in the same nucleus, and (3) the omission of the homeotypic division. As a result microspores of normal chromosome constitution were rarely formed and very little good pollen was produced.

In diploid tissue on a haploid plant three bivalents were formed in many PMC's but non-conjunction of one or more chromosome pairs was a frequent occurrence. This lack of pairing between presumably completely homologous chromosomes is of great theoretical interest, for it shows that complete homology does not necessarily result in bivalent formation at meiosis.

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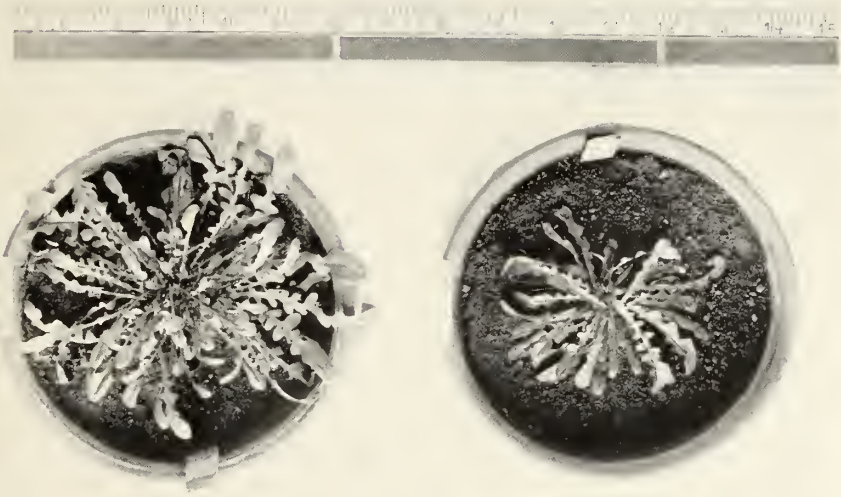
PLATE 6

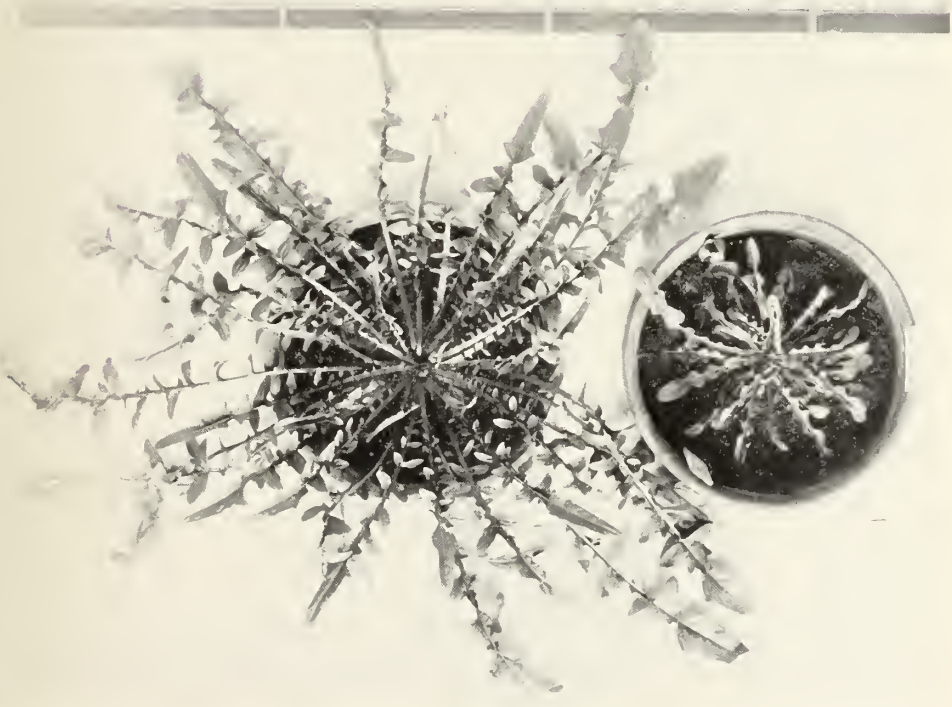
Crepis capillaris.

a, Haploid plants at the rosette stage.

b, Haploid and diploid plants of the same age.



a



b

PLATE 7

Crepis capillaris.

Diploid plant at late maturity.

PLATE 8

Crepis capillaris.

Haploid plant at early maturity showing the tall chimeral(?) branch with large heads.