INTERSPECIFIC HYBRIDS IN CREPIS. II.
A PRELIMINARY REPORT ON THE RESULTS OF HYBRIDIZING *CREPIS SETOSA* HALL. WITH *C. CAPILLARIS* (L.) WALLR. AND WITH *C. BIENNIS* L.

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TABLE OF CONTENTS

INTRODUCTION

In the first paper of this series (BABCOCK and COLLINS 1920) the F_1 hybrid of *Crepis capillaris* (L.) Wallr. $(N=3)$[1] × *Crepis tectorum* L. $(N=4)$[1] was described in detail. It was pointed out that the compatibility between these two species was so low that the two haploid sets of chromosomes were unable to function together, with the result that the F_1 plants were unable to grow beyond the seedling stage. The present paper presents data on two other species hybrids obtained by crossing *Crepis setosa* Hall. with *C. capillaris* (L.) Wallr. and with *C. biennis* L., both of which are able to complete growth to maturity. These hybrids are of especial interest because they involve (1) a cross between two species which differ from one another by one pair of chromosomes, *setosa* $(N=4)$ × *capillaris* $(N=3)$, and (2) a cross between two species differing by 16 pairs of chromosomes, *setosa* $(N=4)$ × *biennis* $(N=20)$. Although back-cross and F_2 plants have been obtained, this report is necessarily preliminary, since anything like a complete analysis of the problems which such material involves will occupy a considerable period.

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[1] N is the haploid number of chromosomes.

MATERIAL AND METHODS

The oriental species of the genus have been divided by BOISSIER (1875) into three sections largely on the basis of the achene characters. Section I, Eucrepis, includes those plants having achenes all similar, the apex sometimes more or less narrowed or attenuated but never beaked. Both *Crepis capillaris* and *C. biennis* are in this section. Section II, Barkhausia, includes the plants having all or at least the central achenes beaked, the pappus being borne at the end of the slender beak. *Crepis setosa* belongs in this section. Section III, Gatyona, includes species having achenes either beaked or non-beaked, but placed radially with a conspicuous wing or keel on the ventral face of the achene. None of the species reported upon are representatives of this third section.

Crepis capillaris (L.) Wallr. is an annual, producing a stem, single below and paniculately branched above or branching from the crown of the root as well as along the stem. The plant varies in height from a few inches to four feet. The leaves are generally considered as glabrous but in reality have a fine scattered pubescence over the surface which becomes much more pronounced on the midrib of the radical leaves. These leaves are generally lanceolate in form, the margins of those on different plants varying from entire or merely toothed to deeply pinnatifid or bipinnately compound. The cauline leaves are sagittate or sub-sagittate. The involucre is composed of two series of foliaceous bracts the outer of which are smaller, forming an appressed calyculus. The bracts of the inner series are larger and enclose the florets. The keel of these bracts is covered with short gland-tipped hairs.[2] The achenes are 10-ribbed, tapered at both ends, without a beak, length about 2.5 mm (figure 1 b). The pappus is pure white.

Crepis biennis L. is also in the Eucrepis section. It is a biennial under ordinary conditions. The plant is larger and coarser in all parts than the corresponding parts in *C. capillaris* but differs very little in morphological characters, when size is not considered. Erect radical leaves are characteristic of our *C. biennis* material, while they are seldom seen in *C. capillaris*; the cauline leaves in *C. biennis* are not sagittate. On the other hand, the stem habit is approximately the same for both species, but the plant-pubescence and leaf-form variation exhibit some differences, which are in keeping with the larger size. The achenes of *C. biennis* are approximately 3.5 mm in length. The principal features of difference

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[2] Plants lacking this glandular pubescence are known to act as Mendelian recessives when crossed with the normal type.

between the two species, then, is found in the size and in the length of the life cycle of an individual.

Crepis setosa Hall. is in the Barkhausia section, since the achenes are beaked. It is an annual of about the same height and growth as *capillaris*. Stems and leaves are bristly pubescent but not glandular, the bristle-like hairs being conspicuous on the pedicel and involucre. The calyculus is relaxed or spreading (figure 1 a). Radical leaves show considerable variation in degree of pinnate lobing. Cauline leaves are sagittate at the base. The achenes are more slender than in *C. capillaris*; they are usually 10-ribbed and are striate-tuberculate, with the pappus at the tip of the slender beak (figure 1b).

Two methods were used to secure cross-fertilization. One consisted in emasculation of ten to fifteen florets per head, the remaining floret buds being removed. The other method consisted in washing the fresh pollen from the stigmas of the peripheral whorl of florets with a fine stream of water from a syringe; at the same time the central unopened florets were removed. Pollen was applied from one to three days later. In both F_1 hybrids described *C. setosa* was used as the female parent.

The achenes were placed in moist-chamber germinators. When germination had occurred the seedlings were transferred to six-inch clay pots where they remained in the greenhouse. (Cf. COLLINS 1922 for detailed description of the methods employed.)

For chromosome study root tips were fixed in chrom-acetic-urea and stained in Heidenhain's iron haematoxylin. The root tips were usually obtained from the bottom of the pots, but some were from sprouted achenes. BELLING'S (1921) iron-aceto-carmine method proved very useful for pollen mother cells of Crepis.

Crepis setosa HALL. × *C. capillaris* (L.) WALLR.

The F_1 hybrid

The *setosa* characters predominate in F_1 with the one marked exception that the achenes are not beaked (figure 1 b). The rosette leaves of the hybrid have the pinnate lobing intensified (figure 4) while the pubescence throughout the plant is less pronounced than in *C. setosa*.

Crepis setosa, which was used as the pistillate parent in the cross, has four pairs of chromosomes with such marked individuality that there is almost never any difficulty in identifying the homologues in somatic cells. The longest chromosomes always have a semi-detached tip which frequently makes them look like i's or j's. They are readily found in the figures (figure 2 c). The other pairs consist of a very short pair and two pairs of intermediate size, one slightly longer than the other.

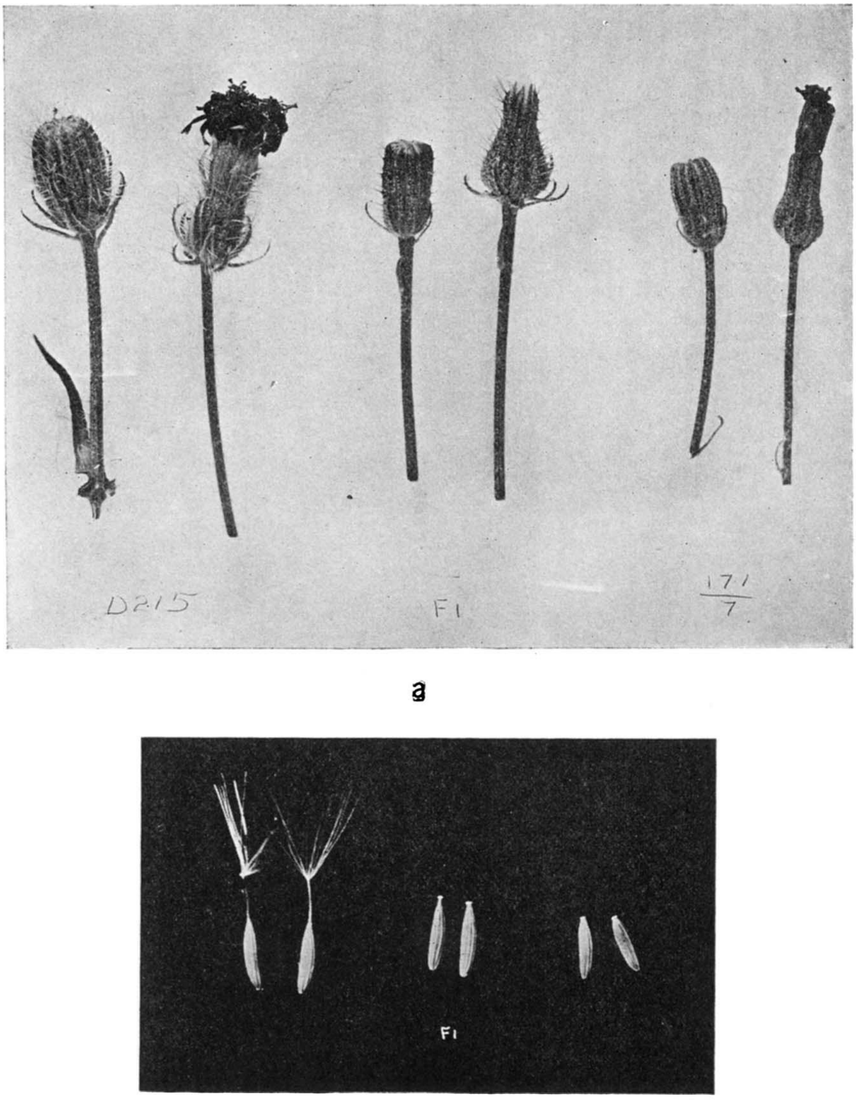

FIGURE 1.—a. Flower heads of *Crepis setosa* (left), *C. capillaris* (right) and F_1 hybrid (center). b. Achenes of *Crepis setosa* (left), *C. capillaris* (right) and F_1 hybrid (center).

Crepis capillaris has three pairs of chromosomes which also show distinct individuality (figure 2 b) as was previously reported by DIGBY (1914), ROSENBERG (1909) and SAX (1918).[3] Here the chromosomes consist of a graded series, one long, one intermediate, and one short pair. The longest chromosome of *C. capillaris* is decidedly longer than the longest of *C. setosa,* and the shortest of *C. capillaris* is much longer than the shortest

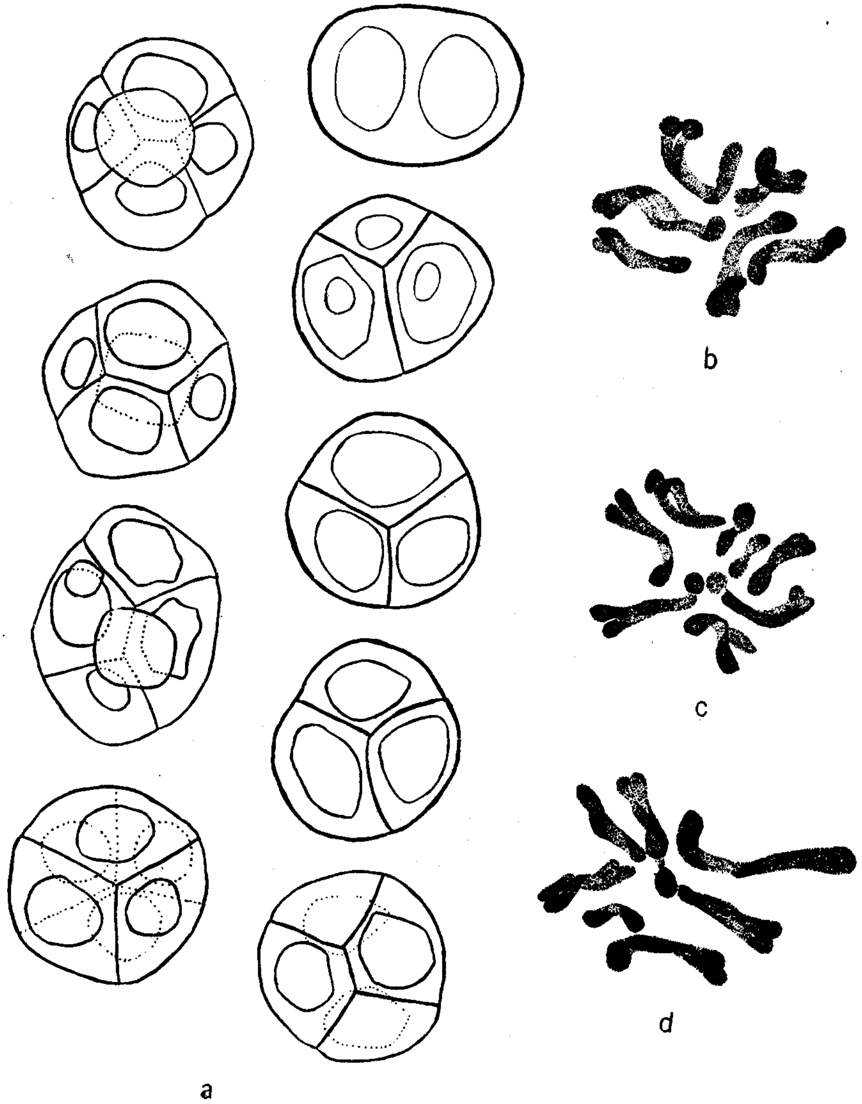

FIGURE 2.—a. Anomalies in pollen formation in the F_1 *Crepis setosa* × *C. capillaris.* b. Somatic metaphase of *C. capillaris.* c. Somatic metaphase of *C. setosa.* d. Somatic metaphase of *C. setosa* × *C. capillaris.*

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[3] Unpublished.

of *C. setosa*. There is little difference in the size of the two intermediate pairs of *C. setosa* and the two shorter pairs of *C. capillaris*.

The F_1 root-tip cells have seven chromosomes, four from *C. setosa* and three from *C. capillaris* (figure 2 d). It is nearly always possible to recognize the long compound one with the partially detached end and the very short chromosome from the *setosa* complex, as well as the longest one from *C. capillaris* but it is impossible to distinguish the two shorter *capillaris* from the two intermediate *setosa* chromosomes. The chromosomes in the pollen mother cells are unpaired in diakinesis and seem to undergo rather less contraction than is usual at this stage (figure 4 a). The first meiotic division is very irregular. The undivided chromosomes are usually distributed in a variable number of large or small groups which are scattered throughout the pollen mother cell and there form from 2 to 6 vesicles or nuclei, a condition which is frequently found in cells under abnormal conditions. In a single case all of the chromosomes had divided, but this is the exception, not the rule. The second division looks much more normal than the first, but it appears to occur only when the chromosomes have previously divided into two rather equal groups. The cytoplasmic divisions usually give rise to the normal tetrad, although about 12 percent result in two, 19 percent in three, 1.4 percent in five and 0.7 percent in six microspores. When three, four, five or six microspores result, they may be very similar or very different in size, as may be seen from figure 2 a. The size of the cell corresponds to the size of the nucleus which it contains.

Back-crosses

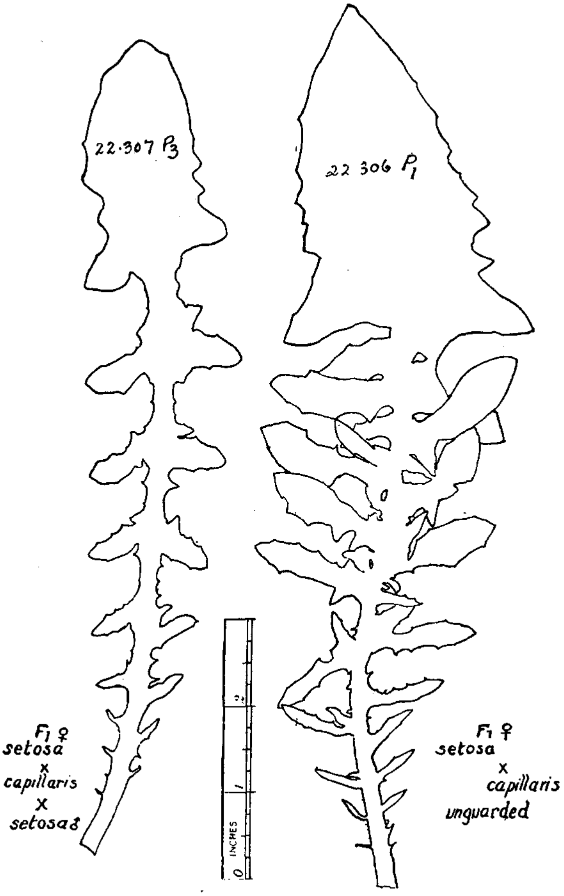
Very little of the pollen appears to mature properly, most of it remaining in the anther locules and there disintegrating. It is to be expected that some of the pollen would be functional yet none of the back-crosses in which the F_1 was used as the pollen parent was successful. That some ovules are functional has been shown by the fact that back-crosses were obtained when the F_1 was used as the pistillate parent. Five such plants are now growing, two of them having 10, two 8, and one 7 chromosomes in the root-tip cells. The different types of 'gametes which are to be expected from a random assortment of the seven chromosomes of the F_1 hybrid during germ-cell formation are shown in table 1. The relative number of each expected type is shown in the first column. All of the 128 gametes are different even though many of them have the same chromosome number. It will be noted in column five that three of the five back-cross plants which were obtained, the two with 8 and the one with 7 chromosomes, belong to the two classes containing the largest number of different gametes. The other two plants must have resulted from the fertilization of egg cells with six chromosomes.

Only one of the back-crosses has flowered, 22.306P$_1$ (figure 3 b). Four pairs of chromosomes appear in diakinesis, and reduction, cytokinesis, and pollen formation proceed normally. This is in accord with the observation that the root-tip cells have the same type of chromosome group as *C. setosa* and that the plant is typically *C. setosa* in appearance. It may thus be expected to maintain itself as such upon inbreeding. The other back-cross with eight chromosomes, 22.307P$_3$ (figure 3 a), has a very similar type of chromosome group in the somatic cells, and the rosette leaves are well within the range of variability which has been observed in *C. setosa*. Until it has flowered, however, we cannot be certain that all of the chromosomes of intermediate length belong to the *setosa* complex. Perhaps the slowness to flower indicates the presence of one or two *capillaris* chromosomes. The plant with seven chromosomes (22.307P$_1$, figure 4) resembles the F$_1$ both in rosette-leaf characteristics and in type of somatic chromosome group (cf. figures 4 b and 2 d). The fact that the entire *setosa* group reappeared together at least once and probably twice and that the F$_1$ type seems to have reappeared among the back-crosses, indicates that back-crosses to *C. capillaris* should give some pure *C. capillaris* plants. Thus far all attempts to make this back-cross have been unsuccessful, but all of the work was done in the greenhouse during the summer, where achenes do not set as readily as they do out-of-doors.

TABLE 1

Showing the chromosome relations when the F$_1$ setosa × capillaris is back-crossed to setosa.

RELATIVE FREQUENCY OF F$_1$ GAMETES	NUMBER OF CHROMOSOMES IN			NUMBER OF ZYGOTES OBTAINED
	F$_1$ gametes	*setosa* gametes	resulting zygote	
1	7	4	11	
7	6	4	10	2
21	5	4	9	
35	4	4	8	2
35	3	4	7	1
21	2	4	6	
7	1	4	5	
1	0	4	4	
128				



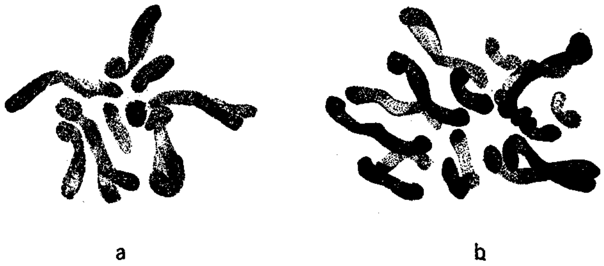
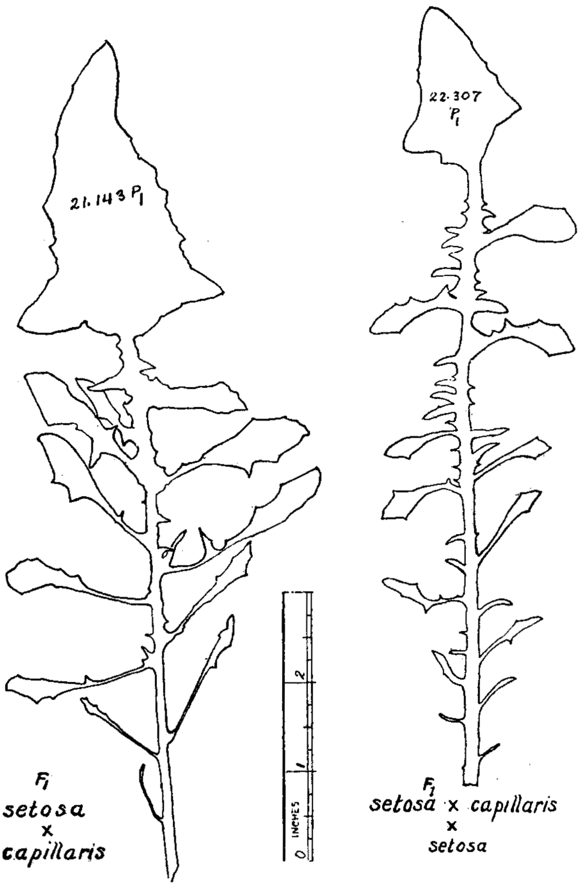


FIGURE 3.—Back-crosses with eight somatic chromosomes. a. Metaphase of 22.307P_3. b. Early anaphase of 22.306P_1. Note correspondence of size and position of divided chromosomes.



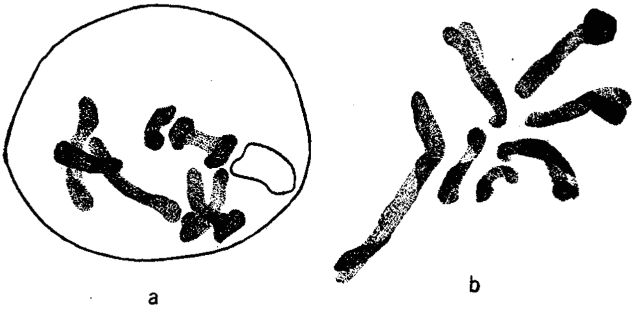


FIGURE 4.—a. Diakinesis group of a pollen mother cell of the F_1 *C. setosa* × *C. capillaris*. The nucleolus is outlined, the chromosomes stippled. b. Somatic group of (*C. setosa* × *C. capillaris*) × *C. setosa*, 22.307P_1.

The two plants containing 10 chromosomes in the root-tip cells (figure 5) were strikingly different in the rosette stage from any of the other plants, but very similar to one another. They are only in the rosette stage at present and have not yet flowered, hence nothing is known regarding their meiotic behavior and fertility. The somatic groups contain two j's and two short *setosa* chromosomes, as well as one long one from *C. capillaris*. The source of the other five chromosomes is still doubtful. The meiotic behavior in the plants resulting from back-crossing the F_1 to *C. setosa* should be of great interest, since one would expect to be able to determine positively the number of unpaired chromosomes in diakinesis. The number of lagging chromosomes in the first meiotic division would also assist in the determination, since univalent chromosomes usually lag while bivalents divide at a more rapid rate. If one of the 10-chromosome back-cross plants were to show only 2 unpaired chromosomes it would indicate that the F_1 gamete contained 4 *setosa*, a haploid set, and 2 *capillaris* chromosomes. If, on the other hand, four unpaired chromosomes were found it would indicate that the F_1 gamete was composed of 3 *capillaris*, a complete haploid set, and 3 *setosa* chromosomes. If the 10-chromosome plants contain 8 *setosa* and 2 *capillaris* chromosomes the gametic series with respect to number and derivation of chromosomes (S = *setosa* and C = *capillaris*) will be 1 (4 S+0 C)+2 (4 S+1 C)+1(4 S+2 C) and the zygotic series produced by self-fertilization of such a plant will be:

1 (8 S+0 C)
4 (8 S+1 C)
6 (8 S+2 C)
4 (8 S+3 C)
1 (8 S+4 C)

Those plants which have one or two pairs of *capillaris* chromosomes plus the four pairs of *setosa* chromosomes would be expected to continue as 5- and 6-pair species, respectively, in subsequent generations.

Crepis setosa HALL. × *C. biennis* L.

The F_1 hybrids

The plants of the F_1 are predominately like the pollen parent, *C. biennis*, but differ in having finer pinnate lobing of the rosette leaves than is the case in *C. biennis*, and in blooming the first year. The hybrids are quite as large and vigorous as the parent which they resemble. Characteristics of *C. biennis* have been given above.

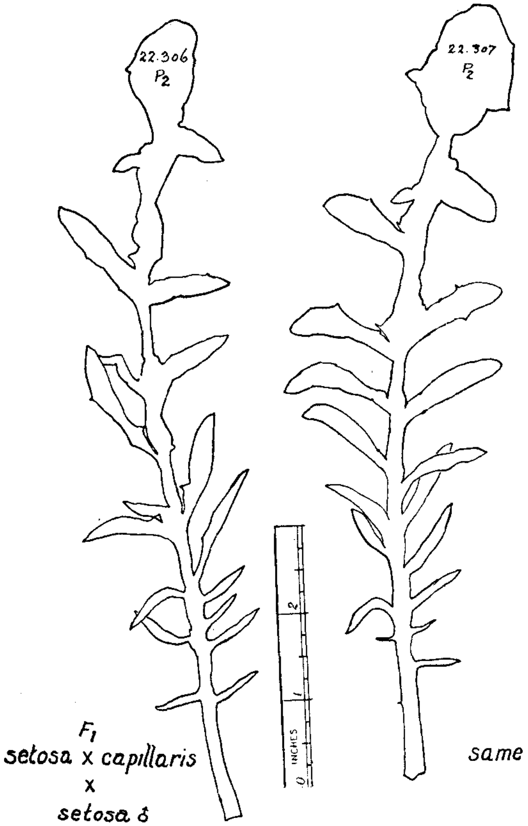


FIGURE 5.—Back-crosses with ten somatic chromosomes. a. Somatic group of 22.307P_2. b. Same of 22. 306P_2.

C. biennis is an outstanding species in the genus in that it has twenty pairs of chromosomes. They are similar in breadth and in length to the chromosomes of most of the other species so that the great increase in number must have resulted from duplication and not from cross-division of the chromosomes. Except for its greater size *C. biennis* does not differ from the four- and some of the five-chromosome species, so that one is tempted to consider it, at least tentatively, as an octoploid species which may have originated in much the same manner as the *gigas* forms of Oenothera and Primula. Such forms have been observed to arise suddenly, as tetraploids, from the normal diploid species, and, at least in certain cases, to maintain the increased chromosome number as well as the *gigas* character in subsequent generations. ROSENBERG (1920), who reported forty-two chromosomes for this species, considered three pairs as a basic number and hence *C. biennis* as a case of 14-ploidy. MARCHAL (1920) counted only sixteen pairs in the pollen mother cells. Counts of the pollen mother cells and root tips of the pure *C. biennis* of our material show that twenty pairs are present in all diploid cells (figure 6). It has been possible to check this count by still another means since a hybrid was obtained between *C. setosa* ($N=4$) and *C. biennis* ($N=20$), in which the root-tip cells contain twenty-four chromosomes, and since four came from *C. setosa*, twenty must have been derived from the *biennis* parent (figure 7 b 2).

The large number of chromosomes in *C. biennis* makes a study of the individuality impracticable at the present time, but it would be of great interest to know whether or not they fall into five size-types as should be the case if it were an octoploid form derived from a five-pair species.

No other hybrid has been described in which there is anything like as great a difference in the chromosome numbers of the parents as there is in *C. setosa* and *C. biennis*. It has frequently been assumed that such crosses would prove impracticable. The fact that these species will hybridize is astonishing enough, but it is especially surprising to find that the divisions of the pollen mother cells are very nearly normal, much more so than in the cross, *C. setosa* ($N=4$) × *C. capillaris* ($N=3$). The microspore groups are invariably tetrads and one rarely finds evidence that chromosomes have been cast out into the cytoplasm. However, a few small extra-nuclear vesicles were noted in pollen mother cells which had not yet undergone cytokinesis.

In most hybrids between species which differ in chromosome number, it has been found that the maternal chromosomes tend to pair with the paternal, leaving the extra chromosomes as univalents. TÄCKHOLM (1922) after

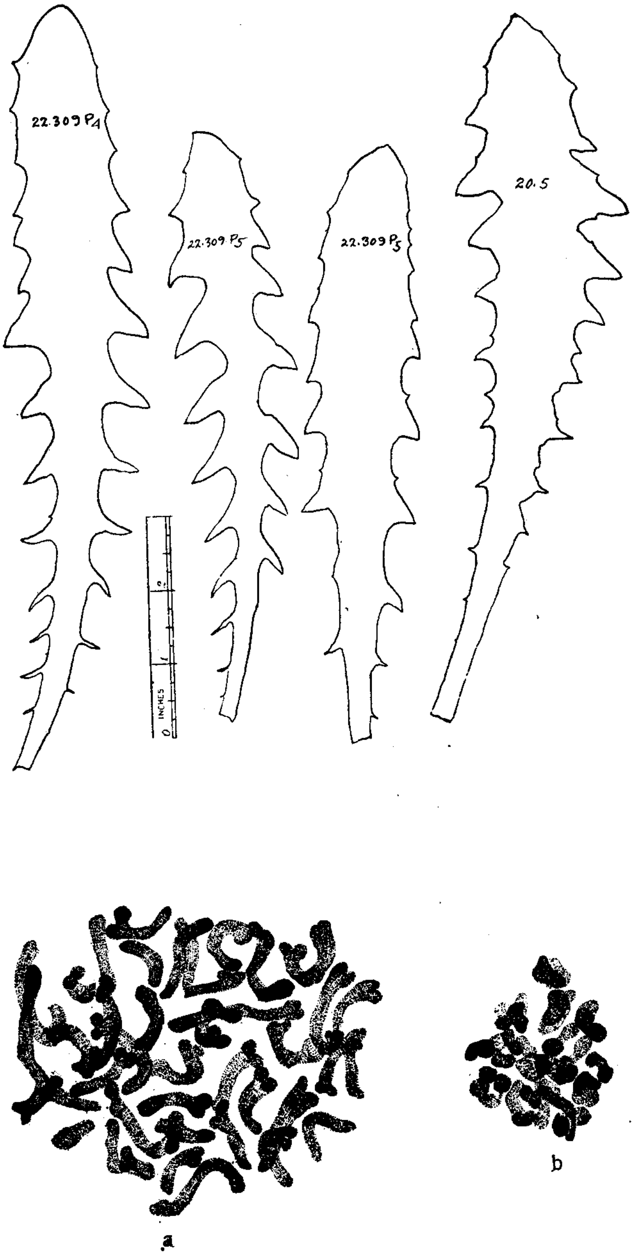


FIGURE 6.—*Crepis biennis*. Variation in leaf types. a. Somatic chromosome group. b. Haploid chromosome group.

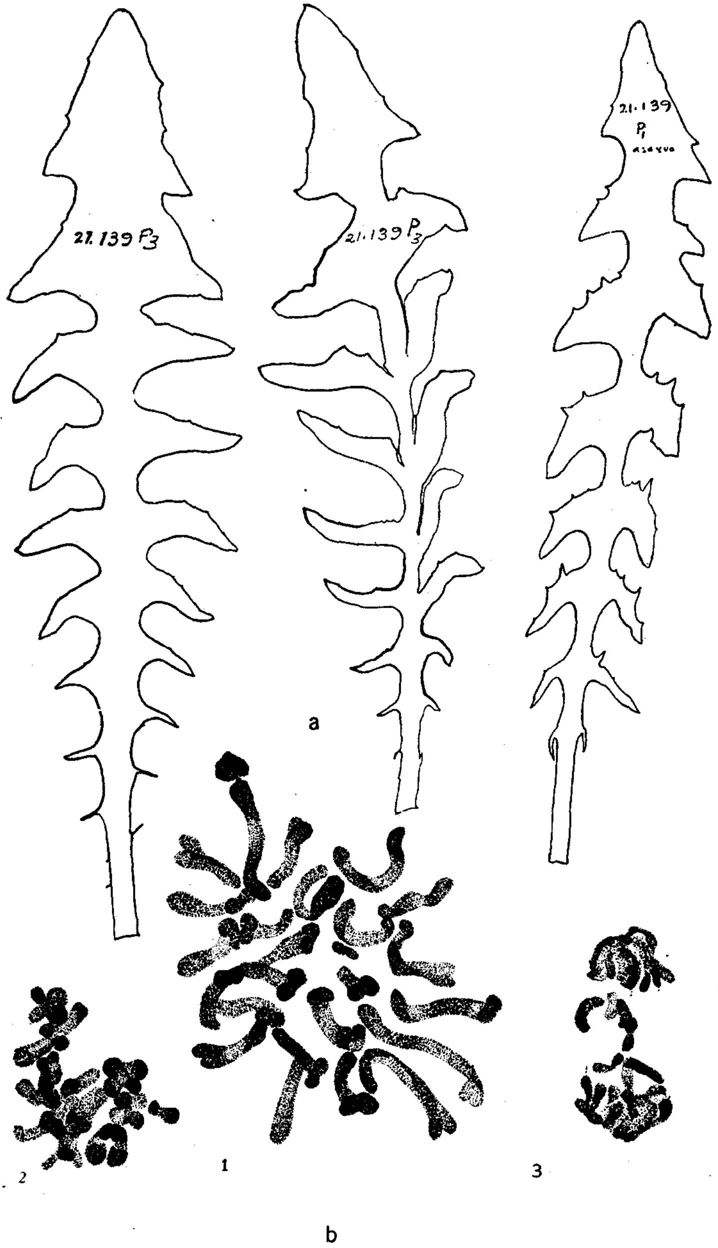


Figure 7.—a. Leaf variations in F_1 *C. setosa* × *C. biennis*. b. Chromosome groups of F_1 *C. setosa* × *C. biennis*. 1. Somatic group. 2. Diakinesis showing eight pairs and four odd chromosomes. 3. Same showing four lagging chromosomes which have divided.

examining the literature concludes that this is the rule. He notes that little or no pairing may occur, but that when it does he believes that it has been shown that maternal and paternal chromosomes mate. Only one exception to this appears in the literature and this TÄCKHOLM seriously doubts, namely that of *Digitalis lutea* ($N=48$) × *D. pupurea* ($N=24$) described by HAASE-BESSEL (1921), which shows 36 pairs in diakinesis. It is obvious that in this case certain of the *D. lutea* chromosomes must have paired with one another. It is of especial interest to note that as many as ten bivalent chromosomes can readily be distinguished in the diakinesis of the pollen mother cells of the F_1 from *C. setosa* × *biennis*. There are also a few obviously univalent chromosomes (figure 7 b). Since *C. setosa* contributes only four chromosomes it is evident that those from *C. biennis* must have paired with one another. This is important, for it indicates a qualitative similarity between what one would usually consider non-homologous chromosomes in *C. biennis*; exactly what one would expect to find if the increased number had been derived by chromosome duplication from a progenitor with a lesser number. The bivalents of the F_1 pollen mother cells are very similar to the bivalents seen in *C. biennis*. At the anaphase of the first division of the pollen mother cells two to four chromosomes of variable size are seen to lag (figure 7 b 3), but eventually, except in rare cases, all of the chromosomes enter one or the other of the two nuclei. The second division is more regular. It seems significant that the number of laggards should not exceed four and that they should show distinct size differences, since this is just what one would expect if the *setosa* chromosomes failed to pair with one another. And since they did not pair in the cross, *C. setosa* ($N=4$) × *capillaris* ($N=3$) there is reason to suppose that they are qualitatively so different that it is impossible for them to pair together. The lagging chromosomes in the *setosa* × *biennis* hybrid sometimes appear to divide, but sometimes seem also to pass undivided to one or the other pole. It is therefore obvious that one should expect gametes to be formed containing 10 *biennis* chromosomes plus 0, 1, 2, 3 or 4 *setosa* chromosomes, provided there is random assortment of the unpaired *setosa* chromosomes. We have shown below in outline the types of progeny expected in the F_2 generation. It will be seen that five types would have no unpaired chromosomes; these should be expected to continue as 10-, 11-, 12-, 13- and 14-paired races. If these could again be crossed with *C. setosa* other interesting types should be produced containing 5, 6, 7, 8 and 9 pairs of chromosomes, if our assumption that *C. biennis* is an octoploid species is correct. If there is independent assortment of the univalent *setosa* chromosomes, as now appears to be the case, the gametes of the F_1 hybrid will conform to the following series:

1 (10 B+0 S)
4 (10 B+1 S)
6 (10 B+2 S)
4 (10 B+3 S)
1 (10 B+4 S)

If these gametes all survive and unite at random in fertilization, the F_2 zygotic series will be:

1 (20 B+0 S)
8 (20 B+1 S)
28 (20 B+2 S)
56 (20 B+3 S)
70 (20 B+4 S)
56 (20 B+5 S)
28 (20 B+6 S)
8 (20 B+7 S)
1 (20 B+8 S)

The F_2 plants

The F_2 plants which have been examined cytologically have 24 or 25 chromosomes (figure 9 b). It is significant that these belong to the largest of the theoretical classes outlined above, although whether this means anything in terms of gamete survival is not clear. The five *setosa* chromosomes must include one or two pairs, the chances being about equal for both alternatives. If these mate it may be possible (1) to reduce the race to a 10-pair species, or (2) to continue it as an 11- or 12-pair species (i.e., 10 pairs of *C. biennis* plus 1 or 2 pairs of *C. setosa*).

Back-crosses

The back-cross of the F_1 to *biennis* presents no difficulty. We should expect different types of plants with respect to somatic chromosome number, since the distribution of the *setosa* chromosomes is somewhat irregular in the F_1. They should contain 30, 31, 32, 33 or 34 chromosomes. The two back-crosses which have been studied cytologically have 32 chromosomes in root-tip cells (figure 8 e), twenty from *biennis* plus 10 *biennis* and 2 *setosa* chromosomes from the F_1. It is conceivable that 15 pairs plus 2 laggards, or 10 pairs and 12 laggards might be found in reducing cells, the behavior depending upon whether or not the 10 unmated *biennis* chromosomes can form 5 pairs. Study of pollen mother cells shows that fifteen pairs are present and chromosome division and cytokinesis proceed normally. Thus we shall expect a 30-chromosome form to result from back-crosses.

It has been more difficult to secure viable achenes when the F_1 is back-crossed to the *setosa* parent. Three such plants have been obtained, all having a different appearance in the rosette stage. One, $22.315P_2$, would pass readily for *biennis*, while $22.315P_1$ closely resembles the F_1 *C. setosa* × *C. biennis* and $22.315P_3$ is unlike anything which we have observed in the parent species. There are 17 chromosomes in the root-tip cells of $22.315P_2$ (figure 8 d), presumably 10 *biennis* and 3 *setosa* chromosomes having come from the F_1 while a normal haploid set of 4 has entered from *C. setosa.* Inasmuch as 10 *biennis* chromosomes give the *biennis* type of plant it seems probable that they contain all of the genes necessary for its development. There should thus be 3 pairs of *setosa* chromosomes. If the 10 *biennis* chromosomes form 5 pairs and the 6 *setosa* chromosomes 3 pairs, we should be able to obtain an 8-paired species plus one laggard. The other back-crosses, $23.315P_1$ and $22.315P_3$, have not yet been studied cytologically. Back-crosses to *C. setosa* should include plants with 14, 15, 16, 17 and 18 chromosomes in somatic cells and by inbreeding might, as indicated above, produce stable races with 10, 12, 14, 16 and 18 chromosomes, respectively.

The fact that the hybrids of these species can be propagated asexually makes it possible to retain any plant, having a particular chromosome complex, for repeated tests and analysis extending over more than one season.

SUMMARY AND CONCLUSIONS

Such material makes it possible to study the effects in the F_1 of (a) extra chromosomes, and (b) decreased chromosome number, on development and somatic appearance.

When the chromosomes are irregularly distributed, as in the meiosis of the F_1 from *C. setosa* × *C. capillaris*, a means is afforded whereby chromosome number may, by subsequent breeding, be increased by one or a few pairs. Thus, breaks in chromosome number series, such as we find in the genus Crepis, may be caused by hybridization, not necessarily by non-disjunction.

If *C. setosa* × *C. capillaris* can be inbred it should be possible to observe the effect of one, two, or three pairs of *capillaris* chromosomes on the characters of the plant.

It has often been assumed, that, if a single pair of chromosomes foreign

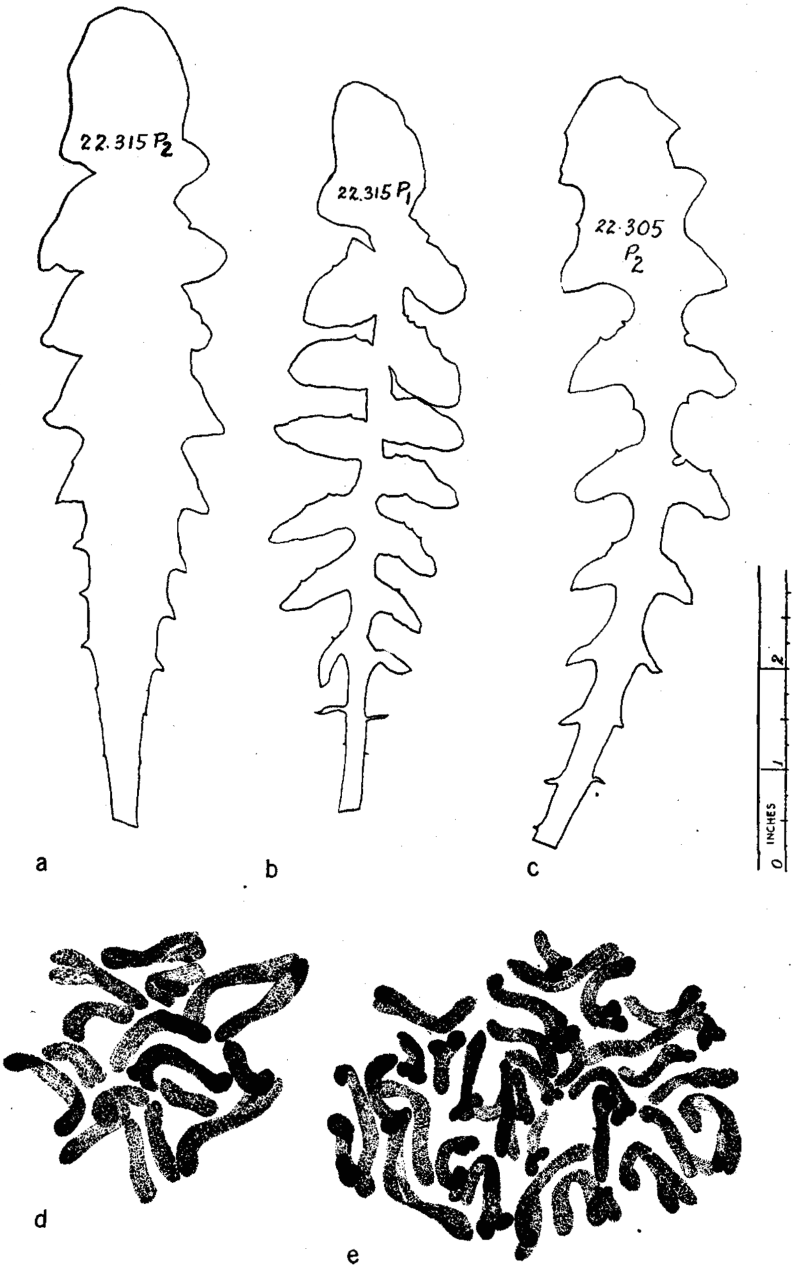


FIGURE 8.—Variations in back-crosses. a and b. F$_1$ (*C. setosa* × *biennis*) × *C. setosa*. c. F$_1$ (*C. setosa* × *C. biennis*) × *C. biennis*. d. Chromosome group of 22.315P$_2$. e. Chromosome group of 22. 304P$_2$.

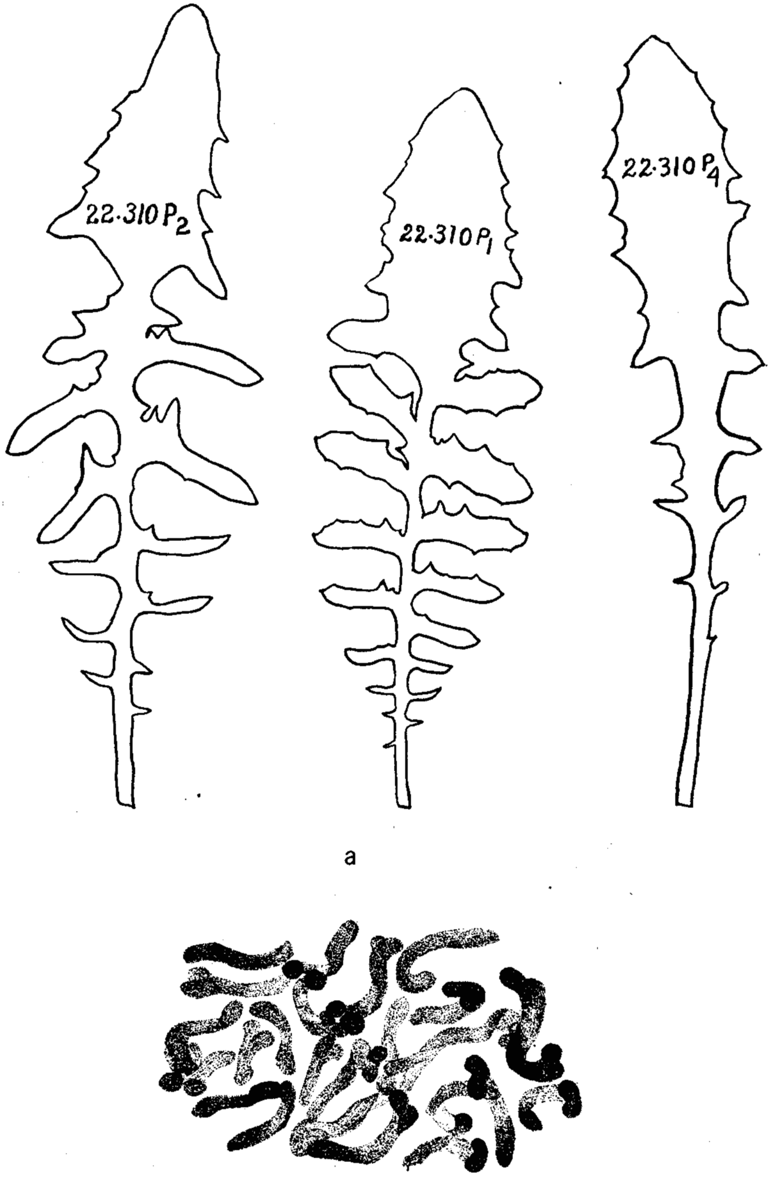


FIGURE 9.—a. Leaf variations in F_2 *C. setosa* × *C. biennis*. b. Chromosome group of F_2 22. 310P_2.

to a group were to be inserted into it, they would automatically maintain themselves. This can now be tested experimentally.

The back-crosses from the F_1 (*C. setosa* × *C. capillaris*) × *C. setosa* indicate that the germ cells of the F_1 have a greater probability of survival if they contain the total *capillaris* or *setosa* complex with or without extra chromosomes.

Since *Crepis biennis* (N = 20) will cross with *Crepis setosa* (N = 4) and give vigorous offspring the possibility of hybridization is obviously not proportionate to the similarity of chromosome number of the parents.

The evidence from *C. setosa* × *biennis* proves that it is possible for the chromosomes from one parent to unite with one another, and shows that plants with half of the normal *biennis* number retain the *biennis* characteristics. This opens the question as to how far this reduction can be carried, and of how such further reduction may affect the somatic appearance.

Since the F_1 of *C. setosa* (N = 4) × *C. capillaris* (N = 3) shows very abnormal reduction phenomena while *C. setosa* × *C. biennis* reduces almost normally, it is evident that normality of reduction does not depend upon similarity of chromosome number, but rather upon likeness of internal composition of the chromosomes.

Plants of *C. biennis* are among the largest and most robust of the genus. The cells are much larger than they are in the species with lower chromosome number.

If *biennis* is considered as an octoploid species the loss of the *gigas* characteristics would not be expected until the 2N condition had been reached. The F_1 *C. setosa* × *C. biennis*, having the *biennis* characters but only a haploid number of *biennis* chromosomes, is as large as *C. biennis*. This may indicate that these plants are still in the tetraploid condition.

The F_1 hybrid, having half of the *biennis* chromosomes, is an annual. This indicates either the activity of the *setosa* haploid set of chromosomes or that reduction of the number of chromosomes in this case results in a change from biennial to annual.

The F_1 *C. setosa* × *C. biennis* cannot revert to the parent species through back-crossing because of the pairing of the *biennis* chromosomes of the F_1 during meiosis. The back-crosses to *C. biennis*, which have ten less *biennis* chromosomes than *C. biennis*, show no *setosa* characteristics in the rosette stage.

In these crosses the species contributing the greater number of chromosomes was dominant. In *C. setosa* (N = 4) × *C. capillaris* (N = 3), *C. setosa* was dominant while in *C. setosa* (N = 4) × *C. biennis* (N = 20) *C. biennis* was dominant.

It is possible to propagate the hybrids and their parents by asexual means.

Self-fertilized seeds were found to set on *C. setosa* × *C. biennis* F_1 hybrids in the garden, but failed to set in the greenhouse. The F_1 *C. setosa* × *C. capillaris* failed to set selfed seed in the greenhouse but was not tested in the field.

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