together with a random number from the haploid set of the other species. The regular conjugation of the *biennis* chromosomes to form 10 pairs in F_1 prevents the recovery of the parent species in subsequent generations as is possible in the majority of partially fertile species hybrids, and at the same time sets up a mechanism for the production of constant forms having 10 pairs of *biennis* chromosomes with or without chromosomes from the other species. As reported in the preliminary account, these F_1 hybrids when backcrossed with *biennis* produce plants having 30 *biennis* chromosomes which form 15 pairs during gametogenesis. Additional evidence is now available (detailed later in this paper) which indicates clearly that the 10 *biennis* chromosomes in the F_1 gametes may conjugate to form 5 pairs. There are, therefore, in the gametes of *biennis* four sets of chromosomes each containing five members which can form bivalents under appropriate conditions. We now have additional evidence to support the view that *bennis* is an octoploid species.

ORIGIN OF CREPIS ARTIFICIALIS (N=12), A CONSTANT HYBRID FORM FROM BIENNIS (N=20) × SETOSA (N=4)

The F_1 plants from the cross *biennis* × *setosa* were similar in phenotype to *biennis*. Plants of the F_2 and subsequent segregating generations exhibited great diversity in phenotype and fertility including *biennis*-like plants, plants showing *setosa*-like types on an enlarged scale, and plants with some *setosa* characters superimposed upon *biennis* characters.

The formation of viable seeds in a number of Crepis species appears to be influenced by environmental conditions at the time of pollination. A given plant may set seed well at one time and at another with changed conditions (cool, cloudy weather) appear sterile or almost so. It has, therefore, been impossible to determine accurately the degree of fertility of hybrid plants. However, those with more pronounced *setosa*-like characters were regularly less fertile than plants which more closely resembled *biennis*. Due to this situation the subsequent generations consisted largely of *biennis*-like plants. Occasional fertile, or partially fertile plants having some *setosa* characters intermingled with *biennis* characters have appeared. One such F_4 plant ($26.47P_2$) obviously had formed a working combination of chromosomes from both *biennis* and *setosa*. This plant was the beginning of the new form which is referred to here as *Crepis artificialis* for convenience in reference and because it represents a distinct new type. (The taxonomic treatment of this form will be published later).

MORPHOLOGY OF C. ARTIFICIALIS

Crepis artificialis is an annual, first forming a rosette from which the flowering stalk is produced. The rosette leaves are pinnately divided with large lyrate terminal lobe, see figure 3. They show the developmental variation common to this type of plant and also perhaps some genic heterogeneity exists. The leaves are more petiolate than are *biennis* leaves and are covered with a fine pubescence.

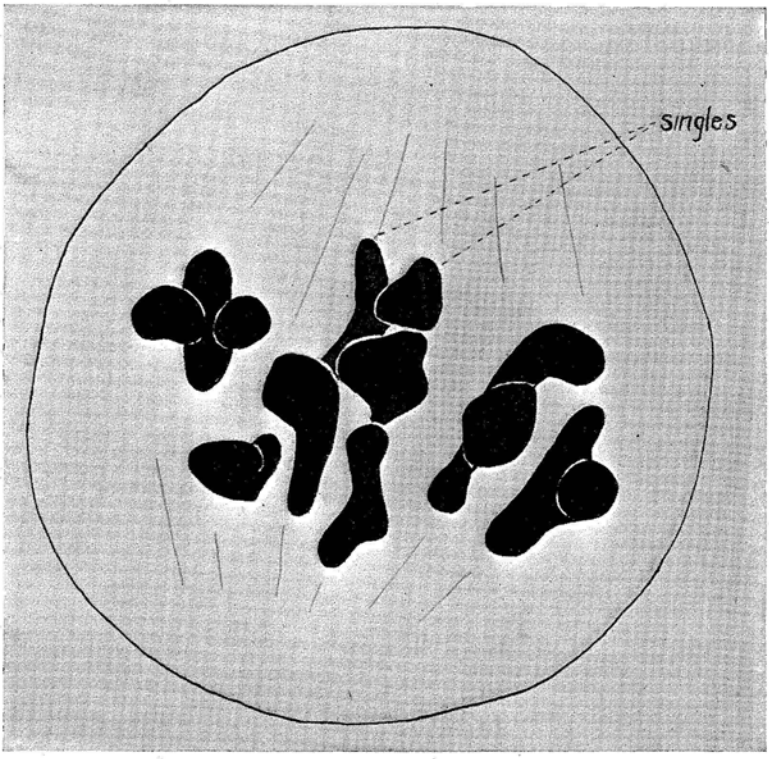

FIGURE 2.—A meiotic metaphase in a pollen mother cell of an F_1 plant, *C. artificialis*×*C. setosa*, (27.86 P_1) showing 7 pairs and 2 singles. Magnification, × 3700.

The stems which are sparsely hairy with *setosa*-like hairs are from 30 to 60 cm. tall depending upon growing conditions. The buds bear long, non-glandular hairs on the bracts. The flower heads are from 25–38 m.m. in diameter when open, which is much larger than *setosa* flowers and about the size of *biennis* flowers. The stigmas are dark colored like those of *setosa* and the achenes while, large like *biennis*, are not beaked. A comparison of the characters of *artificialis* with those of its parent

species shows *artificialis* to be *biennis*-like in about seven characters and *setosa*-like in about eight and to be intermediate or compound in some four other characters. See table 2.

A TRIPLOID PLANT OF C. ARTIFICIALIS

One of the extra chromosome plants listed in table 1 is a triploid *artificialis*, having 36 chromosomes. This plant ($26.040P_{29}$) was slightly more

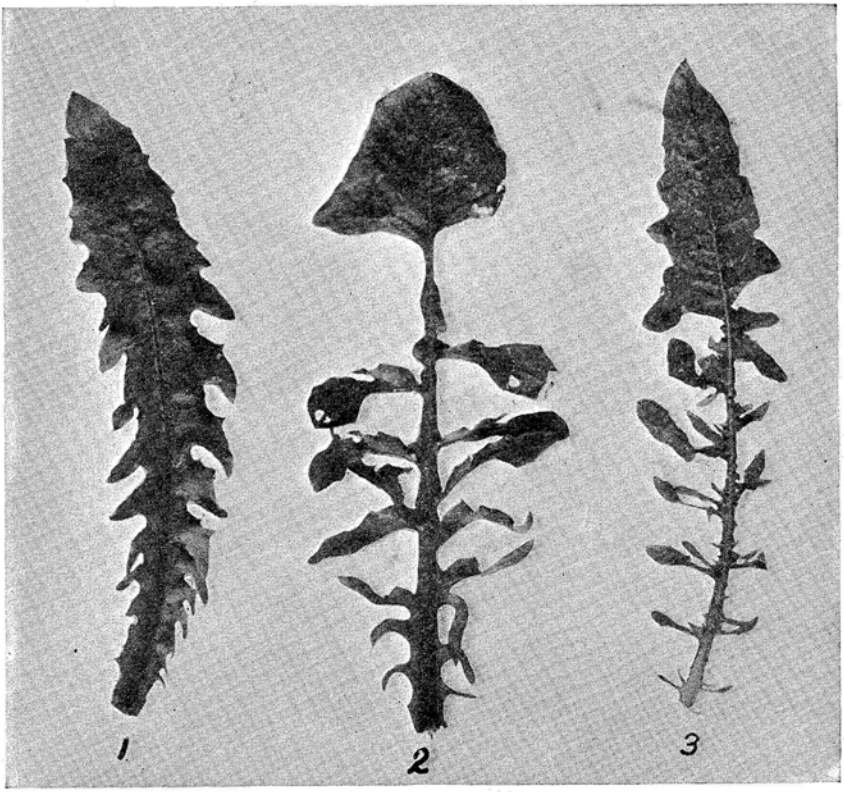

FIGURE 3.—Typical rosette leaves from 1, *C. biennis*, 2 *C. artificialis* and 3 *C. setosa*. Magnification approximately, ×1/2.

robust than the 24 chromosome plants of the same culture. The five achenes in the bottom group of figure 4 are from this triploid and are slightly larger than the average of the others which are from 24 chromosome plants.

It has been shown that *C. artificialis* contains 10 pairs of *biennis* and 2 pairs of *setosa* chromosomes. Meiosis in the triploid presented some

TABLE 2

A comparison of the principal characters of Crepis artificialis with those of C. setosa and C. biennis.

CHARACTER	*setosa* (n=4)	*biennis* (n=20)	*artificialis* (n=12)
Habit of growth	annual	biennial	annual
Stems	slender, bristly hairy, leafy, sharply angular, much branched.	stout, rough coarse hairy, and soft white tomentum, less leafy than *setosa;* branched in upper half.*	semi-stout, sparsely hairy angular, less leafy than *setosa*, branches on upper half.*
Height	23–60 cm.	45–120 cm.	30–60 cm.
Radical leaves	hairy, not rough, petiolate, often lyrate.	rough hairy, slightly petiolate only, seldom lyrate.	rough hairy, petiolate, lyrate.
Cauline leaves	sagittate and clasping	narrow only slightly clasping.	like *biennis*, narrow and clasping.
Peduncles	slender, angular, hispid with long hairs, and canescent puberulent.	stout, not hairy or only sparsely so.	stout, hispid with sparse long *setosa*-like hairs and wooly white tomentum.
Receptacle	alevolate, the alveolae small with short-ciliate margins, at maturity almost glabrous.	alveolate, alveolae large, with laciniately long fringed margins.	alveolate like *biennis* but less well developed

TABLE 2 cont'd

CHARACTER	*setosa*	*biennis*	*artificialis*
Heads	14–16 mm. long, 19 mm. in diameter when open. Involucral bracts hoary from a fine pubescence, all bracts setose hirsute with long yellowish glandless hairs, bracts keeled.	larger than *setosa*, 25–38 mm. diameter when open. Stiff short black hairs, sometimes glandular, on bracts Outer bracts have no keel, inner have weak keel about ½ its length.	25–38 mm. in diameter when open, pubescence of two kinds like *setosa* (not glandular), bracts keeled.
Florets	red sometimes appears on back of ligule, stamen-tube yellow, stigmas blackish green	no red on back of ligule, stamen tube yellow.	no red on back of ligule, stamen tube yellow stigmas dark greenish black.
Achenes	grayish brown, spindle shaped, beaked, 10 equal ribs, 2 sizes of achenes, 4 mm. and 5 mm.	dark or light brown, long columnar, slightly narrowed at tip, not beaked. 10–13 ribs with alternate stronger and weaker. Achenes average 5 mm. but show variation in size. Not two distinct size classes.	brown, spindle shaped, attenuate at both ends, sometimes a very short beak, 10–13 ribbed equal in size, size more like that of *setosa* with two means at 4 mm. and 5 mm.

* Old plants of these species also show branching from lower part of the plant.

unusual features. No trivalent chromosomes were found at diakinesis but cells showing 18, 19 and 20 chromatin units at the first metaphase were observed of which 19 was the most frequent number. These could clearly be distinguished as 17_{II} and 2_{I}. The plates with 18 units consisted of 17_{II} and 1_{I}, the other single probably being obscured. Where 20 units were observed there appeared to be four singles present. In some of the first metaphase plates singles appeared to be dividing. (This would give rise to the extra univalent chromosomes.) Here, as in the backcross of $F_1 \times$ *biennis*, the 30 *biennis* chromosomes form 15 pairs, while the 6 *setosa* chromosomes form 2 pairs and 2 singles instead of two trivalent units, although each *setosa* chromosome is certainly present three times.

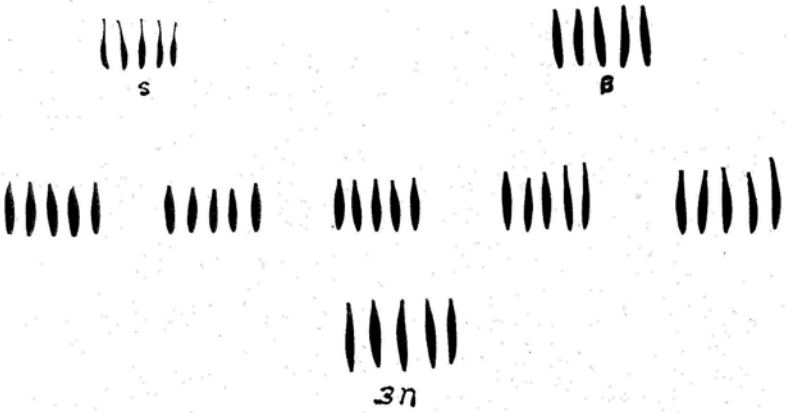

FIGURE 4.—Typical achenes of *C. setosa* (S), *C. biennis* (B), above, with achenes from six different plants of *C. artificialis*, the lowest group (3n) contains achenes from a triploid plant of *C. artificialis*. Magnification, ×1.5.

Triploids are usually very low in fertility but due to the large number of bivalent chromosomes (17) formed here, the fertility is quite high as indicated by the large amount of seed produced and from examination of anthers which showed only 30–38 percent bad pollen. The apparently good pollen showed variation in size.

The progeny of this triploid exhibited two distinct types in the seedling stage in about equal numbers. One group of 55 seedlings were normal in regard to cotyledon leaves; the other of 49 plants had abnormally developed cotyledon leaves, which were usually more or less coalesced. The two types are illustrated in figure 5. The rosettes of nearly mature plants exhibit much variation in size and type of leaves.

From the type of meiosis observed we should expect the progeny to have a range in chromosome number from 34 to 38. At the present time

the number in nine plants is as follows: five with 34 chromosomes, two with 31 and one each with 33 and 35 chromosomes. The failure to find plants with 36 to 38 chromosomes was very probably correlated with the presence of micronulcei and microcytes frequently observed at the tetrad stage.

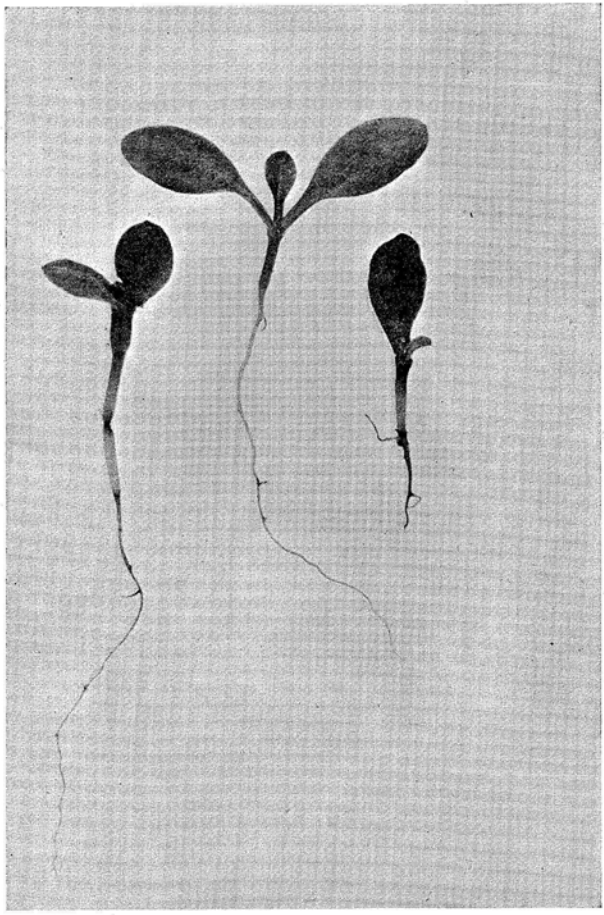

FIGURE 5.—Seedlings of the *C. artificialis* triploid plant showing a normal seedling and on each side seedlings with abnormal cotyledon development. Magnification, ×2.

We are not yet able to account definitely for the numbers lower than 34. The plants having 34 chromosomes should be the origin of a new form having 30 *biennis* chromosomes with 4 *setosa* chromosomes. They represent *artificialis* plants to which 10 additional *biennis* chromosomes have been added. Two of these 34 chromosome plants have been placed

in an isolated field at Davis, California, to determine their ability to reproduce under natural field conditions.

DISCUSSION

Crepis artificialis has the same number of chromosomes (24) as the *biennis*×*setosa* F_1 hybrid and each has 20 chromosomes from *biennis*. The F_1 has four univalent *setosa* chromosomes, while *artificialis* has two bivalent chromosomes from *setosa*. Although there is only this small difference in the chromosomes, the plants are quite distinct in phenotype. The F_1 plants are essentially *biennis* in appearance while *artificialis* shows some *setosa*-like characters more or less modified in their expression by the presence of some *biennis*-like characters. In the F_1 resulting from crossing *artificialis* with *setosa*, plants containing 10 chromosomes from *biennis* and 6 from *setosa* were secured. The latter included the two pairs present in *artificialis* plus one member of each of the two pairs not represented in *artificialis*. These plants were more like *setosa* than is *artificialis*.

Of the three outstanding distinctive characters of *setosa*, (a) pubescence (b) lyrate terminal lobe of the rosette leaves and (c) the beaked achenes, the first two are present in *artificialis* in a marked degree, while the third is not present or only to a very slight degree (see figure 4). In other hybrid strains from the same species cross beaked achenes are present, usually with no or only a small development of the *setosa* type of pubescence. Consequently it may be concluded that the major multiple genes for beak production are not present in *artificialis*, while those for pubescence must be largely located in the two pairs of *setosa* chromosomes included in the *artificialis* complex. (In the F_2 of *biennis*×*setosa* and subsequent generations there were plants showing different degrees of expression of beak and pubescence which suggested the operation of cumulative multiple genes for these characters).

These experiments have also added to our knowledge concerning the chromosomes of *biennis*. The normal diploid number appears to be 40 but plants of this species have been found to have 39, 41, 42, 43 and 45, (including counts made by M. NAVASHIN). LONGLEY (1927) has studied the occurrence of spernumerary chromosomes in maize where the normal diploid number is 20 but plants with one, two and three additional chromosomes have been found more or less frequently. These extra chromosomes appear to be repetitions of a single type, the smallest of the maize set. We have not been able to identify the extra chromosomes in *biennis* as repetitions of a single type but that chromosome elimination