CYTOLOGICAL STUDIES OF FIVE INTERSPECIFIC HYBRIDS OF CREPIS LEONTODONTOIDES

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University of California Publications in Agricultural Sciences
Volume 6, No. 5, pp. 135–167, 18 figures in text
Issued December 10, 1930

University of California Press
Berkeley, California

Cambridge University Press
London, England

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INTRODUCTION

Cytological investigations in *Crepis* have been primarily concerned with the somatic chromosomes, their low number and well marked individuality being particularly favorable for such studies. Less extensive investigations have been carried on in regard to meiotic phenomena in interspecific hybrids by Collins and Mann (1923), Navashin (1927), Babcock and Clausen (1929), and Hollingshead (1930*a*). The study of this phase of the chromosome cycle involves greater difficulties than that of the somatic and must often be inferior on the quantitative side to similar studies in other more easily handled genera. Nevertheless, certain apparently significant facts are very strikingly demonstrated in the meiotic as well as the somatic divisions of the hybrids of low-chromosomed species. It is therefore in illustration of these facts that the present account is given of cytological observations on five F_1 hybrids in which a single species, *Crepis leontodontoides*, served as one parent in the cross.

It is a pleasure to acknowledge my indebtedness to Professor E. B. Babcock for advice and interest as well as for facilities which made possible the studies reported here. I am also indebted to Mr. C. W. Haney for three of the hybrids used in these investigations.

Material and Methods

Two accessions (1682 and 1807) of seed from Italy were the source of the *C. leontodontoides* plants used in securing the hybrids concerned in the present study. The plants of the other species used were those belonging to strains grown in pure line in the Genetics gardens at the University of California (*C. tectorum*, 1498 and 1622; *C. capillaris* X-strain; *C. parviflora*, 1533; *C. marschalli*, 1532; *C. aurea*, 1636).

Root tips from young plants were used as material for the study of somatic chromosomes. These were killed and fixed in chrom-acetic formalin according to formula 1 given by Hollingshead and Babcock (1930, p. 3), and imbedded in paraffin in the usual way. Sections were cut 8μ thick and stained with Haidenhain's iron-alum haemotoxylin.

For the study of meiotic behavior, PMC's were used, three different procedures being followed. In a few cases, and especially for tetrad counts, aceto-carmine smears of buds of the proper stage were used. Most frequently, however, the buds of approximately the right stage were fixed in Carnoy's fluid for 3–12 hours, rinsed in the higher alcohols, and stored in 70 per cent alcohol. These buds were then used for making smears with aceto-carmine as described by Hollingshead (1930*a*). One objection to this procedure is the large loss of PMC's in hybrids where material is apt to be scarce. In these cases some buds were fixed in chrom-acetic-formalin, or in Carnoy followed by chrom-acetic-formalin as described by Babcock and Clausen (1929). After imbedding, these buds were sectioned 10–12μ in thickness and stained with either haemotoxylin or gentian violet. All drawings were made from aceto-carmine smears, the sectioned material being used to supplement these in the study of meiotic behavior.

The somatic chromosomes were drawn at a magnification of 3400 and reduced one-fourth in reproduction. The meiotic phases were drawn at the same magnification (except figs. 5*a* and 5*c*, × 3700) and reduced one-half in reproduction.

The Species Used in the Crosses and Their F_1 Hybrids

The species hybrids used in the present study were made between *Crepis leontodontoides* and five other *Crepis* species belonging to three subgenera. *C. leontodontoides* has been placed in the subgenus *Eucrepis* because it has a spongy thickened mid-rib on the inner involucral bracts, and the achenes found in some forms are beakless. However, the very short beaks of the achenes in certain other forms have caused this species to be classified under *Barkhausia* in several works. In fact *C. leontodontoides* is really a border-line species with reference to the three large subgenera of *Crepis*, for the evidence herein reported certainly indicates a derivation in common with one or more species of *Catonia*. To the subgenus *Eucrepis* belong the species *C. capillaris*, *C. tectorum*, and *C. parviflora*, with all of which species F_1 hybrids

with *C. leontodontoides* were obtained. *C. aurea* is the only species of the subgenus *Catonia* with which hybrids were secured, although extensive crosses were made with *C. tingitana*. F_1 hybrids were also secured with the *Barkhausia* species *C. marschalli*.

In every case the F_1 hybrids possessed features characteristic of each of the two parental species. In three cases the hybrid resembled one parent more closely than the other in its gross morphology.

Fig. 1. Rosette leaves of *Crepis leontodontoides, C. capillaris* and between them their F_1 hybrid.

Thus the hybrids between *leontodontoides* and *aurea* and between *leontodontoides* and *marschalli* were closer to *leontodontoides* than to the other parent; while the F_1 *leontodontoides* × *parviflora* resembled *parviflora* more closely. In the other two cases, F_1 *leontodontoides* × *capillaris* and F_1 *leontodontoides* × *tectorum*, the hybrid was intermediate in habit and in all character expressions. This is well shown by a comparison of the rosette leaves of *C. leontodontoides, C. capillaris* and their F_1 hybrid (fig. 1).

In the F_1 hybrid between *C. leontodontoides* and *C. tectorum* a lethal Mendelian factor was operative, causing the death in the cotyledon stage of all the hybrids from four different *tectorum* plants, and of one-half the hybrids from two *tectorum* plants. In one case all

the hybrids from one *tectorum* plant were viable. The genetic analysis of the same lethal factor operating in the F_1 hybrid between *C. tectorum* and *C. capillaris* has been made by Hollingshead (1930*b*).

A summary of the vigor, fertility, and morphological characters of these F_1 hybrids as determined in the present investigation has been given by Babcock and Navashin (1930, pp. 59–63). Their possible significance, in connection with the cytological evidence presented here, for the determination of phylogenetic and taxonomic relationships has also been pointed out in this report (p. 62).

The group of hybrids thus available for study possessed the haploid chromosome complement of *C. leontodontoides* in combination with five different genoms belonging to *Crepis* species of various degrees of taxonomic relationship.

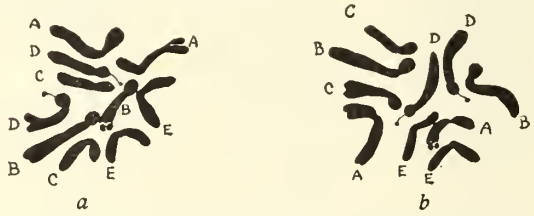

Fig. 2. Somatic metaphases of *C. leontodontoides*.

The Somatic Chromosome Complement of C. Leontodontoides

The characteristic morphology of the somatic chromosomes of *C. leontodontoides* was studied in considerable detail in order to facilitate their recognition in the chromosome complements of the hybrids, and make possible their comparison with chromosomes of other species.

In individuality the chromosomes of *C. leontodontoides* are less well marked than are those of most *Crepis species* with low chromosome number. This is largely due to the smaller size of the chromosomes and the lack of great differences in size within the complement. A study of many somatic plates showed, however, that each of the members of the five pairs can be distinguished, chiefly on the basis of the fiber attachment constriction. It was nevertheless difficult to find plates in which all ten chromosomes were in a position to show their characteristic morphologies (figs. 2*a* and 2*b*).

In the *leontodontoides* haploid set of five, three chromosomes differ little in total length, but they may be distinguished by the point of constriction where the spindle fiber is attached. Following Navashin's scheme, A has been used to designate one of the long chromosomes

of the set, having a submedian point of constriction about one-third of the distance from the proximal to the distal end, giving the chromosome a J-shape (fig. 2). A chromosome of about the same length, but with a subterminal constriction forming a head is designated B. Because of the position of the spindle fiber attachment, this chromosome often lies unbent in the plate and appears to be longer than the A-chromosome. When, however, it is bent, the B-chromosome is very similar to the A-chromosome in appearance and may be distinguished from it only if the subterminal constriction is evident. The third of the long chromosomes is slightly shorter than the other two, and is characterized by a median constriction which typically gives a V shape to this E-chromosome.

The D-chromosome is intermediate in length, but is only slightly shorter than the E-chromosome. It is, however, well marked because it bears a small but distinct satellite attached by a slender thread to the proximal end of the chromosome. The constriction is subterminal, forming a small head to which the satellite is attached, but this point of constriction is often less well marked than are those of the other chromosomes. Typically, the D-chromosome lies unbent and nearly straight in the plate, but it sometimes bends at a point other than that of constriction.

The shortest C-chromosome is distinctly shorter than any of the rest. It has a submedian constriction forming arms which hold about the same relation to each other as those of the A-chromosome, i.e., 2:1. It is the only chromosome which can be identified from size relations alone.

F_1 *C. leontodontoides* × *C. tectorum*

The Somatic Chromosomes

None of the five chromosomes of *C. leontodontoides* resembles any of the four chromosomes of *C. tectorum* in somatic figures. The difference between the chromosomes of the two species is striking in the somatic cells of the hybrid. Here the *leontodontoides* chromosomes seem small in comparison to those of *tectorum,* and also the slight differences in length within the *leontodontoides* complement as compared with the greater differences in *tectorum* are evident (fig. 3).

The total length of the five *leontodontoides* chromosomes is less than three-fourths the length of the four *tectorum* chromosomes as measured in the same somatic cells of the hybrid. Each of the four *tectorum* chromosomes is easily recognized, but often the slight differ-

ences between the *leontodontoides* chromosomes are not evident, especially since the D-chromosome loses its satellite in the hybrid. The D-chromosome of *tectorum* retains its satellite unaltered, but in no case was a satellite found on the *leontodontoides* chromosome, a phenomenon (amphiplastie) which seems to be characteristic of certain interspecific hybrids as first described by Navashin (1928). Figure 3 shows a somatic plate in which the differences between the two haploid sets are evident, and each of the chromosomes from the two parents may be identified.

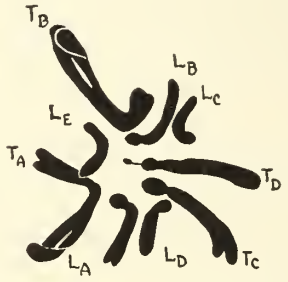

Fig. 3. Somatic metaphase of F_1 *C. leontodontoides-tectorum.*

Meiosis

With such morphological differences between the parental chromosomes, there is little reason to expect conjugation of the chromosomes of the two species at the meiotic divisions in the hybrid. Accordingly, at diakinesis and metaphase of the first meiotic division the nine chromosomes of the hybrid are frequently unpaired. In figure 4*a* a diakinesis stage shows nine unpaired units of which the four larger *tectorum* chromosomes are distinct from the five smaller and rounder *leontodontoides* chromosomes. Occasionally a stage immediately following the disappearance of the nuclear membrane shows the nine units arranged in a semicircular fashion, suggesting a telosynaptic arrangement (fig. 4*b*). Where no pairing has occurred up to diakinesis, there is apparently little tendency for the formation of a definite first metaphase plate. Thus a scattering distribution of the nine unpaired chromosomes (fig. 4*c*) seems to follow directly upon such a late diakinesis as that shown in figure 4*b*. Rarely a I–M is seen in which all the nine units are rather definitely arranged in an equatorial plate, and here the four large *tectorum* chromosomes are distinct from the five small *leontodontoides* chromosomes (figs. 4*d* and 4*e*). Only instances of random distribution of the unpaired chromo-

somes to the two poles were seen, with occasional laggards which sometimes divide. It seems probable, however, that here, as in some of the other hybrids, all nine chromosomes occasionally divide in the first division, giving rise to dyads and diploid gametes. At the tetrad stage about 7 per cent dyads are present, the proportion varying from 5.2 to 8.9 per cent.

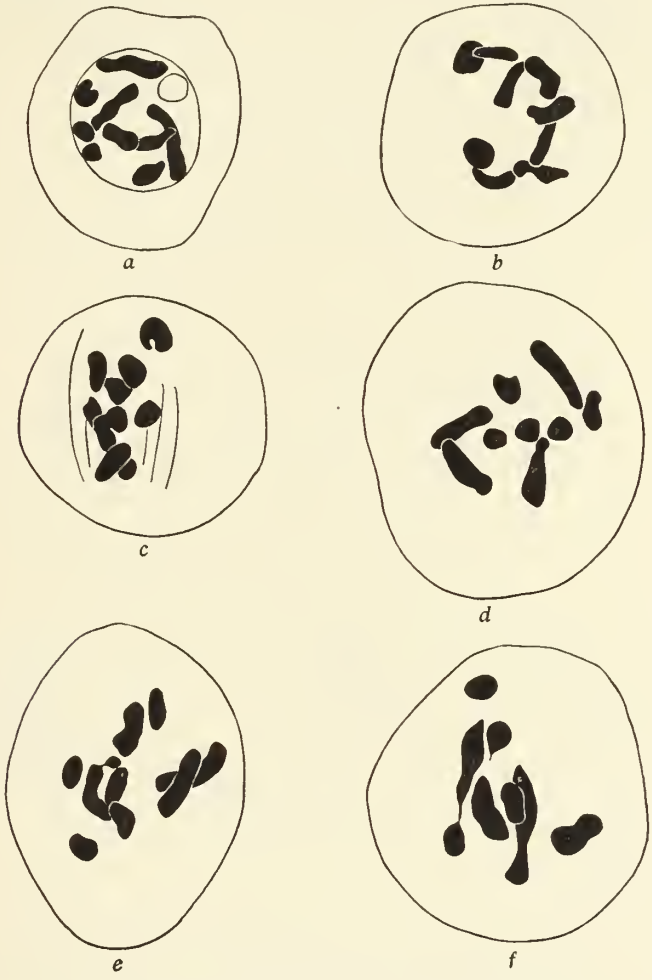

Fig. 4. Meiosis in F_1 *C. leontodontoides-tectorum.*

a, diakinesis, no bivalents; *b*, early I–M, no bivalents; *c*, I–A distribution following no pairing in I; *d*, and *e*, I–M, no bivalents, showing four large *tectorum* and five smaller *leontodontoides* chromosomes; *f*, I–M, showing one bivalent, one loosely conjugated unequal pair, and five unpaired chromosomes.

Although the behavior of the chromosomes in meiosis just described was rather frequently seen in the hybrid, it was far from being the

characteristic behavior at the reduction division. All degrees of association between the chromosomes of the two sets were observed, from $1_{II} + 7_I$ to $4_{II} + 1_I$. Sometimes "loose" pairing of two chromosomes added to the irregular appearance of the first metaphase. A tabulation of 54 PMC's in diakinesis and I–M in which the number of pairs and singles was readily interpreted (table 1) showed that $2_{II} + 5_I$ were most frequent, 9_I and $4_{II} + 1_I$ about equally frequent, and $1_{II} + 7_I$ and $3_{II} + 3_I$ least, although only slightly less, frequent. Examples of these types of pairing are shown in figures 4*f* and 5. In figure 4*f* there is $1_{II} + 7_I$, with two unequal univalents showing loose association; in figure 5*a*, $2_{II} + 5_I$; in figure 5*c*, a condition intermediate between the last two is shown, there being $1_{II} + 1$ loose$_{II} + 5_I$; in figure 5*b* there are $3_{II} + 3_I$; in figure 5*d* a diakinesis shows $4_{II} + 1_I$; and in figure 5*e* a first metaphase shows $4_{II} + 1_I$ with one pair loosely joined.

TABLE 1

SUMMARY OF CHROMOSOME BEHAVIOR IN F_1 HYBRIDS

F_1 Hybrid	Number of Bivalents at I-M						Total PMC	Per cent* tetrad irregularities
	0	1	2	3	4	5		
C. leontodontoides x *tectorum*	11	10	14	8	11	.....	54	7
C. leontodontoides x *parviflora*	6	0	5	4	11	.....	26	7
C. leontodontoides x *capillaris*	11	4	5	5	.....	.....	25	23.5
C. leontodontoides x *marschalli*	17	9	13	12	5	.....	56	20.5
C. leontodontoides x *aurea*	0	0	0	2	12	39	53	.7

*Not including micronuclei.

The pairing is clearly between the chromosomes of the two species and not within the haploid set of either parent. Thus where there is $1_{II} + 7_I$, three large *tectorum* and four small *leontodontoides* chromosomes remain unpaired (fig. 4*f*); where there are $2_{II} + 5_I$, two large *tectorum* and three small *leontodontoides* chromosomes remain unpaired (fig. 5*a*); and with $3_{II} + 3_I$, the univalents are one large *tectorum* and two small *leontodontoides* chromosomes (fig. 5*b*).

Fig. 5. Meiosis in F_1 *C. leontodontoides-tectorum.*

a, I–M, with two bivalents and five univalents; *b*, I–M, with three bivalents, and three univalents; *c*, I–M, with one bivalent, one loose pair, and five univalents; *d*, early diakinesis and *e*, I–M, with four bivalents and one univalent chromosome; *f*, and *g*, late I–A.

The results of such different types of behavior at I–M are evident at I–A where the unpaired chromosomes are frequently seen to lag and divide. Thus a I–A probably following a I–M with $4_{II} + 1_{I}$ is shown in figure 5*f*. Here four chromosomes are at each pole while one small *leontodontoides* chromosome has lagged and divided in the equatorial region. In figure 5*g* three chromosomes are seen dividing in the equatorial region, while six halves of univalent chromosomes are at each pole. Such an anaphase probably leads to the formation of diploid or near diploid gametes, as evidenced by the presence of 7 per cent dyads at the tetrad stage. Although lagging of unpaired chromosomes is frequent, microcytes are rare at the tetrad stage. Micronuclei are, however, frequent.

The per cent of good pollen grains, filled with protoplasm and taking aceto-carmine stain, varied at different times, from plant to plant and from flower to flower. Under usual conditions, the average per cent of good grains was 5.5 varying from 3.8–10 per cent. After a period of warm weather, however, the proportion in two plants was found to be 21.3 and 23.7 per cent respectively. Even the apparently good pollen grains, however, were incapable of producing viable offspring, no progeny being obtained from the few seeds set after numerous backcrossings of the hybrid with both parents.

F_1 *C. leontodontoides* × *C. parviflora.*

Somatic Chromosomes

In somatic cells of the hybrid, the two longest (A and B) of the four chromosomes of the *parviflora* parent are distinct from all the

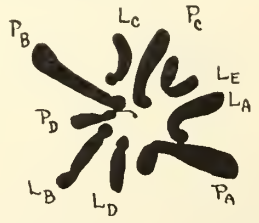

Fig. 6. Somatic metaphase of F_1 *C. leontodontoides — parviflora.*

leontodontoides chromosomes owing to their greater length. The *parviflora* satellited D-chromosome, however, is shorter than any of the *leontodontoides* chromosomes. This is of interest in connection with its suggested origin by fragmentation from the satellited chromosome of *C. capillaris* (cf. Babcock and Navashin 1930). It retains its satel-

lite on a long thread, and is thus easily identified. The D-chromosome of *leontodontoides* loses its satellite, as in the hybrid with *tectorum*. The C-chromosome of *parviflora* is so similar to the B-chromosome of *leontodontoides* in morphology that distinction between the two is not usually possible (fig. 6).

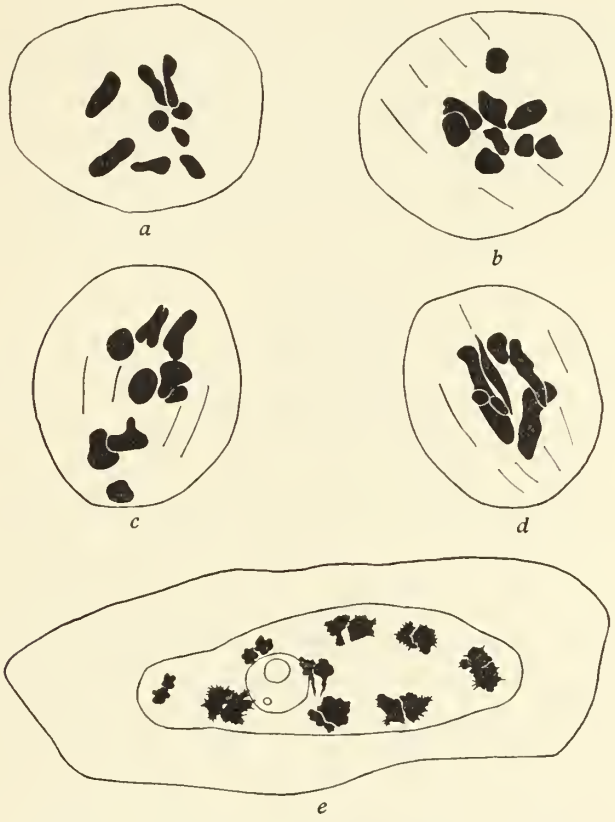

Fig. 7. Meiosis in F_1 *C. leontodontoides-parviflora*.

a, I–M, with no bivalents; *b*, and *c*, I–A, showing nine univalent chromosomes; *d*, I–M, with four bivalents and one univalent chromosome; *e*, tapetal cell showing diakinesis-like stage.

Meiosis

In the meiotic divisions the distinction between the *leontodontoides* and *parviflora* chromosomes is not so great as in the hybrid with *tectorum*, but the behavior of the chromosomes is rather similar. The same variation in the amount of pairing occurs, but more regular pairing is more frequent. Thus at diakinesis and I–M, $4_{II} + 1_I$ are seen more frequently than in the hybrid with *tectorum*, but 9_I are also

rather frequent, and intermediate amounts of pairing with $1_{II} + 7_{I}$, $2_{II} + 5_{I}$ and $3_{II} + 3_{I}$ occur (figs. 7*a*–7*d*). The types of pairing observed in 26 PMC's are listed in table 1.

The average per cent of dyads at the tetrad stage in the plants examined was again 7, but the variation from plant to plant was great and that from bud to bud of the same plant only slightly less. Thus the per cent of dyads varied from .5 to 17.7, the majority of counts showing 3–7 per cent. There were exceedingly few microcytes but micronuclei were frequent. A few triads and pentads were also seen.

The average proportion of good pollen grains in mature pollen was 6 per cent, but the variation was from 1–20 per cent. Flowers on a single plant showed a variation from 4–20 per cent. Most of the good pollen grains were extra large indicating that they came from dyads which probably contained a diploid complement of chromosomes.

In this hybrid a very striking example of a diakinesis-like stage in a tapetal cell was observed. Winge (1917) has found diakinesis-like stages in nuclei of the tapetum of *Humulus japonicus* and other species, which he regards as "a special method of mitotic nuclear division, normally including a typical diakinesis stage, presumably due to anticipated chromosome splitting." The tapetal cell observed in the present case had the size and shape of the normal tapetal cells and was much larger and more oblong than the PMC's. It was observed, however, in an aceto-carmine smear, so that its place of development is unknown. Within the large oval nucleus were nine distinct pairs of short thick chromosomes, lying close to the nuclear membrane (fig. 7*e*). A vacuolated nucleolus was present as at diakinesis in a PMC. The edges of the chromosomes were somewhat "fringed" as in a typical diakinesis. The fact that nine apparent pairs of chromosomes were present here suggests that a longitudinal division had taken place giving rise to apparent bivalents, the total number of chromosomes being twice that of the somatic cells of the hybrid. This corresponds closely with Winge's observations in *Humulus*, and no doubt here as in *Humulus* the diakinesis-like stage is not followed by reduction, but by further chromosome division.

F_1 *C. capillaris* × *C. leontodontoides.*

Somatic Chromosomes

In somatic cells of the hybrid, the three chromosomes of *capillaris* are morphologically distinct from the *leontodontoides* chromosomes, all three being larger than any of the *leontodontoides* chromosomes. The *capillaris* chromosomes maintain their individuality, the satellite always being present on the D-chromosome. However, the satellite on the D-chromosome of *leontodontoides* was never seen (fig. 8).

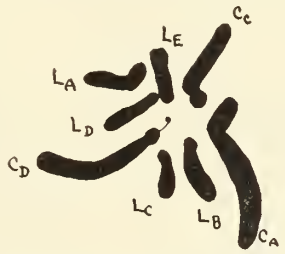

Fig. 8. Somatic metaphase of F_1 *C. capillaris-leontodontoides.*

Meiosis

The great difference in size between the *capillaris* and *leontodontoides* chromosomes makes it possible to distinguish the chromosomes of the two parents in PMC's as well as in somatic tissues. Thus in figure 9*a* three large *capillaris* and five smaller *leontodontoides* chromosomes are seen in an early metaphase where no pairing occurred. As a rule the meiotic divisions in this hybrid are very irregular. Eight unpaired chromosomes can frequently be seen at diakinesis or early first metaphase, and only very rarely can any true pairing be found, although a loose association at I–M occasionally takes place. Thus in figure 9*b* two typical pairs have been formed and another pair of chromosomes is loosely associated leaving two small *leontodontoides* chromosomes unpaired.

It is more usual to find some or all of the chromosomes dividing in the first division, and apparently the unpaired chromosomes frequently enter a distributional anaphase in which they may divide without having formed as definite a I–M plate as that shown in figure 9*a*. Thus in figure 9*c*, a 4–4 distribution is taking place at I–A but

four of the chromosomes have already divided, and the other four are in the process of division, probably resulting in an interkinesis somewhat like that in figure 9*d*. Here there was probably an 8–8 distribution of halves of univalent chromosomes, but in one nucleus three chromosomes are again dividing and in the other nucleus one chromosome appears to be doubly dividing. In this one large chromosome both longitudinal and cross-division seem to be taking place, and many other PMC's give evidence of fragmentation as well as early

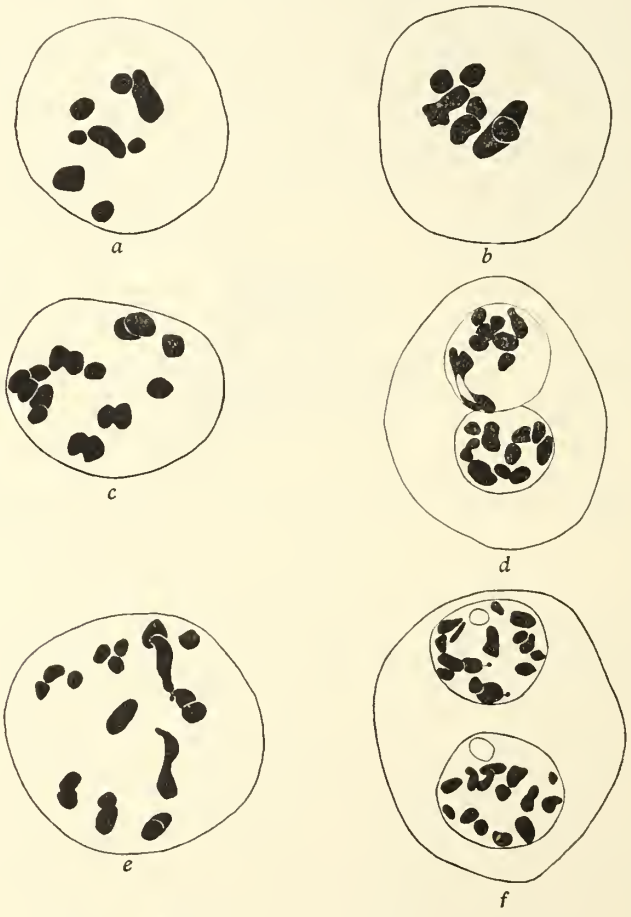

Fig. 9. Meiosis in F_1 *C. capillaris-leontodontoides.*

a, I–M, with no pairing between the three large *capillaris* and five small *leontodontoides* chromosomes; *b*, I–M, with two bivalents, one loose pair, and two univalents; *c*, I–A; *d*, interkinesis, showing products of double division or fragmentation; *e*, I–A, where fragmentation has given rise to at least 20 units; *f*, interkinesis, at least fourteen units in each nucleus.

division of chromosomes. Thus figure 9*e* apparently corresponds to a I–A but division or fragmentation is giving rise to at least twenty units. That double division or fragmentation occurs in the first meiotic division is shown by the interkinesis in figure 9*f*, where at least fourteen units, some extremely small, are seen in each nucleus.

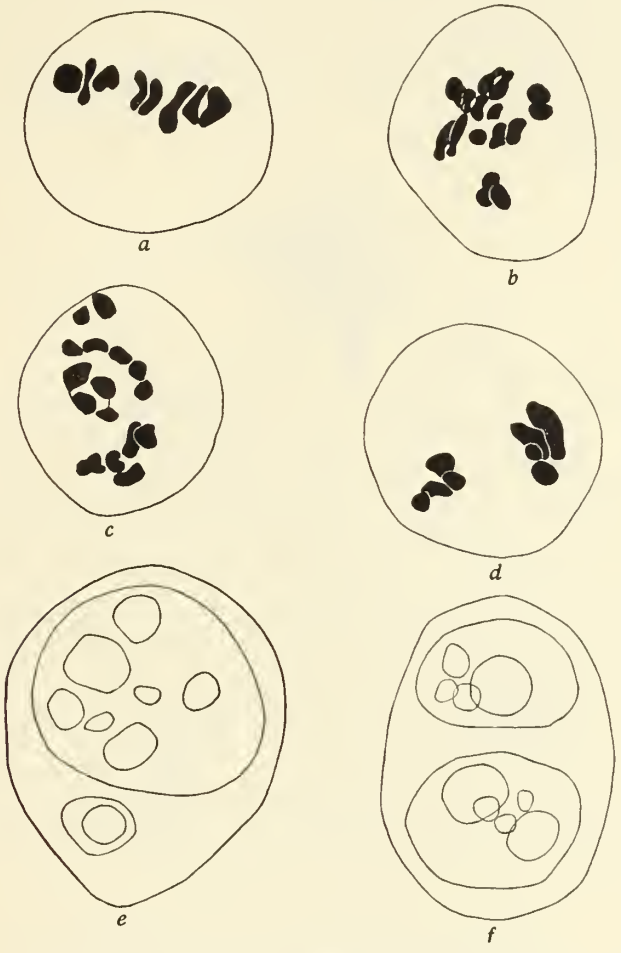

Fig. 10. Meiosis in F_1 *C. capillaris-leontodontoides.*

a, I–M, eight univalent chromosomes forming an equatorial plate; *b*, late I–M, eight univalent chromosomes dividing; *c*, I–A, irregular division of chromosomes; *d*, I–T, showing 4–4 distribution of univalent chromosomes; *e*, monad, with microcyte, five large, and three small nuclei; *f*, dyad with three large and six small nuclei.

Occasionally a metaphase is found with the eight chromosomes forming an equatorial plate and undergoing division, as shown in figures 10*a* and 10*b*. Usually, however, the division seems to be

accomplished more irregularly at various stages of I as shown in figures 9*e*, 9*f* and 10*c*. The latter figure shows a I–A where six chromosomes have already divided, five halves being at one pole, two at the other, and five in between the plates, and in addition two chromosomes are just completing their division in the equatorial region. Such irregular division leads to various numbers of chromosome units at II–M. Only rarely are I–T or II–T stages seen in which a total of only eight units can be identified, but the PMC in figure 9*d* shows a I–T with four units in each plate, no division or fragmentation having taken place.

Fig. 11. Somatic metaphase of F_1 *C. leontodontoides-marschalli.*

The irregular meiotic behavior is reflected in the tetrad stage. Micronuclei are frequent in all cells of the tetrads, and where four cells are formed there is considerable variation in their size. Dyads and triads are frequent, an average of about 22.4 per cent being counted, the variation in four buds from one plant being from 17.3 to 26.9 per cent. The dyads contain many nuclei or micro-nuclei, eight or nine usually being present. Thus in figure 10*e*, a monad with a microcyte has eight nuclei of various sizes and in figure 10*f* a dyad has three large and six small nuclei. Such behavior at meiosis can, of course, seldom lead to the formation of good pollen grains. Most of the mature pollen consists of small empty grains, and 3 per cent was the highest number of stainable grains observed.

F_1 *C. leontodontoides* × *C. marschalli.*

The Somatic Chromosomes

In somatic cells of the hybrid, three of the four *marschalli* chromosomes are distinct from all the *leontodontoides* chromosomes because of their greater length. The satellited chromosome of *marschalli*, however, is of about the same length as the *leontodontoides* chromosomes. It retains its satellite and is thus to be distinguished from the *leontodontoides* chromosomes. The leontodontoides satellite

again disappears in this hybrid. In figure 11 a somatic plate from a rather old root is shown. Here all the chromosomes are contracted so that the individuality of the *leontodontoides* chromosomes is not evident, but the distinction between the parental sets is obvious.

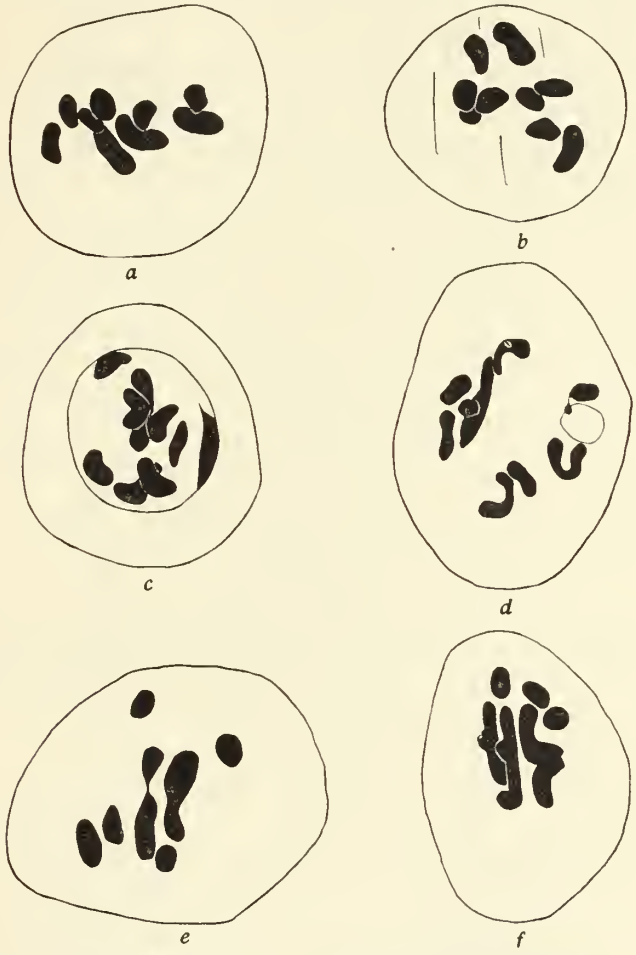

Fig. 12. Meiosis in F_1 *C. leontodontoides-marschalli.*

a, I–M, with no bivalents, three of the *marschalli* chromosomes appear larger than the rest; *b*, I–A; *c*, diakinesis with nine unpaired chromosomes; *d*, late diakinesis with one bivalent and seven univalents, one with a satellite on the nucleolus; *e*, I–M, with two bivalents; *f*, I–M, with three bivalents.

Meiosis

In PMC's of the hybrid the same size relations are found, three large and six smaller units being evident at I–M where no pairing occurs (figs. 12*a* and 12*b*). No pairing of the nine chromosomes is

the most frequent behavior at diakinesis (fig. 12*c*) and I–M, but here the complete range of types of pairing was observed to take place, there being little significant difference between the frequency of each type of pairing seen. Thus of 56 PMC's in which the type of pairing could be determined, there were 17 with 9_I, 9 with $1_{II} + 7_I$, 13 with $2_{II} + 5_I$, 12 with $3_{II} + 3_I$, and 5 with $4_{II} + 1_I$.

In figure 12*d*, a late diakinesis shows one pair and seven single chromosomes. A small chromosome seems to have a satellite attached which is close to the nucleolus. This is probably the *marschalli* satellited chromosome. Such an origin of satellites on the nucleolus has been described by Kuhn (1928) and Navashin (1927). Figure 12*e* shows $2_{II} + 5_I$. One of the pairs is loosely joined, showing that the synaptic mates are in reality chromosomes quite distinct in size. In figure 12*f*, there are $3_{II} + 3_I$. The three pairs appear to have the characteristic form of bivalents in *Crepis*, although one of the members of each pair is conspicuously smaller than the other. In figure 13*a* the formation of $4_{II} + 1_I$ shows that the chromosomes of the two species are occasionally capable of forming normal pairs to the fullest extent possible.

An anaphase in which the three large *marschalli* chromosomes are distinct from the rest is shown in figure 13*b*. Here no division of univalents has taken place. In figure 13*c* is shown a II–A after an apparent 6–3 distribution at I–A. Five chromosomes are at each pole in one half of the cell with one delayed chromosome dividing between the plates, and two chromosomes at each pole in the other half of the cell with a chromosome dividing between.

Laggard chromosomes are frequent at I–T and II–T, and result in frequent micronuclei at the tetrad stage. A II–T with five large and two small nuclei is shown in figure 13*d*. The four cells of the tetrad are often unequal in size. Dyads are frequent and often contain microcytes which vary in size up to that of the other two cells resulting in a triad. The average per cent of dyads and triads was 20.5, ranging from 12.4 to 25.3. The average per cent of good pollen grains was 5.7, and here again most of the good grains were much larger than normal.

Fig. 13. Meiosis in F_1 *C. leontodontoides-marschalli.*

a, I–M, with four bivalents; *b*, I–A, showing three large *marschalli chromosomes*; *c*, II–A, after a 6–3 distribution at I–A; *d*, II–T, five large and two small nuclei.

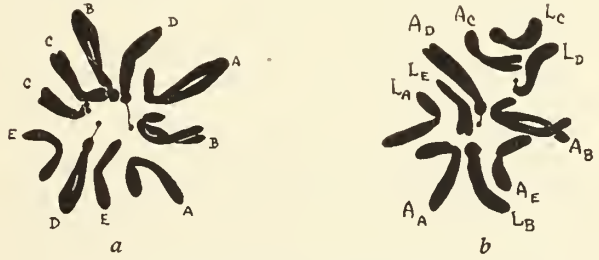

Fig. 14. Somatic metaphases.

a, of *C. aurea*; *b*, of F_1 *C. leontodontoides-aurea.*

F_1 *C. leontodontoides* and *C. aurea.*

The Somatic Chromosomes

The chromosomes of *C. aurea* resemble those of *leontodontoides* in more than number, which is $2n = 10$ in both species. The same morphological classes of chromosomes are found in *aurea* as in *leontodontoides* (fig. 14). Thus the three pairs of long chromosomes are similar in length but are distinguishable on the basis of constrictions and satellites. The A-chromosome has a submedian constriction forming a J-shaped chromosome, while the B-chromosome has a subterminal constriction forming a small head, and the E-chromosome has a median constriction giving it a V-shape. The D-chromosome is nearly equal to the B-chromosome in length, and has a somewhat smaller head to which a satellite is attached, while the C-chromosome is somewhat shorter and has a subterminal constriction deeper than that of the D-chromosome. The whole complex bulks somewhat larger than that of *leontodontoides*, but the types of chromosomes are the same. The size differences within the sets are not the same, however, the most conspicuous difference being in the comparatively greater length of the D-chromosome in *aurea*. The satellite is also larger and usually attached by a longer thread than in *leontodontoides*. Each of the chromosomes of *aurea* is slightly larger than the corresponding chromosome of *leontodontoides*.

In somatic cells of the hybrid there is little difference between the two parental sets of chromosomes, and it is only rarely that every chromosome can be definitely assigned to one or the other of the parental sets. The A- and B-chromosomes of *aurea* usually appear a little larger than the rest of the chromosomes, and the larger satellite makes the D-chromosome of *aurea* distinguishable. The C- and E-chromosomes of the two sets appear so much alike, however, that only rarely is the slight difference in size evident enough to make distinction possible. In most plates the only visible satellite is that of *aurea*, but in several instances the small satellite of *leontodontoides* could also be seen although it was always close to the body of the D-chromosome and never separated from it by the usual thread. It therefore seems that the satellite of *leontodontoides* does not disappear so completely in this hybrid as in the others examined (fig. 14*b*).

Meiosis

In meiotic divisions the chromosomes of the two species cannot be distinguished. In contrast to the other hybrids there is great regularity in meiosis. At diakinesis 5_{II} or $4_{II} + 2_{I}$ are seen. In figure 15*a* one pair of chromosomes appears to be only loosely associated

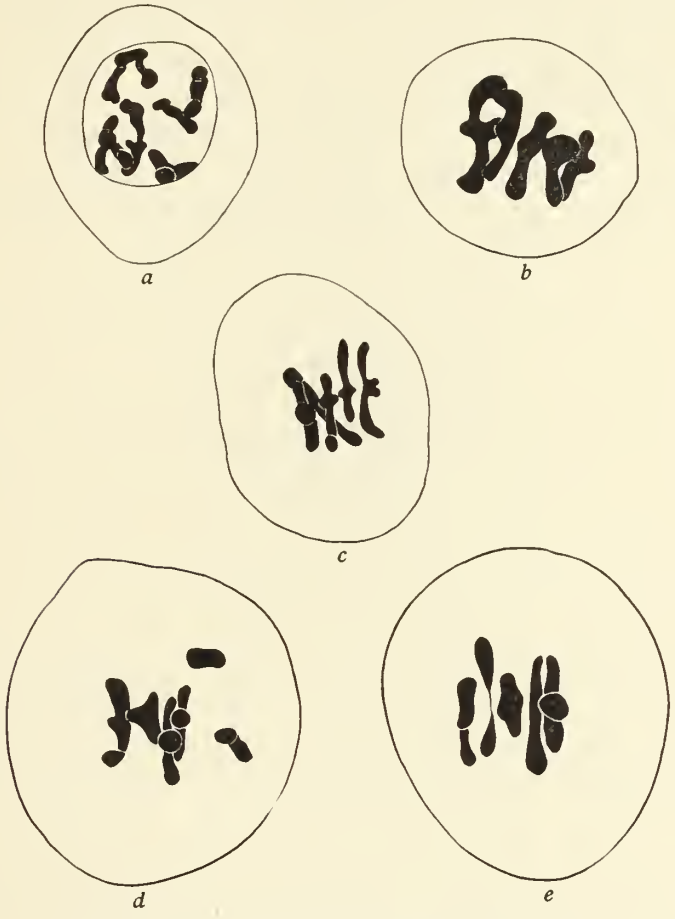

Fig. 15. Meiosis in F_1 *C. leontodontoides-aurea.*

a, diakinesis, with five pairs, one pair loosely associated; *b*, and *c*, I–M, with five bivalents; *d*, I–M, with four bivalents; *e*, I–M, with four bivalents and one pair loosely conjugated.

while the other four pairs are normally conjugated. The same amount of variation in pairing is found at the first metaphase, 5_{II} being most frequent (figs. 15*b* and 15*c*), but $4_{II} + 2_{I}$ also occur (fig. 15*d*) together with many cases of four pairs plus two loosely associated chromo-

somes (fig. 15*e*). Rarely two pairs of chromosomes show loose association. Of 53 PMC's in which the type of pairing could be distinguished at diakinesis and I–M, 39 showed 5_{II}, 12 showed $4_{II} + 2_{I}$ (including cells showing one loosely joined pair), and two showed three pairs plus two loosely associated pairs.

As would be expected from such behavior at I–M, the I–A and II–A show few irregularities. Occasionally a single chromosome lags, or a pair is late in disjoining at I–A. One or two chromosomes may rarely be left out of the daughter nuclei at II–T. The tetrads are consequently very regular as compared with those of the other hybrids. Micronuclei are occasionally seen, but microcytes are extremely rare. Dyads are formed as in the other hybrids, but to a very small extent, 2 per cent being the highest number counted, and .5 per cent being the average number in 2158 PMC's.

The number of good stainable pollen grains was exceedingly few in all seven hybrids examined. The range observed was from 1.8 to 3.7 per cent, the most showing 2–3 per cent. Some other factors besides irregularities in chromosome distribution must be operating here to produce inviable pollen grains. The per cent of good grains might have been higher under more favorable weather conditions, as was found in the case of other hybrids. At any rate, a larger per cent of female gametes must have been capable of functioning since these hybrids set more viable seed than any others upon open pollination when growing next to *C. leontodontoides.*

The contrast between the *leontodontoides-aurea* hybrid and all other hybrids studied is great. The partial fertility permitting recombinations of parental characters in backcrosses of F_1 is probably directly connected with the more regular meiosis due to the greater amount of normal pairing. This was the only hybrid both of whose parents had somatic chromosomes of the same number and types, and of very nearly the same size. The fact that morphological similarity between the somatic chromosomes is followed by conjugation of the chromosomes to a large extent at meiosis would indicate that here morphological similarity of the chromosomes bears some relation to genetic homology.

RESULT OF CROSSES OF C. LEONTODONTOIDES WITH C. TINGITANA

Because of the apparent relationship between *C. leontodontoides* and *C. aurea,* attempts were made during two seasons to obtain hybrids between *C. leontodontoides* and *C. tingitana,* another species with five pairs of chromosomes belonging to the subgenus *Catonia* and morphologically close to *aurea.* No hybrids were obtained the first year, and the second year more extensive attempts were made using various plants of both species. However, no hybrids were obtained from crosses involving sixty-two heads.

Fig. 16. Somatic metaphase of *C. tingitana.*

The failure to obtain hybrids between *leontodontoides* and *tingitana* does not necessarily mean that the relation between the two species is too distant for the production of such a hybrid. The comparative morphology of their somatic chromosomes would suggest, however, that there is a greater difference between the chromosomes of *C. leontodontoides* and *C. tingitana* than between *C. leontodontoides* and *C. aurea.*

All the chromosomes of *tingitana* are considerably larger than the corresponding chromosomes of *leontodontoides* and *aurea.* The difference in size between the chromosomes of *tingitana* and *aurea* is much greater than that between those of *aurea* and *leontodontoides.* However, the same five types of chromosomes are found in *tingitana* as in the other two species. The satellited chromosome is somewhat shorter here as compared with the A- and B-chromosomes than in the other species, being very nearly of the same length as the D-chromosome of *aurea.* With this exception the size relations within the set

are close to those found in the other two species, but the total length of the chromosomes, and the total bulk of chromatin, are much greater in *tingitana* (fig. 16). In figure 17 one chromosome of each type has been drawn from a single somatic cell of each of the three five paired species. Here the similarities and differences in the chromosome complements are evident.

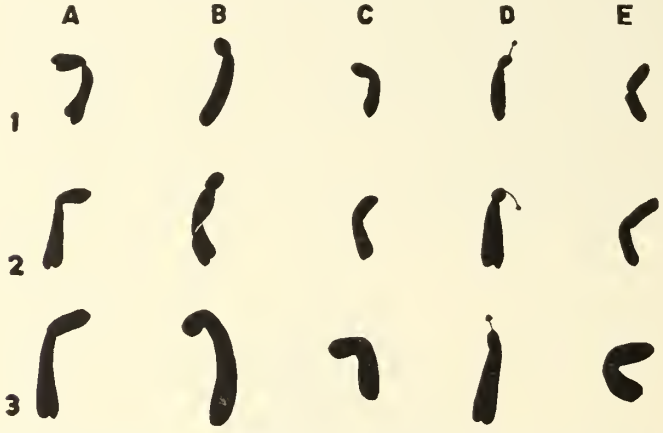

Fig. 17. Somatic chromosomes of (1) *C. leontodontoides*, (2) *C. aurea*, (3) *C. tingitana*. The chromosomes which are similar morphologically are placed under the same letter designations.

Discussion

Three features observed in these five F_1 hybrids deserve consideration, namely, the sharpness of the distinction in morphology between the chromosomes of the parental sets involved, the conjugation of morphologically distinct chromosomes, and the variable amount of chromosome conjugation. The difference in size between the chromosomes of the paternal and maternal sets is sufficiently great to permit the recognition of practically all the chromosomes as belonging to one genom or the other throughout not only the somatic but also the meiotic divisions in all the hybrids except the F_1 *leontodontoides-aurea*. For this reason the study of the behavior of the parental chromosomes in the meiosis of the hybrids is of particular interest.

The pairing of chromosomes in these hybrids takes place between chromosomes which are morphologically unlike, and is variable in its extent. This raises the question as to the fundamental nature of the synaptic union, but only indirectly contributes to the solution of this increasingly important problem.

The large number of careful observations which have been made on the meiotic phases in plants and animals in recent years, together with evidence from genetic and taxonomic studies, has led to the development of the view that when the chromosomes of the two parental sets can be shown to be composed of essentially similar genic material, and are morphologically alike, they will conjugate to form pairs of chromosomes in the prophase of the meiotic division. It is for this reason that all the chromosomes of a pure species normally conjugate to form pairs. Whether genic dissimilarity will cause chromosomes to fail to pair when it has reached a certain point, is not clear from the experimental and observational evidence. Nevertheless, the view of Gates (1928) seems justified, that the conjugation of two chromosomes is evidence of the mutual specific attractions between their similar genes, while lack of conjugation shows dissimilarity in genic constitution. This familiar point of view will be referred to as the "genic attraction" theory.

In the case of species hybrids, different degrees of conjugation between the parental chromosomes have been observed, and it is necessary to explain the differences according to the genic attraction theory if this theory be accepted for the pairing of chromosomes in a pure species. A few species hybrids are known (e.g. *Nicotiana alata* × *langsdorffii*) in which all the chromosomes of one parent pair with all the chromosomes of the other parent. In these cases the chromosomes of the two species are of the same number and of similar morphology. According to the genic attraction theory, we must infer that the basic genic constitution of the conjugating chromosomes of the two species is similar, and account for divergences in external characters leading to specific distinction through gene mutations distributed throughout the respective genoms. The number of gene mutations in such cases is supposed to be within the limits which affect chromosome conjugation.

In species hybrids where the parental species differ in chromosome number and the *Drosera* type of chromosome conjugation occurs, it would seem that the precise pairing of all the chromosomes of the species of lower chromosome number with an equal number of chromosomes of the species with the high number indicates a similar genic constitution of the conjugating chromosomes. Accordingly, it is possible to suggest that the species with the higher chromosome number has been derived by amphidiploidy from a hybrid between two species with lower chromosome number, one of which or a derivative of

which, was a parent of the hybrid concerned. *Nicotiana tabacum* is a species which may have been derived in this way according to Goodspeed and Clausen (1928), who have used the type of pairing found in the hybrids between *N. tabacum*, *N. sylvestris*, and *N. tomentosa* to support this suggestion.

In rare cases (e.g. *Crepis biennis* × *setosa*) it has been found that the chromosomes of one of the parental species conjugate *inter se* in the F_1 hybrid with another species. Such behavior suggests the polyploid nature of the species whose chromosomes exhibit autosyndesis, for the duplication of a chromosome complement followed by only slight alterations within each complement would allow the chromosomes to attract each other when independent of their more genically similar homologues.

TABLE 2

THE OCCURRENCE OF A VARIABLE NUMBER OF PAIRS OF CHROMOSOMES IN MEIOSIS IN PLANTS

	Parental Chromosome Numbers	Number of pairs at I-M	Investigator
Aegilops ovata x *Triticum vulgare*	14+21	0–3	Bleier, 1928.
ovata x *Triticum monococcum*	14+ 7	0–5	Bleier, 1928.
ventricosa x *Triticum villosum*	14+ 7	0–4	Bleier, 1928.
Crepis aspera x *bursifolia*	4+4	0–4	Babcock and Clausen, 1929
aspera x *aculeata*	4+4	3–4	Babcock and Clausen, 1929
taraxaeifolia x *tectorum*	4+4	1–4	Babcock and Clausen, 1929
capillaris x *tectorum*	3+4	0–3	Hollingshead, 1930a
Nicotiana rustica x *tabacum*	24+24	few	Christoff, 1928
bigelovii x *nudicaulis*	24+24	4–14	Webber, 1927
Papaver atlanticum x *dubium*	7+14	1–3	Ljungdahl, 1922
somniferum x *nudicaule*	11+7	3–4	Yasui, 1927
Polypodium aureum x *vulgare*	34+90	0–30	Farmer and Digby, 1910
Solanum nigrum haploid	36	3–12	Jörgensen, 1928
Triticum dicoccum x *monococcum*	14+7	4–7	Kihara, 1924
dicoccum x *aegilopoides*	14+7	4–7	Kihara, 1924
turgidum x *monococcum*	14+7	3–7	Thompson, 1926
spelta x *monococcum*	21+7	0–5	Melburn & Thompson, 1927
vulgare x Secale cereale	21+7	0–3	Kihara, 1924 Thompson, 1926
Verbascum blattaria x *Celsia bugulifolia*	15+17	12–15	Håkansson, 1926
Viola arvensis x *tricolor*	17+13	13–15	Clausen, 1922

The table given by Renner (1929, p. 107) was used as a basis for the list given here.

Complete failure of all the chromosomes of one set to pair with any of the chromosomes of the other set is not of infrequent occurrence in interspecific hybrids. This occurs where the chromosomes of the parents are the same in number and morphology, or different. In the first case, the presumption is that the species have become distinct through the accumulation of genic differences of sufficient magnitude to destroy the mutual attraction of homologous chromosomes. Thus in the case of the hybrids between *Raphanus* and *Brassica* (Karpechenko 1927) where the parental species belong to different genera, the chromosomes of the two genoms are similar in number and morphology but fail to show any mutual attraction at the heterotypic division. Where the chromosomes of the two genoms which fail to pair differ in number or morphology or both, other processes besides gene mutation have obviously been concerned in the differentiation of the chromosome complements of the species. These processes may be included under the general term "transformations," and will be considered below.

The formation of a variable number of pairs between the chromosomes of the two parental sets, whether they are of the same or of different number and morphology, has been reported as occurring in a number of interspecific hybrids. A list of instances of variable pairing in the case of plant hybrids is given in table 2. The significance of this type of behavior has been variously interpreted (cf. Farmer and Digby, 1910; Harrison and Doncaster, 1914; and Winge, 1917), but no interpretation in accordance with modern genetic and cytological knowledge has as yet been suggested which seems adequate to account for the occurrence of the variable pairing characteristic of the *Crepis* hybrids as described above.

The evolutionary processes which it seems reasonable to assume have been largely responsible for the differentiation of the distinct chromosome complements of *Crepis* species, must also be responsible for the differences between the genoms of the species which cause the formation of a variable number of pairs of chromosomes in meiosis in their hybrids. Hollingshead and Babcock (1930), after a study of the somatic complements of some seventy *Crepis* species, have pointed out that the differences between the genoms of these species can be accounted for only on the basis that transformational processes have been at work which induce changes in chromosome number and morphology. These transformational processes include mechanical changes in chromosome structure, such as inversion, trans-

location, deletion, duplication, union, and fragmentation, which have been observed to occur both under natural conditions and after subjection to high frequency radiations in *Drosophila* and *Datura*.

An illustration of the extent of the change in a chromosome complement which these processes might produce if operating over long periods of time is given in figure 18. Here, through the interference of fragmentation, translocation, inversion, deletion, and duplication, a genom has been evolved which differs in chromosome number, size, and shape, from the original complement. Yet the chromosomes of this "transformed" genom possess segments which are genically similar to segments of the chromosomes of the original complement.

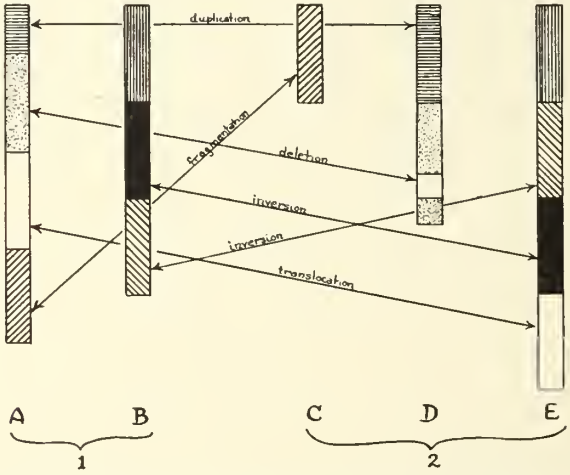

Fig. 18. Diagram showing the possible change in chromosome number and size of a genom brought about through transformational processes. Chromosome segments which are similar in genic constitution in the original and the transformed genom are similarly shaded.

These segments are now borne by chromosomes of different length and morphology. These processes operating under different external conditions over a similar period of time on the same original chromosome complement would produce transformed genoms of other types, all of which, in common with the two illustrated, would possess segments of chromosomes essentially alike in genic constitution. The similar genes borne by different transformed genoms must be responsible for the generic characters common to the species possessing these different genoms. Deletions and duplications of genes, together with gene mutations taking place concurrently with these transformational processes, and not illustrated in the diagram, may in most cases be responsible for the character differences between the species.

According to this view, pairing between the chromosomes of complements which are not alike as to number or morphology is due to the residual genic similarity of these chromosome segments. The larger or more numerous the segments which are genically similar in the case of two chromosomes belonging to different species, the greater is their mutual attraction and the more constant their pairing, while the smaller or fewer the similar segments, the weaker is their attraction and the more variable their pairing, ending in complete failure to pair when the genic similarity is less than a certain minimum. Thus we might explain different extents of chromosome conjugation in the meiotic divisions of the hybrid between two species with the chromosome complements shown in figure 18, upon the assumption that the chromosomes of the last archesporial division enter the resting stage with their orientation with reference to one another a chance one. The segments of chromosome A of species 1 genically similar to those of chromosome D of species 2 might then be of sufficient extent to attract this chromosome and permit at least loose conjugation with it, if the two chromosomes are near each other in the early prophase of the heterotypic division. If, however, the two chromosomes are widely separated, the mutual attractions of their genes may be insufficient to permit the chromosomes to conjugate.

The question as to whether or not the chromosomes in mitosis and meiosis are arranged in the spireme stages and the metaphase plates purely by chance, or assume a more definite arrangement dependent upon homology or size, does not seem to have been adequately answered as yet. Kuwada (1929) and his co-workers have shown that the chromosomes in meiosis tend to assume an arrangement characteristic of a like number of magnetized needles of corresponding sizes in a polarized field. Accordingly, the arrangement of chromosomes in both mitosis and meiosis is supposed to be rather definite, and determined by chromosome size and number. Although definite space relations may be the rule, it would seem that in hybrids such as those of *Crepis* where the chromosomes form a graduated series as to size, there must be several alternative balanced arrangements. The orientation of any one of the large chromosomes in reference to the other chromosomes must also be dependent somewhat on chance, so that proximity in prophase might well be the deciding factor in the conjugation of two chromosomes containing genically similar segments. Cleland (1928) has shown that in *Oenothera* it is probable that the chromosomes are definitely arranged in the early prophase

of the meiotic division according to their homologies and parental derivation, but no cytological proof of such definite arrangement in early prophase has been secured in *Oenothera* or any other organism.

Thus the evidence from the mode of chromosome conjugation in meiosis of interspecific hybrids supports the conclusion drawn from the study of the somatic chromosome complements of sixty-seven species that chromosome transformation has been an important method of differentiation of specific genoms in *Crepis*.

SUMMARY

1. Hybrids between *Crepis leontodontoides* and species belonging to three subgenera were studied cytologically in both somatic and meiotic phases. *C. leontodontoides* (n = 5) belongs to the subgenus *Eucrepis* and the F_1 hybrids studied were made with the *Eucrepis* species *tectorum* (n = 4), *parviflora* (n = 4) and *capillaris* (n = 3); with the *Barkhausia* species *marschalli* (n = 4), and the *Catonia* species *aurea* (n = 5).

2. The chromosomes of the two parental species can be distinguished in somatic figures in all the hybrids, although the distinction is slight in the F_1 *C. leontodontoides-aurea*.

3. The somatic chromosomes of *C. leontodontoides* and *aurea* are of the same morphological types, but those of *aurea* are slightly larger. The chromosomes of *C. tingitana*, a *Catonia* species close to *aurea*, are of the same number and shape as those of *leontodontoides* and *aurea* but are considerably larger. Efforts to secure hybrids between *C. leontodontoides* and *tingitana* were unsuccessful.

4. The satellite disappears from the D-chromosome of *leontodontoides* in the F_1 hybrid with *tectorum*, *parviflora*, *capillaris*, and *marschalli*, but is sometimes evident close to the D-chromosome in the F_1 *leontodontoides-aurea*.

5. All the chromosomes can be identified as belonging to one or the other of the parental genoms throughout meiotic as well as somatic divisions, in the F_1 *capillaris-leontodontoides*, and the F_1 *leontodontoides-tectorum* owing to the great size difference between the chromosomes of the two complements. In the F_1 *leontodontoides-parviflora* and the F_1 *leontodontoides-marschalli* all but one or two of the chromosomes of the species with larger and fewer chromosomes can be identified in the meiotic divisions.

6. The number of bivalents formed in meiosis varied in different PMC's from complete conjugation between the parental chromosomes to entire absence of conjugation in all hybrids except the F_1 *leontodontoides-aurea*. In this hybrid, the greater extent and regularity of chromosome conjugation indicates that the morphological similarity of the chromosomes bears some relation to genetic homology. In all other hybrids the pairing is obviously between chromosomes of dissimilar morphology.

7. It is suggested that the variable pairing characteristic of these hybrids is a reflection of the transformational processes presumably responsible for the differentiation of the specific genoms.

LITERATURE CITED

Babcock, E. B., and Clausen, J.
1929. Meiosis in two species and three hybrids of *Crepis* and its bearing on taxonomic relationship. Univ. Calif. Publ. Agr. Sci., 2:401–432.

Babcock, E. B., and Navashin, M.
1930. The genus *Crepis*. Biblio. Genetica, 6:1–90.

Bleier, H.
1928. Zytologische Untersuchungen an seltenen Getreide- und Rübenbastarden. Verh. V. Internat. Kong. Vererb. Berlin, 1927, 1:447–452.

Christoff, M.
1928. Cytological studies in the genus *Nicotiana*. Genetics, 13:233–277.

Clausen, J.
1922. Studies on the collective species *Viola tricolor* L. II. Botanisk Tidsskrift, 37:363–416.

Cleland, R. E.
1928. The genetics of *Oenothera* in relation to chromosome behavior with special reference to certain hybrids. Verh. V. Internat. Kong. Vererb, Berlin, 1927, 1:554–567.

Collins, J. L., and Mann, M. C.
1923. Interspecific hybrids in *Crepis*. II. A preliminary report on the results of hybridizing *Crepis setosa* Hall. F. with *C. capillaris* (L) Wallr. and with *C. biennis* L. Genetics, 8:212–232.

Farmer, J. B., and Digby, E.
1910. On the cytological features exhibited by certain varietal and hybrid ferns. Ann. Bot., 24:191–212.

Gates, R. R.
1928. The relations of cytology to genetics in *Oenothera*. Verh. V. Internat. Kong. Vererb. Berlin, 1927, 1:749–758.

Goodspeed, T. H., and Clausen, R. E.
1928. Interspecific hybridization in *Nicotiana*. VIII. The *sylvestris-tomentosa-tabacum* hybrid triangle and its bearing on the origin of *tabacum*. Univ. Calif. Publ. Bot., 11:245–256.

Häkansson, A.
1926. Zur Zytologie von *Celsia* und *Verbascum*. Lunds Univers. Årsskr., 21:3–47.

Harrison, J. W. H., and Doncaster, L.
1914. On hybrids between moths of the geometrid subfamily *Bistoninae* with an account of the behavior of the chromosomes in gametogenesis in *Lycia* (*Biston*) *hertaria*, *Ithysia* (*Nyssia*) *zonaria* and in their hybrids. Jour. Genetics, 3:229–248.

Hollingshead, L.
1930*a*. Cytological investigations of hybrids and hybrid derivatives of *Crepis capillaris* and *Crepis tectorum*. Univ. Calif. Publ. Agr. Sci., 6:55–94.
1930*b*. A lethal factor in *Crepis* effective only in an interspecific hybrid. Genetics, 15:114–141.

Hollingshead, L., and Babcock, E. B.
1930. Chromosomes and Phylogeny in *Crepis*. Univ. Calif. Publ. Agr. Sci., 6:1–53.

Jörgensen, C. A.
1928. The formation of heteroploid plants in the genus *Solanum*. Jour. Genetics, 19:133–211.

Karpechenko, G. D.
1927. The production of polyploid gametes in hybrids. Hereditas, 9:349–368.

Kihara, H.
1924. Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, 1:1–200.

Kuhn, E.
1928. Zur Zytologie von *Thalictrum*. Jahrb. f. wiss. Bot., 68:382–430.

Kuwada, Y.
1929. Model experiments with floating magnets and some theoretical considerations on the problem. Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, 4:199–264.

Ljungdahl, H.
1922. Zur Zytologie der Gattung *Papaver*. Svensk. Bot. Tidskr., 16:103–114.

Melburn, M. C., and Thompson, W. P.
1927. The cytology of a tetraploid wheat hybrid (T. spelta × T. monococcum). Am. Jour. Bot., 14:327–333.

Navashin, M.
1927. Über die Veränderung von Zahl und Form der Chromosomen infolge der Hybridisation. Zeit. f. Zellforsch. u. Mikrosk. Anat., 6:195–233.
1928. "Amphiplastie"—eine neue karyologische Erscheinung. Verh. V. Int. Kong. Vererb. Berlin, 1927, 2:1148–1152.

Renner, O.
1929. Artbastarde bei Pflanzen. Handb. der Vererb., 2:1–161.

Thompson, W. P.
1926*a*. Chromosome behavior in a cross between wheat and rye. Genetics, 11: 317–322.
1926*b*. Chromosome behavior in a triploid wheat hybrid. Jour. Genetics, 17: 43–48.

Webber, J. M.
1927. Interspecific hybridization in Nicotiana. Cytological features of two F_1 hybrids, Bigelovii–nudicaulis and Bigelovii–tabacum, 24 × 24 combinations. MS thesis filed in the library of the University of California.

Winge, O.
1917. The chromosomes, their numbers and general importance. Compt. Rend. des. Trav. du Lab. de Carlsberg, **13**:131–275.

Yasui, K.
1927. Further studies on genetics and cytology of artificially raised interspecific hybrids of *Papaver*. Bot. Mag. Tokyo, **41**:235–261.