MEIOSIS IN *CREPIS*.

I. PACHYTENE ASSOCIATION AND CHIASMA BEHAVIOUR IN *CREPIS CAPILLARIS* (L.) WALLR. AND *C. TECTORUM* L.

By M. MARGARET RICHARDSON.

(*Division of Genetics, University of California, and John Innes Horticultural Institution, Merton.*)

(With Thirteen Text-figures and One Graph.)

CONTENTS.

I. Introduction.

Meiosis in *Crepis* has already been examined in many species and hybrids (Collins and Mann, 1923; Navashin, 1927; Babcock and J. Clausen, 1929; Hollingshead, 1930; Avery, 1930; Poole, 1931, 1932; Collins, Hollingshead and Avery, 1929), but, with the exception of the work of Babcock and Clausen on two species, no attention has been paid to the early stages. Bivalent form at metaphase has only been briefly described, and the majority of the studies have merely been concerned with the proportions of bivalents and univalents in various hybrids. These have been regarded as an indication of the degree of affinity between parental species. We have no knowledge of pachytene association, nor of bivalent form or chiasma behaviour in post-pachytene stages in this genus.

The low number of chromosomes in many species of *Crepis*, together with the frequently dissimilar morphology of all members of the complement, should provide exceptionally favourable material for the study of all stages. A more detailed investigation of meiosis in this genus has therefore been made in the light of recent advances in our knowledge of meiotic behaviour.

Crepis capillaris ($n=3$) and *C. tectorum* ($n=4$) have been used in the present investigation. The former is especially valuable for a study of chiasma behaviour, since it is possible for the first time to follow frequency and movement of chiasmata in each kind of bivalent from diplotene to metaphase. This has hitherto only been partially attempted (*Spironema fragrans*, Richardson (1934); *Fritillaria Meleagris*, Newton and Darlington (1930); *Vicia Faba*, Maeda (1930 *a*); *Stenobothrus*, Darlington and Dark (1932)). *C. tectorum* is closely related, with some similar somatic chromosomes.

II. Material and methods.

The florets are extremely small and it is impossible to obtain individual anthers without the use of a dissecting microscope. Smears were unsuccessful, and the best preparations were obtained with aceto-carmine after previous fixation in 1 part glacial acetic acid to 3 or 4 parts of absolute alcohol.

The floret is cut into pieces before squashing in aceto-carmine, in order that the chains of pollen mother cells may emerge more freely. For pachytene observations, the florets should not remain in the fixative for more than two days, and the slide should be heated several times to a temperature just under the boiling-point of the aceto-carmine. For diakinesis and the later stages of meiosis, the florets may apparently be left in the fixative for longer periods of time, but less heat and less iron in the aceto-carmine are required.

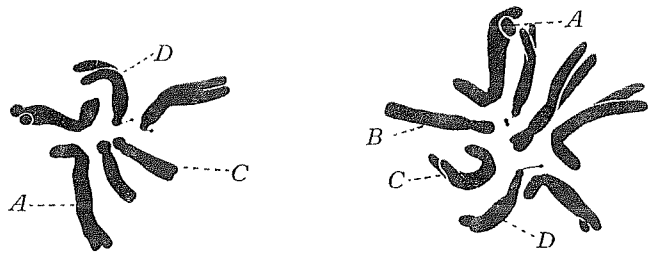
The plants used in this investigation were morphologically typical members of their species, and flowered under rather high temperature conditions in a greenhouse at Berkeley, California, during a hot June.

All illustrations were made with the aid of a camera lucida at bench level using a magnification of $\times 3600$ and reduced to $\times 2400$.

III. Somatic chromosomes.

Crepis capillaris has three pairs of morphologically distinct chromosomes. *C. tectorum*, to which it is closely related, has four pairs—also individually identifiable (Rosenberg, 1909, 1918; Digby, 1914; Marchal, 1920; Collins and Mann, 1923; Mann, 1925; *et al.*).

For the sake of uniformity, Navashin's (1925) scheme of nomenclature has been adopted. The following measurements of somatic chromosomes have been taken from Mann (1925) (see Table I), who merely groups the chromosomes according to size differences, but in the following table I have superimposed Navashin's designations of types to Mann's figures.



C. capillaris *C. tectorum*

Fig. 1. Somatic chromosomes in root tips of *C. capillaris* and *C. tectorum*. Reproduced from Hollingshead (1930).

TABLE I.

Position of spindle attachment	Mean total length of somatic chromosomes		
	C. capillaris	*C. tectorum*	
A, subterminal	26·2	28·1	
B, subterminal	—	23·2	22·8
C, subterminal	14·8	17·2	
D, terminal, satellite	20·4	20·2	
Mean total length of haploid chromosome set	61·4	88·7	

Figures represent average from ten somatic polar metaphases.

IV. OBSERVATIONS.

A. *General description of pachytene and the subsequent stages of meiosis in* Crepis capillaris (23–13, 23–23), *and* C. tectorum (29–23).

Pachytene.

Synapsis at pachytene was observed to be completely regular in all cases for both species, a large number of cells being examined. No traces of univalent threads or non-homologous association were seen. There is a fairly considerable contraction in length of the paired chromosomes from early to late pachytene, but even at the later pachytene stages the paired chromosomes are still too long to be followed separately throughout their whole length. The chromomeres are visible in well-fixed and stained preparations, but no knobs at all comparable in appearance to those in

Zea were observed (cf. McClintock, 1931). A colourless spherical region, presumably that of the spindle attachment chromomere, is present. In *C. capillaris* the *D* chromosomes, which Hollingshead (1930) and Navashin (1929) have shown to be attached to the nucleolus, have a darkly stained large chromomere at the point of attachment. No material of *C. tectorum* was available for a detailed study of pachytene, as the buds had been kept too long in the fixative. It could only be determined that the threads were closely paired throughout their length.

Subsequent stages of meiosis.

Behaviour is quite normal. Chromosomes are twisted about one another in a spiral manner at diplotene. The characteristic appearance of the bivalents at this stage is illustrated in Figs. 2 *a*, 3 *a* and *b*, and 4 *a* and *b*; the other illustrations represent bivalents in which there was less twisting, and interpretation was thus easier. The ends of the bivalents may lie free from one another, or they may lie very close together, but the frequency of such associations could not be accurately determined. Chiasma frequency could not be quantitatively analysed at the early stages owing to twisting and the swollen nature of the chromosomes in aceto-carmine. Occasionally bivalents with single interstitial chiasmata were recognised at early diplotene, and by late diplotene it could be seen that the majority of bivalents had one or two chiasmata. A few of the *A* bivalents in *C. capillaris* gave indications of having three chiasmata, but I was unable to be completely satisfied that they were not twists in all cases.

The chromosomes untwist, and by late diplotene bivalents are found in which the number of twists varies from nil or a half-twist in which the arms of a bivalent lie over one another to as much as two complete spirals. Untwisting is completed by mid-diakinesis, and at this, the stage of maximum repulsion (Darlington and Dark, 1932), a change of plane between loop and free arms is clearly evident (see Figs. 2, 3 and 4). The nucleolus disappears during the later stages of diakinesis.

Contraction is high at metaphase and it is frequently difficult to analyse bivalent structure in the aceto-carmine. The *C* bivalent of both *C. capillaris* and *C. tectorum* is most commonly found in the centre of the plate in side views of metaphase, and separates towards the poles at anaphase before the longer *A* and *D* bivalents of *C. capillaris*.

Chromosome individuality can once more be recognised by the mid-prophase of the second meiotic division, and homologues are seen to be united at the point of spindle attachment. All four chromosomes were distinguished in *C. tectorum*, the *D* chromosomes are united terminally

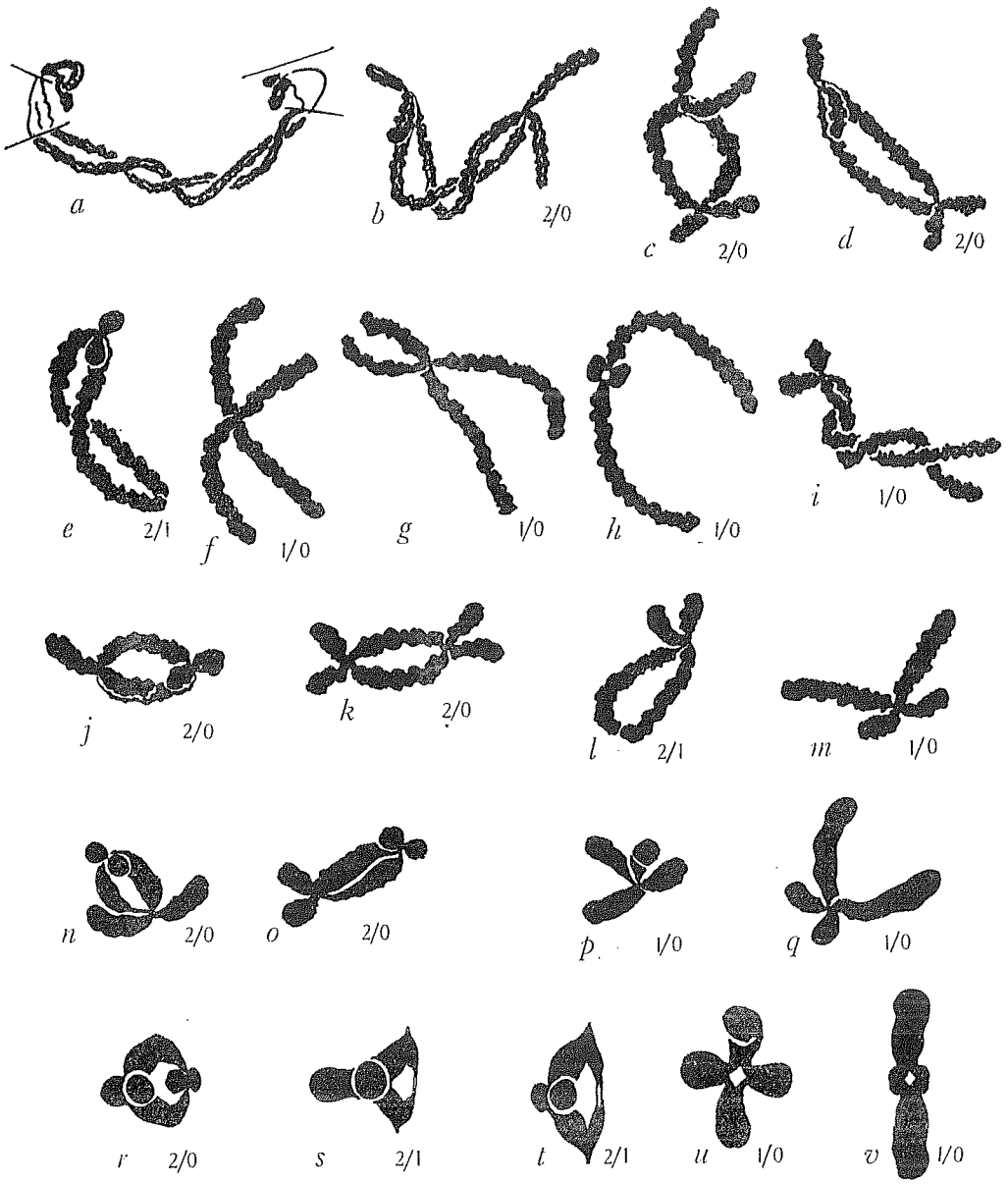


Fig. 2. Configurations in the *A* bivalent from diplotene to metaphase in *C. capillaris* 23–23. *a*, mid-diplotene; *b*, late diplotene; *c–i*, early diakinesis; *j–m*, mid-diakinesis; *n–q*, late diakinesis; *r–v*, metaphase, side views.

and are attached to the nucleolus (Fig. 7). At the earliest stage of contraction at which the individuality of the chromosomes is distinguishable, the two homologues lie apart and are frequently twisted into spirals or kinks (Fig. 7, chromosome *A*), but at the later stages of contraction these are lost.

The nucleolus disappears before contraction is finally completed (Fig. 8), and at metaphase the morphological form of the chromosomes is very closely similar to that of somatic metaphase chromosomes in root

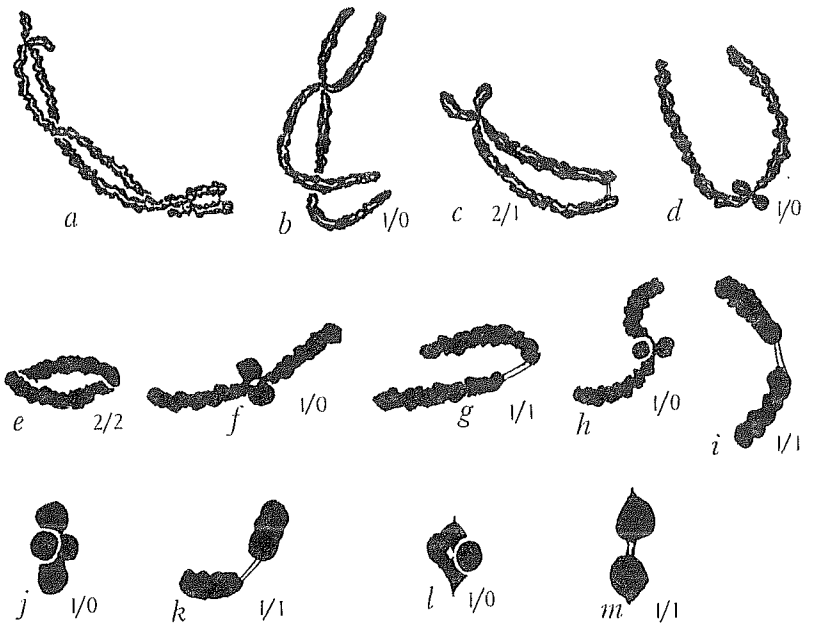


Fig. 3. Configurations in the *C* bivalent from diplotene to metaphase in *C. capillaris* 23-23. *a–b*, mid-diplotene; *c–d*, late diplotene; *e–g*, early diakinesis; *h–i*, mid-diakinesis; *j–k*, late diakinesis; *l–m*, metaphase, side view.

tips, with the following differences: (1) no satellite could be discerned on the *D* chromosomes, (2) the arms of daughter chromosomes, which in prophase lie apart, come to be closer together at metaphase, but they are never in such close juxtaposition as in mitotic chromosomes.

Discussion of general observations.

The coiling of the two chromosomes of a bivalent about each other during diplotene has been observed in many plant genera. In *Crepis* this feature has been seen in *C. aspera*, and *C. bursifolia* (Babcock and Clausen, 1929), where a single bivalent had as many as five twists at diplotene.

Uncoiling and contraction occurred concurrently. Newton in *Tulipa* (1927), Maeda in *Lathyrus* (1930 *a*), Moffett in *Anemone* (1932) and others have all shown the presence of this feature in addition to chiasma formation. The fact that the bivalents in these *Crepis* species have pairs of

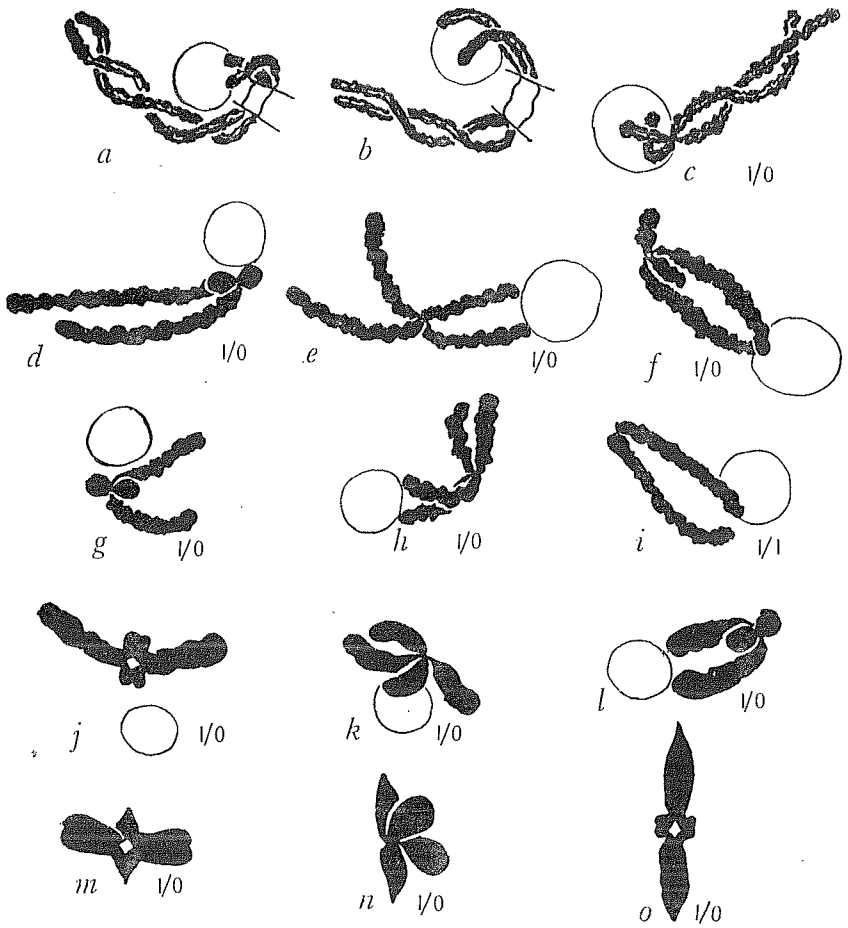


Fig. 4. Configurations in the *D* bivalent from diplotene to metaphase in *C. capillaris* 23–23. *a–b*, mid-diplotene; *c*, late diplotene; *d–f*, early diakinesis; *g–i*, mid-diakinesis; *j–l*, late diakinesis; *m–o*, metaphase, side view.

paired chromatids at diplotene in closer juxtaposition than seems to be common, is apparently due to a higher degree of coiling.

The work of Heitz (1931), McClintock (1931), and others has shown the relation between the nucleolus and the satellite chromosomes. More

especially in *Crepis*, Navashin (1929) and Hollingshead (1930) have shown its attachment to the *D* chromosome in somatic and meiotic divisions of *C. capillaris*. The present observations indicate that it is also attached to the satellite chromosomes during the prophase of the second meiotic division.

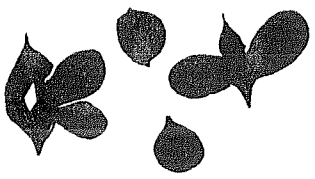


Fig. 5.

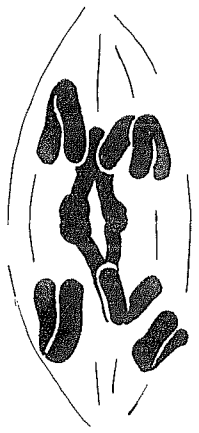


Fig. 6.

Fig. 5. Early first anaphase, *C. capillaris*.
Fig. 6. Early first anaphase, *C. tectorum*.

B. *Analysis of post-pachytene chromosome association in* C. capillaris.

(1) *Classification of bivalents.*

The *C* bivalent may be distinguished at all stages by its small size. The *D* bivalent has already been shown to be attached to the nucleolus (above), and it is clearly intermediate in size. At metaphase it can be distinguished from the *A* bivalent by its smaller size, and by the position of the spindle-fibre attachment, which is seen to be terminal in side views.

(2) *Chiasma frequency for the whole complement and for each kind of bivalent.*

Two plants have been examined. Behaviour is normal and there is no statistically significant change in chiasma frequency at successive stages of contraction for the whole nuclear complement in either plant, or between the two plants (Table II). Difficulties of interpretation, owing to twisting at diplotene and contraction at metaphase, prevented a quantitative analysis of these stages being made, but general morphological observations indicate that there is no change in chiasma frequency at the earlier stages.

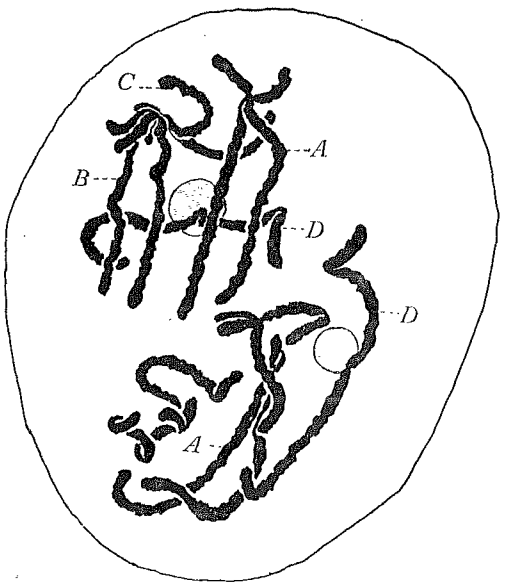


Fig. 7.

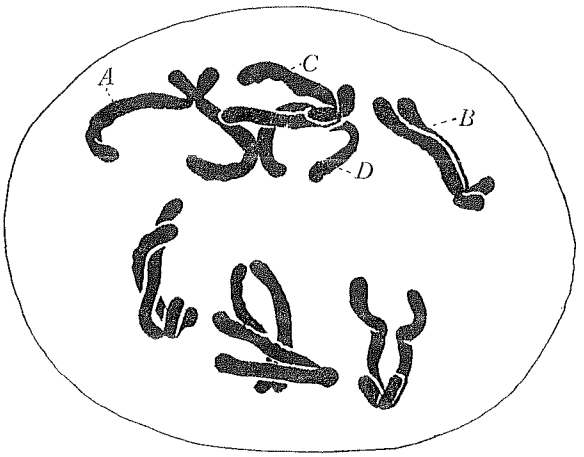


Fig. 8.

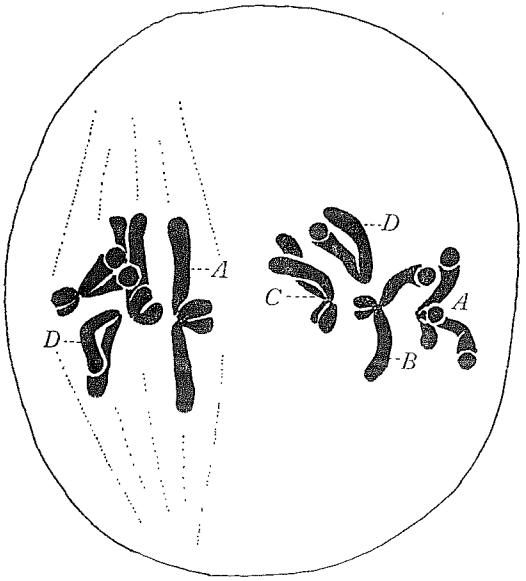


Fig. 9.

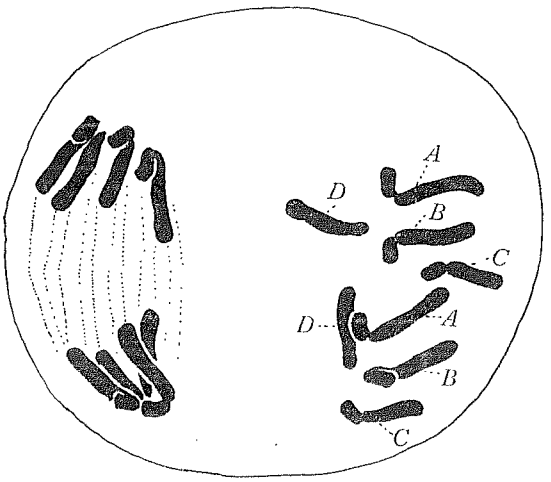


Fig. 10.

Figs. 7–10. *C. tectorum*, second meiotic division. 7. Mid-prophase, *D* chromosomes are attached to nucleoli. 8. Late prophase. 9. Second metaphase. 10. Second anaphase.

TABLE II.

Chiasma frequency and numbers of terminal chiasmata analysed for the whole nuclear complements at successive stages of meiosis—C. capillaris *and* C. tectorum.

Plant	Stage	No. of nuclei	Xma. frequency 3	4	5	6	7	T.Xma. frequency 0	1	2	3	Total Xta.	Total T.Xta.	Mean no. of Xta.	Mean no. of T.Xta.	Term. coeff.
C. capillaris																
23–13	E.DK.	4	2	1	—	1	—	3	—	1	—	16	2	4·0	0·50	0·13
	M.DK.	23	8	14	1	—	—	12	10	1	—	85	12	3·7	0·52	0·14
	L.DK.	13	4	8	1	—	—	7	5	1	—	49	7	3·8	0·54	0·14
23–23	M.DK.	84	13	46	22	3	—	50	27	5	2	351	43	4·17	0·51	0·12
	L.DK.	40	9	25	6	—	—	22	15	3	—	157	21	3·92	0·52	0·13
C. tectorum																
29–23	E.DK.	1	—	—	1	—	—	1	—	—	—	5	0	5·0	0·0	0·0
	M.DK.	10	—	—	7	—	3	4	4	2	—	56	8	5·6	0·8	0·14
	L.DK.	10	—	—	6	3	1	4	2	4	—	55	10	5·5	1·0	0·19
	M.	20	—	1	9	10	—	—	—	—	—	109	—	5·45	—	—

Abbreviations used in Tables II–VI: Xma. = chiasma, T.Xma. = terminal chiasma, Xta. = chiasmata, E.DK. = early diakinesis, M.DK. = mid-diakinesis, L.DK. = late diakinesis, M. = metaphase.

Chiasma frequency is shown for each kind of bivalent in Tables III and IV.

TABLE III.

Mean number of chiasmata, terminal chiasmata, and proportion of terminal chiasmata in each kind of bivalent. C. capillaris.

Plant	Stage	No. of nuclei	Mean no. of Xta. per bivalent *A*	*C*	*D*	Mean no. of T.Xta. per bivalent *A*	*C*	*D*	Term. coeff. *A*	*C*	*D*
23–13	M.DK.	23	1·65	1·00	1·08	0·08	0·29	0·04	0·05	0·29	0·04
	L.DK.	13	1·69	1·00	1·07	0·15	0·30	0·07	0·09	0·30	0·07
23–23	M.DK.	84	1·85	1·00	1·33	0·22	0·23	0·05	0·12	0·24	0·04
	L.DK.	40	1·73	1·00	1·15	0·05	0·40	0·10	0·03	0·40	0·09

TABLE IV.

Chiasma frequencies for different bivalents. C. capillaris.

	Plant 23–13						Plant 23–23						
		A		*C*	*D*			*A*			*C*	*D*	
No. of T.Xta.	No. of nuclei	1	2	1	1	2	No. of nuclei	1	2	3	1	1	2	3
M.DK. 0	—	8	13	14	21	1	—	17	47	2	64	58	21	—
1	—	—	2	9	—	1	—	—	15	2	20	—	4	1
2	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Total	23	8	15	23	21	2	84	17	62	5	84	58	25	1
L.DK. 0	—	4	7	9	12	—	—	11	27	—	24	33	3	—
1	—	—	2	4	—	1	—	—	2	—	16	1	3	—
Total	13	4	9	13	12	1	40	11	29	—	40	34	6	—

(3) *Positions and terminalisation of chiasmata.*

Terminalisation is low in this species (Tables III and IV). This is especially so in bivalents with only one chiasma. These may be supposed to show little movement of chiasmata, since the forces of repulsion between paired chromatids at diplotene and diakinesis which are operative in causing terminalisation are less effective between free arms than in a system of loops (Darlington and Dark, 1932, electrostatic theory of the movement of chiasmata).

In the analysis of behaviour in each kind of bivalent it is found that the proportion of terminal chiasmata is much higher in the *C* bivalents than in the *A* or *D* (Table III). Terminal chiasmata are only found at

TABLE V.

Positions of chiasmata in each of the three bivalents in C. capillaris. *Diakinesis and later stages* (Figs. 2, 3 and 4).

		A	*C*	*D*
1 Xma.	1/0	Random position on long arm	Random position	Random position; when subterminal, more frequently proximal to the nucleolus
	1/1	Only observed at M. On the long arm, once on the short arm	Observed at all stages, seen in side views of M. to be on long arm	At the end away from the spindle-fibre attachment
2 Xta.	2/0	Observed	Not observed	Observed
	2/1	T.Xma. on short arm at M. and probably also at DK.	Observed at E.DK., position of T.Xma. not clear	T.Xma. at the end away from nucleolus
	2/2	Not observed	Observed at E.DK.	Not observed
3 Xta.	3/0	Observed at M.DK.	Not observed	Not observed
	3/1	Observed at M.DK. Position of T.Xma. unknown	Not observed	Observed, T.Xma. at the end away from nucleolus
	3/2	Observed at M.DK.	Not observed	Not observed

mid and late diakinesis in bivalents with two chiasmata in the *A* and *D* chromosomes, whereas single terminal chiasmata are found in the *C* bivalents from late diplotene.

Table V shows the positions of the chiasmata in different bivalents. The exact position in relation to the spindle-fibre attachment region at diakinesis has been deduced in some bivalents by analogy with the known position evinced in similar configurations in side views of metaphase (Figs. 2, 3 and 4).

Bivalents of all three kinds may be recognised with a single interstitial chiasma at late diplotene. The incidence of chiasma formation is therefore low in this species. This is strikingly different to conditions in Liliaceous plants (*Lilium*, *Hyacinthus*, Belling, 1927, 1931; *Tulipa*,

Newton, 1927; *et al.*); and in *Vicia Faba* (Maeda, 1930*b*), *Lathyrus odoratus* (Maeda, 1930*a*), and *Fritillaria imperialis* (Darlington, 1931) and other genera, where there are several chiasmata per bivalent at diakinesis, and up to a mean of eight in *Vicia Faba*.

It has been shown that single interstitial chiasmata may be terminalised in the *C* bivalents by early diakinesis, whereas they are not terminalised in the *A* or *D* bivalents until metaphase. The few cases of the last condition which were observed may possibly be examples of an early anaphasic split in which the chromatids were obscured owing to the swelling caused by the aceto-carmine. Behaviour in the *A* and *D* bivalents is therefore similar to that in *Tulipa* (Darlington and Janaki-Ammal, 1932), where single interstitial chiasmata are not terminalised, and the *C* bivalent is different. On the theory that a terminal association always represents the terminalisation of a chiasma which has previously been interstitial this may be explained in the following manner: There is a certain rate of movement of chiasmata which is the same in all three bivalents and, although very slow, is sufficient to bring about terminalisation by early diakinesis in this class of bivalent owing to the shorter distance. This is found in fragments of *Fritillaria imperialis* (Darlington, 1930). Morphological observations indicate that movement is always slight, since all three classes of bivalent show configurations in all stages from mid-diplotene to metaphase in which chiasmata occupy relatively similar positions (Figs. 2, 3 and 4).

C. *Behaviour in* C. tectorum.

(1) *Classification of bivalents.*

The *D* chromosome has been shown earlier to be attached to the nucleolus in the prophase of the second meiotic division, and by analogy with this, and the behaviour of the satellite *D* chromosome in *C. capillaris* I have assumed that the bivalent attached to the nucleolus in all stages up to late diakinesis is composed of the *D* chromosomes. It can also be recognised in side views of metaphase owing to the position of the spindle fibre. The *C* bivalent may be recognised by its smaller size, but there is difficulty in differentiating between the *A* and the *B*. No attempt has therefore been made to separate these three bivalents when analysing chiasma frequency.

(2) *Chiasma frequency. Plant* 29–23.

There is no significant change in chiasma frequency for the whole nuclear complement between mid-diakinesis and metaphase. Behaviour

is similar to that in *C. capillaris*, chiasma frequency is low at diakinesis, the majority of bivalents having single chiasmata. The mean number of chiasmata for the whole complement varies between four and seven (Table II). The *D* bivalent has a mean very close to that of the *D* in *C. capillaris*, and the *A*, *B* and *C* bivalents together have a mean lower than that of *A* in *C. capillaris* (see Table VI and Graph 1).

TABLE VI.

Mean numbers of chiasmata and terminal chiasmata per bivalent in C. tectorum 29–23.

		A, *B* and *C* bivalents					*D* bivalent				
Stage	No. of nuclei	No. of bivalents	Total no. of Xta.	Total no. of T.Xta.	Mean no. of Xta. per bivalent	Mean no. of T.Xta. per bivalent	No. of bivalents	Total no. of Xta.	Total no. of T.Xta.	Mean no. of Xta. per bivalent	Mean no. of T.Xta. per bivalent
M.DK.	10	30	43	5	1·43	0·17	10	13	1	1·3	0·1
L.DK.	10	30	42	7	1·4	0·23	10	11	3	1·1	0·3

(3) *Positions and terminalisation of chiasmata.*

No data as to the number of terminal chiasmata are available for the metaphase stage owing to difficulties of interpretation due to high contraction. The mean number of terminal chiasmata increases very slightly for the complement as a whole (Table II), and in each class of bivalent from mid to late diakinesis (Table VI), but this increase may not be statistically significant owing to the small number of cells under investigation.

Types of configurations similar to those of *C. capillaris* were found at all stages. Single terminal chiasmata were seen at metaphase on the ends of the long arm, or at the end distal to the spindle-fibre attachment in the *D* bivalents (Figs. 11, 12 and 13).

D. *Chiasma frequency in relation to chromosome length.*

There is an almost directly proportional relationship between chromosome length and chiasma frequency at mid-diakinesis in *C. capillaris* and *C. tectorum* (Graph 1), as in *Fritillaria imperialis* (Darlington, 1930). Although the numbers of chiasmata are unknown at the earliest stage, this is probably the true relation between size and chiasma frequency, since morphological observations show that there is little movement of chiasmata, and consequently of reduction in the number of chiasmata.

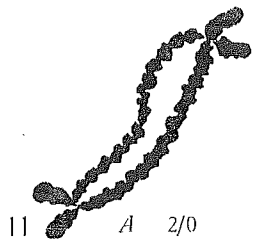


Fig. 11.

Fig. 12.

Figs. 11, 12. *C. tectorum*, *A*, bivalent at late diplotene.

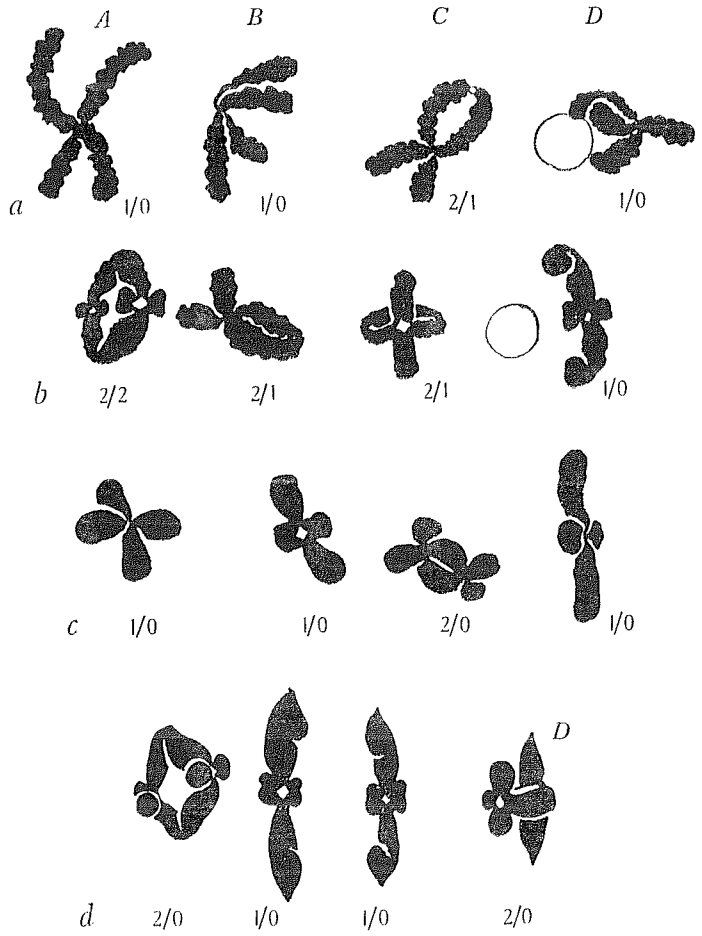
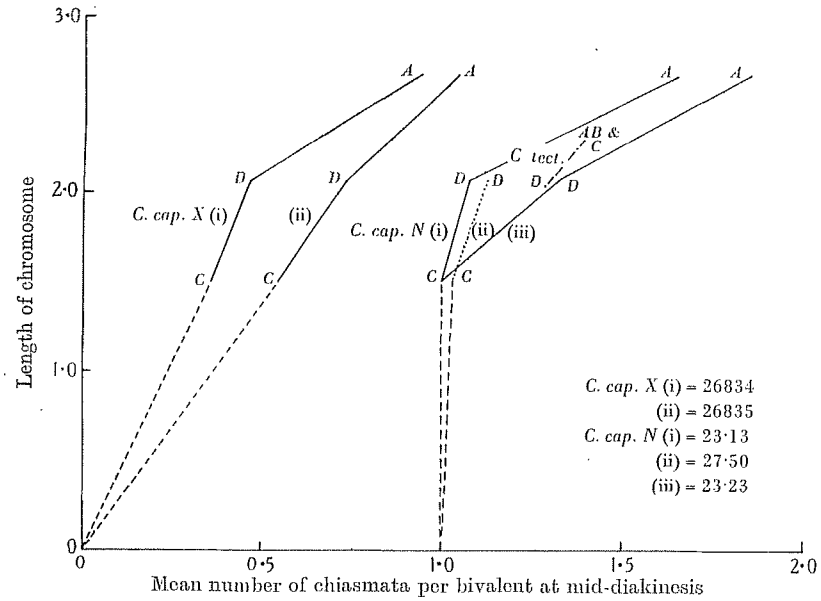


Fig. 13. *C. tectorum*, whole nuclear complements. *a*, mid-diakinesis; *b*, late diakinesis; *c*, prometaphase; *d*, metaphase.

V. SUMMARY.

1. Meiosis is normal and has been followed through all stages from pachytene to second metaphase in *Crepis capillaris* (L.) Wallr. and *C. tectorum* L. A quantitative analysis of chiasma behaviour has been made for each kind of bivalent. Chiasma frequency is low, the majority of bivalents in *C. capillaris* having only one chiasma.

2. The satellited *D* chromosomes in both species are observed to be attached to the nucleolus at both the first and the second meiotic divisions.



Graph 1. Showing the relation between chiasma frequency and chromosome length at mid-diakinesis. (The measurements of chromosome length have been taken from Mann, see Table I, and are not given in μ.)

3. The two chromosomes of a bivalent are coiled about one another in the early stages. Uncoiling is gradual and complete by diakinesis.

4. Bivalents of the *C* chromosomes have single terminalised chiasmata at mid-diakinesis, whereas single chiasmata in the longer *A* and *D* bivalents rarely terminalise.

5. Similar chromosomes of *C. capillaris* and *C. tectorum* show closely similar mean chiasma frequencies during diakinesis, and the same types of bivalent configuration.

6. Chiasma frequency at mid-diakinesis is almost directly proportional to length.

VI. Acknowledgments.

The author is indebted to Profs. E. B. Babcock and R. E. Clausen and Dr Darlington for their help and interest, and to the first for providing material and facilities for research.

REFERENCES.

Avery, Priscilla (1930). "Cytological studies of five interspecific hybrids of *Crepis leontodontoides*." *Univ. Calif. Publ. agric. Sci.* **6**, 135–67.

Babcock, E. B. and Clausen, J. (1929). "Meiosis in two species and three hybrids of *Crepis* and its bearing on taxonomic relationship." *Ibid.* **2**, 401–32.

Belling, J. (1927). "The attachments of chromosomes at the reduction division in flowering plants." *J. Genet.* **18**, 177–205.

—— (1931). "Chiasmas in flowering plants." *Univ. Calif. Publ. Bot.* **16**, 311–38.

Collins, Julius L. (1920). "Inbreeding and crossbreeding in *Crepis capillaris* (L.) Wallr." *Univ. Calif. Publ. agric. Sci.* **2**, 205–16.

Collins, J. L., Hollingshead, Lillian and Avery, Priscilla (1929). "Interspecific hybrids in *Crepis*. III. Constant fertile forms containing chromosomes derived from two species." *Genetics*, **14**, 305–20.

Collins, J. L. and Mann, Margaret C. (1923). "Interspecific hybrids in *Crepis*. II. A preliminary report on the results of hybridising *Crepis setosa* Hall. with *Crepis capillaris* (L.) Wallr. and with *C. biennis* L." *Ibid.* **8**, 212–32.

Darlington, C. D. (1930). "Chromosome studies in *Fritillaria*. III. Chiasma formation and chromosome pairing in *Fritillaria imperialis*." *Cytologia*, **2**, 37–55.

Darlington, C. D. and Dark, S. O. S. (1932). "Origin and behaviour of Chiasmata. II. *Stenobothrus parallelus*." *Ibid.* **3**, 169–85.

Darlington, C. D. and Janaki-Ammal, E. K. (1932). "The origin and behaviour of chiasmata. I. Diploid and tetraploid *Tulipa*." *Bot. Gaz.* **93**, 296–312.

Digby, L. (1914). "Critical study of the cytology of *Crepis virens*." *Arch. Zellforsch.* **12**, 97–146.

Heitz, E. (1931). "Die Ursache der gesetzmässigen Zahl, Lage, Form und Grösse pflanzlicher Nukleolen." *Planta*, **12**, Heft 4.

Hollingshead, Lillian (1930). "Cytological investigations of hybrids and hybrid derivatives of *Crepis capillaris* and *Crepis tectorum*." *Univ. Calif. Publ. agric. Sci.* **6**, 55–94.

Maeda, T. (1930 *a*). "The meiotic divisions in pollen mother cells of the sweet pea (*Lathyrus odoratus*) with special reference to the cytological basis of crossing over." *Mem. Coll. Sci. Kyoto*, **5**, 125–37.

—— (1930 *b*). "On the configurations of gemini in the pollen mother cells of *Vicia Faba* L." *Ibid.* **5**, 125–37.

Mann, Margaret Campbell (1925). "Chromosome number and individuality in the genus *Crepis*. I. A comparative study of the chromosome number and dimensions of nineteen species." *Univ. Calif. Publ. agric. Sci.* **2**, 294–314.

Marchal, E. (1920). "Recherches sur les variations numériques des chromosomes dans la série végétale." *Mém. Acad. R. Belg.* sér. 2, **4**, 1–108.

McCLINTOCK, BARBARA (1931). "Cytological observations of deficiencies involving known genes, translocations and an inversion in *Zea mays*." *Bull. Mo. agric. Exp. Sta.* No. 163, pp. 2–30.

MOFFETT, A. A. (1932). "Chromosome studies in *Anemone*. I. A new type of chiasma behaviour." *Cytologia*, **4**, 26–37.

NAVASHIN, M. (1925). "Morphologische Kernstudien der *Crepis*-Arten in Bezug auf die Artbildung." *Z. Zellforsch.* **6**, 195–233.

—— (1927). "Über die Veränderung von Zahl und Form der Chromosomen infolge der Hybridisation." *Ibid.* **4**, 171–215.

—— (1929). "Studies on polyploidy. I. Cytological investigations on triploidy in *Crepis*." *Univ. Calif. Publ. agric. Sci.* **2**, 377–400.

NEWTON, W. C. F. (1927). "Chromosome studies in *Tulipa* and some related genera." *J. linn. Soc.* (*Bot.*), **47**, 339–54.

NEWTON, W. C. F. and DARLINGTON, C. D. (1930). "*Fritillaria Meleagris*: chiasma formation and distribution." *J. Genet.* **22**, 1–14.

POOLE, CHARLES F. (1931). "The interspecific hybrid, *Crepis rubra* × *C. foetida*, and some of its derivatives. I." *Univ. Calif. Publ. agric. Sci.* **6**, 169–200.

—— (1932). "The interspecific hybrid, *Crepis rubra* × *C. foetida*, and some of its derivatives. II. Two selfed generations from an amphidiploid hybrid." *Ibid.* **6**, 231–55.

RICHARDSON, M. MARGARET (1934). "The origin and behaviour of Chiasmata. X. *Spironema fragrans*." *Cytologia*, **5**, 337–54.

ROSENBERG, O. (1909). "Zur Kenntniss von den Tetradenteilungen der Compositen." *Svensk bot. Tidskr.* **3**, 64–77.

—— (1918). "Chromosomenzahlen und Chromosomendimensionen von der Gattung *Crepis*." *Arch. Bot.* **15**, 1–16.