Chromosoma (Berl.) 52, 89—101 (1975)

Aneuploidy and Isolation in Two *Hypochoeris* Species

J. S. Parker

Department of Plant Biology and Microbiology, Queen Mary College, University of London, Mile End Road, London E1 4NS, England

Abstract. The annual species *Hypochoeris glabra* ($2n=10$) and the perennial *H. radicata* ($2n=8$) hybridise readily in nature and in experiment. During meiosis in F_1 hybrids the maximum association is a chain of seven and a bivalent indicating that at least three interchanges differentiate the two genomes. The nucleolar chromosomes in the two species are homologous and form a ring bivalent. They are, however, differentiated since in the F_1 hybrid only one nucleolar-organiser region is expressed. Although chromosomal differentiation reduces the egg fertility of F_1 hybrids to about 1%, viable backcross hybrids to *H. radicata* as pollen parent have been experimentally produced and occur in natural populations. Backcrosses with 8, 9 and rarely 13 chromosomes are found and those with $2n=8$ are fully interfertile with *H. radicata.* Gene flow may therefore take place in natural populations across an aneuploid barrier. The direction of gene flow in *Hypochoeris* is probably unidirectional from the annual to the perennial.

Introduction

The nature of the aneuploid chromosome differences which are frequently found between related diploids can be established from studies of meiosis in F_1 hybrids. Unequal interchange coupled with gain or loss of centromeres, centric fusion and fission have all been implicated in the origins of aneuploidy (John and Lewis, 1968; Jones, 1974). In the genus *Hypochoeris* (Compositae) a perennial, self incompatible species with $n=4$ and an annual, self compatible species with $n=5$ are found in mixed populations where they frequently hybridise. The chromosomal relationships of these species and the efficiency of structural chromosome changes as isolating mechanisms operating during meiosis in F_1 hybrids are examined in this paper.

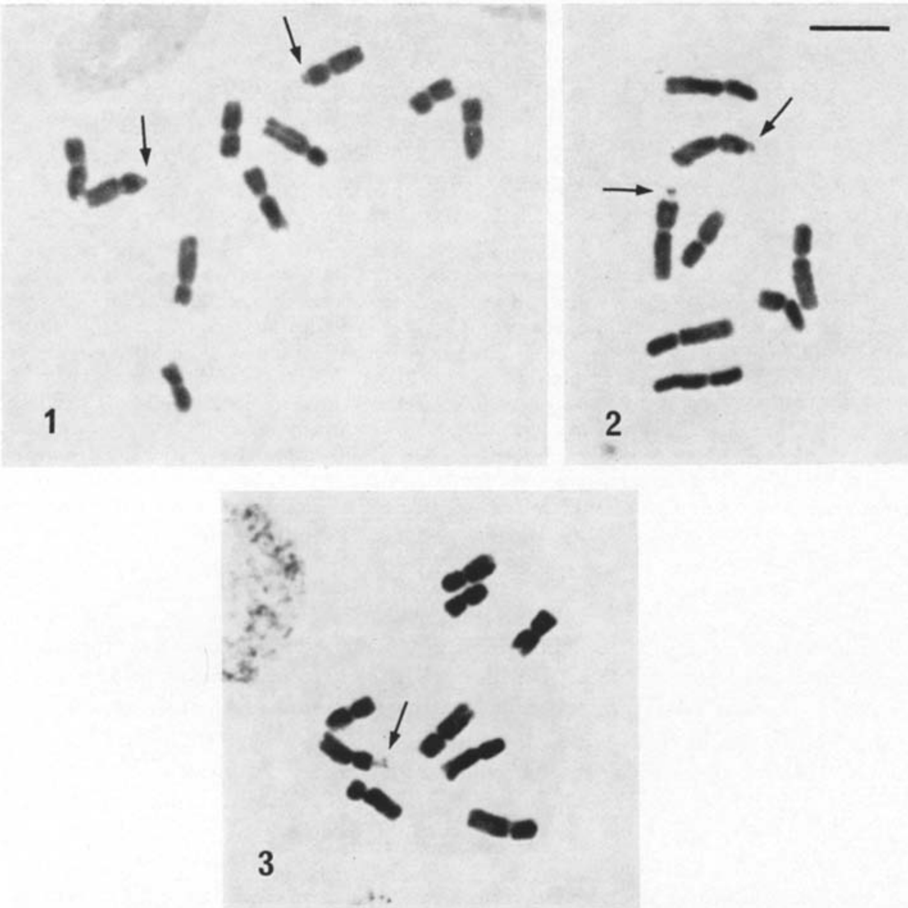
Materials and Methods

(i) The Plants. Hypochoeris radicata, is a perennial, strictly self-incompatible species with numerous capitula (flower heads) each 2–3 cm in diameter. *H. glabra* is annual, self-compatible and the less numerous capitula are generally much less than 1 cm in diameter. *H. radicata* produces about ten times as much pollen per anther as *H. glabra* and, in the wild, has four or five times as many florets per capitulum.

(ii) Hybridisations. Plants from two British and one French population of *H. radicata* were crossed with *H. glabra* plants collected in Britain, Portugal and Sweden. Hybrids can be produced easily by rubbing fully-open capitula together without emasculation. When *H. glabra* is used as the female parent hybrid frequency is 1–2%, the remainder being selfs. Hybrids can be distinguished morphologically from selfs at the second true-leaf stage in seedlings and hybridity is confirmed by a chromosome count. The reciprocal cross, with *H. radicata* as female parent, has been successfully accomplished only once.

Natural hybrids have been obtained from three British populations, two in Norfolk and one in Suffolk.

(iii) Chromosome Studies. For mitotic analysis, root-tips were pretreated with 0.05% colchicine for two hours, fixed in acetic-alcohol and stained in lactopropionic orcein after cold hydrolysis for 5–10 minutes in 5N HCl. Capitula were fixed in Carnoy and stained with lactopropionic orcein or acetocarmine.



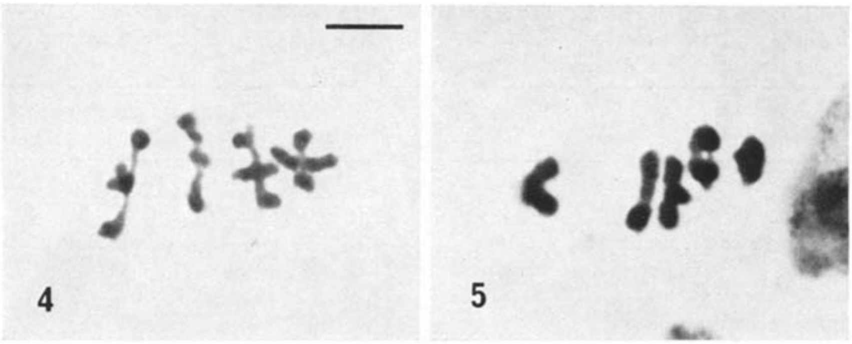
Figs. 1—3[1]. Somatic chromosomes of two *Hypochoeris* species and their F_1 hybrid Fig. 1. *H. glabra*, 2n = 10. Fig. 2. *H. radicata* 2n = 8. Fig. 3. F_1 hybrid 2n = 9. The satellite chromosomes are arrowed

Results

1. The Karyotypes

There is an aneuploid difference between the two species, *Hypochoeris glabra* having 2n = 10 and *H. radicata* 2n = 8. The total chromosome lengths at mitotic metaphase are, however, very similar (Table 1). Each complement has one pair of nucleolar-organising chromosomes with a small satellite on the short arm. These chromosomes are almost identical in arm ratio and mitotic length (Figs. 1 and 2). The chromosomes of the parental species cannot be distinguished unambiguously at mitosis (Fig. 3) in the hybrid (2n = 9) where only one secondary constriction is evident although two are visible in each parental species. Since the nucleolar chromosomes are so similar in morphology it is unfortunately impossible to decide

1 The scales in all figures represents 5 μm



Figs. 4 and 5. Metaphase-I in PMC's of *Hypochoeris* species. Fig. 4. *H. radicata*. Fig. 5. *H. glabra*. Notice the difference in chiasma frequency and distribution between the two species

Table 1. Chromosome complements of *Hypochoeris glabra* and *H. radicata*

Species	n	Total haploid length (μm)	Range (μm)	Nucleolar chromosome	
				Length (μm)	Arm ratio
H. glabra	5	13.00	2.2–2.85	2.75	1:1.80
H. radicata	4	12.65	2.52–3.72	3.05	1:1.76

whether the satellite-expressing chromosome in every cell and each hybrid is derived from the same parent. It is probable, however, that this is a case of specific competitive suppression of secondary constrictions as first observed in *Crepis* by Navashin (1934).

2. Chiasma Frequency and Position in Parents and Hybrids

In the perennial *H. radicata* mean chiasma frequencies from 4.15 to 6.28 per PMC (1.04—1.57 per bivalent) have been recorded in population plants. Chiasmata are sometimes highly proximal and usually interstitial (Fig. 4). The terminalisation coefficient, expressed as the proportion of terminal chiasmata per paired arm (Rees, 1955) is very low (3–15%) (Table 2). In the annual *H. glabra* mean chiasma frequencies from 7.16 to 9.04 per PMC (1.44—1.81 per bivalent) have been found. The terminalisation coefficient is about 50% and the non-terminal chiasmata are rarely proximal (Fig. 5).

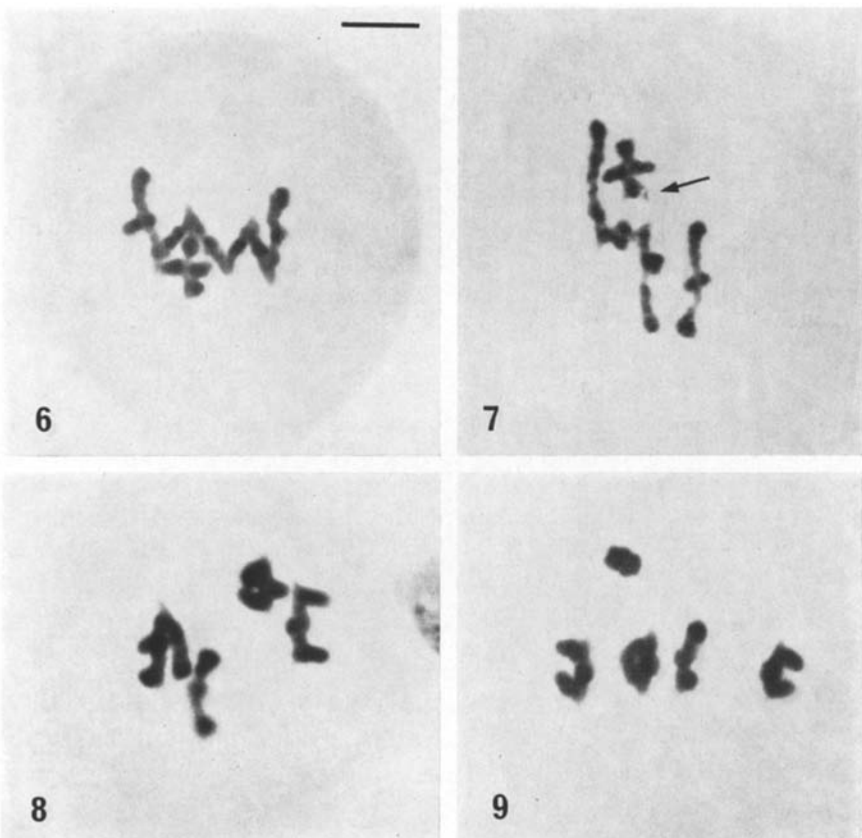
The chiasma frequencies of F_1 hybrids are equivalent to bivalent chiasma frequencies in the range 1.11–1.42 and thus fall within the limits of the *H. radicata* parent. The terminalisation coefficients are, however, generally intermediate between the parental values (Table 2).

3. Pairing Patterns in F_1 Hybrids

The maximum metaphase-I association recorded in seven of the eight hybrids was a chain of seven chromosomes and a bivalent (Fig. 6); in the remaining hybrid the largest configuration found was a chain of five and two bivalents (Table 3).

Table 2. Chiasma frequencies and terminalisation in *Hypochoeris glabra* and *H. radicata*, F_1 hybrids and backcross hybrids to *H. radicata*. Ranges of mean chiasma frequencies in parentheses

Generation		Number of plants	Mean chiasma frequency	Terminalisation coefficient (%)
Parental	*H. glabra*	10	8.00 (7.16–9.04)	44.2–55.6
	H. radicata	64	4.75 (4.15–6.28)	4.0–15.8
F_1		8	5.76 (5.00–6.40)	13.4–32.2
Backcross 1	2n = 9	6	5.80 (5.27–6.40)	19.0–33.8
	2n = 8	19	4.81 (4.28–5.50)	6.4–21.3



Figs. 6—9. Metaphase-I associations in the F_1 hybrid *H. glabra* × *H. radicata* 2n = 9. Fig. 6. VII + II. Fig. 7. V + 2II. A satellite is visible on one short arm of a bivalent (arrowed). Fig. 8. III + 3II. Fig. 9. 4II + I

Table 3. Metaphase-I pairing patterns in eight F_1 hybrids of *Hypochoeris glabra* × *H. radicata* and a single plant of the second backcross generation. Two PMC's have been omitted from the table, one with 3II + 3I (Hybrid 2), the other with VI + II + I (Backcross 2)

Hybrid number	Metaphase-I pairing pattern									Total PMC's	Mean chiasma frequency
	4 II + I	III + 2II + 2I	III + 3II	2III + II + I	IV + 2II + I	IV + III + II	V + II + 2I	V + 2II	VII + II		
1	18	4	54	1	3	1	1	19	—	101	5.00
2	2	—	5	—	—	—	—	3	1	12	5.50
3	1	1	19	—	1	—	—	5	1	28	5.64
4	1	3	17	—	—	1	1	21	6	50	5.78
5	—	—	47	—	3	5	—	39	6	100	5.96
6	—	—	8	—	—	1	—	10	1	20	6.05
7	—	—	16	—	2	1	—	23	8	50	6.28
8	1	—	15	—	—	3	—	25	6	50	6.40
Totals	23	8	181	1	9	12	2	145	29	411	5.76
Back-cross 2	1	—	8	1	1	19	—	6	13	50	6.10

Significantly this plant had the lowest chiasma frequency and the highest proportion of PMC's with univalents. In all hybrids the most common associations are a chain of three with three bivalents and a chain of five with two bivalents (Figs. 7 and 8). The majority of bivalents are rods with single interstitial chiasmata and these often appear slightly heteromorphic. Ring bivalents are found infrequently and never more than one per PMC (Fig. 9). The average number of associations per PMC declines with increasing chiasma frequency and extrapolation of a regression line fitted to this data indicates that a hybrid with a mean chiasma frequency of 8.13 would have a chain of seven in all cells (Fig. 10). Clearly, the low chiasma frequencies of F_1 hybrids limit the formation of the maximum association.

4. *The Later Meiotic Stages in F_1 Hybrids*

Despite the variety of pairing patterns and the occurrence of univalents the chromosomes segregate 5:4 at anaphase-I in almost all cells (Table 4). Univalents often occupy polar positions when the bivalents are congressed and they rarely divide during the first division. Abnormal anaphase separations are no more common than in the parents and have been seen in five PMC's three of which contained a side-arm bridge and two a bridge and fragment. Anaphase-I laggards and interphase micronuclei are rare, indicating a low frequency of chromosome loss at first division. At anaphase-II the chromatid products of first division may occasionally be lost but in most PMC's the chromatid distribution is 4: 4:5:5. After cytokinesis tetrads usually contain four microspores of similar size although occasionally only three are found.

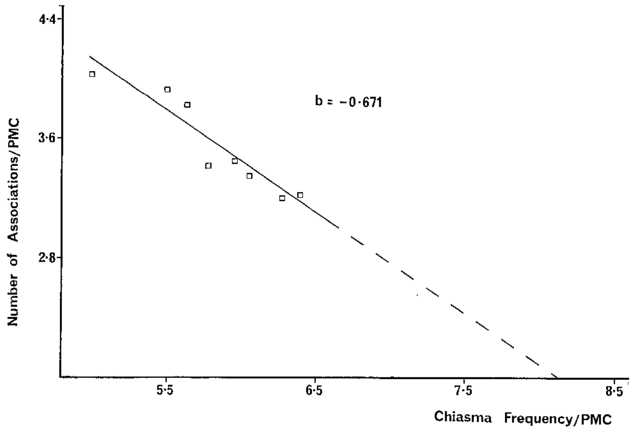


Fig. 10. Regression of the mean number of associations per PMC on mean chiasma frequency in 8 F_1 hybrids

5. Chromosome Relationships of H. glabra and H. radicata

It is clear from meiotic pairing behaviour in the F_1 hybrid that one pair of submetacentric chromosomes has undergone little differentiation during the evolution of these species. Both arms of this pair are still at least partially homologous which can result in the formation of a ring bivalent during meiosis. The chromosomes of these species normally lack convenient markers so unequivocal identification of this pair is not usually possible at metaphase-I of meiosis. However, inspection of the karyotypes suggests that the pair concerned may be the nucleolar chromosomes which are of similar overall size and proportions in the two species (Table 1).

Unequivocal evidence of the nucleolar nature of the homologous pair has been provided by a plant of the second generation backcrossed to *H. radicata.* At meiosis, this second-backcross plant behaved in its maximal pairing as a typical F_1 hybrid with a chain of seven chromosomes and a bivalent. It was unusual, however, in the high frequency of PMC's with a chain of four, a chain of three and a bivalent (Table 3; Fig. 11). In this plant the satellite was clearly visible during metaphase-I of meiosis. In all PMC's with a chain of seven chromosomes and a bivalent the marker could be seen on the short arm of the single bivalent. In PMC's with less than the maximal multiple, the marker chromosome was always bivalent-forming (Fig. 11). Similar observations have been made in an F_1 hybrid, although in this plant the satellite was not visible in every PMC (see Fig. 7).

Table 4. Distribution of chromosomes ('') and chromatids (') at anaphase-I and metaphase-II in F_1 hybrids of *Hypochoeris glabra* × *radicata*

Meiotic stage	Chromosome distribution				Total PMCs
	3'':6''	4''+1':4''+1'	4'':5''	4'':4''+laggard	
Anaphase-I	1	0	60	1	62
Metaphase-II	2	4	40	—	46

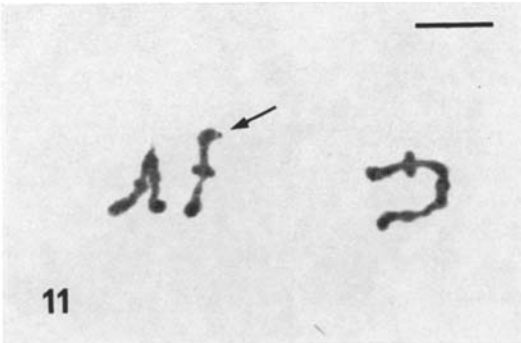


Fig. 11. Metaphase-I in a hybrid of the second generation backcrossed to *H. radicata* showing IV + III + II. A satellite on one of the short arms of the single bivalent is arrowed

Table 5. Chromosome numbers of backcross progeny to *H. radicata* as pollen parent

	Chromosome number			Total
	8	9	13	
Number of plants	32	25	1	58

Considerable redistribution of chromosome material has evidently taken place during the evolution of this pair of species, so that homologies are now shared amongst seven chromosomes. Partial homology of seven chromosomes coupled with a difference in basic number can most simply be effected by three reciprocal but unequal interchanges with the loss or gain of a small chromosome.

6. Hybrid Fertility

The amount of stainable pollen at anthesis in F_1 hybrids determined both with acetocarmine and tetrazolium salts ranges from 8% to 15%. These methods estimate the proportion of living pollen but probably overestimate germination ability. Egg fertility estimated by seed set is much lower. Seeds have not been obtained by self-fertilisation but are occasionally produced by backcrossing to *H. radicata* as pollen parent. About 0.7% of florets are fertile on backcrossing. Since the capitula of F_1 hybrids contain about thirty florets the majority are therefore completely sterile.

7. Backcrosses to H. radicata

Backcross hybrids to *H. radicata* as pollen parent have been found with $2n = 8$, $2n = 9$ and, a single individual, $2n = 13$ (Table 5).

a) 2n = 8. The backcrosses are self-incompatible and are morphologically similar to *H. radicata*. During meiosis four bivalents are formed regularly and the frequency of univalents is only 0.02 per PMC. Chiasma frequencies are within the range of *H. radicata* although terminalisation coefficients are often higher (Table 2). Both pollen and egg fertility in these plants is fully restored to the *H. radicata* level.

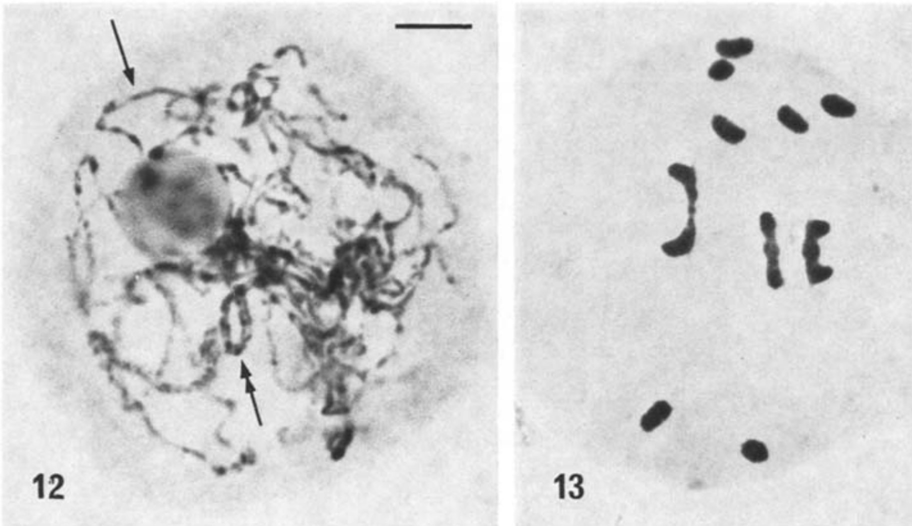
These backcrosses are evidently derived from gametes containing the three non-nucleolar chromosomes contributed to the F_1 hybrid by the *H. radicata* parent. The expected frequency of such gametes can be approximately calculated by making certain assumptions about anaphase-I behaviour: no centric division, no chromosome loss and a random 4:5 distribution of centromeres. The segregation of a particular group of three from seven will occur 1 in 35 PMC's, and thus 1 in 70 gametes should carry three *H. radicata*-derived chromosomes. Two factors may alter expectation although in opposite directions: i. alternate orientation of multiples will increase the frequency of this gamete type. ii. if the *H. glabra*-derived nucleolar chromosome cannot function in such gametes then this will set the lower limit on frequency at 1 in 140 gametes. The observed frequency of such gametes is approximately 1 in 250. Evidently many four-chromosome gametes are inviable as a result of recombination between the haploid complements.

b) $2n = 9$. Backcross hybrids identical in chromosome number and pairing pattern to the F_1 hybrid should occur with the same frequency as those with $2n = 8$. Although the frequencies of 8- and 9-chromosome backcrosses are approximately equal (Table 5) not all 9-chromosome plants have the meiotic pairing typical of F_1 hybrids. Maximum pairing in these backcrosses may be VII with a single ring bivalent, V with two ring bivalents or III with three ring bivalents. Evidently, chromosomes derived from *H. glabra* can be replaced by those of *H. radicata* in functional 5-chromosome gametes. It is not yet known, however, whether apparently identical meiotic pairing patterns conceal chromosomal heterogeneity. Overall it is clear that there is selection against gametes with five chromosomes. Although the chromosomes of *H. radicata* and *H. glabra* retain considerable homology the species are genetically well-differentiated so that crossing-over in the pairing segments may result in recombinant chromosomes with genotypes inimical to the survival of gametes with five chromosomes.

c) $2n = 13$. The course of meiosis in this backross is highly irregular. Zygotene and pachytene are characterised by long asynaptic regions (Fig. 12) and there is a correspondingly low frequency of chiasmate associations at late prophase-I and metaphase-I. The mean chiasma frequency of 4.41 per PMC, equivalent to a frequency of 0.68 per bivalent, is lower than that of any F_1 hybrid and the majority of *H. radicata* plants despite the higher number of chromosomes.

In organisms such as *H. radicata* with a high frequency of unichiasmate bivalents, the distribution of PMC chiasma numbers is highly skewed. For full meiotic efficiency one chiasma must form per bivalent and PMC's with less than four chiasmata are rare: selection is rigorous in maintaining this distribution since sterility results from univalence. In this chromosomally-unbalanced backcross hybrid, however, the normal constraints on chiasma formation appear to have been relaxed. PMC's with 0 to 9 chiasmata are found and these exhibit a symmetrical distribution (Fig. 14).

Eighteen different pairing configurations have been observed at metaphase-I but five types accounted for 83% of PMC's (Table 6). In about half the cells bivalents and univalents were found, about one third had a single trivalent and a variable number of bivalents, and less than 10% of PMC's had two or more trivalents. Quadrivalents were seen in only two PMC's and no higher multiples were



Figs. 12 and 13. Meiotic behaviour in a backcross hybrid to *H. radicata* with 2n = 13. Fig. 12. Pachytene showing paired (double arrow) and unpaired (single arrow) regions. Fig. 13. Metaphase-I showing the most frequent configuration, 3II + 7I. Notice the polar orientation of the univalents

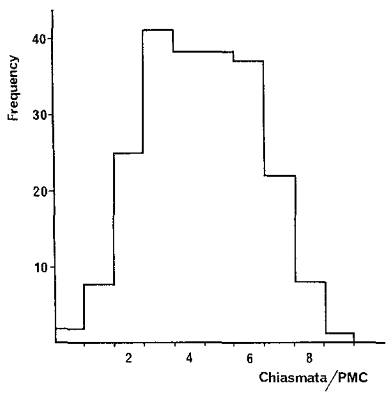


Fig. 14. The symmetrical distribution of chiasmata in 221 PMC's of the backcross hybrid with 2n = 13

found. The most frequently observed pairing pattern was three bivalents and seven univalents (Fig. 13).

This plant must have arisen by fusion of a reduced and a non-reduced gamete and it is most likely that non-reduction occurred in the EMC of the F_1 hybrid. This backcross probably contains a diploid complement of *H. radicata* and a haploid complement of *H. glabra*. Four pairs are totally homologous while partial homology is shared by a group of ten chromosomes and a group of three nucleolar-organising chromosomes. Despite this extensive partial homology the maximal multiples

Table 6. Chromosome pairing at metaphase-I in 219 PMC's of a backcross hybrid with a diploid complement of *H. radicata* and a haploid complement of *H. glabra* (2n = 13). Two PMC's with IV + 3II + 3I omitted from the Table

Number of trivalents	Number of bivalents					
	0	1	2	3	4	5
0	2	9	35	42	32	4
1	2	11	24	30	8	0
2	0	2	12	1	—	—
3	2	2	0	—	—	—
4	1	—	—	—	—	—

are quadrivalents and these are found in less than 1% of PMC's. There must therefore be some preferential pairing, although at least 46% of PMC's show allosyndesis.

8. Hybrids in Nature

Three mixed populations have been examined in eastern England. In each population apparent F_1 hybrids occur at low frequency. The meiotic behaviour of these plants is identical to that of experimentally-produced F_1 hybrids. In addition, F_1 hybrids have been found amongst wild-collected seed of *H. glabra* plants which were growing in two of these mixed populations. In two samples the frequency of hybrids was 1 in 85 and 1 in 226.

Wild F_1 hybrids are of very low fertility but since they carry many more capitula than either parent several viable achenes will probably be produced during the flowering season. Ten plants have been grown from achenes collected on F_1 hybrids growing in natural populations. Seven plants had 2n = 8 and three 2n = 9. These are probably backcrosses to *H. radicata* as pollen parent. The eight-chromosome plants were of full fertility and morphologically like *H. radicata*. In two of the nine-chromosome plants the maximum metaphase-I association was a chain of seven, in the third a chain of five.

Discussion

1. Chromosomal Relationships

Despite the aneuploid difference between these two species, they are closely related chromosomally. The single pair of nucleolar chromosomes has undergone little structural differentiation during the evolution of these species and in F_1 hybrids are associated as a bivalent at meiosis. Both arms of this acrocentric chromosome are still homologous since ring bivalents are occasionally formed. Despite this homology, however, one of the nucleolar-organising regions is suppressed in F_1 hybrids. The remaining seven chromosomes share homology forming a maximal multiple of a chain of seven during meiosis. Precise relationships cannot be established since individual chromosomes are meiotically indistinguishable. It is clear, however, that at least three interchanges differentiate the two genomes. The close chromosomal relationship of the two species is further emphasised by the high frequency of allosyndesis in the 13-chromosome, effectively triploid, backcross hybrid which contains one *glabra* and two *radicata* complements. Ladizinsky (1974) has argued that such hybrids provide a better test of homology between genomes than F_1 hybrids in which pairing of small homoeologous regions may occur. The *Hypochoeris* behaviour is in marked contrast to that in similar hybrids between *Crepis capillaris* and *C. tectorum* in which autosyndesis is complete despite high pairing in diploid F_1 hybrids (Hollingshead, 1930). Despite the extensive chromosomal rearrangements associated with aneuploidy in *Hypochoeris* the total mitotic chromosome lengths are very similar in the two species and it is possible that the complements differ by little more than a centromere.

The origin of aneuploid differences between species by unequal interchange (Darlington, 1937) has been demonstrated extensively in *Drosophila* (Dobzhansky, 1951) and in several species pairs of the genus *Crepis* (Tobgy, 1943; Sherman, 1945). In *Crepis* it has been proposed that unequal interchange and centric loss have led to a progressive reduction in basic number (Babcock, 1947). Similar conclusions have been reached concerning *Haplopappus* (Jackson, 1962, 1965). It is seldom possible from chromosomal evidence alone, however, to deduce the direction of change but additional information on breeding systems, life cycles and distribution may be helpful in assessing evolutionary trends. Kyhos (1965), using such additional evidence, has argued that two annual species of *Chaenactis* (Compositae) with $n = 5$ are both derived from a perennial with $n = 6$ by aneuploid reduction.

In the tribe Cichorieae of Compositae to which *Hypochoeris* belongs Stebbins (1958) has distinguished evolutionary trends of increasing karyotype asymmetry coupled with a reduction in chromosome number. The two species of *Hypochoeris* correspond with these trends since *H. glabra*, $n = 5$, has a more symmetrical karyotype than *H. radicata*, $n = 4$. In the angiosperms, however, inbreeders (*H. glabra*) are derived from outbreeders (*H. radicata*) (Darlington and Mather, 1949). It seems likely, therefore, that *H. radicata* and *H. glabra* are not related as parent and offspring but as sibs. Both may be derived from a perennial ancestor with a basic number of five. These species have no close relatives within the genus with which they can be crossed and both are karyotypically constant. Unless chromosome races are found, or a possible ancestral species discovered, the origins and precise relationships of these species must remain obscure.

2. *Aneuploidy and Gene Flow*

Structural rearrangements of the karyotype in the homozygous state can be exploited as isolating mechanisms acting at meiosis in F_1 hybrids (Lewis and John, 1963). Chromosomal rearrangements between species are widespread in both plants and animals. In the genus *Holocarpha* (Compositae) for example, the numerous species show extreme local differentiation of chromosome structure resulting in the genetic isolation of a patchwork of local races. Hybrids between local races are apparently sterile (Clausen, 1951). Similarly the extensive chromosomal differentiation of *H. glabra* and *H. radicata* reduces the egg fertility of F_1 hybrids to less than 1% and pollen stainability to between 5 and 10%. *Haplopappus gracilis* is exceptioanl in that the *dibivalens* ($2n = 4$) and *tribivalens* ($2n = 6$) forms and their F_1 hybrid with $2n = 5$ co-exist in mixed populations without an attendant drop in fertility (Jackson, 1965) A single interchange apparently differentiates the two chromosome races.

Despite the low fertility of *Hypochoeris* hybrids, natural hybrids produce occasional fertile achenes, probably as a result of backcrossing to *H. radicata*. Backcross hybrids with eight chromosomes have regular meiotic behaviour and are fully fertile. If any of these backcrosses become established they will form part of the breeding population of *H. radicata*. This may therefore lead to the gradual introgression of genes from the annual *H. glabra* into the perennial *H. radicata* across the aneuploid barrier.

Introgression may have more subtle, long-term effects on the population structure of *H. radicata* since backcross hybrids often have an altered pattern of chiasma distribution exemplified by a higher frequency of terminal chiasmata. If differences in chiasma distribution at metaphase-I are a reflection of differences in the positions of chiasmata at their inception rather than the extent of terminalisation then backcross hybrids should produce gametes with a novel genetic spectrum. This in turn will alter the genotypic structure of the population. It is unfortunately not possible to determine the positions of chiasmata in F_1 hybrids and *H. glabra* accurately until diakinesis.

The reverse process of gene flow from *H. radicata* to *H. glabra* via the F_1 hybrid is less likely to occur in natural populations. Pollen production per capitulum of *H. glabra* is only about 5% of that of *H. radicata*, reducing the possibility of transference by insect vectors. The presence of naturally-occurring hybrid seeds on *H. glabra* plants and the wild F_1 hybrids themselves, however, shows that insects occasionally visit these small capitula. Aneuploid differences between diploids, therefore, although severely reducing gene exchange, may not entirely prevent infiltration across the aneuploid barrier.

Acknowledgments. I should like to thank Dr. K. R. Lewis for critically reading this manuscript. I should also like to thank the Trustees of the Druce Bursary for financial support during part of the study at the Botany School, Oxford.

References

Babcock, E. G.: The genus Crepis. Univ. Calif. Publ. Bot. **21**, 1–197 (1947)

Clausen, J.: Stages in the evolution of plant species. Ithaca, N. Y.: Cornell University Press 1951

Darlington, C. D.: Recent advances in cytology, 2nd ed. London: Churchill 1937

Darlington, C. D., Mather, K.: The elements of genetics. London: Allen and Unwin 1949

Dobzhansky, T.: Genetics and the origin of species. New York: Columbia University Press 1951

Jackson, R. C.: Interspecific hybridisation in Haplopappus and its bearing on chromosome evolution in the Blepharodon section. Amer. J. Bot. **49**, 119–132 (1962)

Jackson, R. C.: A cytogenetic study of a three-paired race of Haplopappus gracilis. Amer. J. Bot. **52**, 946–953 (1965)

John, B., Lewis, K. R.: The chromosome complement. Protoplasmatologia VI A. Wien: Springer-Verlag 1968

Jones, K.: Chromosome evolution by robertsonian translocation in Gibasis (Commelinaceae). Chromosoma (Berl.) **45**, 353–368 (1974)

Ladizinsky, G.: Genome relationships in the diploid oats. Chromosoma (Berl.) **47**, 109–117 (1974)

Lewis, K. R., John, B.: Chromosome marker. London: Churchill 1963
Navashin, M.: Chromosome alterations caused by hybridisation and their bearing upon certain general genetic problems. Cytologia (Tokyo) **5**, 169–203 (1934)
Rees, H.: Genotypic control of chromosome behaviour in rye. I. Inbred lines. Heredity **9**, 93–116 (1955)
Sherman, M.: Karyotype evolution: a cytogenetic study of seven species and six interspecific hybrids of Crepis. Univ. Calif. Publ. Bot. **18**, 369–408 (1945)
Stebbins, G. L.: Longevity, habitat and release of genetic variability in the higher plants. Cold Spr. Harb. Symp. quant. Biol. **23**, 365–378 (1958)
Tobgy, H. A.: A cytological study of Crepis fuliginosa, C. neglecta and their F_1 hybrid, and its bearing on the mechanism of phylogenetic reduction in chromosome number. J. Genet. **45**, 67–111 (1943)

Received June 28, 1975 / Accepted by H. Bauer
Ready for press June 30, 1975