Meiotic Irregularities in Tall Fescue Genotypes and Their F_1 Hybrids

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INTERPRETATIVE STATEMENT

This publication represents a detailed analysis on the chromosome behavior in the important forage grass species, tall fescue. Breeders of this species are attempting to utilize hybrid vigor by crossing parent plants of diverse genetic origin and morphology. When genetically diverse types are crossed, the progeny are often sterile. Irregular chromosome behavior resulting in this sterility is reviewed and photographs of chromosome "pairing" relationship are shown. These findings will assist grass breeders throughout the country in the selection and utilization of parents leading to stable progeny, and will guide breeders in the interpretation of sterility when they use diverse types in an approach to the improvement of the species.

Contents

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Meiotic Irregularities in Tall Fescue Genotypes and Their F_1 Hybrids

W. T. W. Woodward and R. V. Frakes

INTRODUCTION

Tall fescue, *Festuca arundinacea* Schreb., is a polymorphic species with wide geographic distribution. It is a multipurpose crop, grown for hay, turf, pasture, and soil conservation. It is considered to be an allohexaploid with a chromosome number of $2n = 42$; $x = 7$. Tall fescue is reported to have three genomes made up of related diploid species of the *Lolium-Festuca* complex (Jauhar, 1975b).

An earlier study of agronomic characteristics in tall fescue was conducted at Oregon State University (Subhanij, 1974), using parent genotypes from two tall fescue cultivars, Fawn and Fortune. Fawn is tall in growth habit, is vigorous, flowers earlier than other varieties, and was released as a cultivar by Oregon State University for use as a forage grass. In contrast, Fortune is shorter in growth habit, less vigorous, later in anthesis date, and was released by Oregon State University for use as a turf grass because of its narrow leaves, dark green color, ability to tolerate frequent clipping, and spreading growth habit.

Many of the F_1 hybrids between these two sources produced little or no seed. Therefore, this study was initiated to cytologically examine the parents and F_1 hybrids for meiotic irregularities which may have caused partial or complete sterility.

REVIEW OF LITERATURE

Meiosis has been studied in many different grass species. Findings range from general statements to detailed observations and frequency of chromosome irregularities.

The formation of multivalents has commonly been reported as meiotic irregularities in allopolyploid species such as tall fescue. Peto (1933) reported meiosis to be regular in tall fescue, observing 21 bivalents with no multivalent associations at metaphase I. In a comprehensive study of meiosis in tall fescue, Crowder (1953a) reported that only 4 percent of the metaphase I cells showed multivalents. On a chromosome basis, only 3 percent of the chromosomes occurred as multivalents. Malik and Thomas

(1966) found the meiotic cycle of 10 exotic tall fescue genotypes, used as parents in the study, to be generally normal with largely bivalent pairing. Similarly, Jauhar (1975b) found meiosis to be regular with 21 bivalents, in 10 geographically isolated tall fescue ecotypes. Evans, Asay, and Jenkins (1973) showed meiosis to be normal in their parental material with a predominance of bivalents at metaphase I. Only two parents had any indication of multivalent associations, and these occurred in only a few pollen mother cells.

Meiosis has been reported to be regular in *Phalaris coerulescens, P. paradoxa, P. conariensis* (Parthasarathy, 1939), *Puccinellia angustata,* (Flovik, 1938) *Andropogon furcastus, A. scoparius, A. virgenicus, A. glomeratus, Festuca capillata, F. elatior* var. *pratensis, Spartina patens* var. *juncea,* and S. *cynosuroides* (Church, 1929a,b).

In contrast to the previous studies, Myers and Hill (1947) found 16-20 bivalents at diakinesis, 0.6-2.8 quadrivalents, and some hexavalents in one tall fescue plant. In separate studies, Lewis (1963), Malik and Thomas (1966), and Jauhar (1975b) found hexavalents, pentavalents, quadrivalents, trivalents, and bivalents in addition to a large number of univalents in hybrids involving exotic ecotypes of tall fescue. Malik and Thomas (1966) found associations of up to 10 chromosomes in their hybrids. Evans, Asay, and Jenkins (1973) reported associations of three, four, five, and six chromosomes to be quite frequent in hybrids between American and North African genotypes. Thomas and Thomas (1973) reported multivalents involving up to eight chromosomes in hybrids from diverse genotypes of tall fescue.

Multivalents have been reported in several species of grasses, including *Agrostis nebulosa* (Tinney, 1936), *Anthoxanthum odoratum* (Ostergren, 1940), *Dactylis aschersoniana* (Muntzing, 1937), *Festuca pratensis* (Simonsen, 1975), *Puccinellia vahliana* (Flovik, 1938), and interspecific and intergeneric hybrids of *Festuca* and *Lolium* (Crowder, 1953a,b; Jauhar, 1957a,b).

The formation of quadrivalents and more complex multivalents in tall fescue and other species could be due to several reasons. One possibility is the genetic system limiting pairing to homologous chromosomes could break down, allowing both homeologous and homologous chromosomes to become associated (Evans, Asay, and Jenkins, 1973; Jauhar, 1975b). Secondly, chromosome differentiation within geographically isolated populations may be the cause of multivalent formation in hybrids (Evans, Asay, and Jenkins, 1973; Malik and Thomas, 1966). Both Myers (1947) and Crowder (1953b) reported that all 28 chromosomes were paired as bivalents in some cells of hybrids between hexaploid tall fescue and diploid *Lolium* and *Festuca* species. Chromosomes of two genomes

of tall fescue would need to be homologous or at least homeologous for this to occur.

Aside from multivalent formation, the most commonly reported meiotic irregularity is the occurrence of univalents at metaphase I, lagging chromosomes at anaphase I and anaphase II, and quartets with micronuclei. Myers and Hill (1947) found the frequency of metaphase I univalents, anaphase I laggards, and quartets with micronuclei to vary considerably in tall fescue. Crowder (1953a) reported 14 percent of the metaphase I cells to possess univalents, but on a chromosomal basis only 0.72 percent occurred as such. Many of the univalents divided at metaphase I, lagged at anaphase I and anaphase II, and formed micronuclei in 6 percent of the microspores. Although Evans, Asay, and Jenkins (1973) found the parental material to be normal, univalents at metaphase I were observed in hybrids and were seen to divide precociously at anaphase I. The high frequency of laggards at anaphase II, resulting in quartets with micronuclei, was attributed to precociously dividing univalents.

Carnahan and Hill (1962) observed quartets with micronuclei to increase with inbreeding. Mean percentage of quartets with micronuclei for the inbred population was 25.8 percent as compared to 11.0 percent for the parental clone. It was suggested that the increase in quartets with micronuclei was due to an increase in metaphase I univalents. Jauhar (1975b) found hybrids between certain diverse ecotypes to show perfectly regular pairing, while other hybrids showed varying degrees of univalent formation. Malik and Thomas (1966) found considerable variation in the average number of univalents per cell in sterile hybrids of intraspecific tall fescue crosses. The range was from 5.7 univalents per cell in one hybrid to 10.9 per cell in another. Lagging chromosomes at anaphase I and up to 12 laggards at anaphase II were observed.

Univalents at metaphase I have been reported in *Agrostis nebulosa* (Tinney, 1936), *Calamagrostis neglecta, Puccinellia phyganodes,* and *Trisetum spiratum* (Rees and Dale, 1974). The behavior of univalents was not reported in these cases. However, a typical behavior is for univalents to become oriented on the metaphase I plate later than the bivalents and to divide equationally at anaphase I. The univalent monads are sometimes left in the cytoplasm at telophase I, but are more often included in the daughter nuclei and lag at anaphase II, resulting in micronuclei in the quartets. This type of univalent behavior occurs frequently and has been reported for *Bromus inermis* (Schertz and Murphy, 1958), *Dactylis aschersoniana* (Muntzing, 1937), *Festuca arundinacea* (Crowder, 1953a; Evans, Asay, and Jenkins, 1973; Malik and Thomas, 1966; Myers and Hill, 1947), *F. pratensis* (Simonsen, 1975), *Phalaris arundinacea* (Carnahan and Hill, 1956), *Paspalum lividum* (Bur-

son and Bennett, 1971), *Pennisetum orientale* (Chatterji and Timothy, 1969b), *P. flaccidum* (Chatterji and Timothy, 1969a), *Agropyron junceum* x *A. repens* (Ostergren, 1940), *Dactylis aschersoniana* x *D. glomerata* (Muntzing, 1937), *Festuca x Lolium* (Crowder, 1953b), *Paspalum urvillei* x *P. juergensii*, and *P. urvillei* x *P. vaginatum* (Burson and Bennett, 1972).

Dicentric chromatid bridges and acentric fragments at anaphase I and, to a lesser extent, at anaphase II occur because of crossing over in heterozygous inversions. Crowder (1953a) observed bridges of this type, but he also reported bridges attributed to chromosome stickiness at anaphase I. Malik and Thomas (1966) and Evans, Asay, and Jenkins (1973) reported variable numbers of bridges with and without fragments. Myers and Hill (1947) suggested that bridges and fragments, which appeared in five of the six plants they examined, may have arisen by crossing over in inverted segments of normally homologous chromosomes. However, some or all of the bridge configurations could have resulted from structural rearrangements in partially homologous chromosomes from different genomes that paired occasionally to form quadrivalents or hexavalents. The two plants with the highest number of bridges and fragments also had the highest number of quadrivalents. Carnahan and Hill (1962) found 10.5 percent of the anaphase I cells to have bridges and/or fragments in the parent clone.

Unexpectedly, the frequency of anaphase I cells with bridges and/or fragments increased to 18.7 percent with inbreeding. In pachytene studies of an intraspecific hybrid, Malik (1970) observed bivalents with looplike structures, probably due to a single inversion. In addition, he observed unpaired segments, loose pairings, translocations, and deletions.

Bridges and fragments have also been observed in *Agropyron junceum, A. repens* (Ostergren, 1940), *Anthoxanthum odoratum* (Ostergren, 1942), *Bromus inermis* (Schertz and Murphy, 1958), *Festuca pratensis* (Simonsen, 1975), *Pennisetum flaccidum* (Chatterji and Timothy, 1969a), *P. orientale* (Chatterji and Timothy, 1969b), *Phalaris arundinacea* (Carnahan and Hill, 1956), *P. brachystachys* (Parthasarathy, 1939), and interspecific and intergeneric hybrids of *Festuca* and *Lolium* (Crowder, 1953b).

Sticky chromosomes, often found at diakinesis, metaphase I, and anaphase I, frequently interfere with proper evaluation of these stages. Crowder (1953a) suggested that stickiness results from a change in the surface properties of the chromosome. Jauhar (1975b) found a high degree of stickiness in some aneuploids. Crowder (1953b) found extreme stickiness and clumping so prevalent in interspecific and intergeneric hybrids involving *Festuca arundinacea* that interpretation of metaphase I

was difficult. Carnahan and Hill (1956) reported that stickiness and clumping of chromosomes interfered with interpretations in hexaploid and octoploid *Phalaris arundinacea.*

MATERIALS AND METHODS

Three selected genotypes from the cultivar Fawn and three from the cultivar Fortune, were crossed in all possible combinations by bagging panicles of two plants together just prior to anthesis (Subhanij, 1974). Six of the possible nine Fawn x Fortune crosses produced sufficient seed for use in the study.

Three plants from each of the six single crosses were randomly selected for detailed analysis of meiotic stages. Panicles were collected at one-quarter to one-half emergence from the boot at mid-morning and fixed in a modified Carnoy's solution consisting of a 6:2:1 ratio of 95 percent ethanol, glacial acetic acid, and chloroform, respectively. After five days, the panicles were transferred to 70 percent ethanol and stored in a freezer until examined.

Pollen mother cells were stained with propiono-carmine and semi-permanent slides were prepared by the use of venetian turpentine mounting median described by Haunold (1968). The techniques for use were similar to those described by Wilson (1945).

For detailed analysis of subsequent meiotic stages, 20 cells at diakinesis, 55 at metaphase I, 30 at anaphase I, 50 at telophase I and anaphase II, and 100 groups of four microspores were examined.

Panicles were collected from 10 plants from each of the six single crosses for pollen study and were stored in 70 percent ethanol. Pollen was classified as normal or abnormal on the basis of starch content when stained with an aqueous iodine-potassium-iodide solution. For the determination of percentage of good pollen, 200 pollen grains from three different panicles (a total of 600 pollen grains per plant), were counted.

Feulgen preparations were made on all parents and F_1 hybrids, and these were used in detailed analyses for determination of chromosome numbers.

Seed set was determined from five open-pollinated panicles per plant. The same 10 plants used for pollen study were used for determining seed set.

Selected cells were photographed on Kodak[1] high-contrast copy film no. 5069, and prints were made on Kodak single-weight Kodabromide F-5 glossy photographic paper.

[1] Use of trademark name does not imply recommendation of the product.

All possible simple correlation coefficients among bridges at anaphase I, univalents at metaphase I, univalents dividing at anaphase I, micronuclei at telophase I, laggards at anaphase II, and micronuclei in quartets were computed on both a chromosomal and cellular basis. The relationship between the percentage normal pollen and seed set under open pollination was also determined by correlation analysis.

RESULTS AND DISCUSSION

Parental Population

Chromosome pairing at diakinesis

All parent plants had the normal somatic hexaploid number of 42 chromosomes except the Fortune II parent, which was a monosomic with 41 chromosomes. Cells at diakinesis for the monosomic Fortune II and the Fortune III parent were too sticky and clumped for interpretation. Various ratios of the components for Carnoy's fixing solution were used to overcome the problem. The 6:2:1 ratio of ethanol, glacial acetic acid, and chloroform proved to be the most satisfactory, but did not solve the problem. The sticky and clumped condition persisted in both the field and greenhouse material. Chromosome pairing was variable for the four remaining parents (Table 1). The average frequency of bivalents per sporocyte ranged from 5.4 in the Fawn I parent to 21 in the Fortune I parent. The Fawn II parent showed predominantly bivalent pairing with a low incidence of univalents, trivalents, and quadrivalents. Figure 1a is a diakinesis of the Fawn II parent, showing asynapsis of one pair of chromosomes, incomplete pairing, and the association of two groups of bivalents. The Fawn III parent had an average frequency of 15.1 bivalents per sporocyte, while the average frequency of quadrivalents was 2.6.

A low frequency of univalents and hexavalents was also observed. Figures 1c, 1d, and 2a-d show quadrivalent and hexavalent configurations at both diakinesis and metaphase I, which were observed in the Fawn III parent. The results obtained differ from those reported by Peto (1933), who found no multivalent associations, and by Crowder (1953a), who found low frequencies of multivalents in *F. arundinacea* ($2n = 42$), but agree with results reported by Myers and Hill (1947), who found both quadrivalents and hexavalents in their tall fescue material. The Fawn I parent was an asynaptic plant with only secondary pairing at diakinesis (Figures 4c-d). An average frequency of 5.4 bivalents per sporocyte was recorded; however, these bivalents were pseudobivalents. Pseudobivalents and pseudomultivalents, which occurred in high frequency, showed only

Table 1. Chromosome numbers and pairing at diakinesis in the parents and their F_1 hybrids

Parents and hybrids	2n	Configurations I	II	III	IV	V	VI	>VI	No. of cells analyzed
Fawn I	42	10.9	5.4	2.4	0.9	0.5	0.6		20
Fawn II	42	0.4	20.4	0.1	0.2				20
Fawn III	42	0.4	15.1		2.6		0.2		20
Fortune I	42		21.0						20
Fortune II*	41								
Fortune III*	42								
Fawn I x Fortune II									
Hybrid 3	42	0.6	20.3	0.1	0.2				20
Hybrid 8	42	1.1	16.2	0.3	1.6	0.1	0.2		20
Hybrid 9	42	0.5	17.4	0.1	1.4		0.2		20
Fawn II x Fortune II									
Hybrid 3	40	0.4	6.0	0.2	0.8		0.4	1.0	20
Hybrid 5*	41								
Hybrid 10*	42								
Fawn II x Fortune III									
Hybrid 1*	42								
Hybrid 2*	42								
Hybrid 8	42	0.5	19.8		0.5				20
Fawn III x Fortune I									
Hybrid 1	42	1.0	7.2	0.2	1.4		0.3	0.8	20
Hybrid 2*	42								
Hybrid 3	42	0.6	17.1	0.1	1.4		0.2		11
Fawn III x Fortune II									
Hybrid 1	42	3.0	19.5						20
Hybrid 6*	42								
Hybrid 7	42	0.3	20.8						20
Fawn III x Fortune III									
Hybrid 3	42	0.4	20.6	0.1	0.1				20
Hybrid 6	42	1.6	14.7	0.2	0.4	0.1	0.7	0.4	20
Hybrid 7	42	0.2	14.4	0.1	1.1		0.9	0.2	20

* Data not available because of chromosome stickiness at diakinesis.

secondary pairing. A high average univalent frequency of 10.9 per sporocyte was recorded, which would be expected from an asynaptic plant. These were univalents with no secondary associations.

Late diakinesis better illustrated the presence of univalents, pseudobivalents, and pseudomultivalents with only secondary pairing (Figures 5a-d and 6a). Frequently, large multivalents in the form of rings or chains

occurred in the Fawn I parent (Figures 5c,d), which may be evidence for homology or perhaps homoeology among certain chromosomes in the tall fescue genomes. The pairing of all 28 chromosomes in some of the cells in hybrids between hexaploid tall fescue and diploid *Lolium* and *Festuca* species, as observed in separate studies by both Myers (1947) and Crowder (1953b), is evidence for similarities between at least two of the genomes in tall fescue.

The secondary connections exhibited were end to end, end to side, or side to side. In such an association, the univalents were equal or unequal in size. Identification of late diakinesis and metaphase I was difficult because these associations were distributed randomly throughout the cells, occupying no definite position. They were situated on the equatorial plate, near the poles, or between the equatorial plate and the poles. Malik (1967) and Malik and Thomas (1966) observed the same type of associations among chromosomes in tall fescue and called them "false bivalents," while Walters (1954) observed them in *Bromus* hybrids and called them "pseudobivalents." Malik (1967) suggested that the association of univalents of this type reflects their partial or slight homology, leading to secondary associations which could have occurred because of chromosomal structural alterations. If this were the case, a considerable amount of structural alterations would have to occur to form a large multivalent (Figures 5c,d). Malik (1970) also suggested that the associations could be brought about by the matrix connections of nonhomologous, partially homologous, or homologous chromosomes.

Univalents and abnormal bivalents at metaphase I

Univalents at metaphase I were observed in all of the parents, with an average frequency per sporocyte ranging from 0.1 in the Fortune I parent to 14.9 in the Fawn I parent (Table 2). Both the Fawn I and Fortune II parents had univalents in all metaphase I cells observed. The univalents counted in the Fawn I parent were those with no secondary pairing. They varied considerably in the 55 cells analyzed, ranging from 3 to 27. Figures 6a-c, 7a,b illustrate univalents, pseudobivalents, and pseudomultivalents on and off the metaphase equatorial plate.

Frequently bivalents orientated on the equatorial plate were elongated and stretched towards opposite poles (Figures 6a,b and 7a). Thin regions were present between the chiasma and centromere, and often on either side of the chiasma. The chromatin strands between these segmented bivalents appeared thin and stretched. This same type of bivalent was described by other researchers (Malik, 1967; Malik and Thomas, 1966; Ostergren and Vigfusson, 1953; Crowder, 1953a,b; and Walters, 1954). Malik (1967) and Malik and Thomas (1966) suggested

Table 2. Univalents in the parents and their F_1 hybrids at metaphase I

Parents and hybrids	Univalents per cell		Percent of cells with univalents	No. of cells analyzed
	Avg. no.	Range		
Fawn I	14.9	3-27	100.0	55
Fawn II	0.2	0-2	12.7	55
Fawn III	0.4	0-3	20.0	55
Fortune I	0.1	0-2	5.5	55
Fortune II	1.8	1-7	100.0	55
Fortune III	1.0	0-3	87.3	55
Fawn I x Fortune II				
Hybrid 3	1.5	0-6	69.1	55
Hybrid 8	1.7	0-7	63.6	55
Hybrid 9	0.4	0-3	23.6	55
Fawn II x Fortune II				
Hybrid 3	3.6	0-8	96.4	55
Hybrid 5	6.4	0-17	96.4	55
Hybrid 10	3.2	0-6	85.5	55
Fawn II x Fortune III				
Hybrid 1	2.1	0-5	89.1	55
Hybrid 2	1.8	0-6	69.1	55
Hybrid 8	0.9	0-4	40.0	55
Fawn III x Fortune I				
Hybrid 1	2.7	0-9	90.9	55
Hybrid 2	1.6	0-4	72.7	55
Hybrid 3	1.3	0-4	61.8	55
Fawn III x Fortune II				
Hybrid 1	22.4	10-34	100.0	55
Hybrid 6	1.4	0-8	56.4	55
Hybrid 7	1.5	0-6	56.4	55
Fawn III x Fortune III				
Hybrid 3	0.5	0-4	18.2	55
Hybrid 6	1.5	0-5	63.6	55
Hybrid 7	1.1	0-4	47.3	55

that the condition might be caused by lack of normal spiralization in some parts of the chromosomes or by chance fusion of the matrix of two non-homologous, partly homologous, or homologous chromosomes at prophase I. The matrix connections result in the presence of thin regions in the bivalent. Ostergren and Vigfusson (1953), working with *Secale*, suggested thin areas may also appear because of poleward movement of centromeres at early metaphase I. Crowder (1953a,b) assumed the abnormality to result from a physiological change in the surface properties

of the chromosome. Walters (1954), working with *Bromus* hybrids, suggested that the chromosomes were held together by a matrix bond, a thin region which he called a "pseudochiasma," rather than a true chiasma.

Univalents ranged from one to seven, with an average frequency of 1.8, in metaphase I sporocytes of the Fortune II parent. They occurred in combinations of one, three, five, or seven in number and rarely more. This might be expected for a monosomic plant. Chromosomes showed considerable stickiness and clumping, thus making chromosome spreading difficult. Figures 3b-d, 4a illustrate univalents off the equatorial plate at metaphase I. Figure 3c shows the tendency for secondary association among bivalents in the monosomic.

Kempanna and Riley (1964) showed evidence that there was secondary association between genetically related bivalents in *T. aestivum*. The Fawn II parent had a low average frequency of 0.2 univalents per sporocyte and never had more than two univalents present in a metaphase I sporocyte. Figure 1b is a metaphase I of the Fawn II parent with two univalents, which possibly resulted from the asynaptic pair of chromosomes in the diakinesis shown in Figure 1a. The two groups of two associated bivalents and the open bivalent can also be related to the diakinesis. The Fortune III parent had a high percentage (87.3) of metaphase I sporocytes with univalents and an average frequency of 1.0 univalent per cell. The Fawn III and Fortune I parents had a relatively low average frequency of 0.4 and 0.1, respectively.

Lagging chromosomes and bridges at anaphase I and micronuclei at telophase I

Dividing univalent chromosomes were noted in all parents (Table 3). The frequency of cells with dividing univalents was less than the frequency of cells with univalents at metaphase I in every case except the Fortune I parent. This suggests that some chromosomes that divided or remained undivided probably moved with the dyads. The percent of cells with dividing univalents ranged from 3.3 in the Fawn II and Fawn III parents to 79.3 in the Fawn I parent. The average frequency of dividing univalents for the Fawn I parent was lower than expected, considering the asynaptic properties of the plant and the high number of univalents at metaphase I.

Good anaphase I cells were difficult to find in the Fawn I parent, and frequently there was considerable misdivision and fragmentation (Figure 7c); however, telophase I cells with no micronuclei were often found (Figure 7d). All of the metaphase I cells showed only secondary pairing among chromosomes; possibly, most of them moved as dyads at anaphase I. Occasionally, all 42 univalents divided equationally at anaphase I

Table 3. Dividing univalents and bridges at anaphase I in the parents and their F_1 hybrids

Parents and hybrids	Dividing univalents per cell		Percent of cells with div. univ.	Percent of cells with bridges	No. of cells analyzed
	Avg. no.	Range			
Fawn I	5.3	0-21	79.3	20.7	29
Fawn II	0.1	0-2	3.3	0.0	30
Fawn III	0.1	0-1	3.3	0.0	30
Fortune I	0.1	0-2	10.0	3.3	30
Fortune II	0.9	0-3	56.7	0.0	30
Fortune III	0.9	0-3	60.0	0.0	30
Fawn I x Fortune II					
Hybrid 3	1.8	0-6	73.3	16.7	30
Hybrid 8	1.3	0-6	53.3	3.3	30
Hybrid 9	1.4	0-6	46.7	3.3	30
Fawn II x Fortune II					
Hybrid 3	4.0	0-12	96.7	0.0	30
Hybrid 5	4.6	0-13	89.3	67.9	28
Hybrid 10	5.2	0-11	96.7	3.3	30
Fawn II x Fortune III					
Hybrid 1	3.4	0-11	83.3	0.0	30
Hybrid 2	3.2	0-9	96.0	20.0	25
Hybrid 8	1.1	0-4	50.0	6.7	30
Fawn III x Fortune I					
Hybrid 1	1.4	0-10	47.8	4.4	23
Hybrid 2	0.8	0-7	33.3	0.0	30
Hybrid 3	0.9	0-4	46.7	0.0	30
Fawn III x Fortune II					
Hybrid 1	22.1	18-26	100.0	0.0	30
Hybrid 6	5.8	1-11	100.0	6.7	30
Hybrid 7	3.0	0-18	83.3	26.7	30
Fawn III x Fortune III					
Hybrid 3	0.3	0-4	20.0	40.0	30
Hybrid 6	5.9	0-10	93.3	0.0	30
Hybrid 7	1.5	0-5	50.0	0.0	30

and, with some lagging, moved toward respective poles (Figure 10a). The monosomic Fortune II parent had 56.7 percent of the cells with dividing univalents, with an average frequency of 0.9 per cell. Figure 4b shows seven dyad laggards which might have resulted from a metaphase I cell with seven univalents such as the one shown in Figure 4a. Dividing univalents were observed in 60 percent of the cells in the Fortune III parent, with an average frequency of 0.9 per cell. The remaining parents were relatively normal. The average frequency of micronuclei at telo-

phase I (Table 4) was about the same as the average frequency of dividing univalents at anaphase I for all but one parent. The Fawn I parent had an average frequency of 0.9 micronuclei per cell as compared to an average frequency of 5.3 dividing univalents per cell at anaphase I. This suggests that although a large percentage of the laggards was observed at telophase I as micronuclei in the cytoplasm, many were included in the nuclei.

Bridges were observed in 20.7 percent of the anaphase I cells in the Fawn I parent (Table 3); however, these were caused by difficulty in

Table 4. Micronuclei at telophase I in the parents and their F_1 hybrids

Parents and hybrids	Micronuclei per cell		Percent of cells with micronuclei	No. of cells analyzed
	Avg. no.	Range		
Fawn I	0.9	0-4	52.0	50
Fawn II	0.1	0-2	8.0	50
Fawn III	0.1	0-2	14.0	50
Fortune I	0.1	0-2	8.0	50
Fortune II	0.7	0-3	54.0	50
Fortune III	0.5	0-3	36.0	50
Fawn I x Fortune II				
Hybrid 3	0.8	0-4	49.0	49
Hybrid 8	0.8	0-3	40.0	50
Hybrid 9	0.8	0-3	42.0	50
Fawn II x Fortune II				
Hybrid 3	4.3	0-10	98.0	50
Hybrid 5	1.4	0-6	82.0	50
Hybrid 10	0.8	0-4	56.0	50
Fawn II x Fortune III				
Hybrid 1	2.9	0-7	92.0	50
Hybrid 2	0.9	0-3	52.0	50
Hybrid 8	0.6	0-4	24.0	50
Fawn III x Fortune I				
Hybrid 1	0.4	0-5	22.0	50
Hybrid 2	0.2	0-2	18.0	50
Hybrid 3	0.5	0-2	32.0	50
Fawn III x Fortune II				
Hybrid 1	0.5	0-4	26.0	50
Hybrid 6	0.9	0-4	46.0	50
Hydrid 7	0.5	0-3	32.0	50
Fawn III x Fortune III				
Hybrid 3	0.0	0-0	0.0	50
Hybrid 6	0.5	0-3	30.0	50
Hybrid 7	0.3	0-2	20.0	50

Table 5. Lagging chromosomes and bridges at anaphase II in the parents and their F_1 hybrids

Parents and hybrids	Laggards per cell		Percent of cells with lag.	Percent of cells with bridges	No. of cells analyzed
	Avg. no.	Range			
Fawn I	21.2	16-24	100.0	—	5
Fawn II	0.8	0-7	24.0	6.0	50
Fawn III	0.4	0-5	16.0	2.0	50
Fortune I	0.0	0-1	4.0	4.0	50
Fortune II	0.5	0-2	36.0	2.0	50
Fortune III	0.6	0-5	32.0	2.0	50
Fawn I x Fortune II					
Hybrid 3	1.6	0-5	72.0	2.0	50
Hybrid 8	1.5	0-6	54.0	4.0	50
Hybrid 9	2.0	0-8	60.0	0.0	50
Fawn II x Fortune II					
Hybrid 3	5.8	2-10	100.0	0.0	50
Hybrid 5	7.4	2-14	100.0	2.0	50
Hybrid 10	9.7	0-18	98.0	2.0	50
Fawn II x Fortune III					
Hybrid 1	4.1	0-8	90.0	0.0	50
Hybrid 2	8.9	1-16	100.0	4.0	50
Hybrid 8	2.2	0-10	48.0	0.0	50
Fawn III x Fortune I					
Hybrid 1	10.2	0-29	98.0	6.0	50
Hybrid 2	7.9	1-19	100.0	0.0	50
Hybrid 3	3.6	0-12	78.0	0.0	50
Fawn III x Fortune II					
Hybrid 1	34.4	8-66	100.0	0.0	50
Hybrid 6	9.4	2-21	100.0	0.0	50
Hybrid 7	1.4	0-8	42.0	0.0	50
Fawn III x Fortune III					
Hybrid 3	0.5	0-4	20.0	0.0	50
Hybrid 6	8.9	0-20	94.0	0.0	50
Hybrid 7	4.1	0-17	90.0	0.0	50

chromosome separation possibly due to stickiness. Crowder (1953a,b) reported "sticky" bridges were the most frequent type seen at anaphase I. Another type of bridge, resulting from crossing over between chromatids in regions heterozygous for a paracentric inversion, occurred in 3.3 percent of the cells in the Fortune I parent. A dicentric bridge with an accompanying fragment is shown in Figure 3a.

Lagging chromosomes and bridges at anaphase II and quartets with micronuclei

Varying numbers of laggards were observed in cells at the anaphase II stage in the parents (Table 5). Laggards were the result of univalents which divided at anaphase I, or did not divide until anaphase II. The average frequency of laggards per cell ranged from 0.0 to 21.2 in the Fortune I and Fawn I parents, respectively. All cells of the Fawn I parent had lagging chromosomes, ranging from 16-24 per cell. Fifty cells were observed, but data from only five cells were used. Because of the high frequency of lagging chromosomes in the Fawn I parent (Figure 8b,c), many chromosomes grouped together and made accurate counts difficult. Frequently, the chromosomes lagged in such a fashion to form a bridge (Figure 8c). Figure 8a shows monads, which become laggards at anaphase II, and dyads on and off the metaphase II equatorial plate. Occasionally, cells were observed with chromosomes appearing to migrate to their respective poles with no cytoplasmic division and some lagging (Figure 8d). The division appeared to go directly from metaphase I to anaphase II. Only 36 percent of the cells showed lagging chromosomes in the monosomic Fortune II parent. Lagging due to the monosome was not as evident as would have been expected.

Bridges were observed in some anaphase II cells in all parents (Table 5). They occurred in a low percentage of the cells, and the most frequent type could be explained by a single crossover within an inverted chromosome region, occurring simultaneously as one in a region between the inversion and centromere. Another type of bridge occurred in the Fawn I parent as a result of the high frequency of laggards grouping together across the equatorial plate (Figure 8c).

Laggards did not move in time to be included in the quartet nuclei but were left to form micronuclei (Table 6). Quartets with micronuclei were observed in all parents, with the average frequency of micronuclei per quartet ranging from 0.1 to 7.9 and percentage of cells with micronuclei ranging from 8.0 to 97.6 in the Fortune I and Fawn I parents, respectively. The average frequency of 7.9 micronuclei for the Fawn I parent is biased downward due to macronuclei which were counted as micronuclei. Forty percent of the quartets had from one to four multilaggard micronuclei. Nuclear bridges as a result of numerous lagging chromosomes at anaphase II (Figure 8c) were observed in 23 percent of the quartets. Nuclear bridges occurred 11 percent of the time on one side (Figure 9a) and 12 percent of the time on both sides of a quartet (Figure 9b). Figures 9c,d illustrate individual micronuclei and large micronuclei observed in the quartets. The remaining parent plants had a relatively low average frequency of micronuclei per quartet.

Table 6. Quartet micronuclei in the parents and their F_1 hybrids

Parents and hybrids	Micronuclei per quartet		Percent of cells with micro.	No. of cells analyzed
	Avg. no.	Range		
Fawn I	7.9	0-17	97.6	84
Fawn II	0.6	0-7	16.0	100
Fawn III	0.5	0-7	25.0	100
Fortune I	0.1	0-2	8.0	100
Fortune II	0.6	0-3	41.0	100
Fortune III	0.7	0-5	44.0	100
Fawn I x Fortune II				
Hybrid 3	1.8	0-6	71.0	100
Hybrid 8	1.4	0-5	53.0	100
Hybrid 9	1.9	0-9	58.0	100
Fawn II x Fortune II				
Hybrid 3	4.8	0-12	98.0	100
Hybrid 5	5.7	1-13	100.0	100
Hybrid 10	6.5	0-14	97.0	100
Fawn II x Fortune III				
Hybrid 1	4.4	0-14	90.0	100
Hybrid 2	7.7	0-15	99.0	100
Hybrid 8	1.0	0-7	31.0	100
Fawn III x Fortune I				
Hybrid 1	5.3	0-16	99.0	100
Hybrid 2	4.8	0-11	96.0	100
Hybrid 3	4.1	0-10	83.0	100
Fawn III x Fortune II				
Hybrid 1	6.0	0-17	99.0	100
Hybrid 6	8.0	2-14	100.0	100
Hybrid 7	1.5	0-6	42.0	100
Fawn III x Fortune III				
Hybrid 3	0.4	0-3	22.0	100
Hybrid 6	5.0	0-12	93.0	100
Hybrid 7	3.2	0-8	91.0	100

Endomitosis

Endomitosis occurred in the Fawn I parent, resulting in pollen mother cells with increased chromosome numbers. Price (1956) suggested three types of syncyte formation in plants: archesporial, migration, and fusion. Archesporial syncyte formation was described to arise through the failure of cytokinesis in the mitotic division which precedes meiosis. Other means by which achesporial syncyte formation might occur were not defined. Migration syncyte formation was defined as the passage of a nucleus from one pollen mother cell to another, and fusion

syncyte formation as the fusion of pollen mother cells or the breakdown of cell walls. These cases appeared not to apply to the syncyte formation which occurred in the Fawn I parent. It was an asynaptic plant with only secondary pairing at diakinesis and metaphase I. Syncytes were not present at early stages of meiosis but occurred at later stages, indicating that syncyte formation was a result of mitosis with no cytokinesis in the sporocytes. Cells with 42 chromosomes in x configurations, which might be found at prophase or metaphase II of meiosis, were observed frequently (Figures 10b,c). Prophases such as those found in mitosis were observed, sometimes leaving chromosomes in the cytoplasm. This indicates that syncytes formed during meiosis rather than before as suggested by Price (1956). Figure 10d shows a syncyte at prophase which has about doubled in size. Note the chromosomes left in the cytoplasm, one of which is attached to a nucleolus. After the first interphase, cells formed with $2n = 84$ chromosomes (Figure 11a), which is twice the normal hexaploid number of $2n = 42$. Syncytes that were observed in an anaphase movement (Figure 11b) could result in a cell which showed no cytokinesis (Figure 11c). Enormous metaphase or early anaphase syncytes were often observed (Figures 11d, 12a). Figure 12b compares two syncytes. The smaller one has doubled once and the larger perhaps twice with an anaphase division, no cytokinesis, and leaving some laggards. The largest cell found was estimated to contain 96 times the basic chromosome number, or a total of 672 chromosomes. Figure 12c shows a syncyte which was estimated to be 48-ploid with 336 chromosomes. Chromosomes of the endomitotic cells were left unpaired and occurred as monads or dyads. Often these giant cells degenerated but many persisted, either in a delayed stage of endomitotic division or as interphase, metaphase, or prophase cells until a cell wall was laid down surrounding the cells. This resulted in a great variation in size of pollen grains, with most in a collapsed state. Giant pollen grains often stained with iodine (Figure 12d).

Pollen stainability and seed set

Percent pollen stainability was above 90 percent for all parents except the asynaptic Fawn I parent (Table 7). Due to the abnormal meiosis and the endomitotic process which occurred in the plant, the 27.5 percent pollen stainability found was higher than expected. In fact, percent pollen stainability was high for all parents considering the meiotic abnormalities present in most. Although the percent pollen stainability does not always reflect the true fertility of a plant, it serves as an estimate.

Seed set was good for all but the Fawn I and Fortune I parents (Table 7). They produced about half as much seed as the Fortune II and Fortune III parents and less than one-third the amount of the

Table 7. Percent stainable pollen and five-panicle seed weight in the parents and their F_1 hybrids

Parents and hybrids	Percent stainable pollen	Five-panicle seed weight (grams)
Fawn I	27.5	0.570
Fawn II	98.0	2.032
Fawn III	91.2	2.159
Fortune I	95.5	0.594
Fortune II	94.0	1.101
Fortune III	93.3	1.158
Fawn I x Fortune II		
Hybrid 1	60.2	0.454
Hybrid 2	0.0	0.000
Hybrid 3*	9.7	0.186
Hybrid 4	62.0	0.938
Hybrid 5	54.0	2.169
Hybrid 6	39.7	0.210
Hybrid 7	34.3	0.155
Hybrid 8*	68.5	1.406
Hybrid 9*	52.5	2.078
Hybrid 10	68.2	1.639
Fawn II x Fortune II		
Hybrid 1	44.8	1.751
Hybrid 2	83.3	2.430
Hybrid 3*	0.0	0.008
Hybrid 4	0.0	0.005
Hybrid 5*	0.0	3.850
Hybrid 6	59.7	0.362
Hybrid 7	0.0	0.004
Hybrid 8	27.8	0.090
Hybrid 9	88.0	0.836
Hybrid 10*	0.0	0.017
Fawn II x Fortune III		
Hybrid 1*	0.0	0.006
Hybrid 2*	0.0	0.013
Hybrid 3	0.0	0.019
Hybrid 4	0.0	0.048
Hybrid 5	0.0	0.009
Hybrid 6	82.3	0.547
Hybrid 7	1.2	0.011
Hybrid 8*	88.0	0.073
Hybrid 9	0.0	0.005
Hybrid 10	0.0	0.034

(*continued next page*)

Table 7—(Continued)

Parents and hybrids	Percent stainable pollen	Five-panicle seed weight (grams)
Fawn III x Fortune I		
Hybrid 1*	0.0	0.000
Hybrid 2*	0.0	0.009
Hybrid 3*	0.0	0.064
Hybrid 4	0.0	0.106
Hybrid 5	0.0	0.042
Hybrid 6	0.0	0.244
Hybrid 7	93.8	2.008
Hybrid 8	59.2	1.286
Hybrid 9	79.3	1.533
Hybrid 10	0.0	0.003
Fawn III x Fortune II		
Hybrid 1*	13.7	0.060
Hybrid 2	1.6	0.066
Hybrid 3	0.0	0.000
Hybrid 4	0.0	0.004
Hybrid 5	0.0	0.019
Hybrid 6*	0.0	0.000
Hybrid 7*	21.0	0.966
Hybrid 8	13.8	1.749
Hybrid 9	12.2	0.483
Hybrid 10	20.3	2.041
Fawn III x Fortune III		
Hybrid 1	0.5	0.000
Hybrid 2	29.7	0.009
Hybrid 3*	89.5	0.064
Hybrid 4	0.0	0.106
Hybrid 5	0.0	0.042
Hybrid 6*	0.0	0.244
Hybrid 7*	0.0	2.008
Hybrid 8	0.0	1.286
Hybrid 9	0.0	1.533
Hybrid 10	67.3	0.003

* Hybrids used for detailed analysis of meiosis.

Fawn II and Fawn III parents. The lower seed set for the Fortune I parent is difficult to explain because of the relatively few meiotic abnormalities in this plant. The Fawn I parent set a relatively large amount of open-pollinated seed per five-panicle sample, considering the abundance of meiotic abnormalities observed in the sporocytes.

Thirty panicles were enclosed in groups of five and selfed under field conditions for the Fawn I parent to determine self-fertility. Only .033 grams of seed were obtained and all had undeveloped caryopses.

Hybrid Population

All hybrids had the normal hexaploid chromosome number of 2n = 42 except hybrids 3 and 5 of the Fawn II x Fortune II cross (Table 1), which had 40 and 41 chromosomes, respectively. Figure 25c shows a somatic cell with 41 chromosomes, and the cell in Figure 25d has the normal 42. Aneuploids might have been expected from the Fawn I x Fortune II cross considering the asynaptic and unstable meiotic properties of the Fawn I parent and the monosomic condition of the Fortune II parent, but none were recorded.

Chromosome pairing at diakinesis

The average frequency of univalents, bivalents, and multivalents was determined for the F_1 hybrids (Table 1). Similar to the Fortune II and III parents, data for eight of the hybrids could not be obtained due to chromosome stickiness or secondary pairing. Figures 20a,b show chromosomes which are condensed enough to be at metaphase I yet maintain a pachytene configuration. This condition of stickiness was often carried over into metaphase I and made analysis difficult (Figures 16c, 20c,d, 22d, 24b). Of the remaining hybrids, the average frequency of bivalents ranged from 6.0 to 20.8. Univalents, quadrivalents, and to a lesser extent trivalents, pentavalents, and hexavalents were observed in the hybrids. Often, larger multivalents were recorded, but these were attributed to stickiness or secondary associations. Because of stickiness and multivalent formation, cells with more regular than "normal" pairing may have been selected for observation. Carnahan and Hill (1961) suggested that this happens when cytologists work with meiotically unstable species.

Figures 14a and 15d show trivalent associations, Figures 14b,c,d, 15a, 17d, and 19b show quadrivalent associations which were of the ring or chain type, and Figures 17b and 24d show cells with hexavalents. Open bivalents at diakinesis (Figure 13a) resulted in rod bivalents at metaphase I (Figure 13b). Diakinesis with open bivalents, univalents, and chromosome associations, which were present in various hybrids, are shown in Figures 13d, 15c, 17a, 19a,c, 21a, and 23a,b.

Univalents and abnormal bivalents at metaphase I

Metaphase I univalents were observed in all of the hybrids, with an average frequency of univalents per sporocyte ranging from 0.4 to 22.4 in hybrid 9 of he Fawn I x Fortune II cross and hybrid 1 of the Fawn III x Fortune II cross, respectively (Table 2). In 14 of the 18 hybrids more than 50 percent of the cells contained univalents. Six of these hybrids were extremely abnormal, with over 80 percent of the cells containing univalents. Hybrid 1 of the Fawn III x Fortune II cross had 100 percent

of the cells showing univalents with a range of 10-34 per cell. For example, Figure 21b shows $5_{II} + 32_{I}$ and Figure 21c shows $7_{II} + 28_{I}$. In addition, 17 univalents can be seen off the metaphase I plate in a monosomic hybrid in Figure 17c. There are two explanations for the occurrence of univalents. One is the failure of pairing due to lack of complete homology, which could be caused by translocations, inversions, or deletions. Secondly, they could be due to lack of genetic control of pairing in the meiotic process; this may be found in monosomics, due to the lost chromosome.

Figures 16a and 17d show metaphase I sporocytes with secondary pairing among bivalents. Riley (1960) and Kempanna and Riley (1964) suggested that secondary associations of this type must be dependent upon attractions determined by residual homology or homoeology. The precise nature of the secondary affinity could not be ascertained, but two causes were suggested. The first was that all homoeologous chromosomes are attracted at zygotene, but pairing only takes place between fully homologous chromosomes. Homoeologues would be attracted throughout prophase and would be revealed as secondary associations at metaphase I. Secondly, secondary association may result from forces of attraction that occur during the migration of bivalents to the metaphase I equatorial plate. The investigators accept this hypothesis as well as the first one because of absence of any contact between secondarily associated bivalents at metaphase I. Figure 16a shows one group of seven, one group of six, and two groups of two bivalents in secondary association. If the first hypothesis is accepted, a high degree of residual homology or perhaps homoeology among chromosomes in tall fescue may exist.

Figures 17b, 21b, and 21c show pseudobivalents similar to those found in the Fawn I parent, and Figure 15b shows association and misdivision of chromosomes at metaphase I. The presence of multivalents, pseudobivalents, and the high frequency of univalents in the hybrids suggests considerable chromosome structural change in either the Fawn or Fortune parents or perhaps in both. However, homoeologous pairing could also result in multivalent and pseudobivalent formation.

Lagging chromosomes and bridges at anaphase I and micronuclei at telophase I

Dividing univalents at anaphase I were observed in varying frequencies in all the F_1 hybrids (Table 3). The average frequency per sporocyte ranged from 0.3 in hybrid 3 of the Fawn III x Fortune III cross to 22.1 in hybrid 1 of the Fawn III x Fortune II cross. In most instances, the frequency of dividing univalents at anaphase I was in good accordance with the frequency of univalents at metaphase I. Thirteen of the eighteen hybrids had 50 percent or more cells with dividing univalents and nine

of these had more than 80 percent. Thirty cells were analyzed for each hybrid at anaphase I, but accurate determination of dividing univalents was often difficult due to a high degree of misdivision in some cells. Only cells which could be accurately analyzed were used for determining frequencies. Figures 16d, 21d, 22a, 23c, and 24c show lagging chromosomes at anaphase I for various hybrids.

Lagging chromosomes at anaphase I appeared as micronuclei in the cytoplasm at telophase I (Table 4, Figure 13c). The average frequency of micronuclei ranged from 0.0 in hybrid 3 of the Fawn III x Fortune III cross to 4.3 in hybrid 3 of the Fawn II x Fortune II cross. The average frequency of micronuclei at telophase I was generally less than the frequency of dividing univalents at anaphase I. This indicated that many of the laggards moved in time to be included in the telophase I nuclei, and that telophase I is not a useful stage for determining the stability of meiosis in tall fescue genotypes.

Bridges at anaphase I were observed in 11 of the 18 hybrids (Table 3). However, they were observed in low frequencies in all but five hybrids and were of the dicentric type. Bridges which appeared to result from difficulty in chromosome separation as a result of stickiness were also noted.

Lagging chromosomes and bridges at anaphase II and quartets with micronuclei

Laggards varied considerably in anaphase II cells of the F_1 hybrids (Table 5). The average frequency ranged from 0.5 in hybrid 3 of the Fawn III x Fortune III cross to 34.4 in hybrid 1 of the Fawn III x Fortune II cross. Six hybrids had laggards in 100 percent of the cells observed, while five others had laggards in at least 90 percent of the cells. In hybrid 1 of the Fawn III x Fortune II cross 100 percent of the anaphase II cells had laggards. The number of laggards per cell ranged from 8 to 66. Anaphase II laggards can be seen in Figures 22b,c and 23d.

A low frequency of bridges at anaphase II was observed in six of the F_1 hybrids (Table 5). The remaining 12 hybrids studied in detail had no anaphase II bridges. If a single crossover occurred within an inverted chromosome, occurring simultaneously as one between the inversion and centromere, the result would be dicentric chromatid movement to the same pole and no bridge at anaphase I. The chromatids would attempt to divide at anaphase II, resulting in a dicentric bridge. A quartet with a chromatin bridge between nuclei is shown in Figure 19d.

Quartets with micronuclei as a result of laggards at anaphase II were observed in all hybrids (Table 6). Eleven of the eighteen hybrids had micronuclei in at least 90 percent of their cells. The average frequency

of micronuclei per quartet varied considerably among hybrids, ranging from 0.4 in hybrid 3 of the Fawn III x Fortune III cross to 8.0 in hybrid 6 of the Fawn III x Fortune II cross. Micronuclei per quartet ranged from 0 to 17 in good accordance with laggards at anaphase II, which indicated that most lagging chromosomes did not move in time to be included in the quartet nuclei. One exception to this was hybrid 1 of the Fawn III x Fortune II cross. It had an average frequency of 22.4 univalents per cell at metaphase I, 22.1 dividing univalents per cell at anaphase I, 34.4 laggards per cell at anaphase II, and only 6.0 micronuclei per quartet. Perhaps cellular division was slowed by the high frequency of univalents, allowing laggards to be included in the quartet nuclei. Quartets with micronuclei are shown in Figure 16b.

Polyspory was frequently observed in hybrid 1 of the Fawn II x Fortune III cross (Figure 18). Quartets with four microspores were usually formed, but occasionally five, six, or seven were present. Polyspory has been reported in *Festuca* x *Lolium* hybrids (Crowder, 1953b) and in *Triticum x Agropyron* hybrids (Marshall and Schmidt, 1954).

Pollen stainability and seed set

Pollen stainability and seed set was observed in 10 F_1 hybrids of each of the six crosses (Table 7). Thirty of the sixty hybrids had collapsed pollen grains with no cytoplasm and no starch grains (Figure 25a). The cross involving the asynaptic Fawn I parent and the monosomic Fortune II parent generally had the most stable meiosis and the highest number of hybrids with stainable pollen. Only one hybrid was completely sterile in this cross. Both the Fawn II x Fortune III and the Fawn III x Fortune I crosses had 7 of 10 hybrids with collapsed pollen grains. Of the 18 hybrids studied in detail, 11 had no stainable pollen.

The detailed study revealed hybrid 8 of the Fawn II x Fortune III cross and hybrid 3 of the Fawn III x Fortune III cross to be the most meiotically stable. These two hybrids had the lowest frequency of micronuclei in the quartets (Table 6) and the highest pollen stainability (Table 7).

Two hybrids of the Fawn II x Fortune II cross were aneuploids with 40 and 41 chromosomes, respectively. Both had irregular meiosis, resulting in collapsed pollen grains. However, the monosomic hybrid 5 had the highest five-panicle seed weight in the study (Table 7). Seed set among the hybrids was variable (Table 7). Only 5 of the 60 hybrids set no seed for five panicles, although many set very little. A correlation coefficient of $r = 0.55$, which was significant at the .01 level of probability, was obtained between pollen stainability and seed set.

Univalent Behavior

A series of photomicrographs of hybrid 1 of the Fawn III x Fortune II cross was prepared to illustrate the univalent behavior which was generally observed throughout the study. At diakinesis, univalents were observed unpaired or secondarily paired (Figure 21a). While bivalents moved to the metaphase equatorial plate, univalents lagged behind, distributed randomly throughout the cytoplasm (Figures 21b,c). As many as 34 univalents were present in metaphase I cells whose secondary pairing was sometimes observed.

After the bivalents divided and moved to their respective poles at anaphase I, univalents, lagging behind the division, would orientate on the metaphase I plate (Figure 21d). At late anaphase I (Figure 22a), the univalents divided equationally and the majority of the chromatids reached the pole at telophase I. The remaining chromosomes were left in the cytoplasm as micronuclei. Only 22 percent of the telophase I cells contained micronuclei, with a low average frequency of 0.4 micronuclei per cell (Table 4). Because of the extremely high number of univalents present, cellular division was probably slowed so that most chromosomes were included in the daughter nuclei. This was not always the case in other hybrids when fewer univalents were involved. Chromatids oriented on the metaphase II plate and lagged at anaphase II (Figure 22b,c). All cells observed had laggards at anaphase II (Table 5). The laggards ranged from 8-66 in the cells and had an average frequency of 34.4 per cell (Table 5). Normally, a high frequency of laggards would appear in the quartet cytoplasm as micronuclei as shown in Figure 16b. Due to an unsynchronized division of bivalents and univalents, a frequency of only 6.0 micronuclei per quartet was recorded. This suggests that many laggards were included in the quartet nuclei. In a majority of the hybrids, the number of micronuclei per cell was in close agreement with the number of laggards per cell at anaphase II (Tables 5 and 6).

Relationships Among Meiotic Irregularity Variables

On a cellular basis, variables—univalents at metaphase I, dividing univalents at anaphase I, micronuclei at telophase I, laggards at anaphase II, and quartet micronuclei—were significantly correlated (Table 8).

Combinations of the variables—univalents at metaphase I, dividing univalents at anaphase I, laggards at anaphase II, and quartet micronuclei —were significantly correlated on a chromosomal basis except the variables univalents at metaphase I and quartet micronuclei. The variable micronuclei at telophase I was not correlated to any other variable on a chromosomal basis.

Table 8. Correlation coefficients of meiotic irregularities on a cellular and chromosomal basis

Variables	Correlation basis[a]	Simple correlation coefficients				
		Univalents at metaphase I	Dividing univalents anaphase I	Micronuclei at telophase I	Laggards at anaphase II	Quartet micronuclei
Bridges at anaphase I	1	.09	.19	.19	.08	.07
	2	.21	.04	.03	.12	.28
Univalents at metaphase I	1		.72**	.66**	.68**	.71**
	2		.87**	.09	.93**	.49
Dividing univalents at anaphase I	1			.70**	.74**	.74**
	2			.12	.89**	.52**
Micronuclei at telophase I	1				.53**	.54**
	2				.05	.30
Laggards at anaphase II	1					.99**
	2					.70**

[a] 1 = Correlation on a cellular basis, 22 d.f., 2 = correlation on a chromosomal basis.
** Significant at the 0.01 level of probability.

The lack of a correlation of variables with micronuclei at telophase I on a chromosomal basis was perhaps due to univalents reaching the poles in time to be included in the daughter nuclei of telophase I. This could also be the explanation for the lack of a correlation on a chromosomal basis between univalents at metaphase I and quartet micronuclei. Bridges at anaphase I had no relationship with the other meiotic irregularity variables. The significant simple correlations indicated that lagging chromosomes and quartet micronuclei resulted predominantly from univalents at metaphase I. This was in agreement with Crowder (1953a), who found significant correlations between all variables on both a chromosomal and cellular basis except univalents dividing at anaphase I and micronuclei at telophase I on the cellular basis.

SUMMARY AND CONCLUSIONS

Six parents and eighteen hybrids derived from six single crosses were cytologically investigated for the possibility of meiotic irregularities causing partial or complete sterility in *Festuca arundinacea* Schreb. Meiotic stages used for detailed analyses included: diakinesis, metaphase I, anaphase I and II, telophase I, and microspore quartets.

An examination of root tips revealed one parent to have 41 and two hybrids to have 40 and 41 chromosomes respectively. Both aneuploid hybrids were the progeny of a monosomic 41-chromosome parent.

Variable numbers of univalents, trivalents, quadrivalents, pentavalents, hexavalents, as well as larger multivalent associations, were observed among the parents and hybrids at diakinesis. The chromosomes were often sticky at diakinesis, and this condition persisted through metaphase I and, to a lesser extent, anaphase I. The reasons for "stickiness" were not determined; however, it could have resulted from the fusion of matrix caused by abnormal surface properties of the chromosomes.

The percent of metaphase I cells with univalents ranged from 5.5 to 100.0 among the hybrids. The average frequency of univalents per cell ranged from 0.1 to 14.9 in the parents and 0.5 to 22.4 in the hybrids. Average frequencies of dividing univalents at anaphase I ranged from 0.1 to 5.3 for the parents and from 0.3 to 22.1 for the hybrids. These univalents often appeared as micronuclei at telophase I, but many moved in time to be included in the nuclei.

Laggards at anaphase II were observed in over 90 percent of the cells in one parent and in 11 of the 18 hybrids studied in detail. The range was from 4.0 to 100.0 percent for the hybrids. The average frequency per cell ranged from 0.0 to 21.2 and 0.5 to 34.4 in the parents and

hybrids, respectively. The frequencies of quartet micronuclei were in good accordance with lagging chromosomes at anaphase II. Significant correlations among meiotic irregularity variables suggested that lagging chromosomes at anaphase II and quartet micronuclei were primarily due to metaphase I univalents.

Dicentric bridges at anaphase I were observed in one parent and in 11 of the 18 hybrids. They occurred in only 3.3 percent of the cells in the parent and from 3.3 to 67.9 percent of the cells in the hybrids. Bridges of this type result from crossing over between chromatids in regions heterozygous for a paracentric inversion. Bridges at anaphase II were observed in 6 percent or less of the cells among the parents and six hybrids. These bridges can be explained by a single crossover within an inverted chromosome region, occurring at the same time as a crossover in a region between the inversion and the centromere. Bridges due to difficulty in chromosome separation because of stickiness were also observed.

The Fawn I parent was an asynaptic plant which produced syncytes with increased chromosome numbers. Evidence showed syncytes to form because of continued mitotic divisions with no cytokinesis. Giant cells ranged from those with $2n = 6x = 42$ to an estimated $2n = 96x = 672$ chromosomes. They often showed indications of anaphasic movements and were observed in prophase and metaphase configurations. The chromosomes appeared only as univalents with some secondary pairing.

Pseudobivalents and pseudomultivalents, involving as many as 36 univalents, occurred in the Fawn I parent; this, along with secondary pairing of bivalents in other plants, was evidence for considerable homology among chromosomes in tall fescue. Pseudobivalents which oriented on the metaphase I plate showed poleward orientation, resulting in "thin regions" between the matrix connections and the centromeres. The condition could have occurred because of early poleward movement of the centromeres at metaphase I, resulting in stretching of the matrix connections in the bivalent.

The occurrence of univalents, multivalents, and more complex associations, including secondary pairing, in the hybrids is indicative of structural rearrangements among the parents. However, multivalents could also result from homeologous pairing.

Polyspory was observed in one of the hybrids. Along with the normal formation of four microspores, abnormal quartets frequently formed five, six, and seven microspores.

Percent stainable pollen was used to estimate pollen fertility and five-panicle seed weight to estimate female fertility. All parents had above 90 percent stainable pollen except the asynaptic Fawn I parent, which had 27.5. Fifty percent of the hybrids had collapsed pollen grains containing

no starch and little cytoplasm. Seed set was variable among parents and progeny, ranging from 0.0 to 3.85 grams of seed for five panicles. Only five hybrids were completely sterile; however, over half of the hybrids set less than one-tenth of a gram of seed for five panicles. A significant correlation coefficient of $r = 0.55$ was found between stainable pollen and five-panicle seed weight.

Sterility among the hybrids was due primarily to high frequencies of univalents and in part to translocations and inversions resulting in chromosome deficiencies in the gametes.

LITERATURE CITED

Burson, Byron L., and Hugh W. Bennett. 1971. Chromosome numbers, microsporogenesis, and mode of reproduction of seven *Paspalum* species. Crop Sci., *11*:292-294.

Burson, Byron L., and Hugh W. Bennett. 1972. Cytogenetics of *Paspalum urvillei* x *P. juergensii* and *P. urvillei* x *P. vaginatum* hybrids. Crop Sci., *12*:105-108.

Carnahan, H. L., and Helen D. Hill. 1956. Cytogenetics of progenies of 35-chromosome reed canarygrass (*Phalaris arundinacea* L.). Agron. J., *48*:356-359.

Carnahan, H. L., and Helen D. Hill. 1961. Cytology and genetics of forage grasses. Bot. Rev., *27*:1-162.

Carnahan, H. L., and Helen D. Hill. 1962. Increased meiotic irregularities in inbred progenies of a *Festuca arundinacea* clone with apparent inversion herterozygosity. *Crop Sci., 2*:445-446.

Chatterji, Asoke K., and D. H. Timothy. 1969a. Microsporogenesis and embryogenesis in *Pennisetum flaccidum* Griseb. Crop Sci., *9*:219-222.

Chatterji, Asoke K., and D. H. Timothy. 1969b. Apomixis and tetraploidy in *Pennisetum orientale* Rich. Crop Sci., *9*:796-799.

Church, G. L. 1929a. Meiotic phenomena in certain Gramineae. I. Festuceae, Aveneae, Agrostideae, Chlorideae and Phalarideae. Bot. Gaz., *87*:608-629.

Church, G. L. 1929b. Meiotic phenomena in certain Gramineae. II. Paniceae and Andropogoneae. Bot. Gaz., *88*:63-84.

Crowder, L. V. 1953a. A survey of meiotic chromosome behavior in tall fescue grass. Amer. J. Bot., *40*:348-354.

Crowder, L. V. 1953b. Interspecific and intergeneric hybrids of *Festuca* and *Lolium*. J. Hered., *44*:195-203.

Evans, G. M., K. H. Asay, and R. G. Jenkins. 1973. Meiotic irregularities in hybrids between diverse genotypes of tall fescue (*Festuca arundinacea* Schreb.). Crop Sci., *13*:376-379.

Flovik, K. 1938. Cytological studies of Arctic grasses. Hereditas, *24*:265-376.

Haunold, A. 1968. Venetian turpentine as an aid in squashing and concomitant production of durable chromosome mounts. Stain Technol., *43*:153-156.

Jauhar, Prem P. 1975a. Chromosome relationships between *Lolium* and *Festuca* (Gramineae). Chromosoma, *52*:103-121.

Jauhar, Prem P. 1975b. Genetic regulation of diploid-like chromosome pairing in the hexaploid species, *Festuca arundinacea* Schreb. and *F. rubra* L. (Gramineae). Chromosoma, *52*:363-382.

Kempanna, C., and R. Riley. 1964. Secondary associations between genetically equivalent bivalents. Hered., *19*:289-299.
Lewis, E. J. 1963. Hybrids between geographical races of *Festuca arundinacea* Schreb. Rep. Welsh Pl. Breed. Sta., 1962, pp. 26-27.
Malik, C. P. 1967. Some abnormal bivalent types in *Festuca* hybrids. The Nucleus, *10*:174-178.
Malik, C. P. 1970. Pachytene studies in the intraspecific hybrid of *Festuca arundinacea* Schreb. Penet. Polon., *11*:379-383.
Malik, C. P., and P. T. Thomas. 1966. Chromosomal polymorphism in *Festuca arundinacea*. Chromosoma, 18:1-18.
Marshall, Harold G., and John W. Schmidt. 1954. A study of the meiotic stability of certain agrotricum hybrids. Agron. J., *46*:383-388.
Muntzing, A. 1937. The effects of chromosomal variation in *Dactylis*. Hereditas, *23*:113-235.
Myers, W. M. 1947. Cytology and genetics of forage grasses. Bot. Rev., *13*:318-421.
Myers, W. M., and Helen D. Hill. 1947. Distribution and nature of polyploidy in *Festuca elatior* L. Bull. Torrey Bot. Club, *74*:99-111.
Ostergren, G. 1940. Cytology of *Agropyron junceum, A. repens* and their spontaneous hybrids. Hereditas, *26*:305-316.
Ostergren, G. 1942. Chromosome numbers in *Anthoxanthum*. Hereditas, *28*:242-243.
Ostergren, G., and E. Vigfusson. 1953. On position correlations of univalents and quasi-bivalents formed by sticky chromosomes. Hereditas, *34*:33-50.
Parthasarathy, N. 1939. Cytogenetical studies in Oryzeae and Phalarideae. III. Cytological studies in Phalarideae. Ann. Bot., *3*:43-76.
Peto, F. H. 1933. The cytology of certain intergeneric hybrids between *Festuca* and *Lolium*. J. Genet., *28*:113-157.
Price, S. 1956. Cytological studies in *Saccharum* and allied genera. I. Syncytes in certain clones of *Saccharum* and *Erianthus*. Cytologia, *21*:21-37.
Rees, H., and P. J. Dale. 1974. Chiasmata and variability in *Lolium* and *Festuca* populations. Chromosoma, *47*:335-351.
Riley, R. 1960. The secondary pairing of bivalents with genetically similar chromosomes. Nature (Lond.), *185*:751-752.
Schertz, K. F., and R. P. Murphy. 1958. Fertility in relation to chromosome constitution and behavior in *Bromus inermis* Leyss. Agron. J., *50*:372-376.
Simonsen, Oystein. 1975. Cytogenetic investigations in diploid and autotetraploid populations of *Festuca pratensis*. Hereditas, *79*:73-103.
Subhanij, T. 1974. The heritability of agronomic characteristics in tall fescue (*Festuca arundinacea* Schreb.). Ph.D. thesis, Oregon State University.
Thomas, P. T., and Hugh Thomas. 1973. Grass cytogenetics. Rep. Welsh Pl. Breed. Sta., 1972, pp. 85-86.
Tinney, F. W. 1936. Chromosome behavior in *Agrostis nebulosa*. Bot. Gaz., *97*:822-833.
Walters, M. S. 1954. A study of pseudobivalents in meiosis of two interspecific hybrids of *Bromus*. Amer. J. Bot., *41*: 160-171.
Wilson, G. 1945. The venetian turpentine mounting medium. Stain. Technol., *20*:133-135.

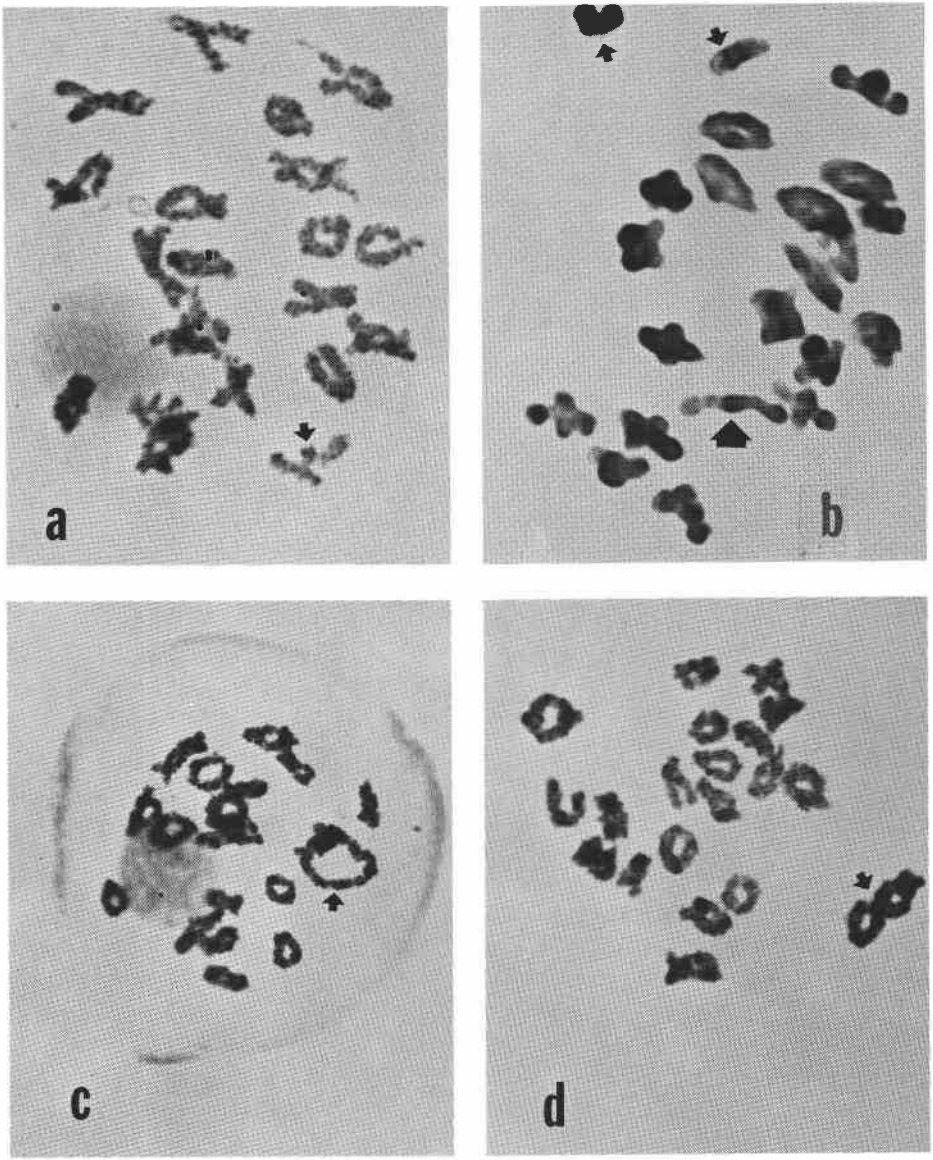

Figure 1. (a) Diakinesis of the Fawn II parent with an asynaptic pair of chromosomes, and an association of two groups of two bivalents (arrow). (b) Metaphase I of the Fawn II parent with two univalents (sm. arrows) possibly resulting from the asynaptic pair at diakinesis, a rod bivalent (lg. arrow) possibly resulting from the incomplete pairing at diakinesis, and two groups of two associated bivalents. (c) Diakinesis of the Fawn III parent with a ring of four chromosomes (arrow). (d) Diakinesis of the Fawn III parent with a figure-eight quadrivalent (arrow).

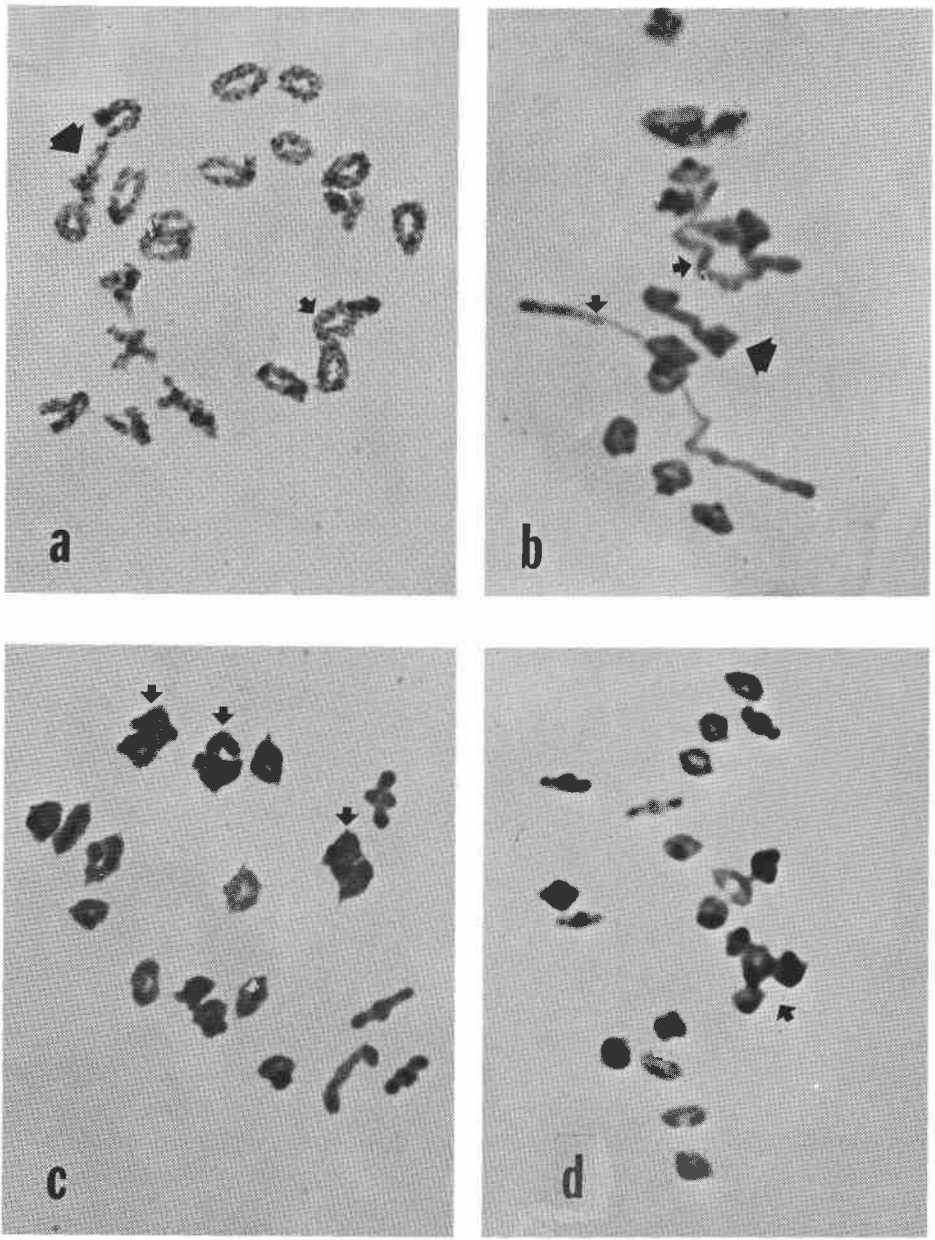

Figure 2. Fawn III parent. (a) Diakinesis with a hexavalent (lg. arrow) and a quadrivalent (sm. arrow). (b) Metaphase I with a hexavalent (lg. arrow) and two chain quadrivalents (sm. arrows). (c) Metaphase I with three groups of two associated bivalents (arrows). (d) Metaphase I with four associated bivalents (arrow).

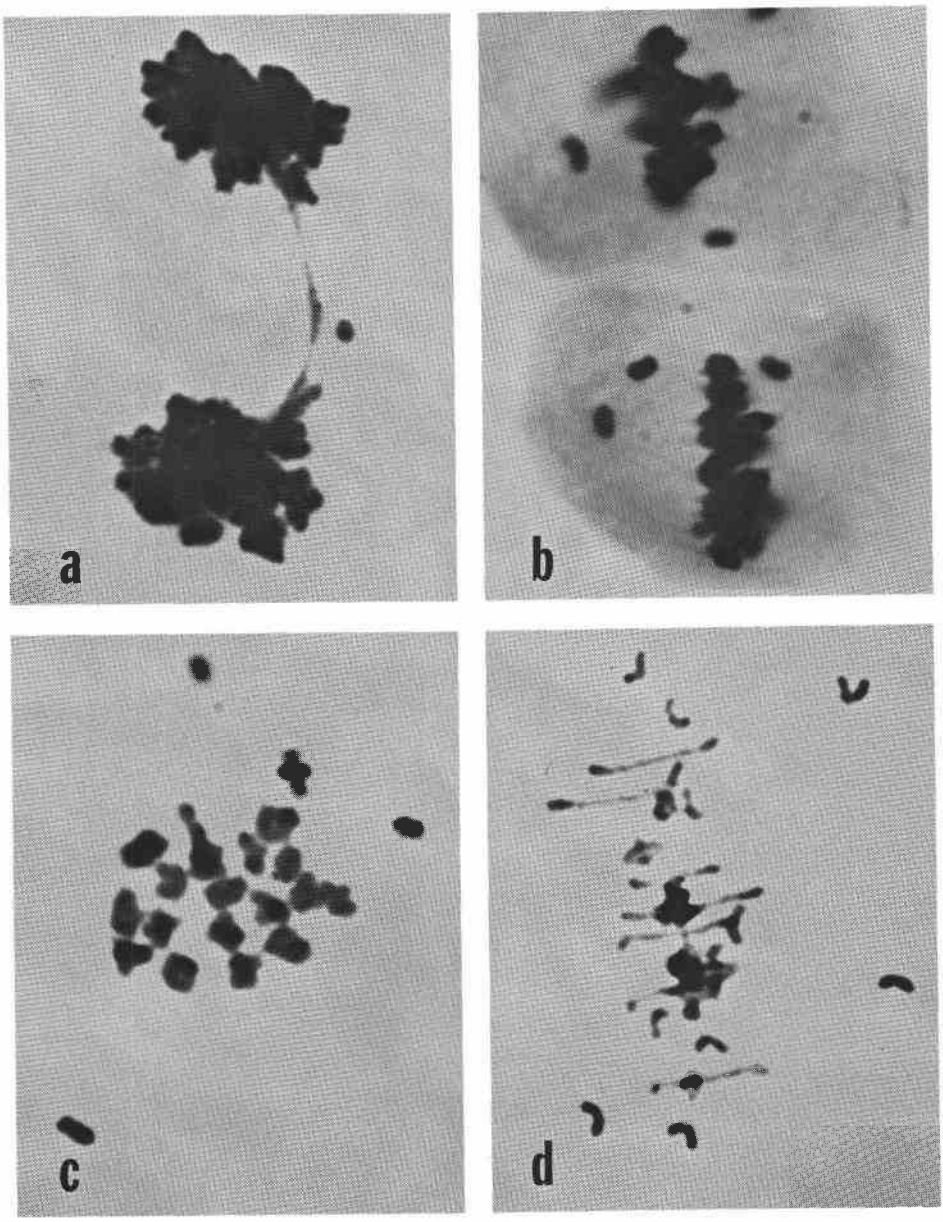

Figure 3. (a) Late anaphase I with a dicentric bridge and an accompanying fragment. (b) Monosomic Fortune II parent with two metaphase I cells showing three univalents off the plate. (c) Metaphase I of the Fortune II parent with three univalents off the plate and secondary associations of bivalents. (d) Metaphase I of the Fortune II parent with univalents and open bivalents.

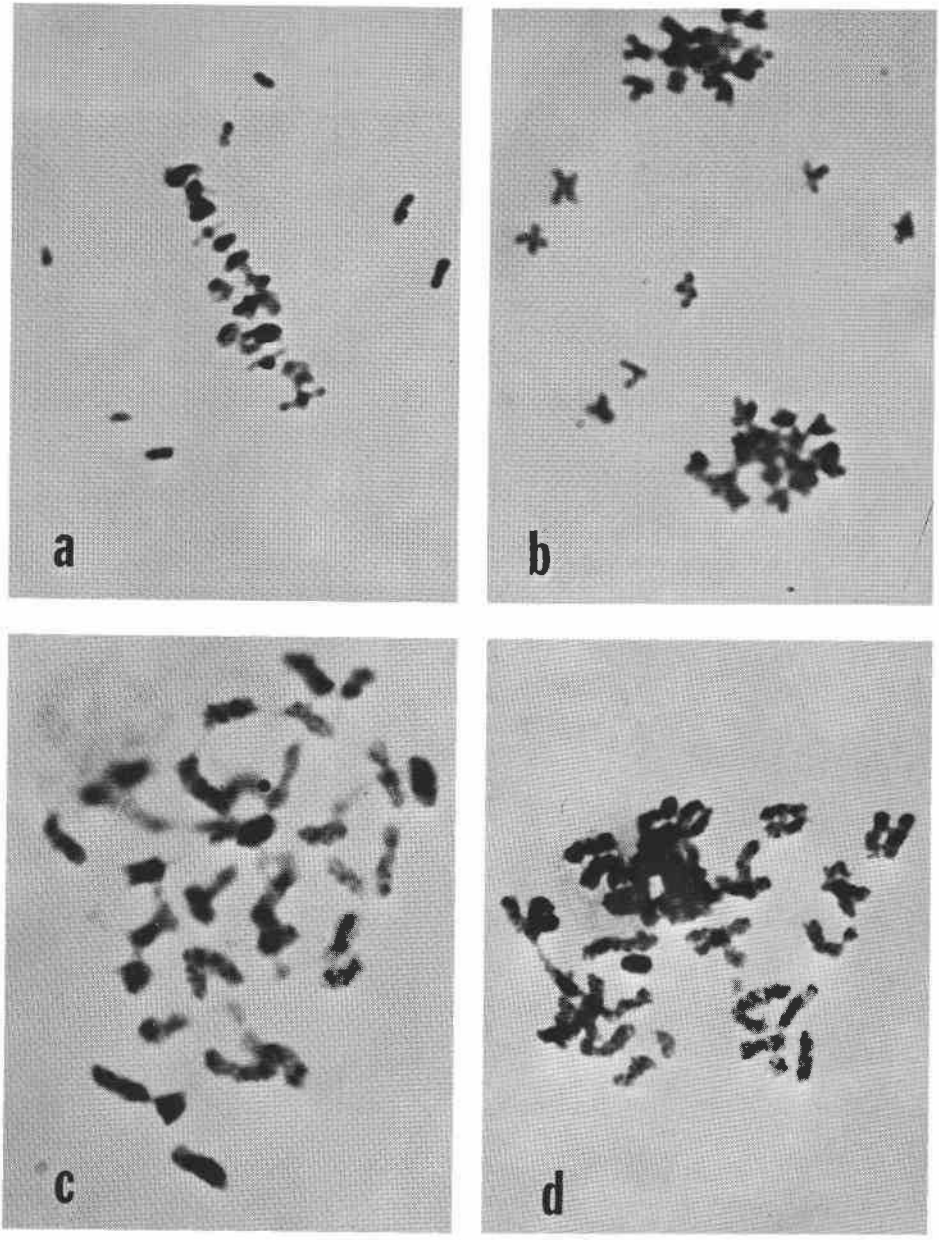

Figure 4. (a) Fortune II parent with seven univalents off of the metaphase I plate. (b) Anaphase I of the Fortune II parent showing seven dyad laggards resulting from seven univalents such as found in Fig. a. (c, d) Diakinesis of the Fawn I parent showing asynapsis and secondary pairing among chromosomes.

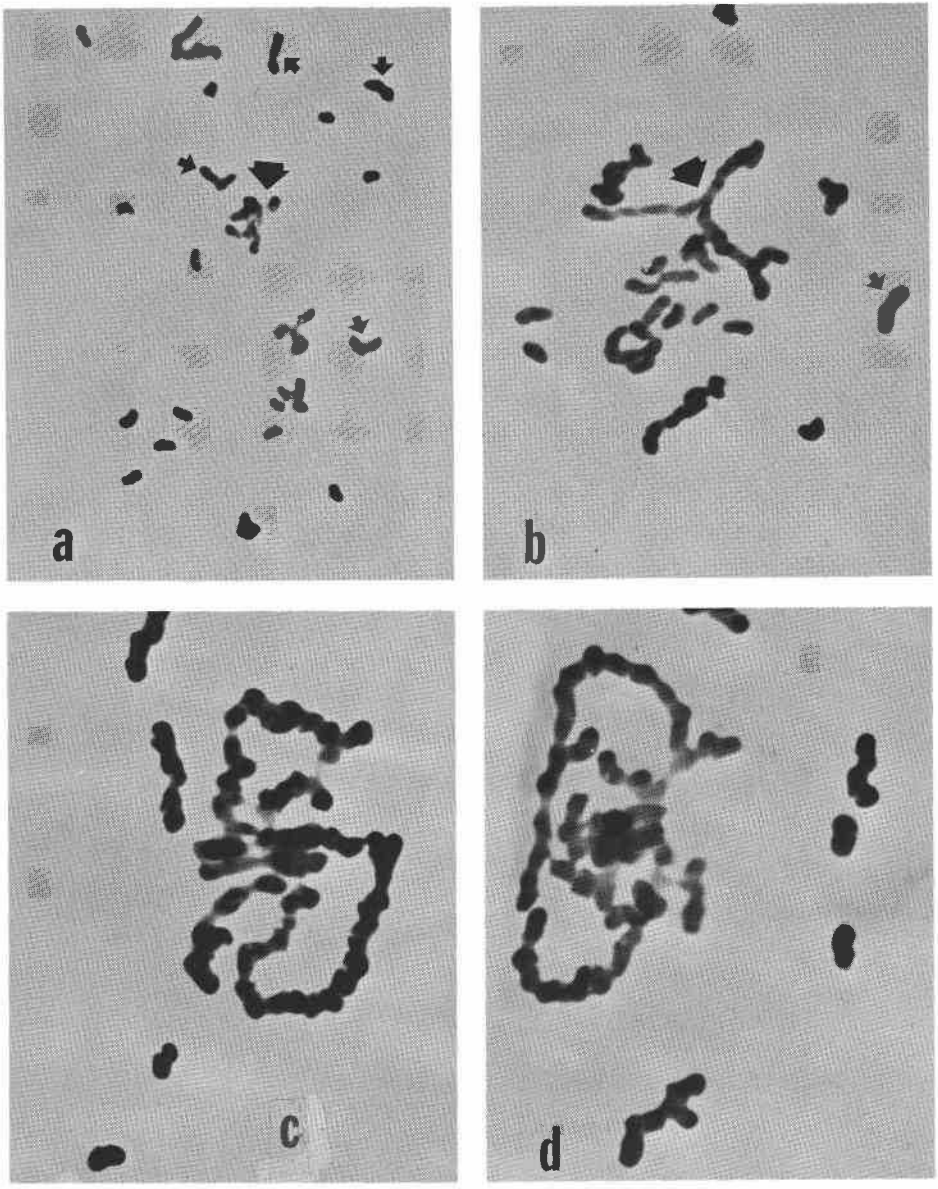

Figure 5. Late diakinesis of the Fawn I parent. (a,b) Univalents, pseudobivalents (sm. arrows), and pseudomultivalents (lg. arrows) showing secondary pairing. (c) Two univalents, two pseudobivalents, and one large pseudomultivalent with secondary pairing. (d) Two univalents, two pseudobivalents, with end-to-end and end-to-side pairing, one pseudoquadrivalent, with side-to-side pairing, and one large pseudomultivalent.

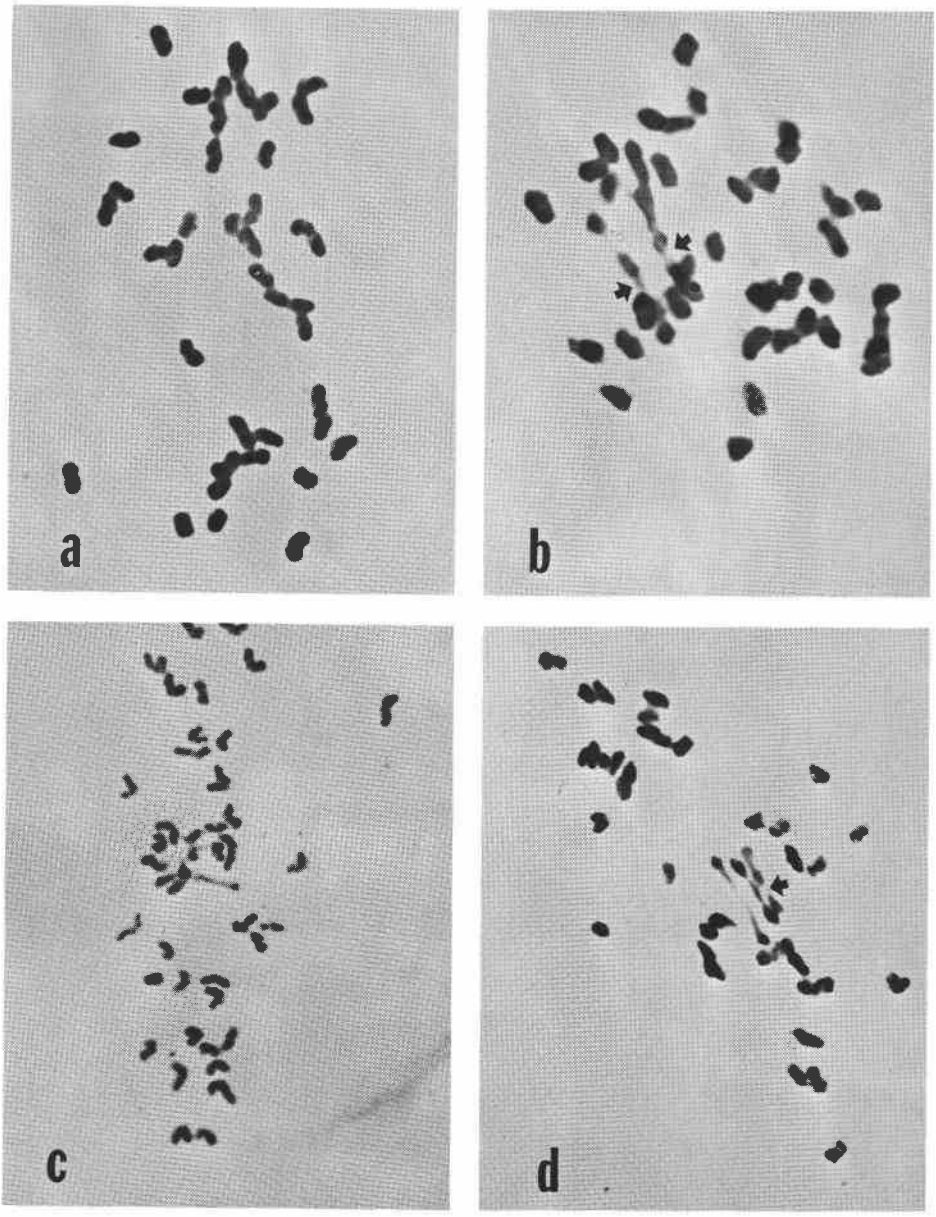

Figure 6. Metaphase I of the Fawn I parent. (a) Univalents, pseudobivalents, and pseudomultivalents situated randomly between the poles. (b) Elongated rod-shaped bivalents with thin regions (arrows). (c) Mostly univalents on the equatorial plate. (d) Bivalents with thin regions situated between the chiasma and the centromeres (arrow).

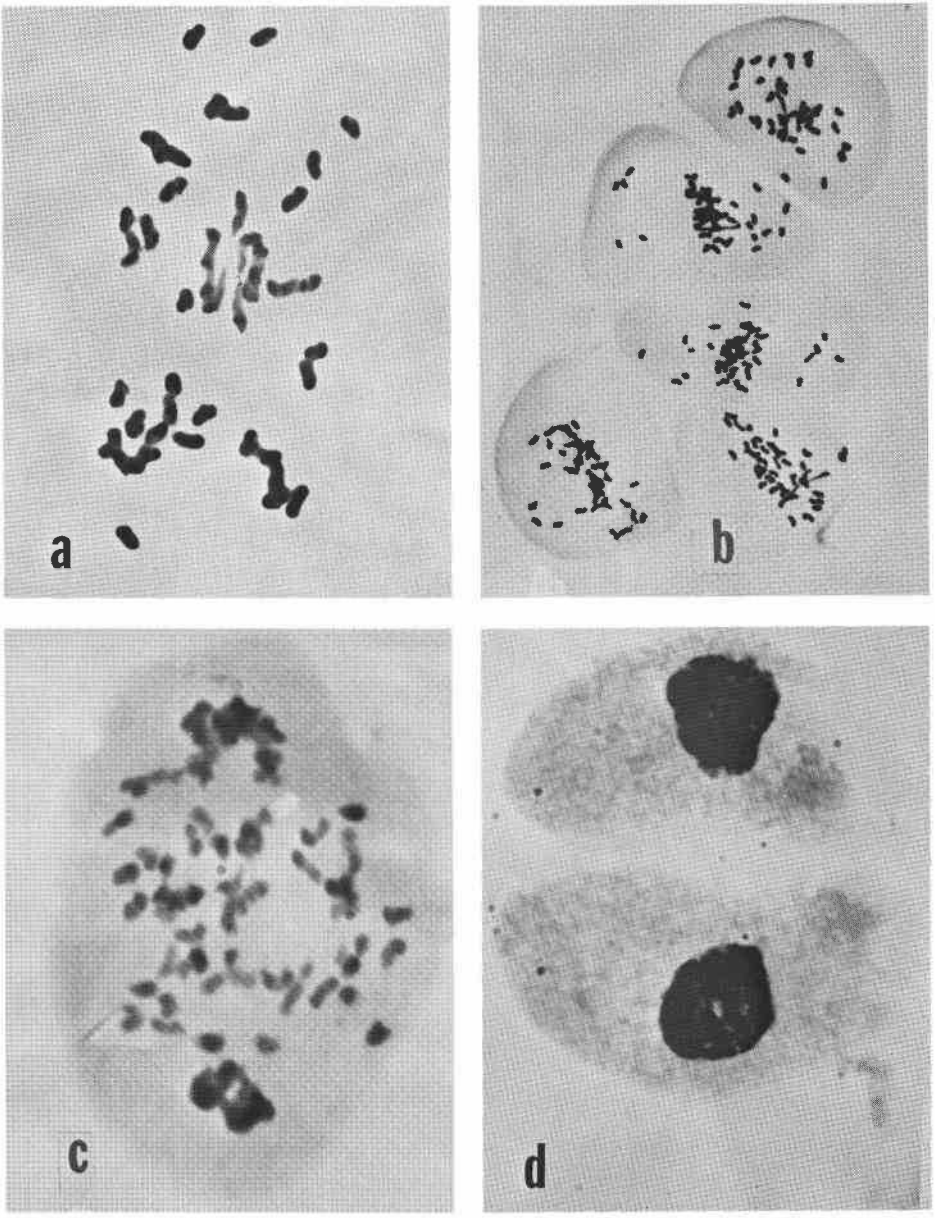

Figure 7. Fawn I parent. (a) Metaphase I with univalents, pseudobivalents, and pseudomultivalents distributed randomly in the cell, and four elongated rod bivalents with thin regions on the plate. (b) Five metaphase I cells with univalents on and off the equatorial plate. (c) Anaphase I with lagging and misdividing chromosomes. (d) Telophase I with no micronuclei.

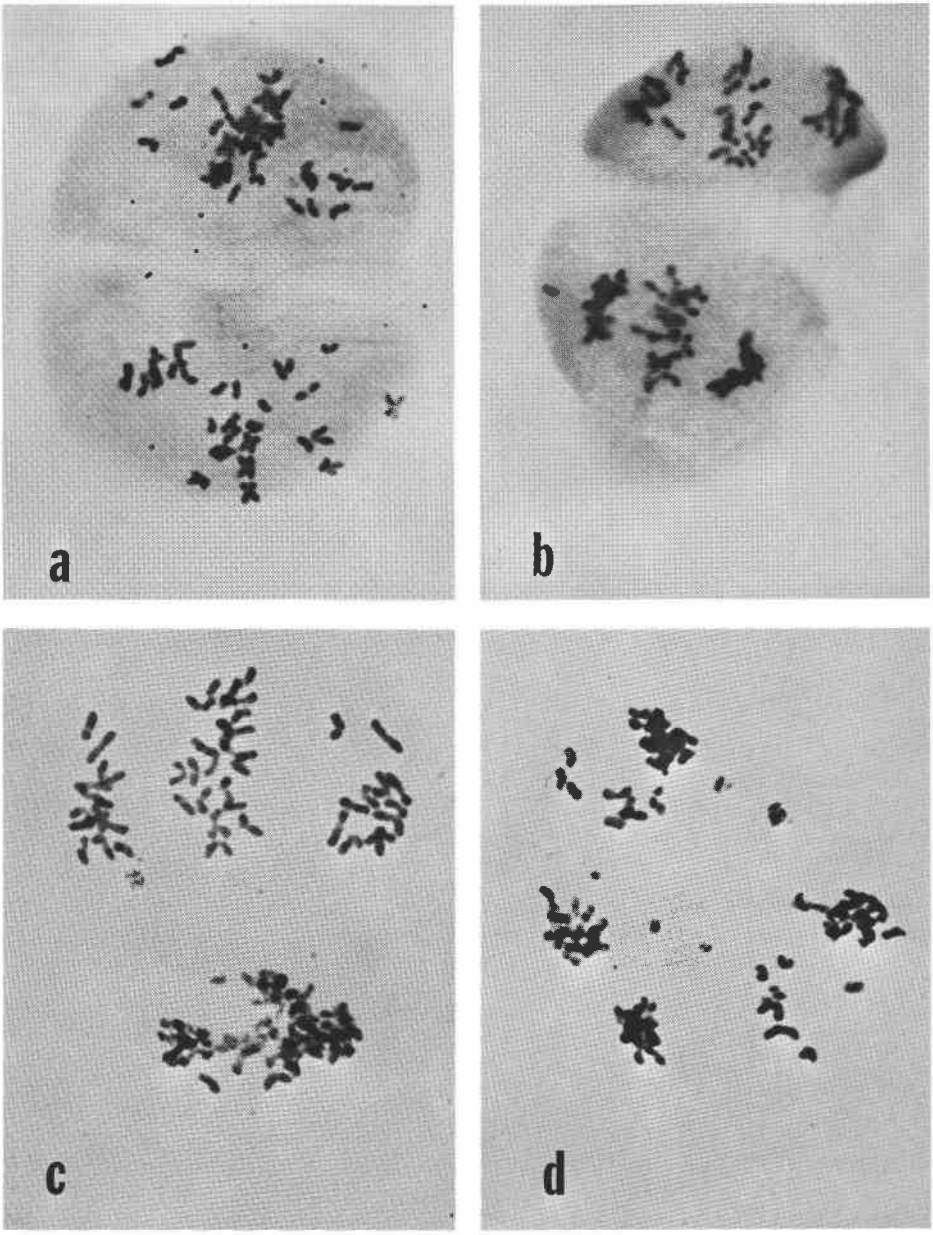

Figure 8. Fawn I parent. (a) Metaphase II with univalent monads and dyads on and off the plate. (b) Anaphase II with laggards left on the plate. (c) Anaphase II with laggards and chromosome clumping forming a nuclear bridge. (d) Migration of chromosomes to poles with no cytokinesis.

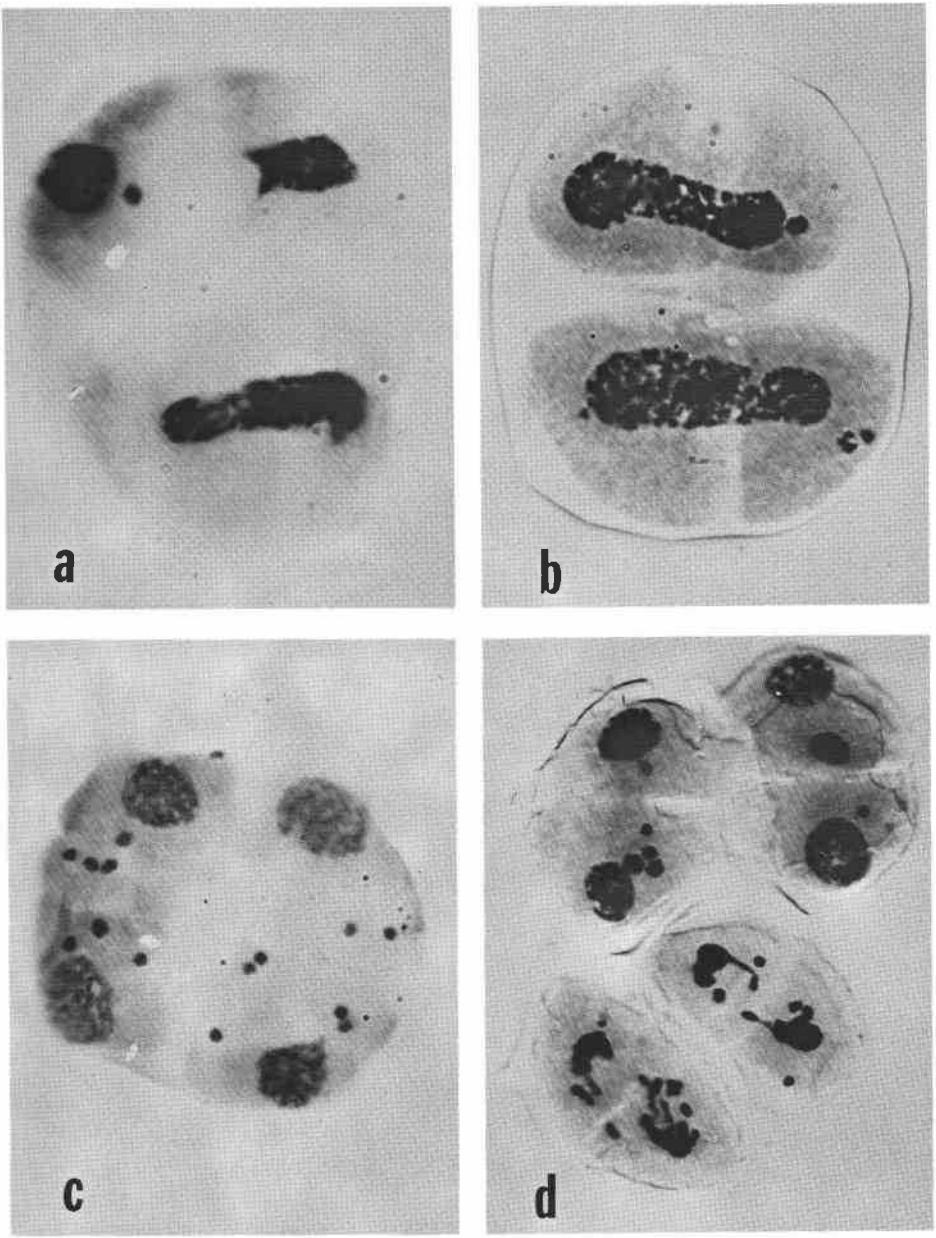

Figure 9. Fawn I parent. (a) Quartet with nuclear bridge as a result of numerous laggards clumping together at anaphase II. (b) Quartet with two bridges. (c) Quartet with individual micronuclei. (d) Two quartets with multilaggard micronuclei.

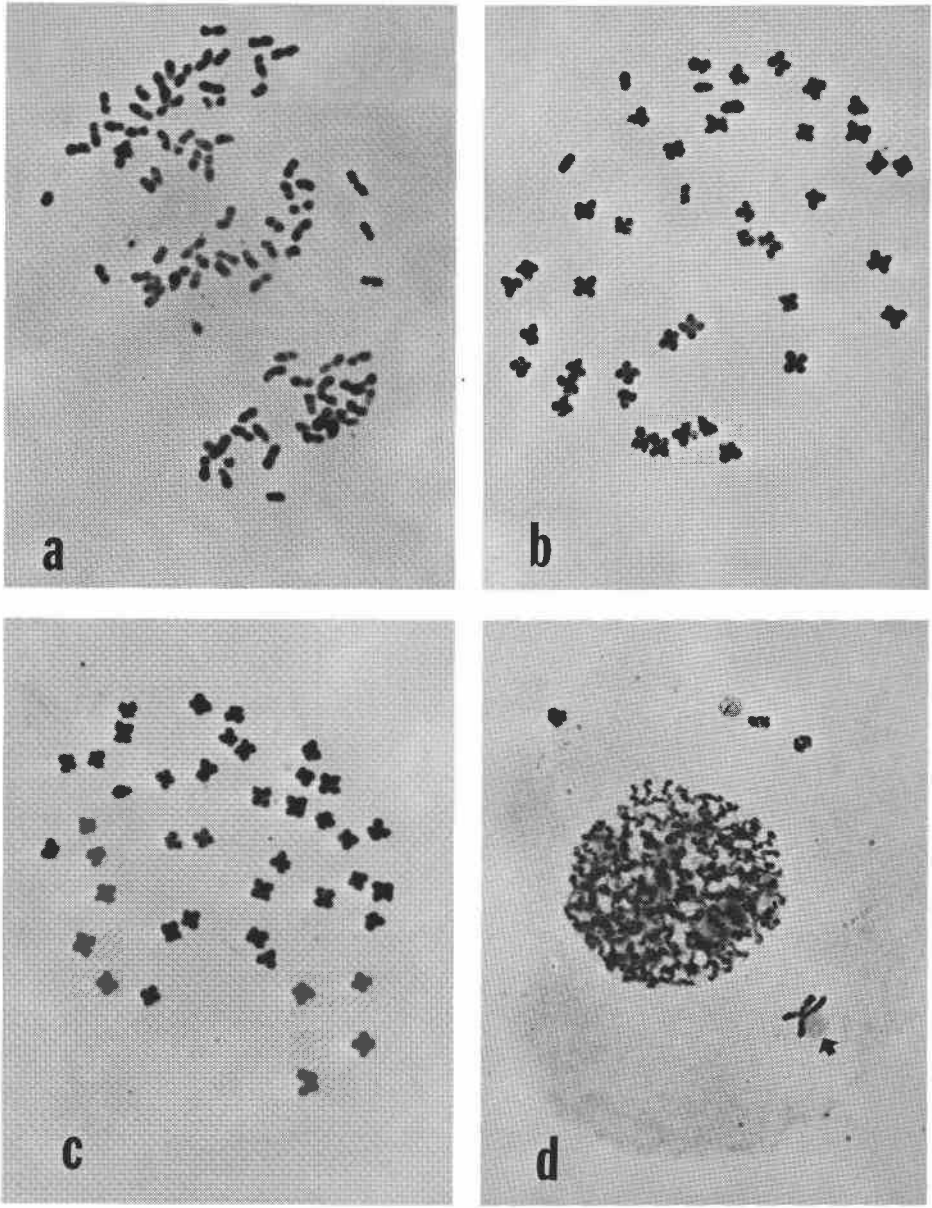

Figure 10. Fawn I parent. (a) Chromatids migrating in an anaphase I fashion. (b,c) X-shaped chromosomes with no polar orientation found at metaphase II of meiosis. The cell is similar to metaphase of mitosis. (d) Giant cell at prophase with chromosome laggards in the cytoplasm. Note the x chromosome with the attached nucleolus (arrow).

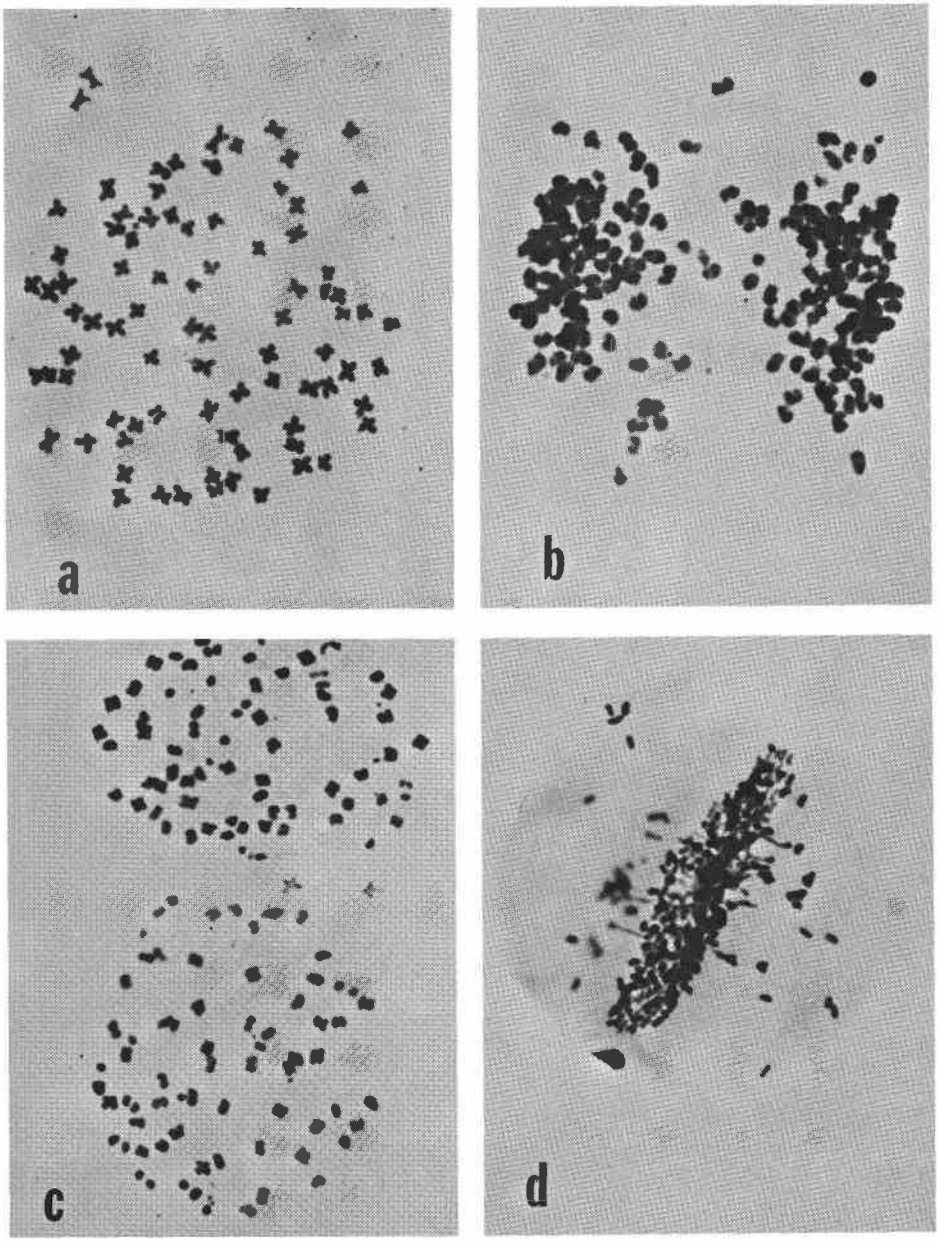

Figure 11. Fawn I parent. (a) Giant cell with 2n = 84 chromosomes. (b) Giant cell at anaphase with 84 chromosomes moving towards each pole. (c) Giant cell with no cytokinesis which resulted after an anaphase division. (d) Giant cell at metaphase.

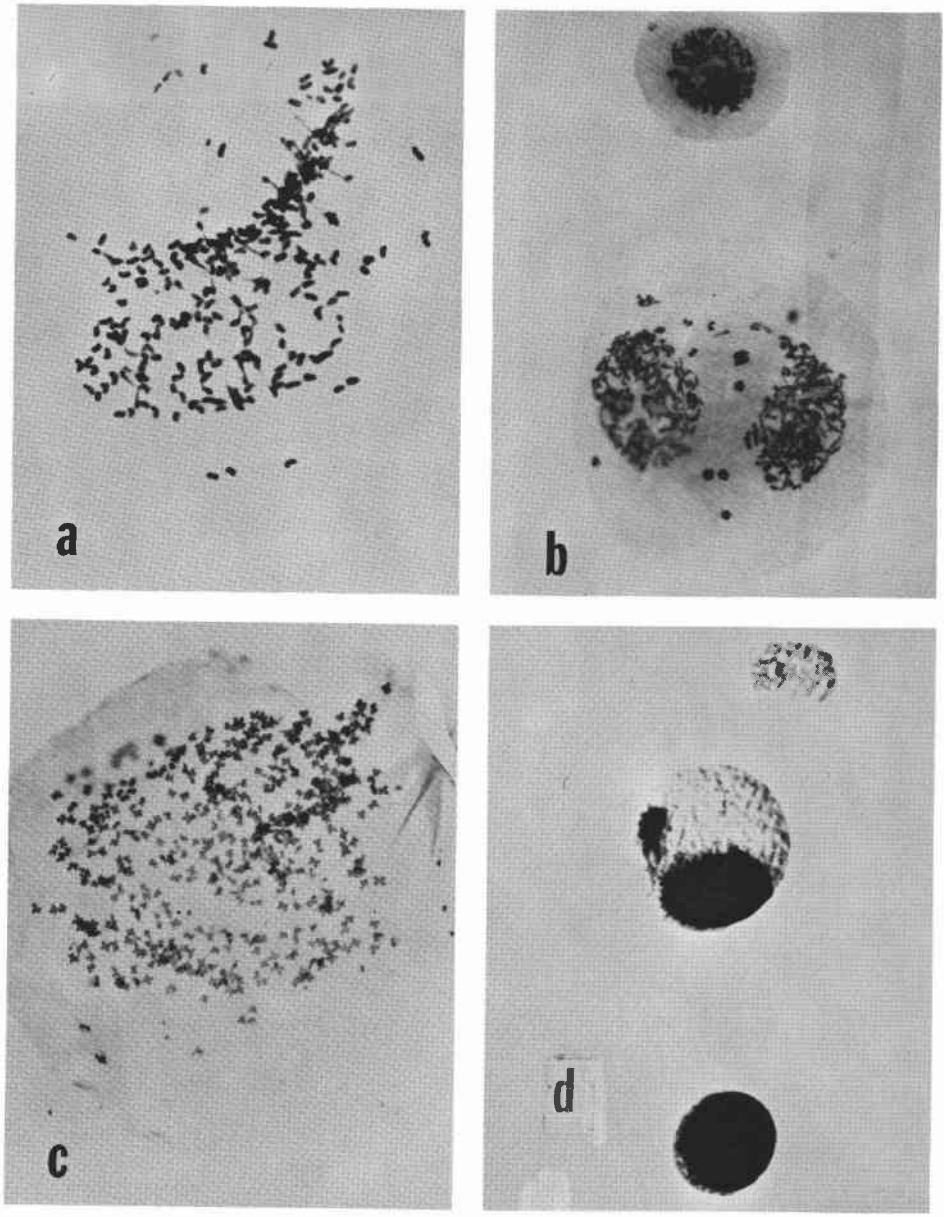

Figure 12. Fawn I parent. (a) Giant cell at metaphase with chromosomes showing secondary associations. (b) Comparison of two giant cells. The smaller one has doubled and the larger one possibly quadrupled after an anaphase division with no cytokinesis. (c) Giant cell which is estimated to have 336 chromosomes. (d) Large pollen grain which resulted from giant cells through endomitosis.

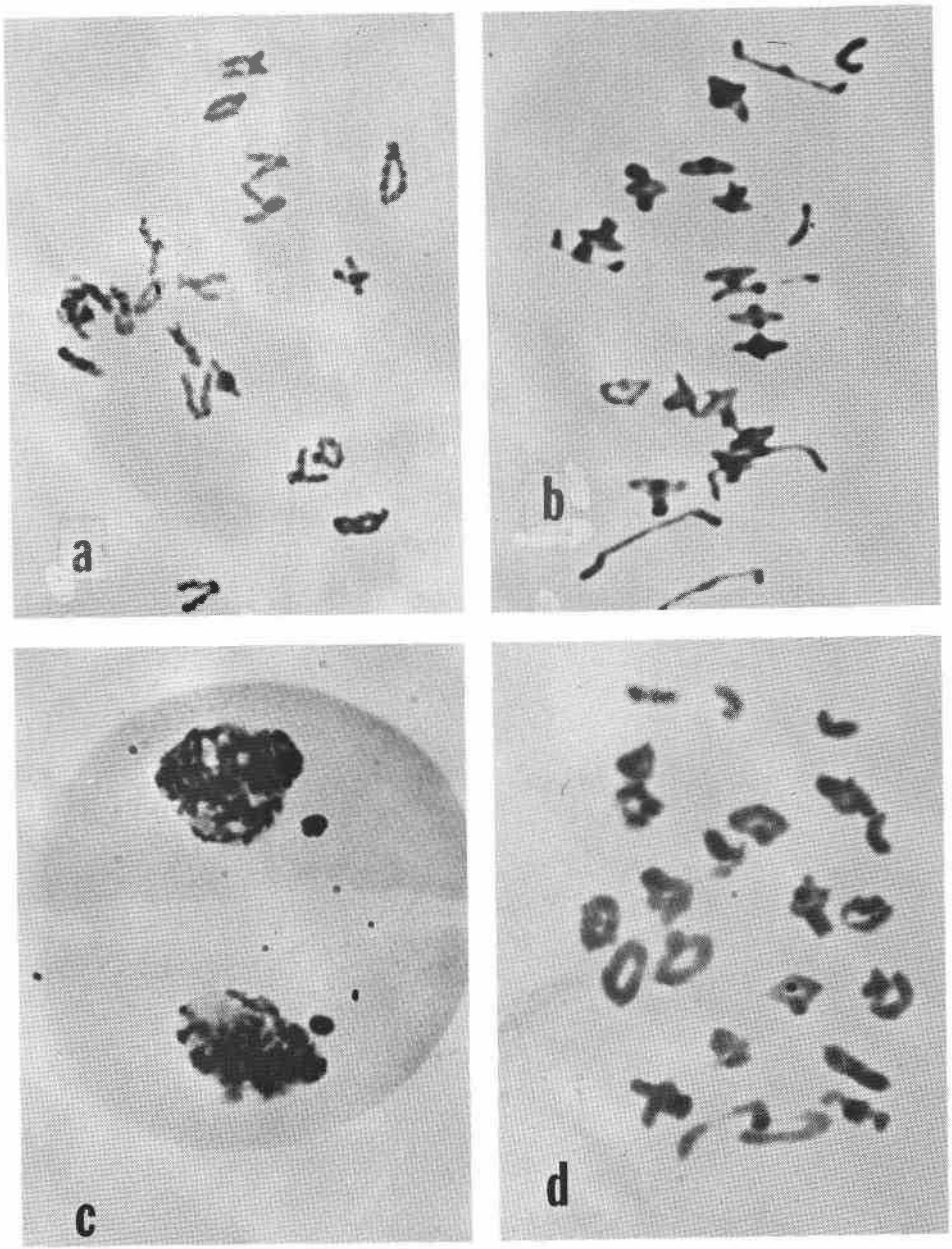

Figure 13. Fawn I x Fortune II hybrids. (a) Hybrid 3 at diakinesis with incomplete pairing of chromosomes. (b) Hybrid 3. Metaphase I with six rod bivalents and two univalents. (c) Hybrid 3. Telophase I with two micronuclei. (d) Hybrid 8. Late diakinesis with four univalents.

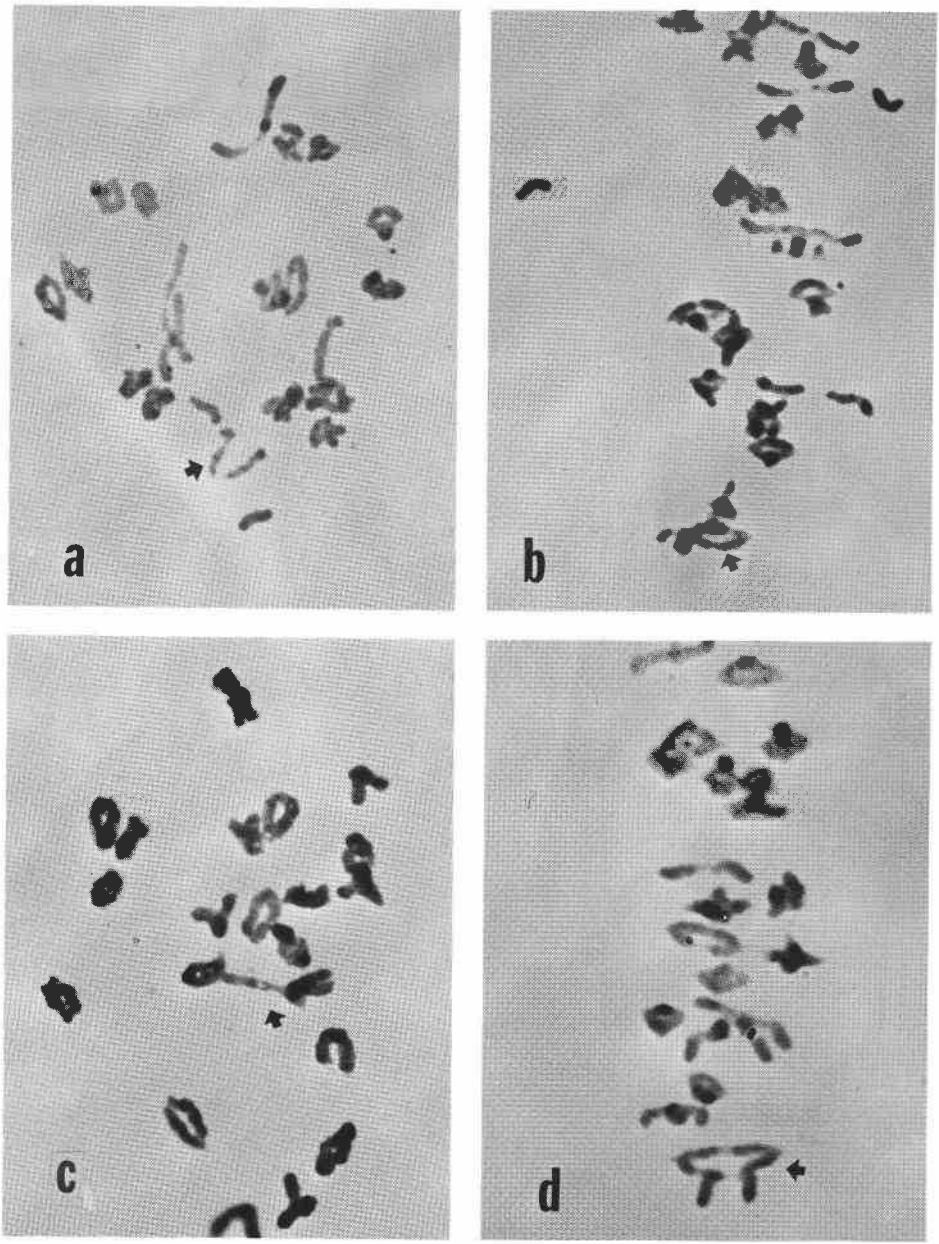

Figure 14. Fawn I x Fortune II hybrid 8. (a) Diakinesis with a trivalent (arrow). (b) Metaphase I with rod bivalents, two univalents, and a quadrivalent (arrow). (c) Diakinesis with a quadrivalent (arrow). (d) Metaphase I with a quadrivalent (arrow).

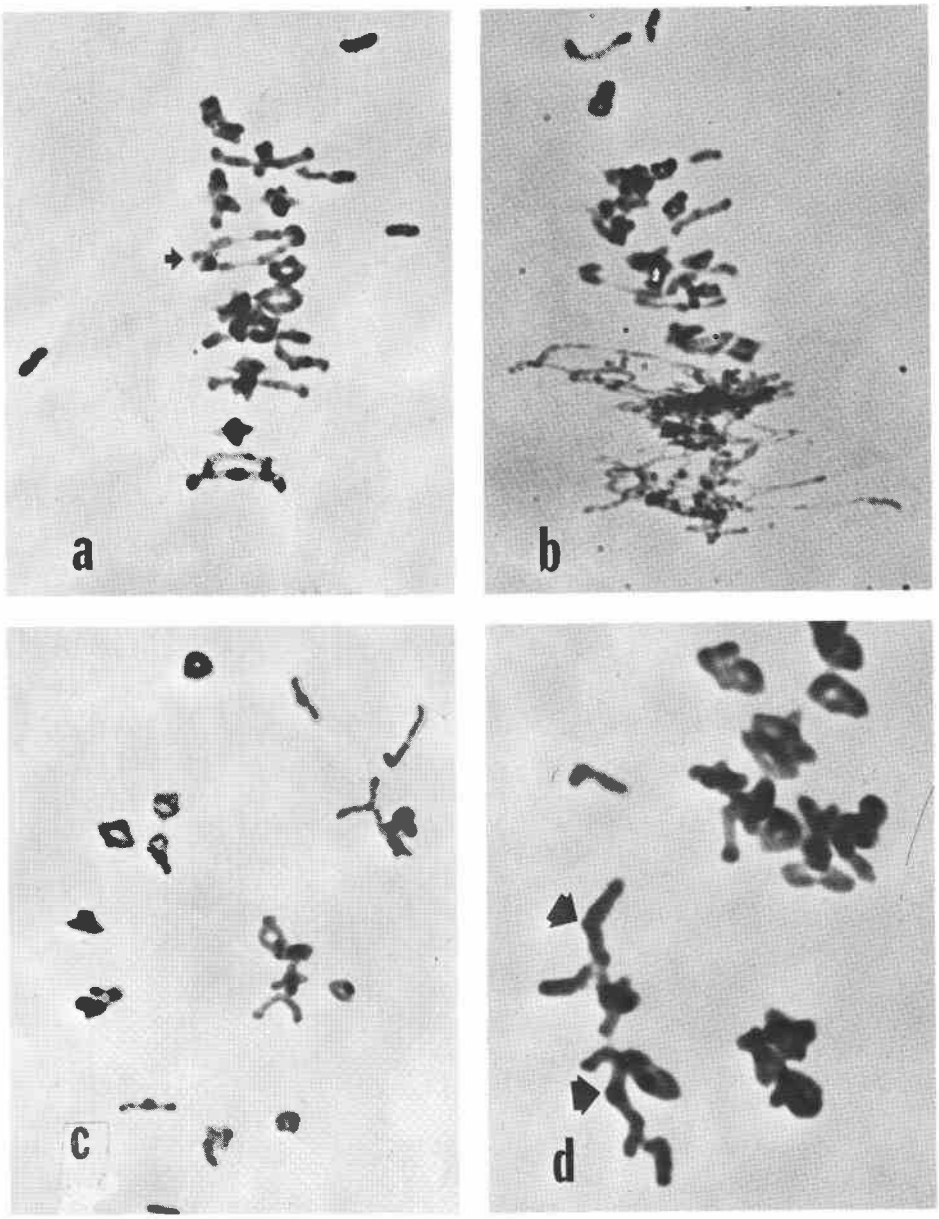

Figure 15. Fawn I x Fortune II. (a) Hybrid 8. Metaphase I with univalents and a quadrivalent (arrow). (b) Hybrid 8. Metaphase I with association and misdivision of chromosomes. (c) Hybrid 9. Late diakinesis showing open bivalents and two univalents. (d) Hybrid 9. Metaphase I with secondary affinity of bivalents and two trivalents (arrows).

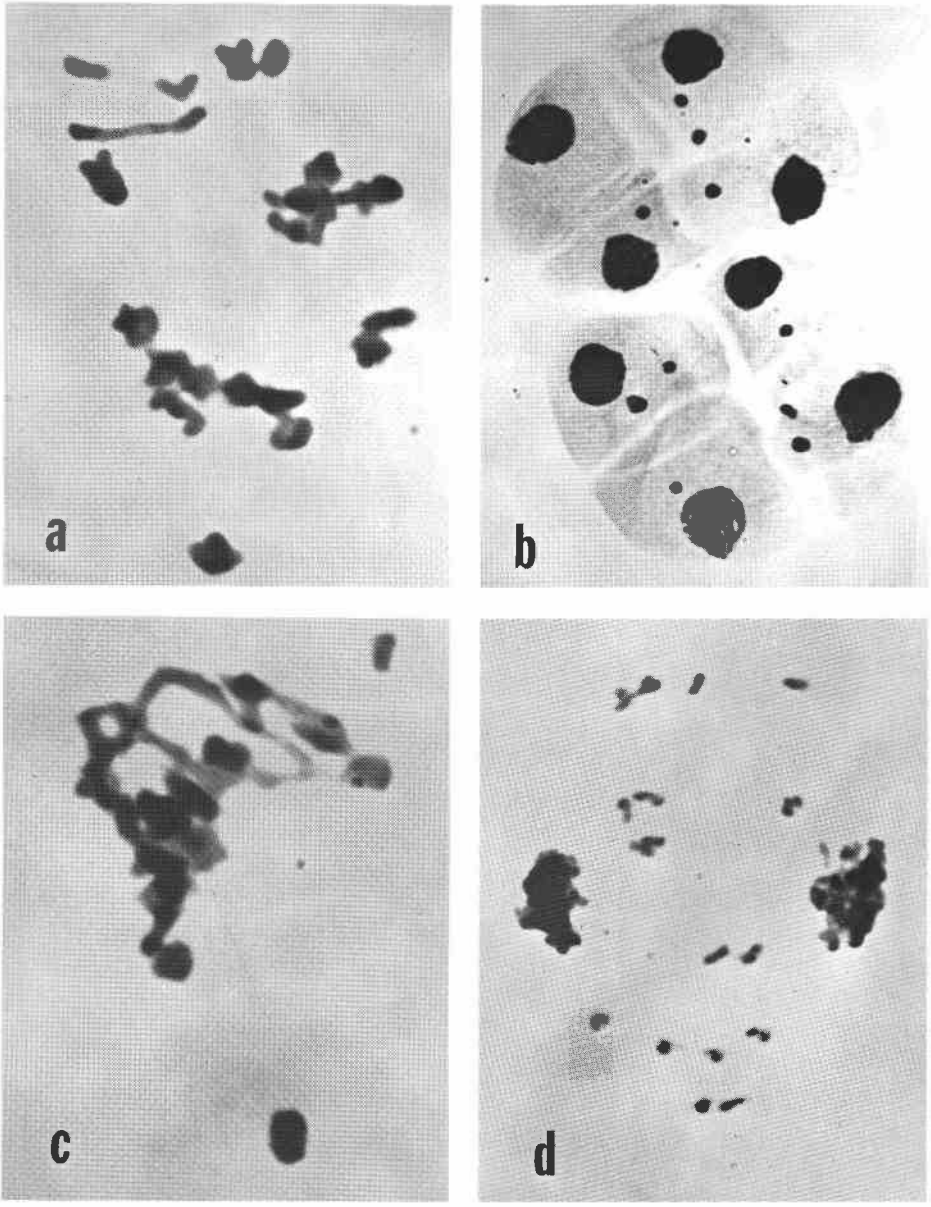

Figure 16. (a) Fawn I x Fortune II hybrid 9. Metaphase I with one group of seven, one group of six, and two groups of two secondarily associated bivalents. (b) Fawn I x Fortune II hybrid 9. Two quartets with micronuclei. (c) Fawn II x Fortune II hybrid 3. Metaphase I with association and clumping of chromosomes. (d) Fawn II x Fortune II hybrid 3. Anaphase I with dividing univalents.

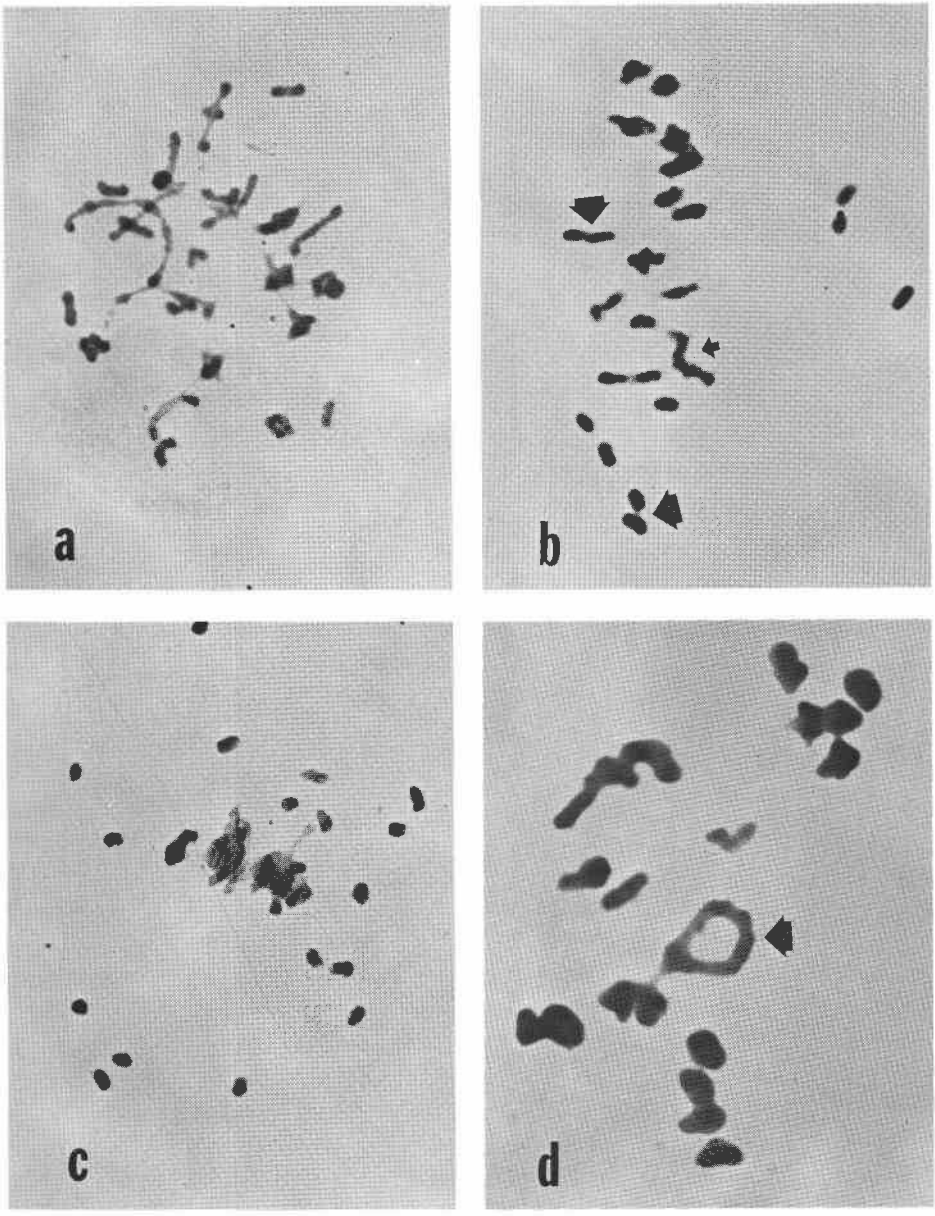

Figure 17. Fawn II x Fortune II. (a) Hybrid 5. Diakinesis with association among chromosomes and matrix connections. (b) Hybrid 5. Metaphase I with a hexavalent (sm. arrow) and pseudobivalents (lg. arrow). (c) Hybrid 5. Metaphase I with 17 univalents off the plate. (d) Hybrid 10. Metaphase I with a ring quadrivalent (arrow) and secondary affinity among bivalents.

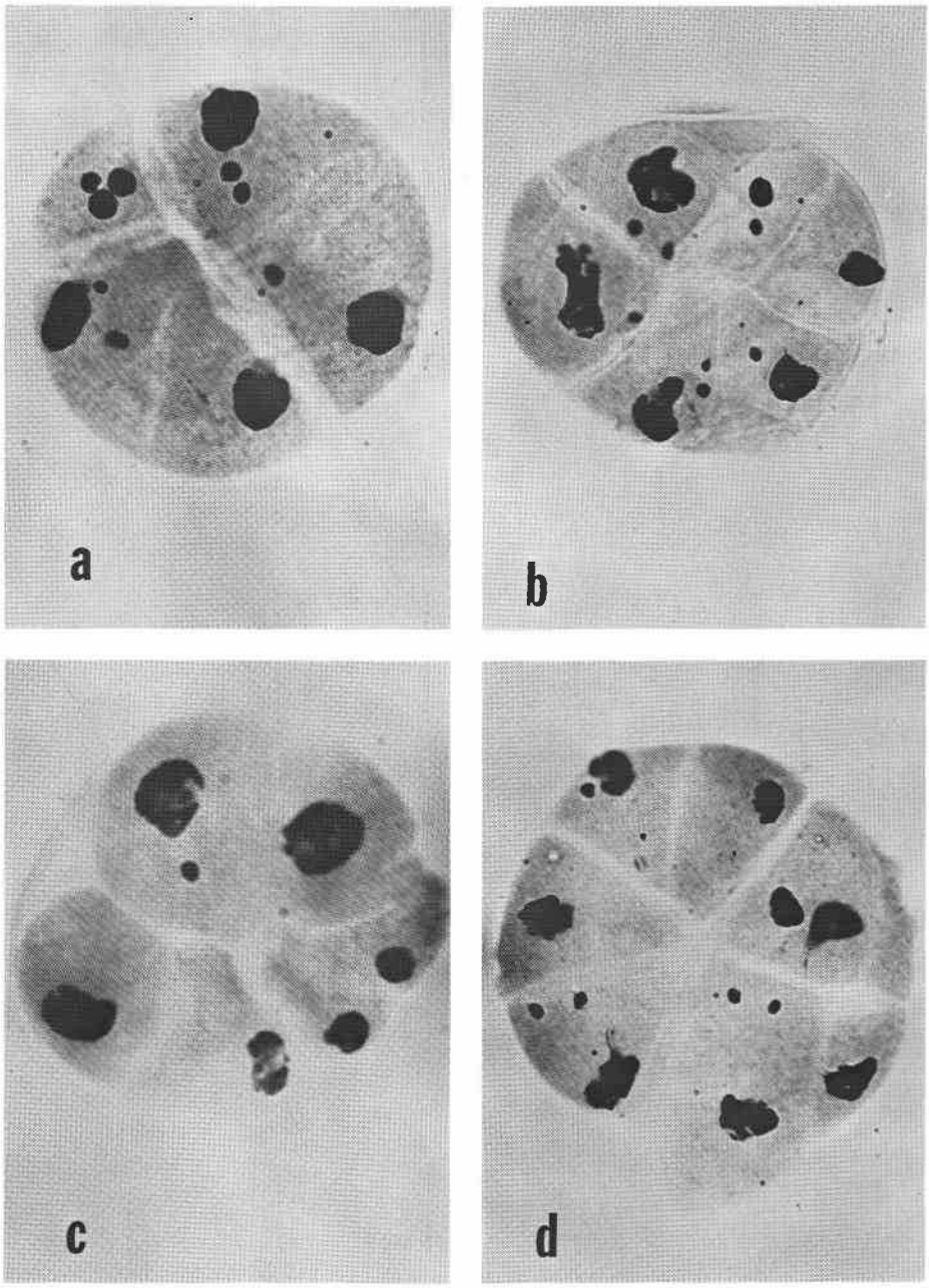

Figure 18. Fawn II x Fortune III hybrid 1. (a-d) Polyspory in the quartets which formed five, six, or seven microspores.

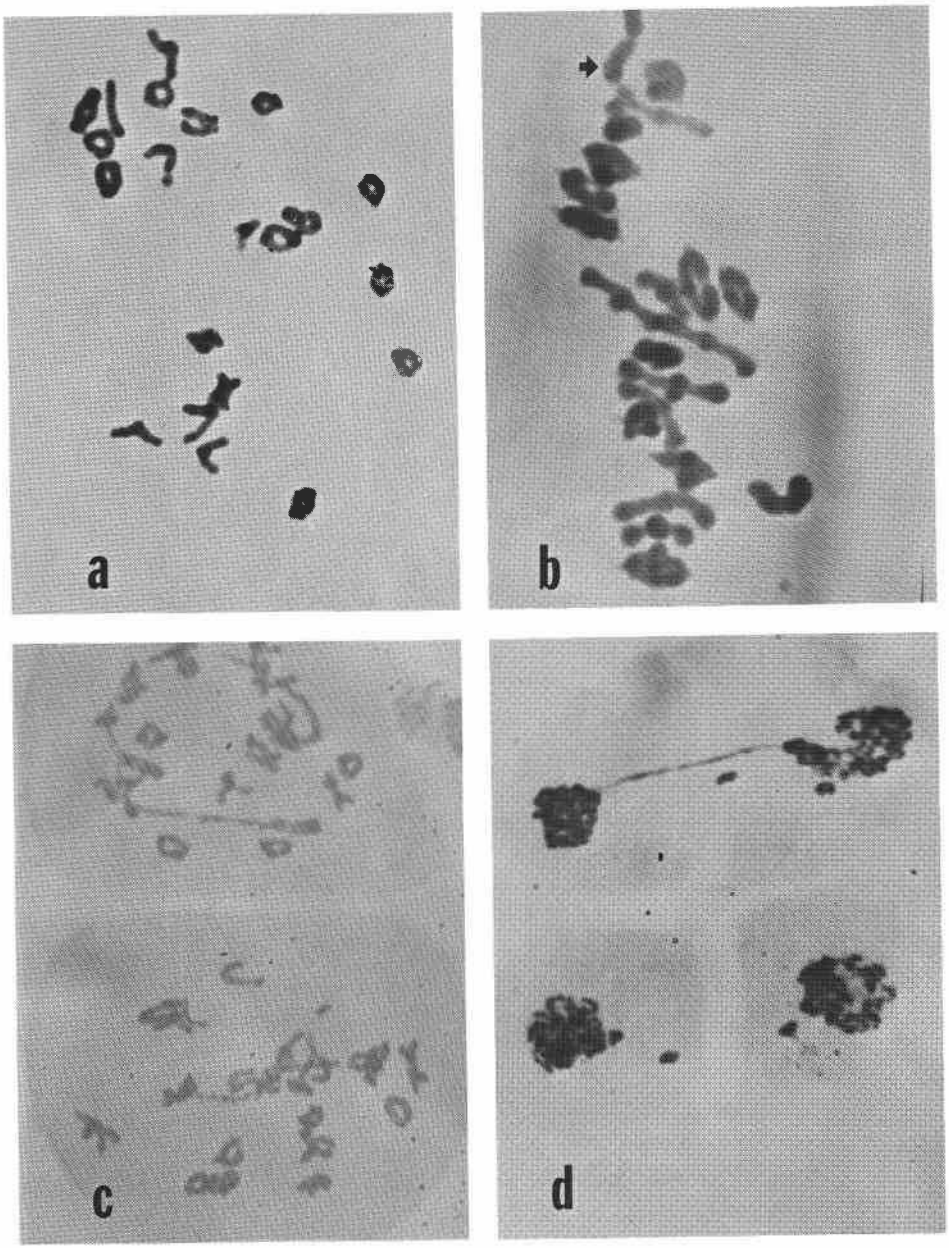

Figure 19. (a) Fawn II x Fortune III hybrid 8. Late diakinesis with bivalent pairing. (b) Fawn II x Fortune III hybrid 8. Metaphase I with a chain-type quadrivalent (arrow). (c) Fawn III x Fortune I hybrid 1. Two diakinesis cells with association among chromosomes. (d) Fawn III x Fortune I hybrid 1. Quartet with a bridge.

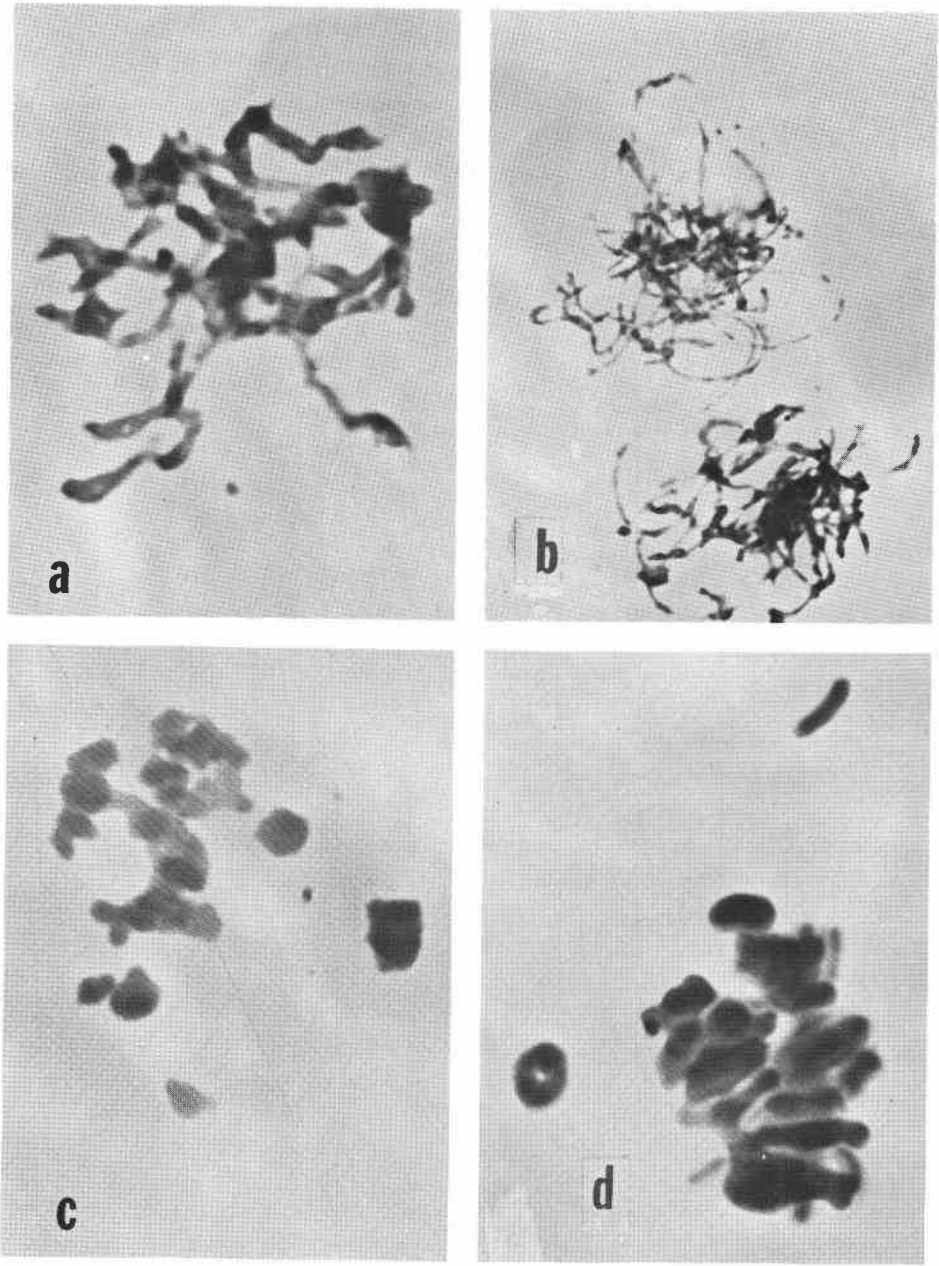

Figure 20. Fawn III x Fortune I hybrid 2. (a,b) Association of chromosomes which are condensed enough to be at metaphase I, but maintain a pachytene configuration. (c,d) Metaphase I with association and clumping of chromosomes.

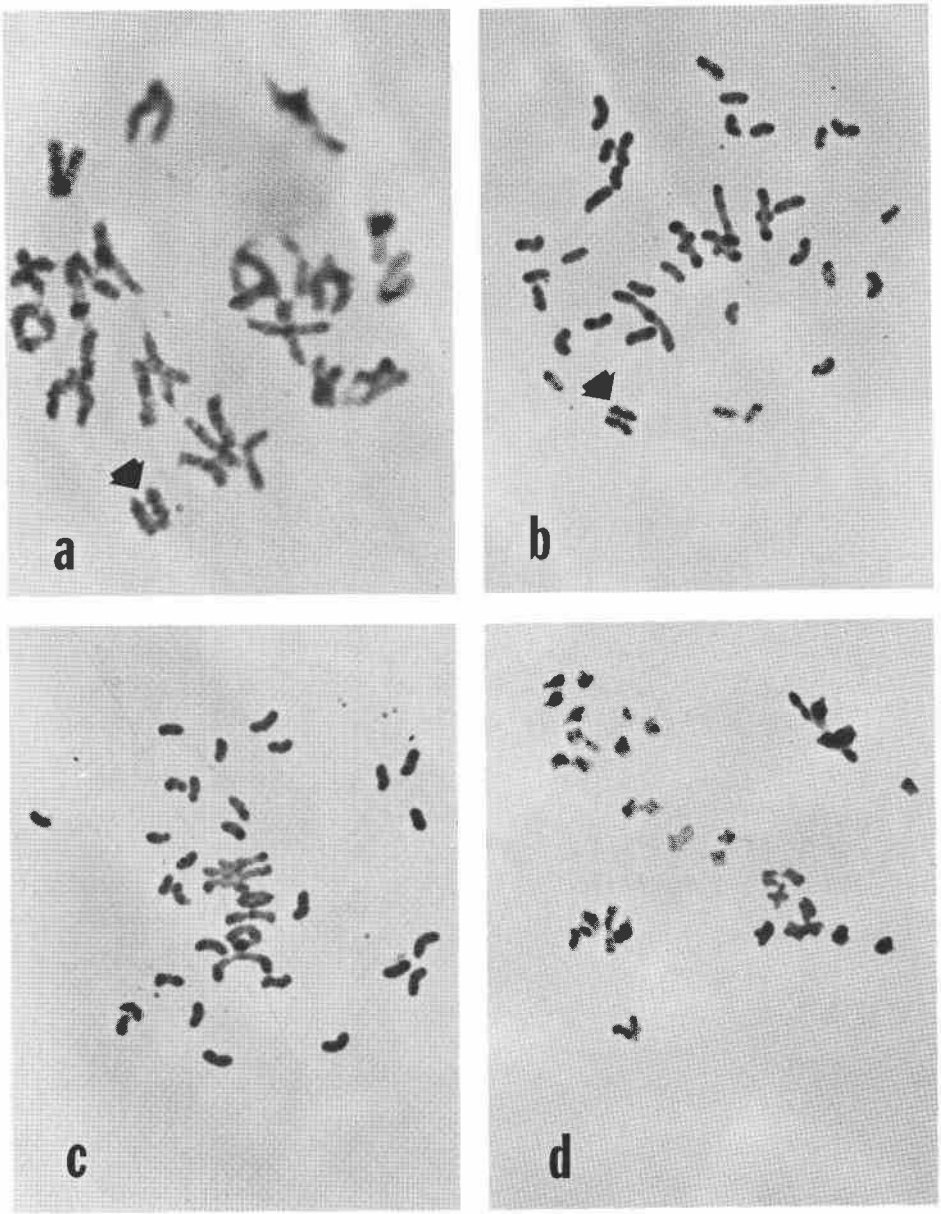

Figure 21. Fawn III x Fortune II hybrid 1. (a) Diakinesis with univalents either singular or secondarily attracted. Note the side-to-side secondary pairing (arrow). (b) Metaphase I with 5_{II} + 32_{I}. Note side-to-side secondary pairing (arrow). (c) Metaphase I with 7_{II} + 28_{I}. Univalents are lagging off the plate. (d) Anaphase I with 24 dyad and 2 monad laggards.

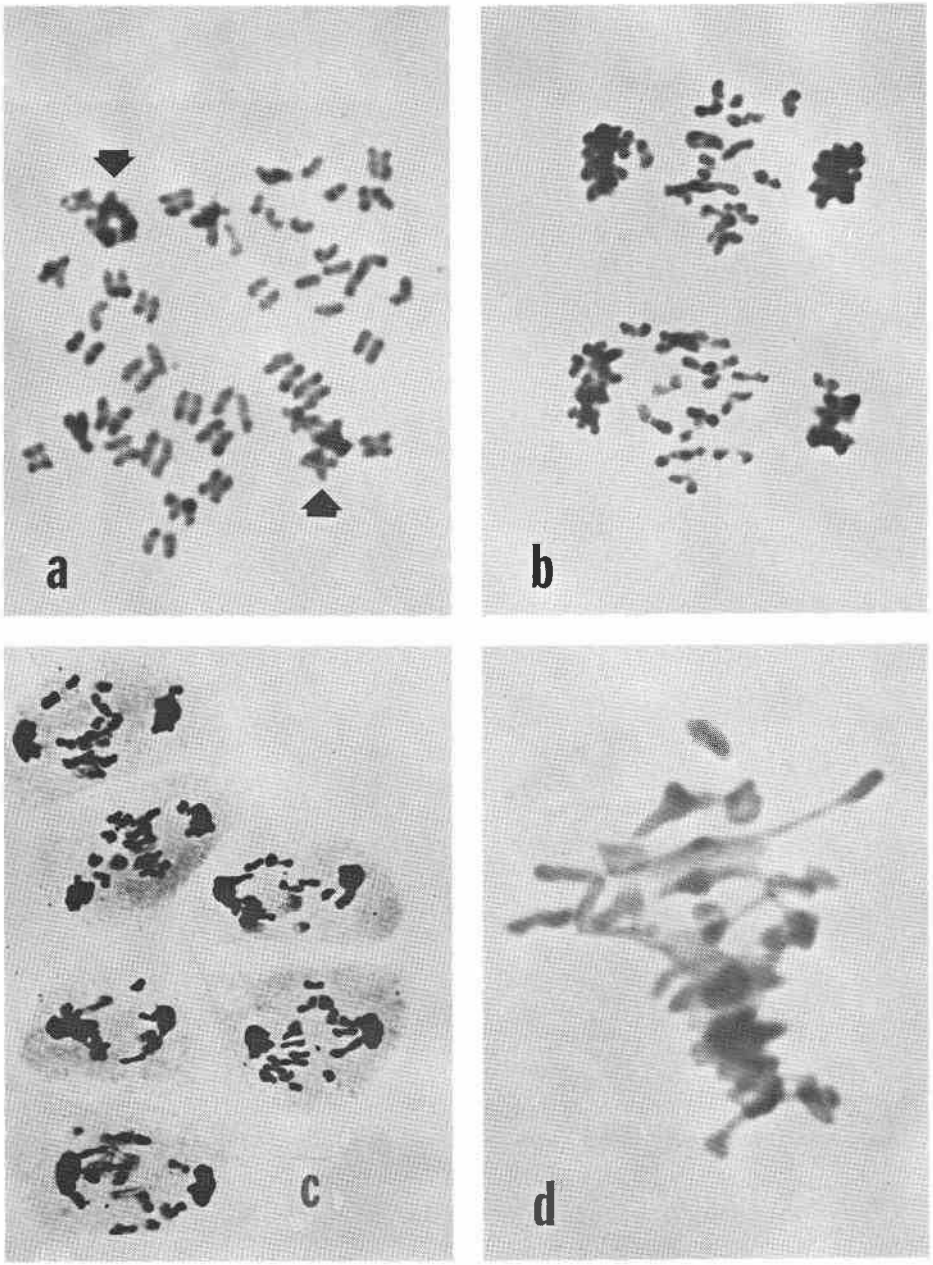

Figure 22. Fawn III x Fortune II hybrid 1. (a) Late anaphase I with univalents dividing equationally (arrows indicate the poles). (b,c) Anaphase II with numerous laggards. (d) Hybrid 6. Metaphase I with association and clumping of chromosomes.

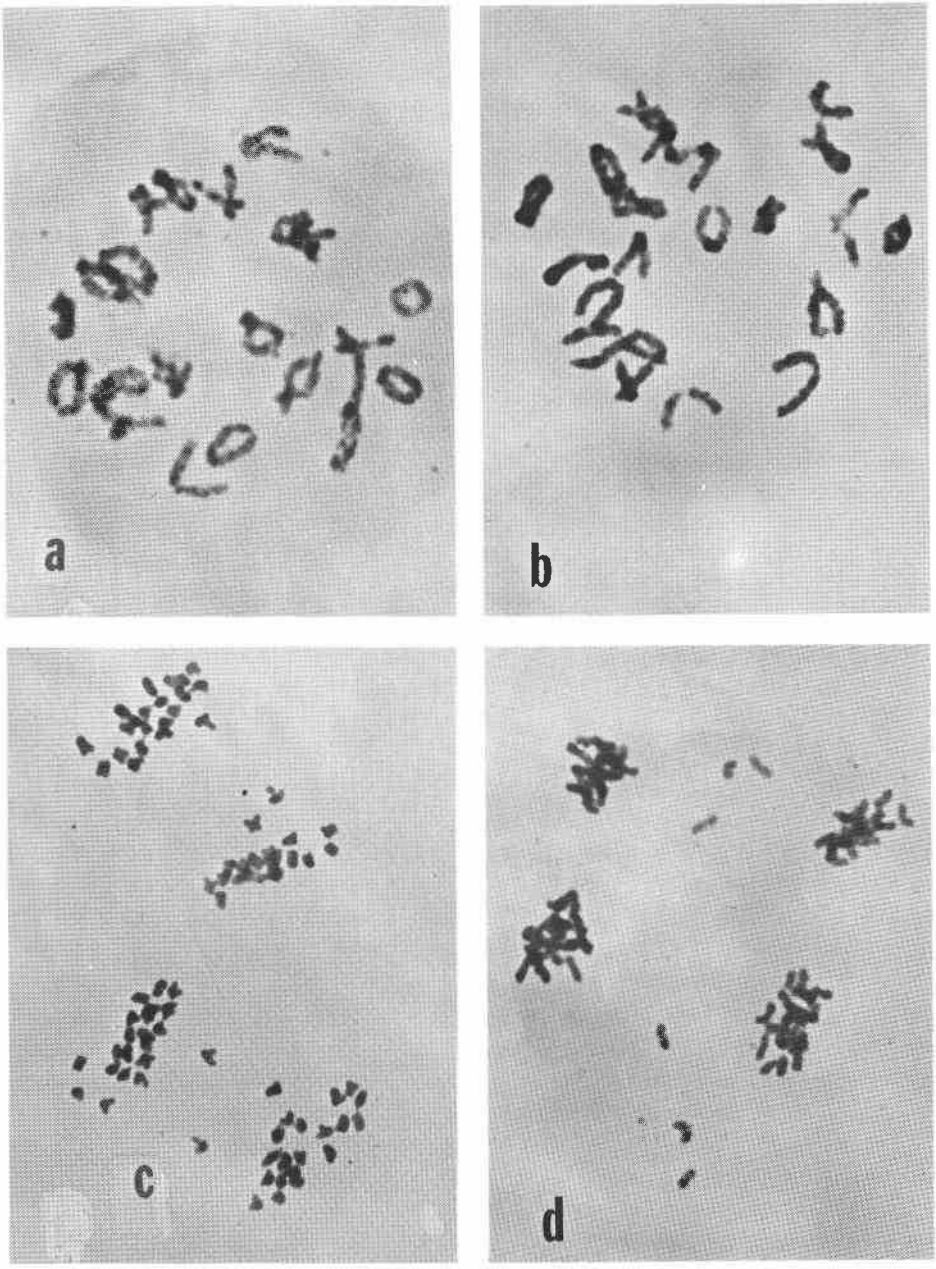

Figure 23. Fawn III x Fortune II hybrid 7. (a,b) Diakinesis with bivalent pairing. Pairing is incomplete in some bivalents. (c) Two anaphase I cells with three dyads lagging only slightly. (d) Anaphase II with six laggards.

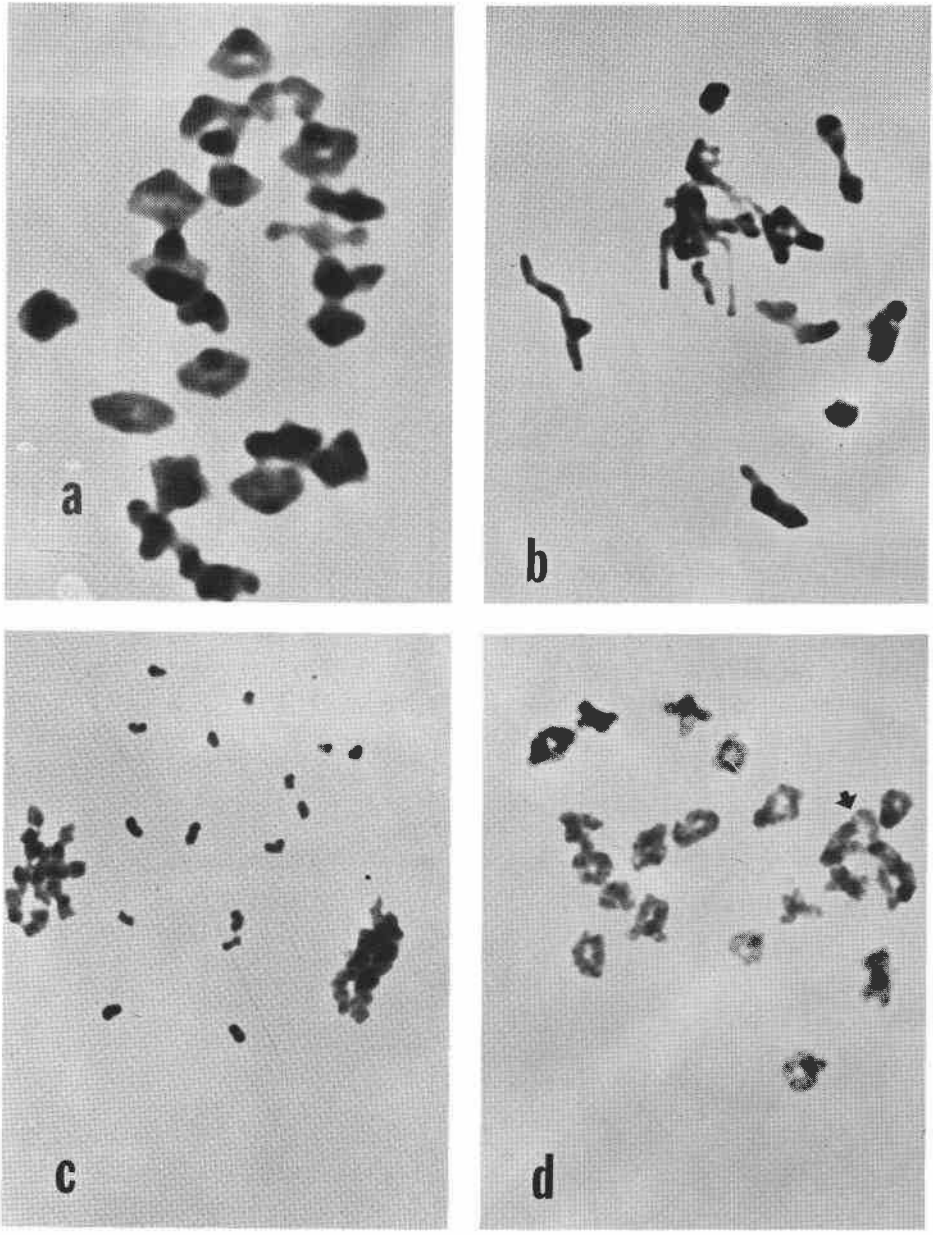

Figure 24. Fawn III x Fortune III hybrids. (a) Hybrid 3. Metaphase I with 21 bivalents. (b) Hybrid 6. Association and clumping of chromosomes. (c) Hybrid 6. Anaphase I with dividing univalents. (d) Hybrid 7. Eighteen bivalents and one hexavalent (arrow).

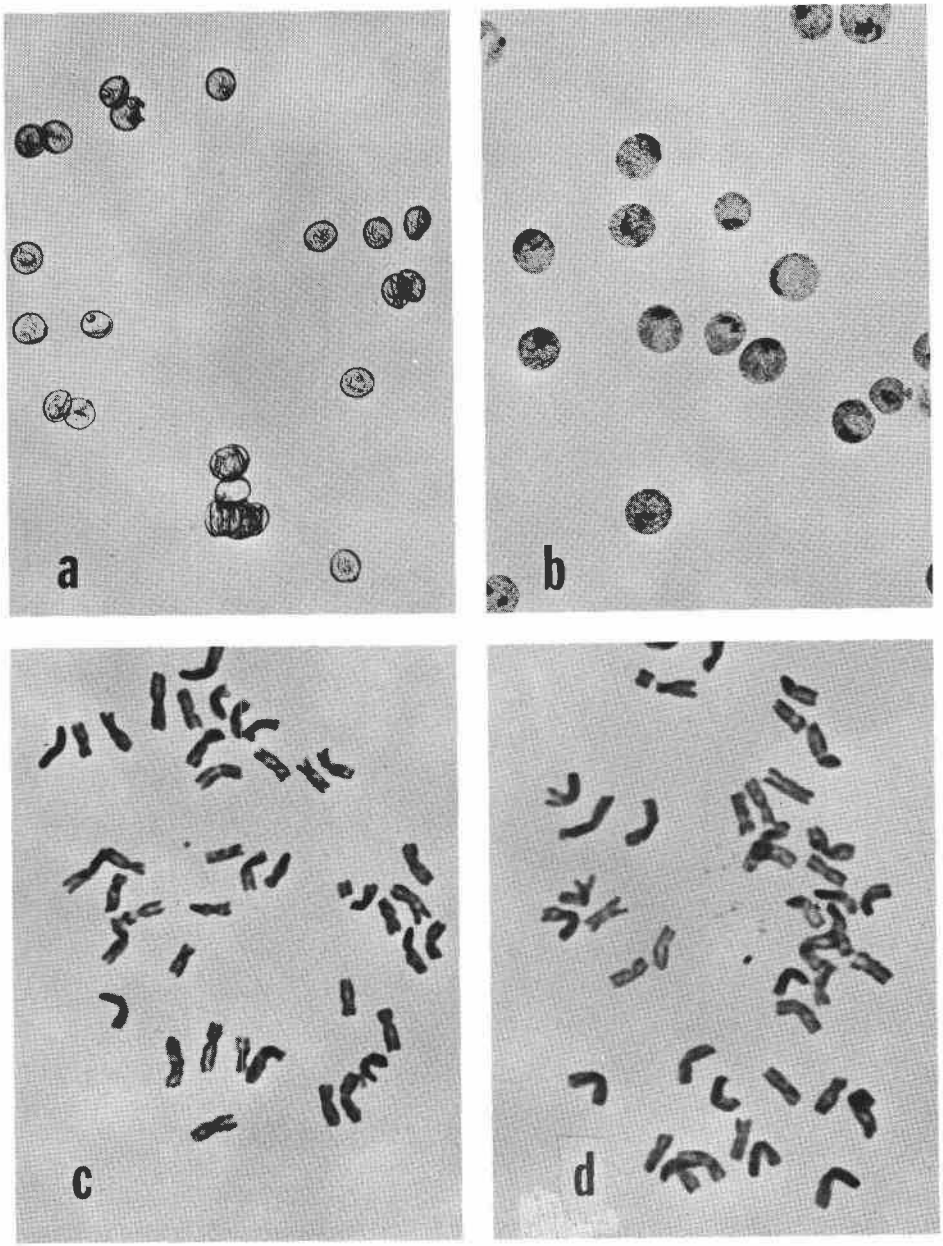

Figure 25. (a) Collapsed pollen grains typical of 50 percent of the hybrids studied. (b) Mature pollen grains with tube nucleus and two sperm nuclei. (c) Somatic cell of the monosomic hybrid with 41 chromosomes. (d) Somatic cell with the normal 42 chromosomes.

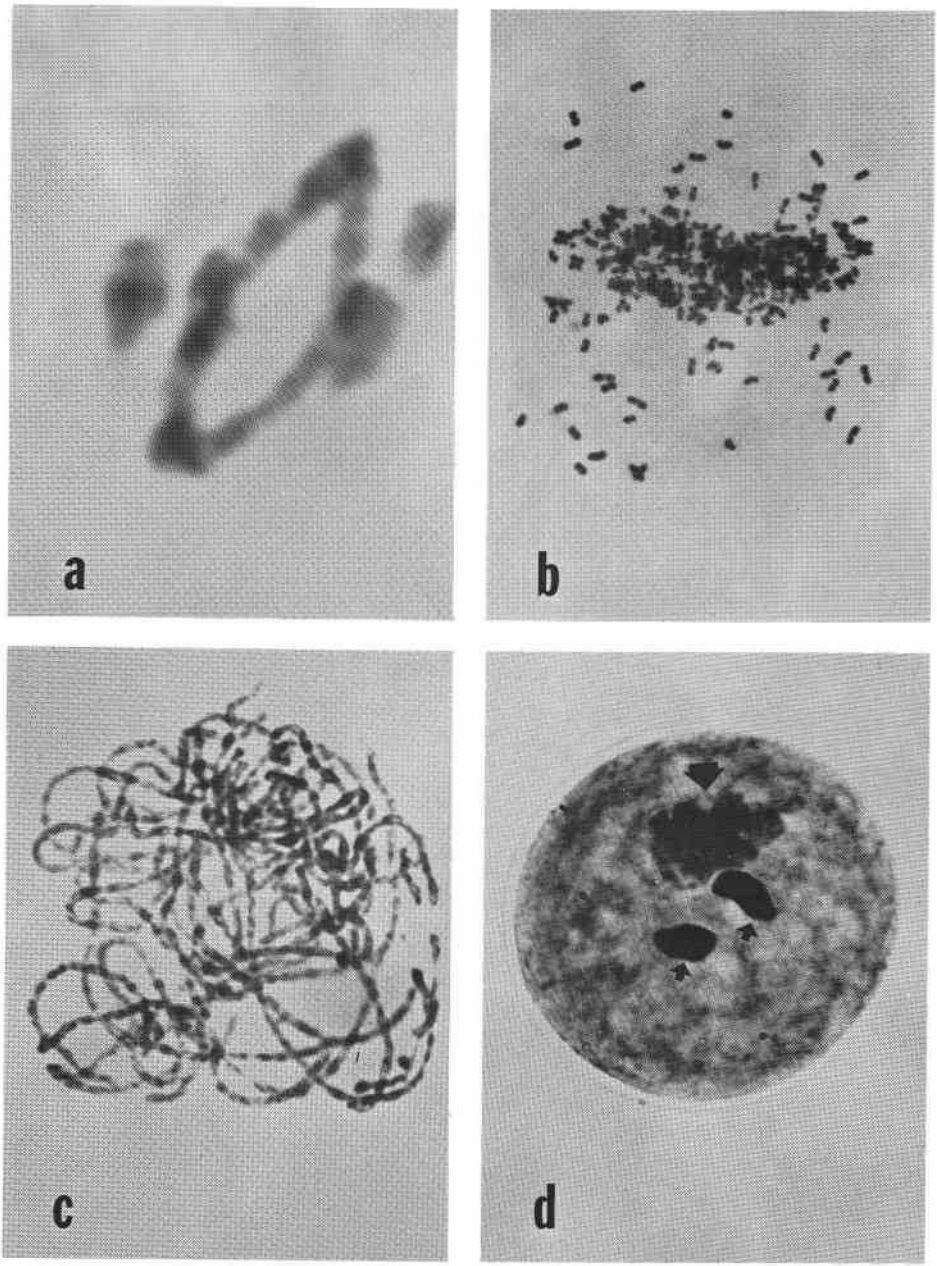

Figure 26. (a) Ring of four translocation at metaphase I. (b) Giant cell at metaphase. (c) Typical pachytene of tall fescue. (d) Mature pollen grain with tube (lg. arrow) and two sperm nuclei (sm. arrows).