CYTOLOGICAL OBSERVATIONS IN WHEAT (TRITICUM AESATIVUM L.) AND IN WHEAT X WHEATGRASS (AGROPYRON ELONGATUM (HOST) BEAUV.) HYBRIDS

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1940

Submitted to the faculty of the Graduate School of
the Oklahoma Agricultural and Mechanical College
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
May, 1953

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ACKNOWLEDGEMENTS

The author wishes to express his deepest appreciation to his major advisor, Dr. A. M. Schlehuber of the Agronomy Department, and to Dr. R. M. Chatters of the Department of Botany and Plant Pathology for their real and intangible assistance during the course of these investigations.

Special thanks are due to Dr. Schlehuber for obtaining the necessary funds and providing laboratory facilities and other materials without which this work would not have been possible. To a no less degree, thanks are also due to Dr. Chatters for providing certain special equipment and for his kind direction of the cytological studies.

The author is further indebted to both Dr. Schlehuber and Dr. Chatters for their counsel and guidance during graduate study.

Dr. Brooks, Dr. Dahms, and Dr. Young have all given helpful advice at various times for which the writer expresses his gratitude.

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INTRODUCTION

Because of its economic importance, wheat has long been of interest to plant breeders and cytologists alike. Each of these groups has built up a separate and tremendous fund of information relatively independent of each other.

The cytologists have concerned themselves with many lines of research chiefly from a theoretical viewpoint. These studies include chromosome counts in species, the study of chromosome behavior during mitosis and meiosis, the homology of chromosomes as demonstrated by their behavior in hybrids, and the artificial induction of aberrations by various means.

Plant breeders on the other hand have devoted their efforts to problems of a more practical nature. As Love (16)[1/] has indicated, most plant breeders use but little the information accumulated by the cytologists and have failed to appreciate the fact that there are cytological techniques which could be used to advantage. In a later paper, Love (17) demonstrated the use of a rapid cytological procedure in making a survey of the meiotic stability of wheats grown commercially and experimentally in Brazil. Theoretically, the investigation was based on cytological studies of various workers which showed that the occurrence of micronuclei in pollen quartets was associated with irregularities during meiosis. Actually, the procedure employed in the survey involved the analysis of young pollen quartets for the frequency of micronuclei by

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[1/] Figures in parentheses refer to "Literature Cited" page 40.

means of the acetocarmine smear technique. The varieties having plants with a high percentage of normal quartets (90% or more) were considered cytologically stable for all practical purposes. The survey revealed that the variety Sinvalocho and related lines were meiotically unstable. Love pointed out that agronomists in the United States have access to Sinvalocho and suggested that this material be examined cytologically before use in a breeding program. This work illustrates in a nice way the application of cytological information and technique to plant breeding problems.

The wheat breeding work in progress at the Oklahoma Experiment Station includes strains of wheat derived from crosses involving certain foreign introductions including Sinvalocho.

Other experimental material of considerable importance consists of lines of wheat derived from an intergeneric cross of Triticum aesativum L.[2/] with Agropyron elongatum (Host) Beauv. Some of this hybrid material is very valuable from the standpoint of rust resistance but it is also extremely variable both as to rust reaction and certain plant characters.

The nature of this material prompted the initiation of a project to obtain cytological information which could be used in the wheat breeding program. This report deals with the observations made in the course of a cytological survey of certain varieties and strains of wheat and of a number of Triticum-Agropyron derivatives.

[2/] Triticum aesativum L. is used as the scientific name of the species since it has priority over the more commonly used Triticum vulgare Vill.

REVIEW OF THE LITERATURE

General Considerations

Purposeful work in cereal cytology began in 1918 with the work of Sakamura who first correctly determined the chromosome numbers of the important species of wheat (21). Since this pioneer work was done, a great deal of information concerning the cytology of wheat and related grasses has accumulated. The literature on the cytology of *Triticum*, especially as it pertains to phylogeny, was reviewed by Aase (2) and by Sears (33). Watkins (41) gave a critical account of the wheat species and their cytological behavior when crossed. More recently Aase (3) reviewed the literature pertaining to polyploids and polyploidogenic agencies. For a comprehensive review of the cytology of the grasses and their hybrids, the reader is referred to the work of Meyers (19). In this report literature pertinent to this study will be reviewed.

Cytology of *Triticum* X *Agropyron* Hybrids

Cytologically the genus *Agropyron* consists of a polyploid series of species with 7 as the basic chromosome number (22, 23, 35). Diploid chromosome numbers of 14 (35), 56 (29), and 70 (23, 8) have been reported for the several biotypes of *Agropyron elongatum*.

Investigations of meiotic behavior in *Triticum* X *Agropyron* hybrids have been reported by Vakar (42, 43, 44). In the F_1 hybrids of *Triticum aesativum* X *Agropyron elongatum* (n=35) associations of 28 bivalents, 21 bivalents plus 14 univalents and 14 bivalents plus 28 univalents were observed. From these and his observations with hybrids of *T. durum* X *A.*

elongatum, Vakar (43) concluded that the genomes of A. elongatum are Aa, Ba, Da, X_1, and X_2 and that the first three genomes are synonymous with those of wheat. Autosyndetic pairing was assumed in those hybrids with 28 bivalents. Cytological analysis of subsequent generations revealed stabilization at 2n=56 chromosomes in the F_3 and F_4 generations.

In the F_1 hybrids of T. aesativum X A. elongatum, Peto (24) reported associations of multivalent chromosomes similar to those observed in A. elongatum but in different frequencies. Meiosis was irregular with numerous micronuclei being formed in the tetrads and pollen grains. Chromosome numbers varied from 54 to 59 (2n) and Peto (25) believed the plants would stabilize at 56=2n chromosomes.

Sapegin (29) used a 56 (2n) biotype of A. elongatum and obtained F_1 hybrids having 21 bivalents and 7 univalents. Microcytes were occasionally observed.

Armstrong and Stevenson (4) compared the cytological behavior of the F_1 and F_5 generations of Triticum aesativum X Agropyron elongatum (n=35) crosses. These authors noted more complete and regular pairing of the chromosomes in the advanced generations. They concluded that the hybrids would stabilize at a 2n chromosome number intermediate between that of the two parents.

Cytological Variability in Strains of Wheat

According to Powers (26), Sapegin, working with pure lines of wheat and F_1 crosses between 42 chromosome wheats, distinguished between 2 types of anomalies which occurred during meiosis. One of these anomalies was characterized by the occurrence of univalent chromosomes; the second by the disorderly arrangement of chromosomes. Sapegin concluded microspore formation does not proceed normally in pure lines of wheat (26).

Powers (26, 27) studied the meiotic behavior of different varieties of Triticum aesativum and found that the cytological aberrations of non-orientation of the chromosomes in meiosis, the occurrence of univalents at metaphase I, and predisjunction led to the occurrence of micronuclei in the pollen quartets. These aberrations, including micronucleus formation, were associated with the coefficients of variability for certain agronomic characters (26).

Meyers and Powers (20) used the phenomenon of micronuclei at the pollen quartet stage as a measure of meiotic instability. They concluded that genetic factors as well as structural differences of the synapsing chromosomes are the main factors determining meiotic instability.

In a cytological survey of Brazilian wheats, Love (17) also used the frequency of occurrence of micronuclei at the tetrad stage as a measure of meiotic instability. In certain unstable lines the frequency of micronucleus formation was associated with the nonorientation of bivalents at metaphase I. Love (17) proposed the term "Meiotic Index" for the percentage of normal pollen quartets and considered any plant with a meiotic index of 90% or more as cytologically stable.

Semeniuk (34) studied the chromosomal stability of hybrids derived from Steinwedel (soft wheat) x T. timopheevi (2n=28). He concluded that differences in meiotic stability are inherited and that it should be possible to select lines which combine high chromosomal stability with vulgare characteristics and resistance to stem and leaf rust. The frequency of micronuclei formation was considered a useful guide in eliminating unstable lines.

Haploids and Monosomics in *Triticum*

The first haploid in wheat was described by Gaines and Aase in 1926 (7). This plant arose parthenogenetically following pollination of *T. compactum* (2n=42) with *Aegilops cylindrica* (2n=28) pollen. Haploids in all three groups of wheat have since been reported (37). They occur with frequencies approaching one percent in diploid wheat (36, 37), but rarely in the other *Triticum* groups. The frequency of occurrence of haploids has been increased by X-ray treatment of pollen and by delayed pollination (37).

Several investigators have reported on the meiotic behavior of haploids in hexaploid wheat (7, 12, 18). Gaines and Aase (7) gave detailed description of meiosis in their haploid. These authors noted that the chromosomes rarely appeared in the typical equatorial plate formation but they were more frequently found distributed over the entire spindle. Random chromosome distribution to the poles with little or no pairing was reported (7). Other investigators, however, have reported varying degrees of chromosome association in haploid wheat (12, 18).

Offspring have been obtained from haploids of both diploid and hexaploid wheats (30, 32, 37, 18). Sears (32) stated that in the hexaploid wheats fertility of the haploids is higher than it is in the other *Triticum* groups. He reported that he obtained as many as 70 viable seed from a single plant following hand-pollination by normal plants. Among the offspring, types with losses or additions of whole chromosomes and with reciprocal translocations predominate (30, 31, 18).

Monosomics are individuals deficient for an entire chromosome (2n-1) and such aberrations have been reported in common wheat by a number of investigators. According to Unrau (39), Kihara in 1924 found monosomics in derivatives of T. polonicum X T. spelta and he described the meiotic behavior of the univalent chromosomes at meiosis. Several different monosomics have been obtained in progenies of crosses between durum and aesativum wheats (26, 20, 14). Meyers and Powers (20) reported that meiotic instability and genetic irregularities were associated with the monosomic state. Others (10, 11, 28) have shown that certain types of speltoids and compactoids in common wheat are associated with the loss of a whole chromosome or a part of a chromosome.

According to Heyne and Livers (9), Sears has produced all 21 of the monosomics in wheat and Sears (31, 32) has published reports on the identification of 17 of the 21 possible monosomic individuals. According to Sears, few of the monosomics differ appreciably from normal 2n plants. When monosomic plants are selfed monosomic, normal and nullisomic progeny are obtained in varying frequencies depending upon the particular monosome. A monosomic plant pollinated with a disomic gives progeny with about 75% monosomic and 25% disomic plants.

Monosomic plants have been used in several studies on the inheritance of various characters in common wheat (32, 39, 9) and these have opened up a new and more direct approach to many genetic problems.

MATERIALS AND METHODS

Description of Materials

The materials included in this survey were divided into two classes. Class I material included 10 varieties and lines of common wheat, *Triticum aesativum* L. and 3 selections of *Triticum-Agropyron elongatum* X Pawnee F_4 hybrids. The complete list of this material together with the numerical designations is given below.

Name or Cross	Numerical Designation
Pawnee	C. I. 11669*
Ponca	C. I. 12128
Triumph	C. I. 12132
Westar	C. I. 12110
Westar Selection	C. I. 13090
Comanche X Blackhull-Hard Federation	C. I. 12517
Comanche	C. I. 11673
Wichita-Sinvalocho X Wichita	C. I. 12702
Bobin-Gaza-Bobin X Pawnee	3345**
Bobin-Gaza-Bobin X Pawnee	3347
Triticum-Agropyron elongatum X Pawnee F_4	3475
Triticum-Agropyron elongatum X Pawnee F_4	3477
Triticum-Agropyron elongatum X Pawnee F_4	3478

*C. I. numbers are the accession numbers of the Division of Cereal Crops and Diseases, U. S. Department of Agriculture.

**1952 Stillwater plot numbers.

Class II material consisted of a heterogeneous group of Triticum X Agropyron derivatives which are listed on page 10. Each of these hybrids was given an entry number which will be used in further discussion.

Hybrids H-1 to H-4 inclusive are selections which stem from seed-stocks of several Triticum spp. X Agropyron elongatum hybrids obtained from the Kansas Experiment Station in 1947. Hybrids H-5 to H-22 inclusive were developed at the Oklahoma Experiment Station as a phase of the cereal breeding program. The Triticum-Agropyron components of these crosses were selections made from plantings of the original Kansas material.

Cytological observations were made on 10 plants of each variety line, or selection of Class I material and on from 4 to 10 plants of each Class II hybrid.

All of this material was collected from various plots and nurseries of the Small Grain Section of the Agronomy Department of Oklahoma A. & M. College.

List of Class II Material

Cross	Entry No.
Triticum-Agropyron elongatum = *T.-A.*	H- 1
Do.	H- 2
Do.	H- 3
Do.	H- 4
T.-A. X Pawnee F_2	H- 5
T.-A. X Ponca F_2	H- 6
Triumph X *T.-A.* F_2	H- 7
Do.	H- 8
Do.	H- 9
C. I. 12517 X *T.-A.* F_2	H-10
(*T.-A.* X Pawnee F_1) X Triumph F_2	H-11
Do.	H-12
(T.-A. X Pawnee F_1) X Pawnee F_2	H-13
Pawnee X (*T.-A.* X Pawnee F_1) F_2	H-14
(*T.-A.* X Pawnee F_1) X C. I. 12517 F_2	H-15
Comanche X (*T.-A.* X Pawnee F_1) F_2	H-16
Ponca X (*T.-A.* X Pawnee F_1) F_2	H-17
T.-A. X (*T.-A.* X Pawnee F_1) F_2	H-18
(*T.-A.* X Pawnee F_1) X *T.-A.* F_2	H-19
T.-A. X Pawnee F_4	H-20
Do.	H-21
Do.	H-22

Experimental Methods

Two or three whole spikes in the early boot stage of development were collected from each of the plants chosen for observation. The spikes were fixed in Carnoy's B fluid and were stored under refrigeration at 0 to 5° C.

The procedure used in making the cytological survey was essentially the same as that suggested by Love (17). The meiotic index (percentage of normal pollen quartets) was determined for each plant. In most cases a total of 500 young pollen quartets were counted for each plant of the Class I material and the number showing micronuclei were recorded. In the analyses of the Class II material, a total of 100 young microspores were analyzed for the frequency of micronuclei. Text Figures 1 and 2 illustrate pollen quartets with and without micronuclei.

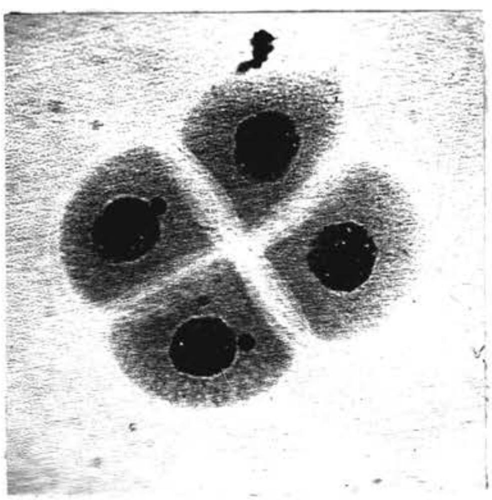

Figure 1. Pollen quartet with micronuclei

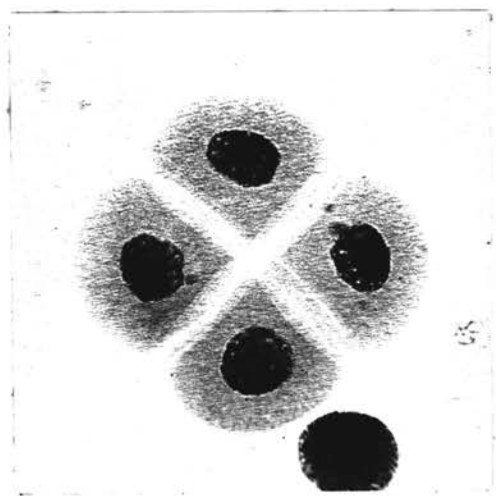

Figure 2. Normal pollen quartet.

Meiosis was studied in detail in some of the plants in order to determine the reasons for the irregularities found in the quartet studies.

Cytological observations were made using the acetocarmine smear technique described by Smith (38). The counts of micronuclei were made at a magnification of about 600X.

Photomicrographs were made from temporary smear preparations with a Leitz "Micam" camera at a magnification of about 1400X.

EXPERIMENTAL RESULTS

Cytological Observations in the Class I Material

The data obtained from the pollen quartet analysis of the several varieties and lines of common wheat as well as the 3 Triticum-Agropyron X Pawnee F_4 hybrids are summarized in Table 1. Individual data for only 2 members of this class are presented in Table 2. The data there show the frequency distribution of micronuclei in the individual plants of Triumph and of one line of Bobin-Gaza-Bobin X Pawnee (3345). Triumph is representative of the stable or normal state while line 3345 illustrates the distribution of micronuclei in one of the more irregular lines of wheat.

If one accepts Love's designation of stable plants as those with a percentage of normal quartets of 90% or more (17) most of the material appeared to be quite stable cytologically. Seven members of this class had all 10 plants with meiotic indices of 91-100 (Table 1). The 10 plants of Triumph were the most stable, the range of the meiotic indices of these plants being 99-100. C. I. 12702, which contained Sinvalocho germ plasm also, was quite stable. The 10 plants of this line had a range of 95-99% normal quartets. The ranges of the other stable lines may be observed in Table 1.

Six of the lines in this class had one or more plants with varying degrees of irregularity. One line of Triticum-A. elongatum X Pawnee F_4, Ponca and Pawnee each had one plant with a meiotic index of 90, 89, and 87, respectively. Limited observations on pollen mother cells (PMC's) failed to reveal any consistent anomaly at meiosis which would cause

Table 1. Meiotic indices of Class I material*

Name or Cross	Number	No. of Plants with Indicated Meiotic Indices 100-91	90-81	80-71	70-61	Number of Plants Examined	Range of Meiotic Indices
Triumph	C.I. 12132	10	-	-	-	10	99-100
Comanche X Blackhull-Hard Federation	C.I. 12517	10	-	-	-	10	98-100
Triticum-*A.* *elongatum* X Pawnee F_4	3475	10	-	-	-	10	97- 99
Comanche	C.I. 11673	10	-	-	-	10	96-100
Wichita-Sinvalocho X Wichita	C.I. 12702	10	-	-	-	10	95- 99
Triticum-*A.* *elongatum* X Pawnee F_4	3478	10	-	-	-	10	92-100
Bobin-Gaza-Bobin X Pawnee	3347	10	-	-	-	10	91- 99
Triticum-*A.* *elongatum* X Pawnee F_4	3477	9	1	-	-	10	90- 99
Ponca	C.I. 12128	9	1	-	-	10	89- 98
Pawnee	C.I. 11669	9	1	-	-	10	87- 97
Westar Selection	C.I. 13090	8	-	2	-	10	75-100
Bobin-Gaza-Bobin X Pawnee	3345	7	1	2	-	10	74- 98
Westar	C.I. 12110	9	-	-	1	10	61- 99

*"Meiotic Index" denotes percentage of normal pollen quartets.

Table 2. Frequency distribution of micronuclei in individual plants of Triumph and one line of Bobin-Gaza-Bobin X Pawnee

Name or Cross	Plant No.	Total No. of Cells	No. of Cells with the Indicated Number of Micronuclei								Total No. of Cells with Micronuclei	Meiotic Index
			1	2	3	4	5	6	7	8		
Triumph (C. I. 12132)	1	500	1	3	-	-	-	-	-	-	4	99.2
	2	"	3	2	-	-	-	-	-	-	5	99.0
	3	"	5	-	-	-	-	-	-	-	5	99.0
	4	"	-	-	-	-	-	-	-	-	0	100.0
	5	"	3	-	-	-	-	-	-	-	3	99.4
	6	"	-	-	-	-	-	-	-	-	0	100.0
	7	"	4	-	-	-	-	-	-	-	4	99.2
	8	"	3	-	-	-	-	-	-	-	3	99.4
	9	"	3	-	-	-	-	-	-	-	3	99.4
	10	"	6	-	-	-	-	-	-	-	6	98.8
Bobin-Gaza-Bobin X Pawnee (3345)	1	500	11	11	1	1	-	-	-	-	24	95.2
	2	"	7 + 1M*	13	2	-	-	-	-	-	23	95.4
	3	"	3	9	4	3	1	1	-	1	22	95.6
	4	"	5 + 1M	9	2	3	-	-	-	-	20	96.0
	5	"	4	5	2	2	-	-	-	-	13	97.4
	6	"	5 + 2M	9	1	3	-	-	-	-	20	96.0
	7	"	10	33	5	8	-	-	-	-	56	88.8
	8	"	55	53	15	5	-	-	-	-	128	74.4
	9	"	15 + 1M	23	9	-	-	-	-	-	48	80.4
	10	"	4	4	1	-	-	-	-	-	9	98.2

*"M" denotes microcytes which are included in the totals. See Plate 3, Figure D.

the formation of micronuclei in the quartets of these plants.

Westar, Westar Selection and Bobin-Caza-Bobin X Pawnee each had one or more plants showing micronuclei (Table 1). These three lines will be considered separately.

In Westar, 9 of the plants were found to have high meiotic indices. The range of these 9 plants was 95 to 99% normal quartets. One plant, however, was found to have a meiotic index of only 61. Many of the quartets were found to possess supernumerary cells or microcytes (Plate 1, Figure D). Twenty-three percent of the cells which contained micronuclei also possessed a microcyte. Other florets of the same spike were examined to determine the cause, the development, and the ultimate fate of the microcytes. Plate 1, Figures A to F illustrate various stages of meiosis observed in this plant. Figure A shows a PMC at telophase I with 2 lagging chromosomes. One of the chromosomes lies just off the equatorial plane while the other is out of focus at the lower left in the cell.

One hundred telophase I cells were counted and approximately 40% of these contained lagging chromosomes situated on or very near the equator (Figures B and C). The cell wall has just begun to develop around the laggards. In Figure B, the phragmoplast appears to terminate at a region just below the laggard while in Figure C the cell wall initials of the dyad are not yet in evidence. Figure D shows the "quartets" with the completely formed microcytes. In Figure E the quartet has developed into young pollen grains while the microcyte has become separated. The final stage of development is shown in F. There, the pollen grains are all mature including the midget which is structurally complete in every detail.

Plate 1

Microcyte formation in a variety of wheat (Westar).

Figure A. PMC at telophase I with 2 lagging chromosomes (one out of focus at lower left).

Figure B.-C. PMC's at telophase I with lagging chromosomes on the equatorial plane. The phragmoplast is evident in (B) and the cell wall surrounding the laggards is just beginning to form.

Figure D. Pollen quartets with laggards appearing as microcytes.

Figure E. Later stage in the development of a quartet with a microcyte. The pollen grains are nearly mature and the microcyte exists as a separate cell.

Figure F. The microcyte has formed a miniature pollen grain which is structurally complete.

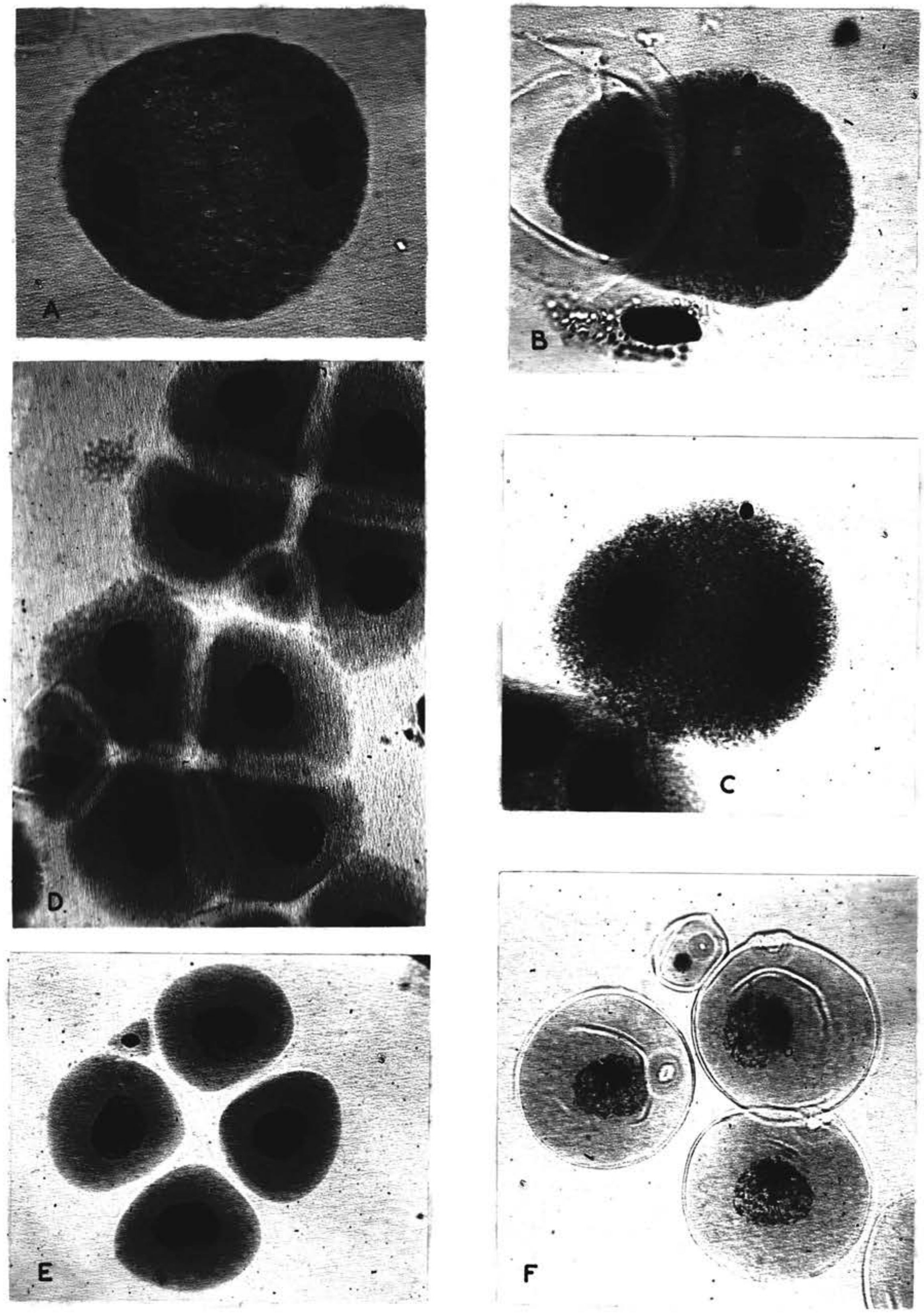

Plate 1

These midget pollen grains were rather numerous. Two thousand large pollen grains were counted and a count of 82 midgets was obtained. Calculated on a 4 to 1 basis the miniature pollen grains were produced 16% of the time in this particular plant.

In the analysis of the plants of Westar Selection, a different situation was observed. Eight of the plants had meiotic indices ranging from 95 to 100 while the other 2 plants had meiotic indices of 75 and 77, respectively. Cytological study of PMC's of these two plants revealed that their meiotic behavior was similar. The photomicrographs of Plate 2 illustrate certain stages of meiosis as observed in them. One to two pairs of univalents were observed at metaphase I (Figure A). These chromosomes moved toward the poles precociously or lagged as in Figure B. Frequently, the lagging univalents divided (Figure C). Figures D and E show dyads in which microcytes were formed only by the laggards which were in a position to deflect the cell wall. On Figure F the lagging chromosomes were sufficiently removed from the equatorial plane so that no microcytes were formed.

Later meiotic stages were unavailable for detailed study, hence, further meiotic behavior in these plants was unobserved.

Bobin-Gaza-Bobin X Pawnee (3345) had plants with meiotic indices which varied from 74 to 98. The distribution of the micronuclei in the individual plants of this line is shown in Table 2. Microcyte formation occurred but slightly and was not confined to those plants with the greatest number of micronuclei.

Cytological observations in the plants with meiotic indices of 74.4 and 80.4 were made. These studies revealed that one or more unpaired chromosomes at metaphase I were probably the main cause of micronucleus formation in those plants.

Plate 2

Pollen mother cells from certain plants
of Westar Selection.

Figure A. PMC at metaphase I with 4 unpaired chromosomes.

Figure B. PMC at anaphase I with the unpaired chromosomes lagging on the plate.

Figure C. Early telophase I showing division of some of the lagging univalents.

Figure D.-E. Telophase I PMC's with microcytes and micronuclei.

Figure F. PMC at beginning of late telophase. All the lagging chromosomes were off the equatorial plane, hence, no microcytes were formed.

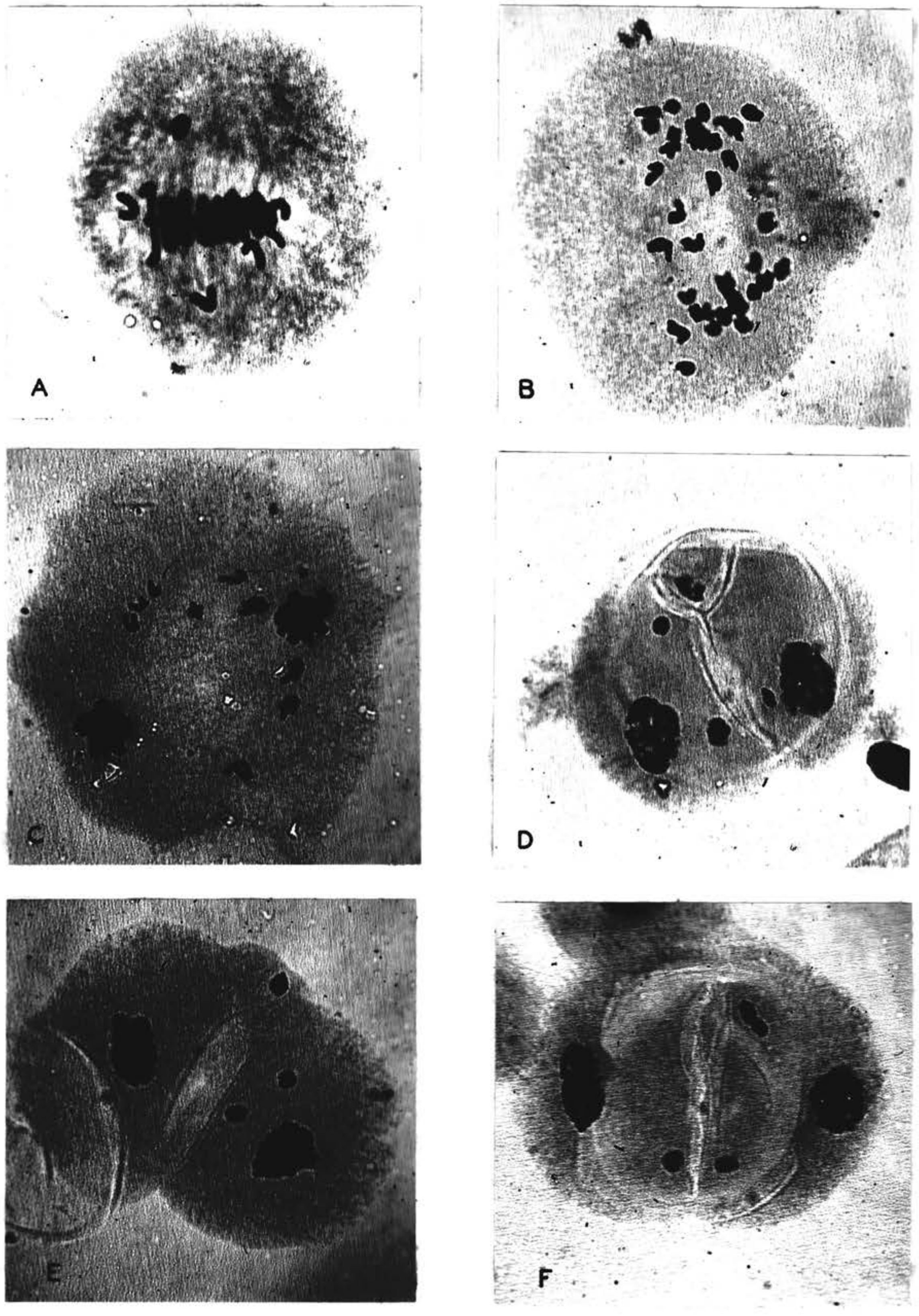

Plate 2

In the course of quartet analysis in the plant with a meiotic index of 88.8 a number of quartets of the type illustrated in Plate 3, Figure G were observed. Cells of this type were found to have occurred with a frequency of 2%. Further studies of other florets of the same spike were made. Certain of the observations are recorded in Plate 3. Figure A is representative of the metaphase I cells which were observed. Approximately 75% of 100 metaphase cells possessed the single univalent lying off the plate as shown. Anaphase I cells were observed to be atypical and were characterized mainly by the single lagging chromosome as illustrated in Figure B. A few cells were seen at anaphase I in which the univalent was dividing (Figure C). There, the dividing univalent may be seen at the left near the equatorial plane while the other 2 groups of chromosomes are distributed equally to the poles. Forty-one chromosomes were counted in several different cells of this plant and it was concluded that it was monosomic (2n-1). In the upper right PMC of Figure D, the lagging chromatids may be observed, and an earlier telophase II cell is shown in Figure E, where apparently one of the lagging chromatids would have been included in the daughter nucleus while the other chromatid would probably appear as a micronucleus in the tetrad stage. An atypical PMC is shown in Figure F. The chromatin material was distributed in unequal masses in the first division. The heterotypic division is just beginning and, were it completed, probably would have formed a hexad with micronuclei as in Figure G.

Detailed cytological study of the material which had a low frequency of micronuclei was as a rule not made. However, the appearance of white-chaffed plants in the field plots of Comanche X Blackhull-Hard Federation (C. I. 12517) which is normally a bronze-colored wheat, prompted a more careful examination of the plants of C. I. 12517.

Plate 3

Meiosis in a monosomic wheat plant
(Bobin-Gaza-Bobin X Pawnee).

Figure A. PMC at metaphase I with monosome.

Figure B. Anaphase I showing the lagging monosome.

Figure C. Polar view of anaphase I. The monosome has divided and appears at the left near the equator.

Figure D. The PMC at anaphase II shows the lagging chromatids formed by division of the monosome in anaphase I and probably would have ultimately formed micronuclei as shown in the quartets.

Figure E. Late anaphase II with one lagging chromatid on the equator. The other chromatid would likely have been included in the nucleus.

Figure F. Atypical PMC at early anaphase II with unequal distribution of the chromatin material.

Figure G. Atypical pollen "quartet" which probably arose from a cell such as is shown in Figure F.

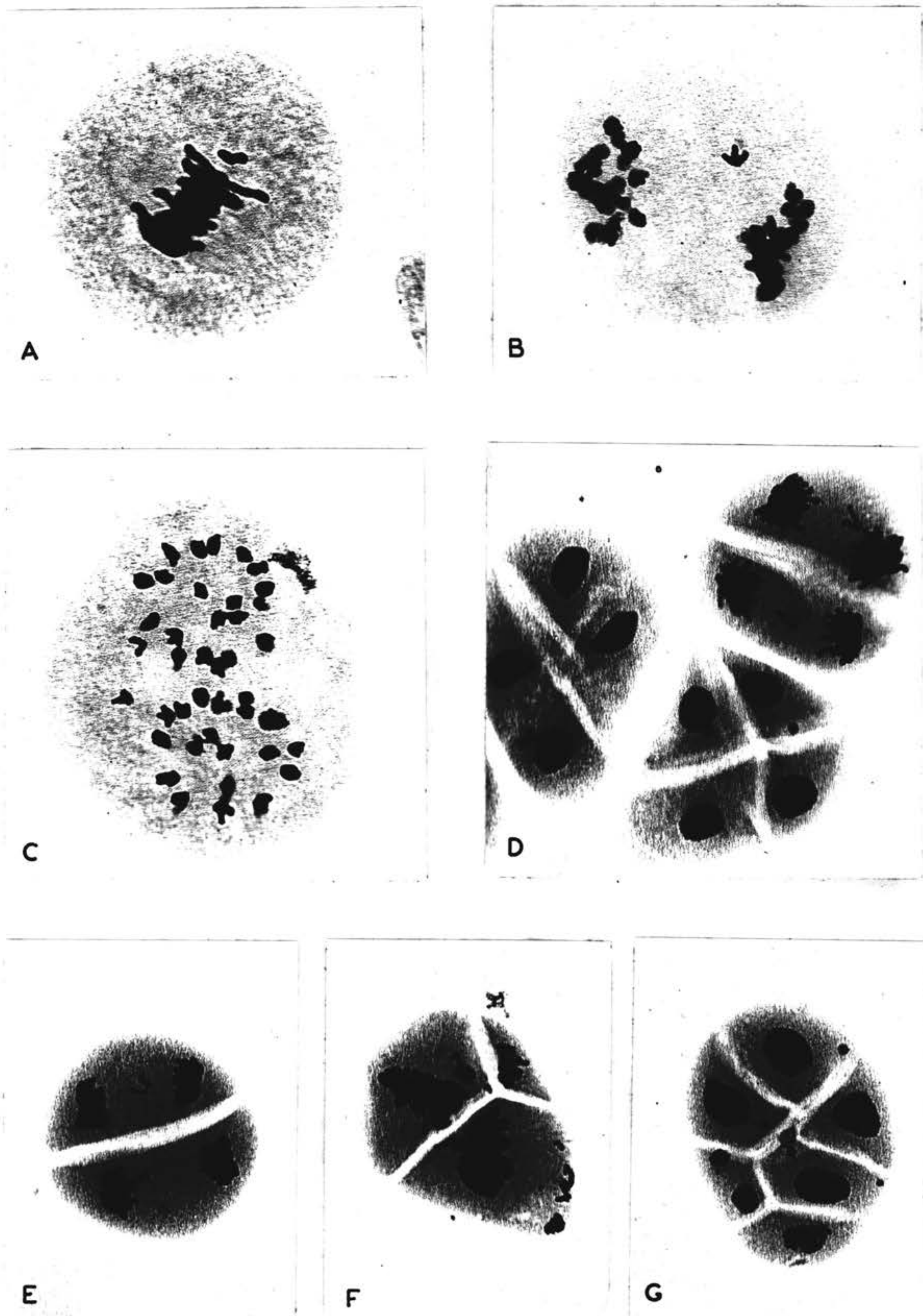

Plate 3

Inasmuch as Comanche appears in C. I. 12517 as the female parent, it also was studied in some detail.

As reported earlier in this section, both C. I. 12517 and Comanche, on the basis of the frequency of occurrence of micronuclei at the tetrad stage were considered as cytologically stable. However, examination of PMC's of these varieties revealed that certain aberrations were common to both. Photomicrographs of PMC's from these varieties are presented in Plate 4. Figures A to C are from C. I. 12517 while Figure D is from Comanche and is included in order to show the great similarity which existed in the meiotic behavior of these plants.

Metaphase I plates in some of the plants of C. I. 12517 were slightly irregular. One or two bivalents or univalents lying off the plate were observed occasionally. Anaphase I stages were irregular and were characterized by a single bivalent stretched across the equator (Figure A). This pair of chromosomes was misshapen in the central region so that the bivalent had a knobbed appearance on one side. As anaphase movement progressed, the ends of the chromosomes with the spindle fiber attachment pulled apart leaving the central irregular portion as a fragment. In Figure B is a late Anaphase I cell which clearly shows the irregular central region about to be detached as a fragment. In some cells the fragment appeared as a microcyte as in Figure C. The marked similarity of the aberration in Figure D (from Comanche) to that in Figures A and B (from C. I. 12517) should be noted.

Several plants of both C. I. 12517 and Comanche exhibited this type of fragmentation. Such an aberration in which portions of chromosomes are lost could very likely lead to the appearance of off-type plants. Since Comanche is normally white-chaffed, phenotypic expression of the deficiency would be unnoticed.

Plate 4

Chromosome fragmentation in a strain of wheat. (C.I. 12517) and its female parent (Comanche)

Figure A.-C. PMC's from C. I. 12517. Figure A shows the irregular bivalent lying across the plate. The knobbed central region of the chromosome pair is evident. In Figure B, disjunction has progressed and fragmentation is underway. In Figure C, the fragment has been excluded as a microcyte.

Figure D. Anaphase PMC from Comanche (compare with Figures A and B).

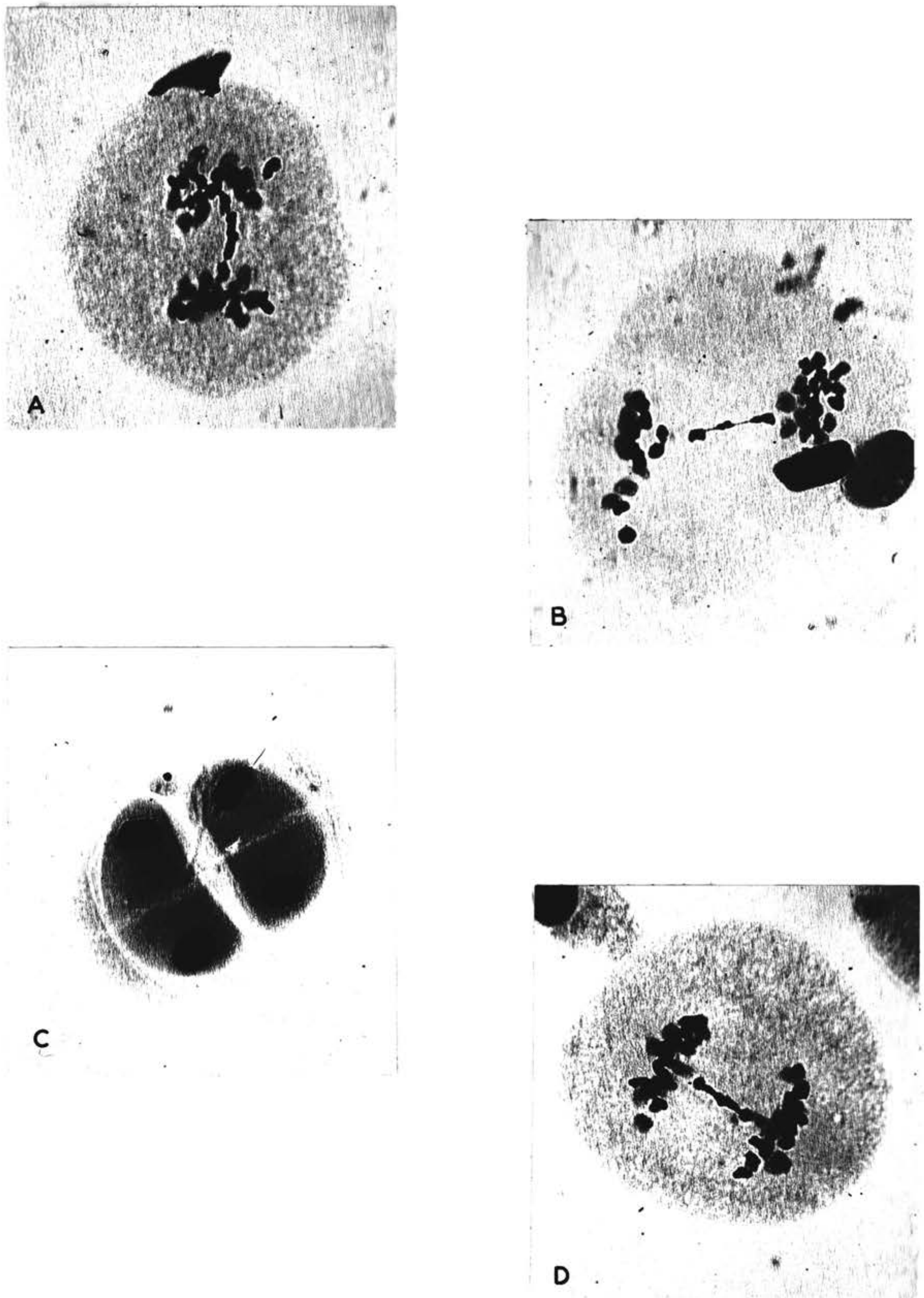

Plate 4

Cytological Observations in Class II Material

The observations in this material were restricted mainly to the analyses of the plants for the presence of micronuclei at the quartet stage. No attempt was made to study in detail the meiotic behavior of all the plants which showed a high frequency of micronuclei. In some cases, however, when the material presented itself, careful examination was made.

The meiotic indices of the various Triticum-Agropyron derivatives are summarized in Table 3. It should be observed that the advanced generation Triticum-Agropyron hybrids, H 1 - H 4, are relatively more stable than the F_2 hybrids with but few exceptions. The F_4 hybrids, H 20 - H 22, are also more stable than the F_2's, and are approximately as stable as hybrids H 1 - H 4.

If the 4 Triticum-Agropyron hybrids are considered as a group, it will be observed that the majority of the plants of H 1 exhibited a moderate frequency of micronuclei. All of the plants of each of the other three lay in the 91-100 range. Counts of 42 (2n) chromosomes were obtained for 4 plants of H 1, 2 plants of H 3 and 1 plant of H 2 and H 4, respectively. This indicated that the chromosome numbers of these plants had stabilized at the 2n number of common wheat.

Hybrids H 5, H 6, and H 7 had identical parentage since they were selections from an F_1 progeny row, and will therefore be considered together. Hybrid H 7 was the most stable of the three, since it had 4 plants in the 91-100 range. Hybrid H 5 was the most irregular with one plant having a meiotic index as low as 14. Cytological studies of PMC's of various plants within this group revealed certain anomalies which help to explain the high frequencies of micronuclei observed in some of them.

Table 3. Meiotic indices of Class II material

Hybrid	No.	Number of Plants with Indicated Meiotic Indices									No. of Plants Examined
		100-91	90-81	80-71	70-61	60-51	50-41	40-31	30-21	20-1	
Triticum-A. elongatum	H 1	2	4	1	-	-	-	-	-	-	7
T.-A.*	H 2	9	-	-	-	-	-	-	-	-	9
T.-A.	H 3	9	-	-	-	-	-	-	-	-	9
T.-A.	H 4	10	-	-	-	-	-	-	-	-	10
Tri. X T.-A. F_2	H 5	-	2	1	2	-	2	-	-	1	8
Tri. X T.-A. F_2	H 6	2	-	-	-	2	3	-	-	-	7
Tri. X T.-A. F_2	H 7	4	-	1	3	-	-	-	1	-	9
C.I. 12517 X T.-A. F_2	H 8	2	-	-	-	1	-	1	2	-	6
T.-A. X Paw. F_2	H 9	1	-	2	2	4	1	1	-	-	11
T.-A. X Ponca F_2	H 10	7	2	-	-	-	-	1	-	-	10
(T.-A. X Paw. F_1) X Tri. F_2	H 11	9	1	-	-	-	-	-	-	-	10
Do.	H 12	1	-	2	2	-	1	-	-	2	8
(T.-A. X Paw. F_1) X Paw. F_2	H 13	3	1	-	1	-	-	-	-	-	5
Paw. X (T.-A. X Paw. F_1) F_2	H 14	7	-	-	-	-	-	-	-	-	7
T.-A. X (T.-A. X Paw. F_1) F_2	H 15	8	-	-	-	-	-	-	-	-	8
(T.-A. X Paw. F_1) X T.-A. F_2	H 16	-	1	1	1	2	-	1	1	1	8
(T.-A. X Paw. F_1) X C.I. 12517 F_2	H 17	4	-	-	-	-	-	-	-	-	4
Com. X (T.-A. X Paw. F_1) F_2	H 18	6	1	-	-	-	-	-	-	-	7
Ponca X (T.-A. X Paw. F_1) F_2	H 19	6	-	-	-	-	-	-	-	-	6
T.-A. X Paw. F_4	H 20	5	2	-	-	-	-	-	-	-	7
Do.	H 21	6	1	-	-	-	-	-	-	-	7
Do.	H 22	6	-	-	-	-	-	-	-	-	6

*Abbreviations:

T.-A. = Triticum-Agropyron elongatum
Tri. = Triumph
C. I. 12517 = Comanche X Blackhull-Hard Federation
Paw. = Pawnee
Com. = Comanche

For example, in hybrid H 5 one plant with a meiotic index of 49 was found to possess 43 (2n) chromosomes. Meiosis in this particular plant was very similar to that observed in the monosomic wheat plant reported earlier in the Class I material. Photomicrographs of PMC's from this plant are presented in Plate 5 (cf Plate 3). At metaphase I (Figure A, Plate 5) the extra chromosome was found off the plate similar to the monosome described previously. At anaphase I the univalent lagged at the equator as in Figure B or moved to one pole or the other. In Figure C the univalent has just begun to divide. Figure D illustrates the condition where the univalent divided longitudinally and the halves migrated to opposite poles. The chromatid near the upper nucleus probably would have been excluded as a micronucleus while the chromatid near the lower nucleus probably would have been included in it. In the PMC in Figure E, the univalent has migrated to the upper pole so that 22 chromosomes are present there while 21 may be observed at the lower pole. The 43 chromosomes may easily be counted in Figure C.

Other plants of hybrid H 5 were examined and 2 of them were found to have the normal 2n complement of 42 chromosomes. One of these 42 chromosome plants had only 64% normal pollen quartets while the other had a meiotic index of 82. Several unpaired chromosomes were found in pollen mother cells of these plants and undoubtedly contributed to the low meiotic index.

In hybrid H 6 the range of the meiotic indices was 41-100. However, 5 of the individuals had meiotic indices of nearly 100. In one plant with a meiotic index of 41, multivalent associations of chromosomes were observed. Photomicrographs of PMC's obtained from this plant are shown

Plate 5

Pollen mother cells from a 43 chromosome Triumph X Triticum-A. elongatum F_2 Hybrid.

Figure A. Metaphase I with the extra unpaired chromosome.

Figure B. Anaphase I with the extra chromosome lagging on the plate.

Figure C. Anaphase I. The additional chromosome has migrated to the upper pole and it appears to be almost completely divided.

Figure D. Late anaphase I PMC showing completed division of the extra chromosomes the halves of which have migrated to opposite poles.

Figure E. Anaphase I polar view. Twenty-two chromosomes may be counted at the upper pole and 21 at the lower.

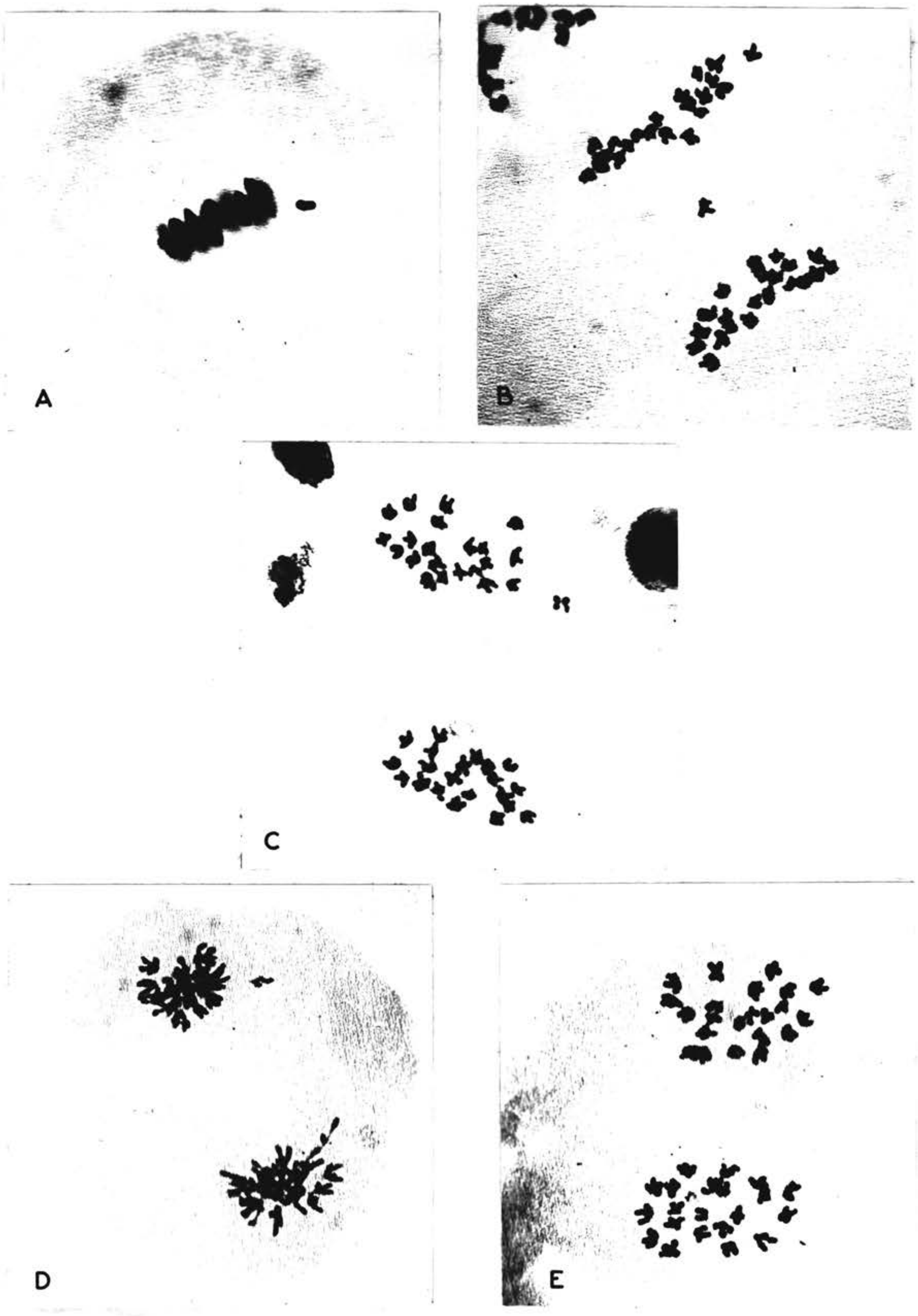

Plate 5

in Figures 3 and 4 below.

Figure 3. PMC with a trivalent and a univalent

Figure 4. PMC with a quadrivalent.

In Figure 3 an association of 3 chromosomes may be observed at the left of the plate while a univalent may be seen below. A quadrivalent configuration is illustrated in Figure 4. Chromosome counts were unobtainable in this plant so it is not known whether additional chromosomes were responsible for the multivalent chromosomes or whether a translocation caused the formation of the chains of 3 and 4 chromosomes. In addition to the multivalents, numerous unpaired chromosomes were observed at metaphase I in this plant but never in the same cell with the polyvalent chromosome.

The meiotic behavior of the plants of hybrid H 7 was not studied; therefore, no explanation can be offered as to the reason for the occurrence of micronuclei.

Hybrids H 8, H 9, H 10 are similar to H 5, H 6, and H 7 in that they are crosses of common wheat with a Triticum-Agropyron derivative. In H 5 to H 8 inclusive common wheat served as the female parent while in hybrids H 9 and H 10 a <u>Triticum-Agropyron</u> derivative was the female. The micronuclei counts in the respective plants of all these hybrids indicate that the direction of the cross had no influence on the frequency of micronuclei in the plants studied. For example, in H 9 and H 10 the <u>Triticum-Agropyron</u> derivative served as the female parents. Hybrid H 9 had only one plant with a percentage of normal quartets above 90 while hybrid H 10 had 7 plants in the 90 to 100 range.

Cytological observations on PMC's from one of the plants of hybrid H 9 showed it to be monosomic. The PMC's of other plants were then studied and chromosome counts of 4 other plants were obtained. Of these 4, three were also monosomic and one was found to have the normal 42 chromosome complement. Meiosis in the 42 (2n) plant was normal with but few micronuclei being formed. The percentages of normal quartets of the 4 monosomics were 32, 53, 55 and 72, respectively. No evidence was obtained as to the cause of the high incidence of micronuclei in other plants of hybrid 9.

The next group of hybrids to be considered are H 11 to H 19 inclusive. These represent crosses in which one of the parents was a <u>Triticum-Agropyron</u> X Pawnee F_1 derivative. With 2 exceptions (H 12 and H 16) these hybrids were quite stable. Repeated crossing with wheat promoted greater meiotic regularity so that fewer micronuclei were formed.

Hybrids H 11 and H 12 were sister selections and a marked difference in stability was noted between them. H 11 had only one of 10 plants with a meiotic index of less than 90, whereas H 12 had only one of 8 plants above 90. Two very irregular plants of H 12 had only 17 and 14% normal quartets, respectively. Limited cytological observations of metaphase I and anaphase I cells of certain plants in H 12 were made. The plant with a meiotic index of 17 had 42 (2n) chromosomes at anaphase I and several unpaired chromosomes were observed at metaphase I.

Similar comparisons of other hybrids of this type might be made but since only one parent is common to some of these hybrids such comparisons would yield but little useful information.

The last group of hybrids is that composed of 3 Triticum-Agropyron X Pawnee F_4 derivatives. Pollen quartet studies showed them to be highly stable. Hybrid 20 had 2 plants with a meiotic index of 90, the remaining 5 plants had a range of 94 to 97% normal quartets. Hybrid 21 had a single plant with a meiotic index as low as 90, while the other 6 plants of this hybrid had a range of 94 to 99. In H 22 all 6 plants were considered stable, the range being 93 to 98% normal quartets.

During the course of the pollen quartet analysis of plants of H 22 PMC's were observed which possessed a haploid complement of n=22 chromosomes. Plates 6 and 7 illustrate PMC's of various stages of meiosis in this haploid plant. No true metaphase I plates were observed but rather the univalent chromosomes were distributed through the cell (Figure A). At anaphase I chromosomes were distributed unequally to the 2 poles. Figure B represents the condition most frequently observed in which 10 univalents passed to one pole while 12 univalents congressed at the other. Frequently cells were observed in which some of the univalents lagged on the equator as in Figure D. Occasionally these lagging chromosomes divided (Figure E).

As a result of nearly equal distribution of the univalents at anaphase I most of the second division anaphase cells appeared as in the left cell of Figure F, Plate 7. Subsequently, pollen tetrads of nearly normal shape were formed (Figure H). Cells of the heterotypic division

Plate 6

Meiosis in a haploid (n=22) *Triticum* X *A. elongatum* X Pawnee F_4 hybrid.

Figure A. PMC showing 22 univalents distributed through the cell.

Figure B. Anaphase I with almost equal distribution of the univalents.

Figure C. Anaphase I with all the univalents congressed at one pole.

Figure D. Anaphase I showing lagging univalent chromosomes.

Figure E. Anaphase I PMC showing division of lagging univalents.

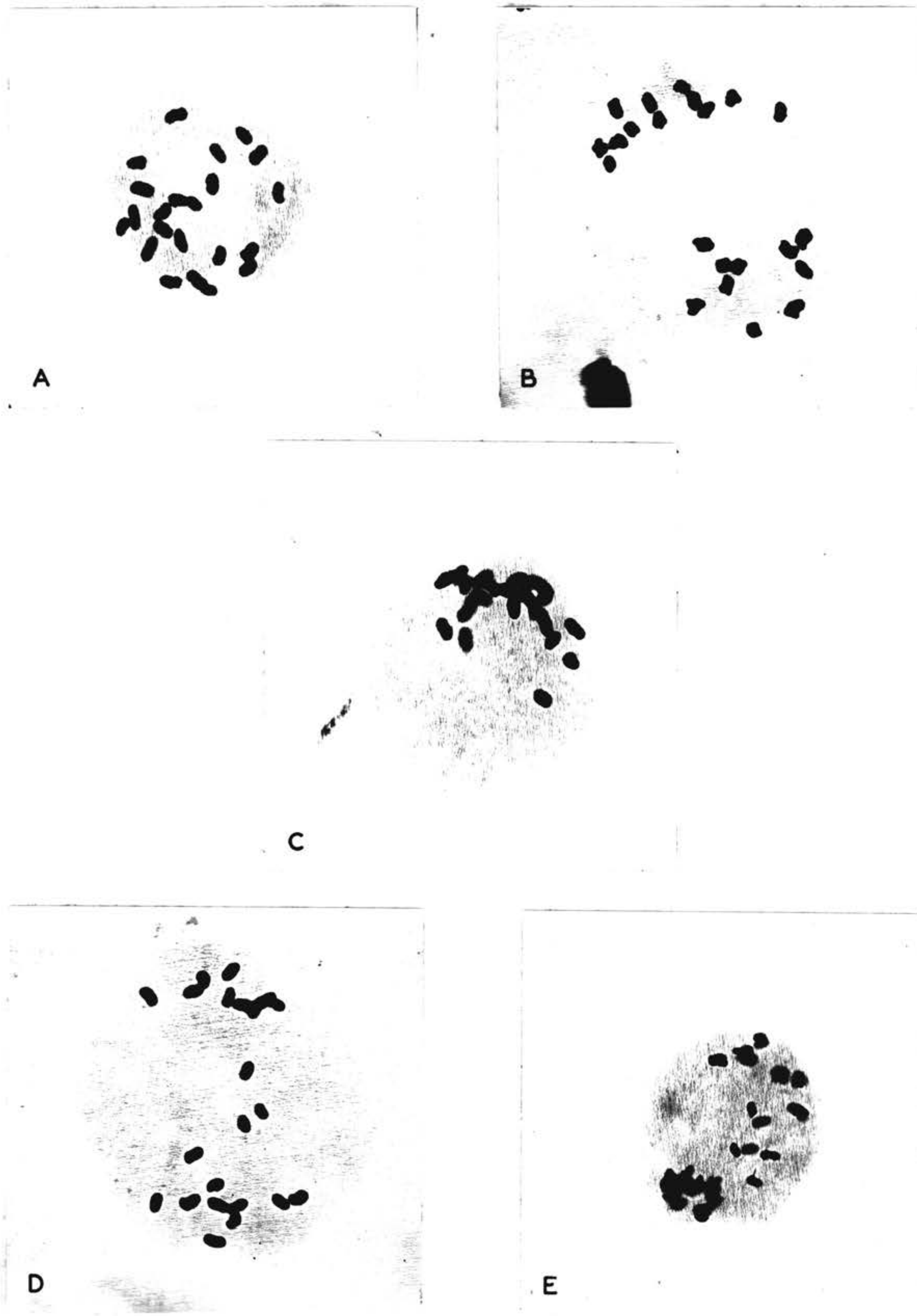

Plate 6

Plate 7

Meiosis in a haploid (Plate 6 Cont'd.)

Figure F. PMC's at early and late anaphase II. The cell at the left is representative of the early anaphase II cells most commonly observed. The cell at the right shows the irregular second division with lagging chromosome fragments.

Figure G.-H. Pollen "quartets" observed in the haploid. Figure H shows the most commonly occurring type of pollen quartet that was observed.

Figure I. Polysporous dyad with the heterotypic division underway. (The "sticky" character of the chromatin should be noted).

Figure J. Hexad derived from the development of such a cell as is shown in I.

Figure K. This is representative of the irregular pollen grains produced by the haploid.

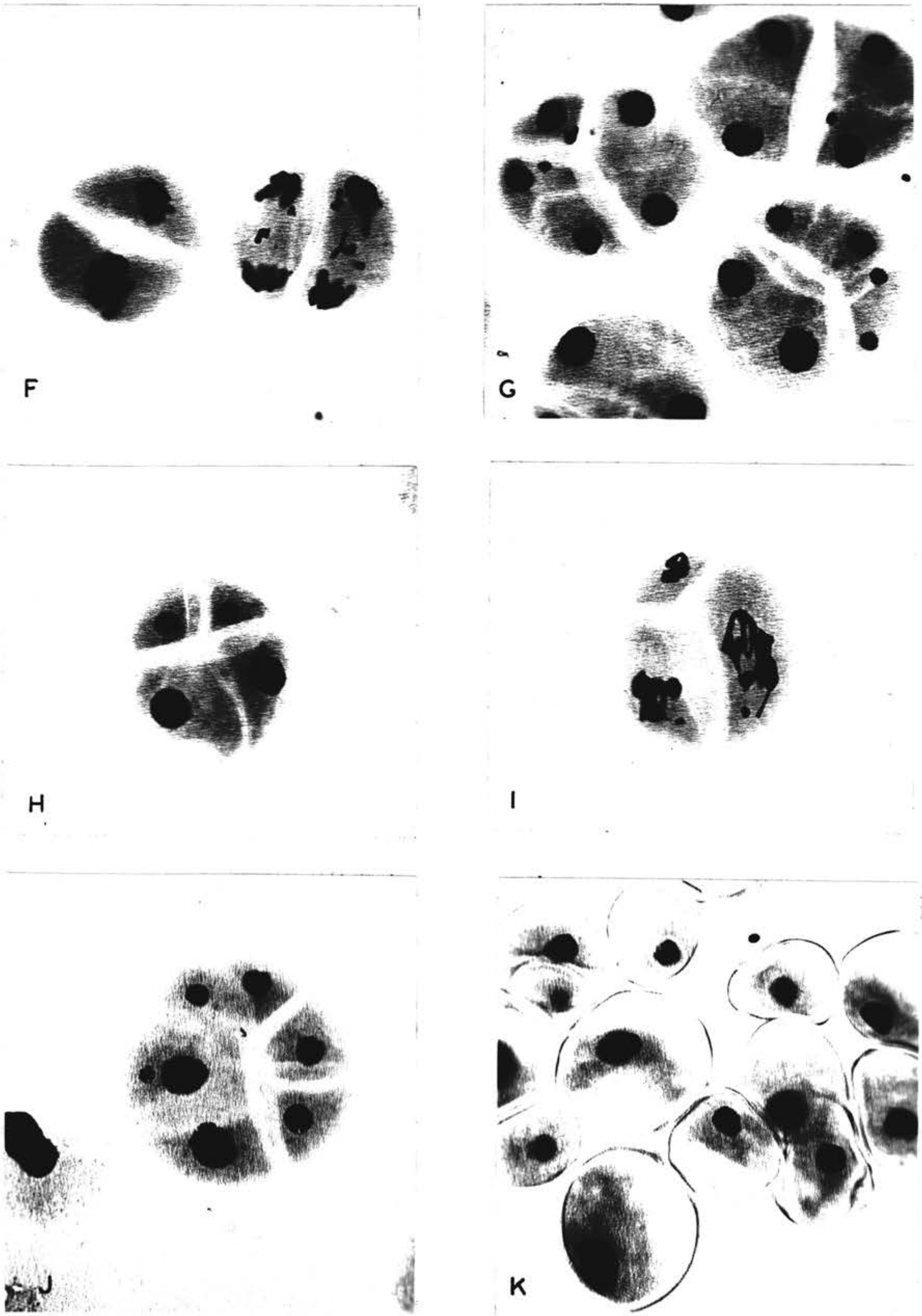

Plate 7

in which laggards occurred were also observed (Figure F, right cell). In Figure G a group of quartets as they usually appeared is shown. Polysporous dyads (Figure I) were quite frequently observed. Such a cell as in Figure I would ultimately produce multi-celled tetrads as illustrated in Figure J. As a result of the great irregularity both in the first and in the second divisions the pollen grains were mostly abnormal as to size and chromatin content (Figure K).

After the haploid plant with an n=22 number of chromosomes was found, a re-examination of the spikes of various plants of H 22 was undertaken in an effort to determine the chromosome numbers of the haploid plants' sibs. Satisfactory material was available from only 2 plants, however, and these were found to possess a 2n complement of 44 chromosomes. Text Figure 5 shows a PMC with 44 chromosomes from one of these plants.

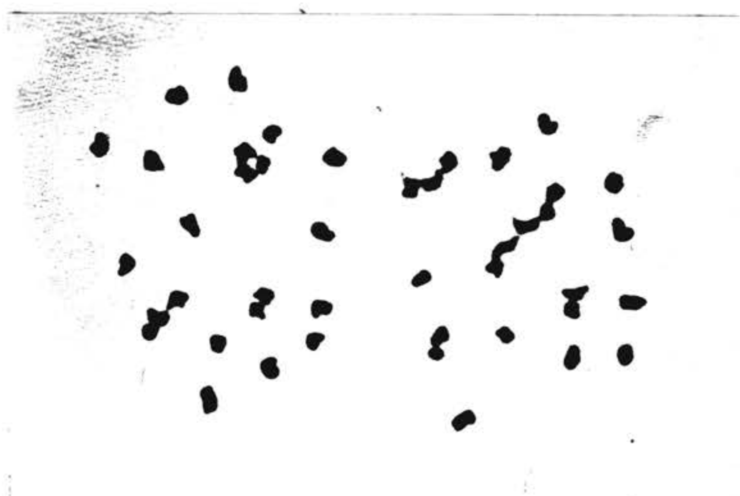

Figure 5. PMC with 44 chromosomes.

The plants of H 21 were also re-examined since H 21 and H 22 originated as head selections from the same F_3 progeny row. Four of the plants were found to have 44 chromosomes, also. Three other plants failed to yield PMC's at the proper stages for counting the chromosomes.

These observations indicate that these hybrids had stabilized at a 2n number of 44 chromosomes.

It might be interjected here that some of the plants of the *Triticum-Agropyron* X Pawnee F_4 line (3477) in the class I material also had 44 chromosomes because line 3477 originated from the same F_3 progeny row as H 21 and H 22.

Further studies of this material are now in progress and should provide more information relative to the stability and meiotic behavior of these hybrids.

DISCUSSION

It has been pointed out by various workers that the percentage of normal pollen quartets may be affected by any disturbance of the physiological process of meiosis. At least two sources of meiotic abnormalities have been pointed out by Love (17). One of these is the failure of pairing due to lack of complete homology as found in plants heterozygous for any number of chromosomal aberrations. The second is the genic disturbance of the meiotic process. However, these two sources of meiotic instability are difficult to separate as Meyers and Powers (20) have pointed out. Just which of these sources of meiotic instability is responsible for the occurrence of micronuclei in the various strains of wheat surveyed is open to question.

For example, in line 3345 of Bobin-Gaza-Bobin X Pawnee the two plants with the highest frequency of micronuclei had several unpaired chromosomes at metaphase I. The question may be asked whether or not failure of pairing was due to lack of homology between the chromosomes which were contributed by the respective parents. This may be possible since one of the parents was a foreign introduction and the other parent a domestic wheat. Certain chromosomal mutations may have occurred in one parent and not in the other and thus have caused sufficient dissimilarity in the chromosomes so that failure of pairing resulted in the intervarietal cross.

Genic disharmony may also have been responsible for failure of pairing of the chromosomes. This seems unlikely, however, since the related line 3347 was entirely stable as measured by the frequency of micronuclei at the tetrad stage.

Lack of pairing of the chromosomes was also responsible for micronucleus formation in certain plants of Westar and in Westar Selection. There is a greater possibility that the meiotic instability is inherited in these plants since Westar Selection is closely related to Westar. The anomaly of microcyte formation which occurred so frequently might conceivably be used as a character to determine whether meiotic instability is an inherited character in Westar. The question of microcyte formation will be discussed further later in this section.

It was pointed out in the Introduction that Love (17) considered Sinvalocho highly unstable and that this instability was inherited. The observations of the writer concerning a line of wheat containing Sinvalocho germ plasm have been reported in the previous section. These results indicated that this material was meiotically stable. Apparently the process of selection and crossing has eliminated the inherent instability of Sinvalocho as noted by Love (17).

The meiotic instability of the Triticum-Agropyron derivatives appeared to be due to the lack of chromosome homology produced as a result of the intergeneric cross. This conclusion is based on the following observations: Some of the advanced generation hybrids as H 2, H 3, and H 4 (Table 3) were very stable. In hybrids such as H 5, H 6, and H 7, where wheat chromosomes were introduced into the hybrid, meiotic instability increased. Then, as additional wheat chromosomes were introduced to form such hybrids as H 11, more regular pairing of the chromosomes resulted and fewer micronuclei were formed.

The cytological observations in C. I. 12517 indicated that a certain type of chromosome fragmentation occurred in that strain of wheat and also in Comanche. It is believed that some chromosomal aberration has altered the morphology of the chromosomes bearing the genes for bronze or red chaff color so that complete terminalization of the chromosomes is prevented. As a result of this interference the chromosomes are stretched at anaphase I and fragmentation occurs (Plate 4, Figure B). Thus, this fragmentation might be responsible for the appearance of white chaff mutants in a manner analagous to the chaff color mutation reported in Dawson's Golden Chaff variety of wheat (13, 15).

Since the microcyte formation occurred so frequently in Westar, some consideration may be given to the reasons advanced by various workers for wall formation around micronuclei. Darlington (5) suggested that cell wall formation was under the control of the centromere. Upcott (40) postulated that in the case of acentric fragments body repulsions may deflect the cell wall. More recently, Frankel (6) reported that acentric fragments in Triticum formed microcytes. He believed that the position and the size of the fragment were the prime factors in determining cell wall formation around micronuclei.

The writer is of the opinion that position of the fragment is chiefly responsible for cell wall formation. In Plate 1, Figure A and in Plate 2, Figure F, the fragments were not directly in the path of the developing cell wall of the pollen mother cell, hence, no microcytes were formed. It would appear that if size of the fragment or the centromere were controlling wall formation, microcytes should have been formed in these instances.

SUMMARY

1. A cytological survey of the meiotic stability of 9 varieties or lines of common wheat _T. aesativum_ L. and of 25 _Triticum-Agropyron_ derivatives was made.

2. The determination of the meiotic stability of the various plants was based on the analysis of the pollen quartets for the frequency of micronuclei.

3. The percentages of normal pollen quartets (Meiotic Indices) were determined for each of the plants.

4. Detailed study of the meiotic behavior of certain of the plants was made and the probable causes for the occurrence of micronuclei were ascertained.

5. The 2n chromosome numbers of several of the plants were obtained. Certain of the _Triticum-Agropyron_ hybrids had 41, 42, 43, and 44 2n chromosomes while one haploid plant with n=22 chromosomes was observed.

6. The results of the survey of the meiotic stability revealed that the varieties or strains of wheat analyzed were generally cytologically stable.

7. The _Triticum-Agropyron_ derivatives were variable in regard to their stability. Certain of the advanced generation hybrids were stable while the F_2 _Triticum-Agropyron_ hybrids exhibited a high degree of instability in most instances.

8. The occurrence of unpaired chromosomes and abnormal chromosome numbers appeared to be the main factors in determining instability of the material studied.

CONCLUSIONS

The method of determining the meiotic stability which is based on the frequency of occurrence of micronuclei at the pollen quartet stage seems to have its greatest value when applied to such material as the intergeneric hybrids. Observations with such material indicate that it would be possible to use this method as an aid in selecting the more stable hybrids for further use. The method fails to measure instability due to genic or minute chromosomal changes unless these changes ultimately lead to lack of homology between the chromosomes and consequent failure of pairing in meiosis.

It is concluded that in order to be most useful, such a method of analysis should be used at the outset of any breeding program involving intergeneric or interspecific crosses and should be applied to the parents involved in the cross as well as to the progeny of succeeding generations.

Inasmuch as some of the hybrids were found to have chromosome numbers differing from the normal 2n complement of common wheat, any future work involving seed stocks of such material should be preceded by cytological study of their chromosome numbers and meiotic behavior.

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THESIS TITLE: CYTOLOGICAL OBSERVATIONS IN WHEAT (*TRITICUM AESATIVUM* L.) AND IN WHEAT X WHEATGRASS (*AGROPYRON ELONGATUM* (HOST) BEAUV.) HYBRIDS

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