Development and structure of Bromus inermis Leyss

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DEVELOPMENT AND STRUCTURE OF
BROMUS INERMIS LEYSS.

by

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A Thesis Submitted to the Graduate Faculty
for the Degree of
DOCTOR OF PHILOSOPHY
Major Subject: Plant Morphology

Approved:

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INTRODUCTION

*Bromus inermis* Leyss., the smooth brome grass, has attained prominence in recent years as a promising grassland and forage crop. The plant is known by a number of common names, Hungarian brome, Austrian brome, Russian brome, awn-less brome, and smooth brome. Its native habitat is variously said to be Eurasia, Russia, and central Europe to China. It was introduced into the United States in 1882 and became widely distributed, especially from 1890 to 1900. Seed was not on the market, however, as late as 1901. Brome grass increased in use in the early part of the twentieth century, but the first world war, with its emphasis on grains, encouraged the plowing up of grasslands rather than their establishment. Brome grass is being utilized with great success in many states today.

Brome grass is a hardy, vigorous, long-lived perennial spreading rapidly by rhizomes. A thick stand is produced in a number of years if moisture conditions are favorable. It remains green all summer in the presence of adequate soil moisture although the plants are more or less dormant after seed production and in mid-summer. Old stands become sod-bound and the plants in such fields are stunted and tend to be chlorotic. In such cases, the yield may be materially reduced.
Brome grass is recognized as one of the best grasses for the prairie and plains states from Canada south to Kansas. In Colorado, the best yields are produced in clay loams but satisfactory growth is also made in sandy soils. It survives under adverse soil conditions and may be considered as adapted to dry, cold climates. Its best growth is made in regions of light to moderate rainfall and low to moderate summer temperatures. Crested wheat grass exceeds brome grass in drought resistance but blue grass is much inferior in this respect. Brome grass has been known to grow at an elevation of 9000 feet.

Brome grass is a nutritious and palatable species with the latter quality persisting up to maturity. It will not pasture as many cattle per acre as sweet clover but its carrying capacity may be greatly increased by planting in combination with alfalfa. In general, it withstands heavy grazing well. Smooth brome grass is used both as a pasture and as a hay grass and strains have been especially selected for these uses. As many as four tons per acre can be obtained with two cuttings.

Because of the increased importance of brome grass as a forage crop in several states, it is desirable to obtain further information regarding its development, morphology, and cytology. Information from this study, particularly the cytological phases, may have a direct application to problems
relating to the development of improved strains through plant breeding.

*Bromus inermis* Leyss. was first described by Leysser (58) in 1761. In a latter work (59), Leysser also mentions the species. The following synonymy was compiled from Hegi (42) and Hitchcock (45): *Festuca inermis* Dc. and Lam. , *F. Leysseri* Moench, *F. poaeformis* Pers., *Schedonorus inermis* Beauv., *Bromus inopinatus* Brues., *B. litoreus* Georgii, *Forasac-
cus inermis* Lunell, and *Zerna inermis* Lindm. Hegi (42) and Piper (78) recognize the following varieties: *pellitus* Beck, *divaricatus* Rohlema, and *pauciflorus* Rohlema. Fernald (31) reduced var. *aristatus* Schur. to forma *aristatus* (Schur.) Fernald and var. *villosum* Mert and Koch. to forma *villosum* (Mert. and Koch.) Fernald. J. W. Moore (63) reported a new form of *Bromus inermis*, forma *bulbiferus* J.W. Moore.
REVIEW OF LITERATURE

The number of papers dealing with aspects of morphology and anatomy in the grasses is large and only those directly concerned with our problem need to be considered here.

Zherebina (104, 105) divided Bromus inermis into a steppe and a meadow type, with the latter subdivided into 1) tall type, 2) bushy type, 3) type with high seed production, 4) type with a low stand of grass. The steppe type was found to be inferior in forage value and succulence to the meadow type but it was superior in drought resistance.

Waldron (90) noted physiological and morphological variation in seedlings of smooth brome grass as well as in members of the same clone. Differences were found in blade length and width, culm height, and crude protein content.

Watkins (93) studied the effects of fertilizers, shade, competition, and photoperiodism in smooth brome grass. In his experiments, fertilizers increased the rate of leaf production, the height and number of shoots, and the dry weight of tops. The number of rhizomes and the weight of the underground parts decreased. Shade decreased the above characters but increased the number of elongated internodes and therefore, the height of the plants. Shading built up the nitrogen but decreased the carbohydrate content. A photoperiod of eighteen hours increased the height of the
plants, the length and size of the rhizomes, the dry weight and percentage and the absolute amounts of carbohydrates. Short-day plants had more shoots than long-day plants. When sown with alfalfa, the number of shoots, the number of rhizomes, and the dry weight increased.

Keyser (53) studied 121 strains of smooth brome grass and was of the opinion that many of the strains bred true. Some progenies, however, were found to break up into strains.

Frolich and Newell (34) noted that smooth brome grass varied considerably in leafiness, height, habit of growth, rhizome development, heat and drought tolerance, disease resistance, and seed-producing qualities. These authors believe that much of the variability in brome grass is environmental.

Waldron (91) compared the coefficient of variation of smooth brome grass with other grasses and found that there was no evident correlation between the homozygous condition of the individuals studied as a population and the amount of variation in regard to height of fertile culms. He found a significant correlation between height and weight.

A few illustrations of variability in other grasses are worth citing here. Wilkins (99) noted that Anthoxanthum and Triticum exhibit morphological variations but that their internal anatomy is uniform. H. Witte (101) found that in Phleum pratense, Dactylis glomerata, Festuca pratensis, and
**Avena elatior**, plants differ among themselves in length and thickness of haulm, leafiness, stooling ability, color, hairiness, inflorescence, winter and rust resistance, time of wilting, and earliness.

Webber (96) found that timothy varies in tallness, stooling ability, number of culms per plant, erectness of culm, number of nodes, length of internodes, length and width of leaves, length and thickness of heads, shape and apex of head, season of maturity and blooming, rust resistance, and growth rates. Hayes and Barker (40) observed that self-fertilized clones of timothy differ widely among themselves. The authors believe this variation is due to genetic causes. Clark (26) had also described variations in timothy.

Gregor and Sansome (36) studied variation in *Phleum*, *Lolium*, and *Dactylis* and found great variation among plants of the same species in regard to erectness of culms and width of leaves. The prostrate character seemed to them to be independent of the environment. The variation exhibited by these three genera was regarded as inherited variation, the phenotype of the plant representing genotypic response to definite habitats.

Brown (18, 19) found that *Poa pratensis* shows morphological variation in open-pollinated plants. He is of the opinion that the low-growing, wide-leaved types originated from the regular hay types by the loss of one genome from the reproductive cycle.
Vinall and Hein (89) recognized that brome grass, orchard grass, blue grass, bent grass, redtop and other grasses are mixed populations of many strains varying in morphological and physiological characters.

Beddows (14) studied flowering and seed-setting in smooth brome grass and came to the conclusion that the species is xenogamous but that pollination is also common between different spikelets of the same plant.

The penetration of the soil by roots of smooth brome grass has claimed the attention of a number of authors. Weaver (95) found that the roots penetrate about 4.7 feet. Ten Eyck (87) recorded a depth of 5.5 feet for two year old plants. Gruber (38) measured a root length of 39 cm. after twelve months. K. Witte (102) found root lengths of as much as 287 cm. Kannenberg (49) noted that after two years in sandy soil, the roots covered 2.48 square meters.

Chrysler (25) found some evidence of a cambium in the nodes of smooth brome grass. Sirrine (83) studied the leaf anatomy of the same species in some detail noting the presence of stomates on both surfaces, thirty-five bundles in the mature leaf, and a difference in the composition of the bundles themselves. Pfitzer (75) and Lohaus (61) also found stomates on both surfaces of the leaf.

The cytology of Bromus inermis has been reported by three authors. Avdulov (7, not seen) reported the normal
diploid complement to be fifty-six. Three years later, the same author (8) confirmed his earlier count. Between Avdulov's first and second papers, Stählin (85) reported forty-two as the diploid number. In 1939, Nielsen (70) confirmed Avdulov's count of fifty-six and added a seventy chromosome race which he discovered. Nielsen noted that the fifty-six chromosome race had thicker and stouter chromosomes and smaller nuclei than the seventy chromosome race. Herbarium specimens of the latter type were larger than those of the other race.

Katterman (50) recorded fifty-six as the diploid number for Bromus erectus var. eu-erectus although Stählin had previously reported the number to be forty-two. A year later, Katterman (51) found evidence that polyvalent chromosomes occur in the variety. Vinall and Hein (89) listed all the chromosome numbers for Bromus known up to 1937, the list including diploids, tetraploids, hexaploids, and octaploids. Nielsen (70) added a decaploid to the series.

Polyploidy is common in other grasses. Agropyron, according to Peto (73) shows a polyploid series having di, tri, tetra, penta, hexa, octa, and decaploid members. There is a wide variation among the plants of a species as well as between the species of the genus. This variation is independent of the environment and is due to natural hybridization. This force also produces intermediate forms.

Fults (35) found six biotypes in Bouteloua gracilis. He
found no relation between the biotype and the chromosome number. One biotype, for instance, was found to have two or three different numbers.

In *Poa pratensis*, Kramer (54) found low correlations between agronomic characters and chromosome numbers. He quoted Müntzing's report that in *Poa alpina* there is no correlation between chromosome number and either vigor or fertility.

Müntzing and Prakken (67) noted that *Secale cereale* is not stable cytologically. This instability was found to be correlated with frequent sterility.

Rancken (79) studied the variation among individual plants in four grasses. In *Festuca pratensis*, nine individuals had a diploid number of fourteen while twenty-one individuals showed a variable number of fragments but the number was constant for each individual. Four individuals of *Poa pratensis* showed a variation in number from sixty-six to sixty-seven. All the plants of *Dactylis glomerata* were constant in number. Nine plants of *Alopecurus pratensis* had a diploid number of twenty-eight but five other plants varied in chromosome number.

Selim (81) reported that five races of *Oryza sativa* have the same chromosome number.

Turesson (88) found that of thirty species examined, five do not have a constant chromosome number.
MATERIALS AND METHODS

The plants used in this study were obtained from the forage crops breeding nursery at the Iowa Agricultural Experiment Station, Ames, Iowa. These plants had been established from open-pollinated single plant selections and strains.

The following plants were examined in the course of the investigation. The first number of the pedigree refers to the accession number of the strain or selection and the last number to the plant in the strain or selection.

255-44, 268-44, 269-39, 272-12, 275-2, 277-6, 291-15,
307-37, 307-45, 307-49, 311-25, 542-17, 542-34,
542-46, 542-47, 542-48, 542-49, 543-1, 543-6, 543-21,
543-28, 543-30, 543-31, 543-34, 543-43, 543-45,
543-46, 543-47, 543-49, 544-6, 544-28, 544-33, 544-34,
544-43, 554-10, 554-21, 554-22, 554-30, 554-39,
554-44, 554-45, 554-49, 555-49.

The above list of forty-nine plants includes sixteen different strains and selections from the following sources:

Strains 554 and 555 were obtained as seed from the Bureau of Plant Industry cooperating with the Washington State Agricultural Experiment Station, Pullman, Washington.

Accession number 307 is a single plant selection made at the Iowa Agricultural Experiment Station, Ames, Iowa. The
plants of this selection are open-pollinated progeny of 307, and hence the male parent is unknown.

Strain 543 originated from a single plant selection made at the Dominion Forage Crops Laboratory, Department of Agriculture, Saskatoon, Saskatchewan, Canada. After selective inbreeding, the third generation inbred progeny of the single plant was increased and distributed under the variety name "Parkland."

Strain 544 also originated at the Dominion Forage Crops Laboratory and was named "University." This strain came from mass selection in ordinary brome grass made with the object of eliminating the widely-creeping type.

Strain 542, called "Superior" was also developed at the Dominion Forage Crops Laboratory.

Accession numbers 255, 268, 269, 272, 275, 277, 291, 296, 298, and 311 refer to single plant selections obtained from old brome grass fields near Ames, Iowa, in 1936.

For the study of chromosome number and behavior in the plants, both root tips and pollen mother cells were studied. Variations of the Nawaschin (Craf) formula, FAA, and Carnoy's fluid were employed as killing agents and a crystal violet-iodine staining technique was used. For the anatomical study of the vegetative organs of brome grass, safranin and fast green were used as stains for the most part. The hot water method of softening embedded tissues was used in the case of the culm, glumes, lemmas, paleas, leaves and other difficult
tissues. Both paraffin and celloidin were used as embedding media.

For the developmental studies, seed was obtained from the nursery and grown in both sand and soil.

A microprojector was used as an aid in outlining some of the drawings.
EXPERIMENTAL RESULTS

Morphological Variation

The following characters were selected for the study of variation:

- rhizomes—creeping or not creeping
- culms—the culms were measured from slightly below the topmost whorl of roots to the tip of the inflorescence, the rachis being considered as the specialized upper, floral part of the culm
- blades—length and width, glabrous or pubescent
- ligules—height, lacerate or not lacerate
- rachises—length from the lowest whorl of flowering branches to the tip, glabrous or pubescent
- secondary branches—glabrous or pubescent
- spikelets—length
- first glumes—length, number of nerves
- second glumes—length, number of nerves
- rachillas—glabrous or pubescent
- lemmas—length, number of nerves, presence or absence of an awn
- paleas—length, number of nerves
- florets—number of fertile and sterile florets in a spikelet
The observations in this study are recorded in table 2 in the appendix. In the preparation of table 2, certain characters were omitted because no marked variability was evident. The rhizomes are always creeping, the rachillas and secondary branches are always pubescent, the paleas are all two-nerved, the lemmas are all five to seven-nerved, the first glume is generally one-nerved, the second glume is three-nerved, the ligule is always lacerate, and the culm is always glabrous except for occasional nodal hairs.

The measurements of the characters are summarized in table 1. Between the strains and selections used, smooth brome grass shows a wide range of variation in the eleven tabulated characters.

Furthermore, within individual strains and selections, there are wide differences as shown in table 2. For example, accession no. 307 shows variation in height of culm, length and width of blade, height of rachis, length of spikelets, and in other characters among the plants of its group. Accession no. 307 was a single plant selection but the plants studied were from open-pollinated seed.
Table 1. Range in Measurements of Various Characters in Bromus inermis by Eight Authors Compared to Measurements of Local Plants Grown at Ames, Iowa.

<table>
<thead>
<tr>
<th></th>
<th>Culm mm.</th>
<th>Sheath</th>
<th>Blade mm.</th>
<th>Ligule mm.</th>
<th>Rachis mm.</th>
<th>Spikelet mm.</th>
<th>First Glume mm.</th>
<th>Second Glume mm.</th>
<th>Lemma</th>
<th>Palea</th>
<th>Floret No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Various Authors</td>
<td>300-1400</td>
<td>glabrous or pubesc.</td>
<td>5-19 wide</td>
<td>.5-2</td>
<td>100-203.2</td>
<td>20-27</td>
<td>4-5</td>
<td>6-8</td>
<td>7-14 equaling lemma</td>
<td>2-10</td>
<td></td>
</tr>
<tr>
<td>Local Measurements</td>
<td>480-1080</td>
<td>glabrous or pubesc.</td>
<td>3.5-9 wide</td>
<td>1-2</td>
<td>80-200</td>
<td>10-30</td>
<td>3-7</td>
<td>4-9</td>
<td>7-13</td>
<td>5-10</td>
<td>3-10</td>
</tr>
<tr>
<td>Total Range</td>
<td>300-1400</td>
<td>glabrous or pubesc.</td>
<td>3.5-19 wide</td>
<td>.5-2</td>
<td>80-203.2</td>
<td>10-30</td>
<td>3-7</td>
<td>4-9</td>
<td>7-14</td>
<td>5-10</td>
<td>2-10</td>
</tr>
</tbody>
</table>
Germination of the Fruit and Development of the Seedling

The following descriptions are representative of the sequence of development of vegetative organs. The indicated rates of development should be understood to represent an average occurring under the favorable and uniform conditions of greenhouse culture.

First and second day after planting: the first observable evidence of germination is the swelling of the entire caryopsis. The radicle grows and pushes the coleorhiza against the pericarp. The coleorhiza then emerges near the base of the dorsal side of the caryopsis. White hairs, less than a millimeter in length, are characteristic of the coleorhiza after emergence. The primary root breaks out of the thin side of the coleorhiza rather than through the denser tip. The primary root thus projects, for a time at least, at right angles to the median plane of the plumule.

Third day: the primary root grows rapidly and is 8 mm. long and the coleoptile is 5 mm. long at this time. The root is densely covered with hairs, except at the tip. Chlorophyll has already formed in the coleoptile.

Fourth day: the first foliage leaf breaks out of the coleoptile to an average length of 4 mm. The upper part of the leaf is chlorophyllous.

Fifth day: the primary root has increased to 18 mm.,
the coleoptile to 10 mm. and the first leaf to 10 mm. Long white hairs occur on both sides of the young leaf, a characteristic feature of all the newly-emerging leaves. The first adventitious root makes its appearance from the region of the scutellar node.

Tenth day: two lateral roots emerge from near the base of the primary root. The adventitious root has no laterals but root hairs are present.

Eleventh day: the first foliage leaf has grown to 75 mm., the primary root has grown to 70 mm., the coleoptile to 20 mm. and the adventitious root to 20 mm. long.

Fourteenth day: the first internode or "mesocotyl" appears and pushes the coleoptile and foliage leaf upward. The lemma, palea, and caryopsis are still adherent to the seedling. The primary root may have eight laterals and be 80 mm. long. The scutellar adventitious root is 30 mm. long. From the coleoptile node, two or three additional adventitious roots arise. The foliage leaf is 85 mm. long.

Seventeenth day: the primary root is now 90 mm. long and bears numerous lateral roots, frequently in recognizable pairs. The scutellar adventitious root is 37 mm. long. The first internode averages 4 mm. in length.

Nineteenth day: the second foliage leaf emerges and grows with striking rapidity.

Twenty-first day: the first foliage leaf has increased
in length to 105 mm. and the second leaf has increased to 72 mm. The first internode is usually 10 mm. long. The ligule on the first foliage leaf is fully-developed, parenchymatous, and soft. It is 1 mm. long and approximately 20 mm. above the coleoptile node.

Twenty-sixth day: the scutellar adventitious root has lateral roots but the coleoptilar roots lack them. The second foliage leaf is 80 mm. long. The coleoptile appears to cover or be continuous with the epidermis of the first internode so that the adventitious roots from the coleoptilar node break through this covering.

Twenty-eighth day: the primary root system comprises the largest part of the root system and is extensively branched, especially at its distal end. The primary root system may have as many as thirteen large lateral roots, many of these branched in turn. By this date, the primary root system may have attained a length of 58 mm. and a width, when fully spread, of 50 mm. The adventitious root system is growing vigorously, and although its largest member is only approximately half as long as the primary root, its diameter is as large.

Thirty-sixth day: many of the adventitious roots from the coleoptile node have now become longer than the primary root system. The second foliage leaf has elongated to 85 mm. and the third leaf has appeared.
Fortieth day: a fourth leaf has emerged. The adventitious roots clearly comprise the larger part of the root system and have approximately the same length as the aerial parts.

Forty-eighth day: the fifth leaf usually emerges at this time and the coleoptile has frequently become shredded off. The first internode and primary roots have turned brownish. The adventitious roots attain a length of 90 mm., there being as many as six roots from the coleoptile node.

Fifty-fourth day: the largest adventitious root is 150 mm. long. Some seedlings planted in pots show three tillers.

Seventy-third day: as many as eight leaves have emerged by this time with the three lowest ones dead.

Ninety-first day: plants in separate pots have five tillers. Seedlings grown in flats have developed no tillers up to this time. The tillers arise from buds in the axils of the lower leaves which break through the lower leaf sheaths, a typical extra-vaginal mode of emergence.

One-hundred eleventh day: as many as ten leaves are present, the lower six being usually dead. The coleoptile node has become greatly swollen as a result of the formation and emergence of adventitious roots. A study was made of seedlings with three tillers. The best developed tiller has a ruptured prophyllum, approximately 5 mm. long, and two
main veins. There are two leaves, each with a distinct sheath 12 mm. long and a blade 3 mm. long. Each leaf has a small ligule. Four other small leaves are present. The second tiller also has a 5 mm. prophyllum. The first or basal leaf, approximately 18 mm. long, has nine veins, no ligule, and no distinction between blade and sheath. Its next highest leaf, which is at least 23 mm. long, has no ligule and no distinction between blade and sheath. The four other leaves have marked distinction between blade and sheath. The third tiller is smaller and younger. Its prophyllum is similar to the others. The first leaf has a sheath 13 mm. long and a 2 mm. blade. The sheath of the second leaf is 23 mm. long and the blade is 5 mm. long. All of the tillers have started to send out roots at their bases.

One hundred twenty-third day: on each culm and tiller there are about as many dead leaves as there are live ones. Each plant has about thirty-eight adventitious roots.

One hundred eighty-ninth day: the primary root is still present but the caryopsis is no longer attached to the plant. Between this date and the two hundred and twenty-first day, two short rhizomes develop, each less than 10 mm. long. The main culm has three tillers at its base and each rhizome has three tillers at its apex. The plant is now well established and shows evidence of spreading. No further studies were made after this date.
Gross Morphology and Anatomy of the Plant

Panicle

The panicle in our specimens varies in height from 80-203 mm. It consists of a central rachis and numerous secondary and tertiary branches. It is wide-spreading but occasionally may be one-sided (Fig. 28). At maturity, the panicle is somewhat contracted. The purplish-brown color of the entire, mature panicle later changes to a straw color.

The secondary branches are arranged in fascicles, each fascicle constituting a half-whorl. The half-whorls are placed on alternate sides of the rachis. The tertiary branches leave the secondary branches singly or they may be in half whorls. In either case, they may terminate directly in a spikelet or branch again before ending in a spikelet.

A single sterile floret is frequently found near the top of the panicle. When present, however, it is overtopped by a normal spikelet.

The rachis is usually glabrous but the secondary and tertiary branches are covered with short, stiff, white, forward-pointing hairs.

Anthesis takes place in late May or early June in Ames, Iowa. On May 1, in the growing season of 1941, the inflorescence was near the ground level and only .5 inch long. On May 4 the paleas, lemmas, and glumes had already developed
and in some cases, the lemmas were awned. The androecia and gynoecia had not differentiated up to that date however. It was noted that panicle primordia arise only in the year of their anthesis.

Anatomically, the rachis is, like the rest of the culm, a hollow cylinder at maturity (Fig. 12). There are two circles of vascular bundles, the outer circle having smaller bundles placed directly within the sclerenchymatous hypodermis. The larger bundles of the inner circle usually alternate with the outer small ones. Each bundle is composed of two to three protoxylem cells and two large flanking metaxylem vessels. Xylem parenchyma, tracheids, phloem, and the thin sheath complete the bundle.

The epidermis is heavily lignified especially on its outer walls. Masses of thin-walled chlorenchyma alternate with the thick-walled hypodermal groups around the periphery of the rachis. Stomates open into these groups of chlorenchyma cells. More chlorenchyma is found in the rachis than in the lower part of the culm. Bridges of thick-walled cells connect the equally-lignified hypodermal groups under the chlorenchyma. The rest of the cortex is composed of thin-walled cells.

In the secondary and subsidiary branches of the rachis (Fig. 11), the epidermal cells are thickened in the characteristic manner, some of them containing silica particles.
Two to three uninterrupted peripheral layers of hypodermal chlorenchyma are found. Centrad to these layers are three to six layers of fiber cells with minute lumens. Imbedded in the outer edge of these fiber layers, there are usually four small, evenly-spaced vascular bundles. The center of the branches is occupied by one to two larger bundles and some thick-walled cells.

Spikelet

The pedunculate spikelet is from 10-30 mm. in length. It consists of two glumes and two to ten florets, and a rachilla. The upper one or two florets may be sterile, consisting of only a lemma, or a lemma and a palea, or a lemma and palea with reduced stamens and pistil.

In shape, the mature spikelets of different clones vary greatly, some being much wider and longer than others. Those plants bearing the larger spikelets are more desirable from the yield standpoint since they have more seeds per spikelet.

The central axis of the spikelet is made up of a disarticulating rachilla. Each segment of the rachilla is about 3 mm. long, and has a convex and a concave side. The latter faces toward the palea while the former always faces out. Rather stiff, white, upward-pointing hairs cover most of the rachilla. The upper end of the rachilla is oblique. At the base of the lemma, a mass of callus occurs, inseparable from the top of the rachilla and apparently fused to it.
**First glume**

The first glume is the smaller of the two bract-like structures at the base of and included in each spikelet. In length, this glume varies from three to seven mm. and is smooth, acute, lanceolate, and has a prominent keel.

Usually, the first glume has one bundle but occasionally glumes are found with three bundles. The chlorenchyma extends over the lower half of the glume, but distally it is confined to the region of the bundle or bundles. Stomates are present on both surfaces.

The internal anatomy (Figs. 19-21) is quite similar to that of the palea and lemma. The outer or lower epidermal cells are heavily lignified on their outer, rippled, tangential walls and on their radial walls, but less so on their inner tangential walls. Silicified cells are scattered in the layer. The hypodermis may or may not be lignified. Below the hypodermis are one to three layers of thin-walled chlorenchyma. The inner or upper epidermal cells are rectangular and thin-walled. The glume margins are usually two cells in thickness.

The bundle contains a few xylem elements, a large mass of phloem, and a bundle sheath which merges with the outer epidermis.
Second glume

The second glume is broader and longer than the first glume, being from 4-9 mm. in length. It is smooth, acute, and lanceolate.

Stomates are present in both surfaces and the distal part of the glume and the margins are free of chlorophyll except in the region of the bundles.

The anatomy (Figs. 17-18) is like that of the first glume except that there are three bundles instead of one.

In the development of the spikelet, the glumes develop before the florets and enclose the whole young spikelet. In maturity, the glumes are much shorter than the spikelet.

Lemma

The lemma (Figs. 24-25), together with the palea, encloses the flower. In length, the lemma varies from 7-14 mm. and it is thicker and greener than the palea. The lemma is elliptical, rounded on the outside, and concave toward the pistil. The margin is translucent, the surface is glabrous distally and pubescent basally.

The tip of the lemma is bifid and may or may not be provided with an awn. The latter, when present, arises from the back, so near the apex that it appears to come from between the lemma tips. The awn may be 2 mm. in length.

There are five to seven nerves or veins, with the center
one and each alternate one larger and hence more conspicuous than those in between. This pattern is similar to that prevailing in the blade itself.

Both the awn and the lemma contain chlorenchyma. In the lemma, it is more abundant near the base and confined to the vascular bundles distally. Chlorenchyma is absent in the margins from base to tip. A thick callus occurs at the base of the lemma.

The outer epidermis is heavily lignified, somewhat more pronouncedly on the rippled outer wall than on the inner wall. Silicified cells, thickened hairs, and stomates are also present.

The hypodermis, of one to two layers of cells, is lignified but to a lesser extent than the epidermis.

Between the hypodermis and inner epidermis there are one to three layers of thin-walled chlorenchyma cells extending the whole width of the lemma.

The inner epidermis consists of rectangular, thin-walled cells without chloroplasts. Stomates occur on both surfaces of the lemma.

The lateral edges of the lemma are composed of a large mass of translucent sclerenchyma cells.

The larger bundles are like those of the palea but the smaller ones have only a few xylem and phloem cells and a narrow bundle sheath.
Pales

The palea (Figs. 22-23) is a bicarinate organ 5-10 mm. in length, protecting the rest of the floret on one side and clasping the caryopsis at maturity. It is concave on its ventral side and its "wings," each about .5 mm. wide, turn back sharply toward the middle of its dorsal side. The keels, one on either side of the concavity, are provided with forward-pointing hairs. In addition, the whole palea is frequently minutely pubescent. The two nerves may be prolonged upward into minute teeth which may cross. In some cases, however, the end of the palea is not split.

The palea is of a more delicate texture than the lemma and is attached to the flower stalk, whereas the lemma is inserted on the rachilla. Both lemma and palea adhere to the fruit in maturity.

The margins of the palea consist of a single layer of slightly lignified cells. This layer of cells appears to be structurally similar to and continuous with the hypodermal layer, a layer which might be considered as the inner layer of a multiple epidermis.

The cell walls of the epidermis proper are thickest on their outer tangential side and on this surface are rippled. Stomates are present in the outer epidermis only.

Below the hypodermis are found one to two layers of chlorenchyma consisting of thin-walled cells. The inner
epidermis contains thin-walled cells also.

The two keels are alike in structure, each having an outer epidermis, a vascular bundle, two to three layers of chlorenchyma, and a inner epidermis. The bundles consist of several xylem elements and a large number of phloem cells. The bundle sheath merges above with the outer epidermis and does not have the endodermis-like layer found in leaf bundles.

Between the keels, the palea is composed of an outer and inner epidermis with a non-chlorophyllous layer in between. The amount of chlorenchyma is greater in the keels than in the margins or in the center.

Lodicule

There are two lodicules in brome grass, inserted on the flower stalk and lying along the basal portion of the inverted "wings" of the palea. They are shorter than the paleas.

During anthesis, the lodicules swell radially, pushing apart the lemma and palea. This action permits the anthers to topple out and the stigmas to protrude.

Vascularization is present in the lodicules, consisting mostly of xylem elements with annular thickenings.
Stamen

The brome grass floret has three stamens, one of which is inserted between the two lodicules (Fig. 7). The filament is short at first but before anthesis it increases several times in length by cell elongation. The filament is composed mainly of parenchymatous tissue with much-elongated nuclei of large diameter. The center of the filament contains two or more annular vessels.

The yellow anther is about 4 mm. long and bifid at both ends. Each anther has two lobes with two locules in each lobe. The anther is basifixed. A small mass of tissue, the connectivum, lies between the two lobes.

The anther wall consists of four layers of cells, epidermis, endothecium, middle layer, and tapetum. The long axis of the epidermal cells is parallel to that of the anther itself. Stomates are present in the connectivum epidermis. The cells of the second or endothelial layer are elongated at right angles to those of the epidermal cells. Thickenings become evident in the endothecium as the pollen grains mature. It is this layer with its thickenings which is responsible for the splitting of the anther apex. The middle layer has the long axis of its cells parallel with those of the epidermis. The tapetum is the innermost layer. At first, the tapetum cells are uninucleate but later they become binucleate by the process of mitosis and the failure of
cell wall formation.

Each pollen mother cell produces four uninucleate, haploid microspores by means of two successive divisions. Each nucleus divides and produces a tube nucleus and a generative nucleus. The latter divides to form two sperms.

The mature pollen grain is spherical in shape, with a granular exine coat and a thick intine coat. There is one germ pore with its opening slightly above the surface. Fresh pollen was found to average 37.6 microns by 42.2 microns but the grains grown on agar were larger because of water imbition.

Fresh pollen stained with aceto-carmine shows two sperms and one tube nucleus. The sperms average 8.25 microns by 4.95 microns while the tube nucleus averages 13.2 microns by 8.25 microns. Starch grains are present in the mature pollen grains.

Pistil

The pistil is inserted on a short flower stalk and consists of a basal ovary and two styles terminating in stigmatic papillae.

The ovary has a high, flattened, ventral side toward the pales and two distinct, shorter lobes on the dorsal or lemma side. The ovary is tricarpellate and uniloculate (Fig. 7). Its dorsal wall is usually six to eight cells
thick with the outer epidermis composed of rather regular cells. The ovary's inner epidermis is chlorophyllous.

The base of the ovary has one large vascular bundle which continues up the ventral lobe, giving off first a branch to the ovule and then a branch to each style. The vascularization in the lobe ceases before the apex of the ovary is reached.

Each ovary contains a single ovule attached directly to the ventral wall, no funiculus being present. The micropyle is directed downward and outward. The ovule is a modified campylotropous type and has two integuments, the outer one disintegrating sometime after fertilization, whereas the inner one finally becomes adherent to the inner ovary wall.

Each style arises from one of the dorsal ovary lobes and branches into feathery, stigmatic branches. Each branch is composed of four rows of elongated, nucleate cells. The distal ends of these cells are free and curved outward, thus forming a receptive surface for the pollen grains.

The upper end of the ovary itself is provided with simple nucleate hairs. These hairs arise at the level at which the lodicules terminate.

**Anthesis**

Flowering in broom grass occurs in late May or early June. An occasional plant may be seen in flower, however,
during later months. Anthesis takes place at Ames, Iowa, in late afternoon. Thermal conditions may play a part in anthesis since one can hasten the process by holding mature spikelets in the hand.

One floret opens each day in each normal spikelet. The duration of flowering for each spikelet is thus dependent upon the number of florets. Flowering in the panicle begins at or near the top and proceeds basally. However, in each individual spikelet, the process progressively proceeds apically.

During the early stages of anthesis, the lodicules absorb water, become turgid, and push the palea and lemma apart. Meanwhile, the filaments have elongated greatly. The three golden anthers tip over, one to one side and two to the opposite side, between the lemma and palea. The two stigmas feather out and one protrudes from each side of the lemma-palea opening.

The distal end of the anther, now hanging downward, splits, and the dry pollen sifts out, aided by the movements of the anthers in the wind.

On windy days, the anthers have been seen to strike their own floret's stigmas. After the pollen is shed, the lips of the anther slit are white.

After shedding, the palea and lemma spring back somewhat, thus protecting the pistil.
Caryopsis

The so-called seed of commerce consists of the caryopsis, palea, lemma, and part of the rachilla. The true fruit or caryopsis is flattened, pointed below, rounded above, and with a tuft of hairs at its distal end. The ventral surface has a ridge. The dorsal surface tends to be slightly concave, and has the embryo at its base.

The caryopsis varies from 6-8 mm. in length, up to 2 mm. in breadth, and almost .5 mm. in thickness.

Only one floret of a spikelet opens each day beginning at the base. The lower caryopses are thus the oldest, and successive stages of maturity occur in a spikelet.

Embryo

The embryo is situated at the base of the dorsal side of the caryopsis, and consists of the scutellum, the coleoptile, one foliage leaf, the stem apex, one primary root, and the coleorhiza. The embryo in soaked seeds is almost 2 mm. long.

The scutellum, which encloses the plumule, has one median bundle (Fig. 8) which branches at the scutellar plate, supplying the primary root, coleoptile, and shoot apex. The posterior or inner surface of the scutellum, in contact with the endosperm, consists of columnar epithelial cells. Most of the scutellar cells are rich in starch.

The plumule has a single, folded foliage leaf, with its
midrib 90 degrees from each coleoptile bundle and 180 degrees from the scutellar bundle. This leaf has three large bundles and two smaller ones (Fig. 8).

The primary root or radicle in the embryo is approximately 0.2 mm. in length. It tapers slightly toward its flattened distal end. A conical coleorhiza covers the tip of the radicle. A meristematic zone, the calyptrigen, lies at the tip of the radicle. The tissues of the coleorhiza in the embryo merge with those of the scutellum. Soon after the coleorhiza has ruptured the pericarp in germination, white hairs develop upon the coleorhiza which adhere to soil particles and hold the seedling in place while the root enters the soil.

Primary root

The primary root, shortly after emergence from the coleorhiza, shows three distinct tissue zones, the epidermis, cortex, and stele.

The epidermis and cortex are composed of thin-walled cells at first. Later, the epidermis and most of the cortex disintegrates while the inner layer of the cortex, the endodermis, becomes lignified. The endodermis is a single layer of cells having greatly thickened radial and inner tangential walls and thin outer tangential walls. The lignification is laminated. Unlignified passage cells are present in the endodermis.
The pericycle consists of a single layer of large, radially-elongated cells between the protoxylem points and usually two layers of smaller cells adjacent to the points. There are commonly four of these smaller cells in a group and these groups lie centrads to the passage cells in the endodermis.

The phloem is radially arranged with respect to the xylem. There are five to six phloem islands each containing three cells. These three cells are arranged together in the shape of a triangle with the apical cell abutting on the pericycle. This apical cell is four-sided, somewhat diamond-shaped, and later enucleate. The phloem forms in this manner: a phloem initial divides to form two cells and soon one of these divides again, making three cells in all.

Between the phloem islands are found enlarged cells which will differentiate into protoxylem vessels. There are one or two of these vessels at maturity between each phloem group. Each vessel is six-sided, smaller than the metaxylem vessels, and is in contact with the small cells of the pericycle.

Almost in the exact center of the root may be seen one or occasionally two metaxyylem vessels. These enlarge before the protoxylem vessels but lignify after them.

In the basal portion of a fourteen day-old root, all of the stelar cells are lignified except the phloem cells
(Fig. 2). At thirty-three days, the protoxylem and metaxylem vessels have developed tyloses. This suggests that the primary root is of little if any importance as a conductive organ by that time.

Adventitious root

The first adventitious roots arise in the five day old seedling at the scutellar node. Other roots arise above the first whorl so that by the fortieth day, their number and length greatly exceed those of the primary system. The adventitious roots form the permanent root system of the plant. They are all fibrous.

The anatomy of the adventitious roots (Figs. 3, 4, 27) is somewhat different from that of the primary root. The epidermis is one cell in thickness and gives rise to root hairs a short distance from the tip. The cortex consists of from six to nine layers of cells, including the endodermis. The cortical cells are elliptical, those nearest the endodermis being flatter. Intercellular spaces are prominent. As the root matures, the cortical cells become flaccid and their walls consequently interlock with each other. The hypodermis also becomes lignified.

In the proximal portion of a fifty-nine day old adventitious root, the endodermis is well lignified and no passage cells are evident.
The pericycle lies inside the endodermis and is considered the outermost layer of the stele. This layer is like that of the primary root, being composed of alternately large and small cells. The small cells are in groups opposite the protoxylem points. They retain their nuclei and cytoplasm longer than do the large cells.

A conspicuous feature of the developing root is the enlargement of a number of central metaxylem cells. As in the primary root, they enlarge before but lignify later than the protoxylem vessels. The number of these metaxylem vessels varies from two to seven with four, five, and six being the more common numbers. They are arranged in a circle around a central mass of cells. All of the stelar cells with the exception of the phloem lignify with age.

The protoxylem originates from enlarged cells adjacent to the pericycle but these cells are smaller in diameter than those of the metaxylem. Each protoxylem point consists of one to two cells, usually one. An interesting feature is that there are frequently twice as many protoxylem cells as metaxylem cells. There may be more than twice as many. One section, for instance, was found to have eleven protoxylem points and four metaxylem vessels.

After the metaxylem vessels enlarge, but before the protoxylem has become conspicuous, the radially-arranged phloem is recognizable. Each phloem group consists of three cells, the outer one being short-lived, probably lysigenous
in character. These three cells form in the same manner as described for the primary root.

The phloem strands are in contact with the larger cells of the pericycle and are alternate with the protoxylem points. There are as many phloem groups as protoxylem points. One cross-section, for instance, showed six metaxylem vessels, sixteen phloem groups and sixteen protoxylem points.

The adventitious roots differ in the following details from the primary root: (1) the adventitious roots are of post-embryonic origin; (2) they have more metaxylem vessels; (3) they have more protoxylem points; (4) they have more phloem groups; (5) the epidermis and cortex functions longer; (6) they live more than one year; (7) they are larger in diameter; (8) they have a pith; (9) there are no passage cells in the endodermis.

First internode

The first internode or "mesocotyl" lies between the scutelllar and coleoptilar nodes. The length of this organ increases with depth of planting, but in no case was it found to exceed 10 mm.

The anatomy of the first internode (Fig. 1) is different from that of the higher internodes. The one-layered epidermis is followed centred by a broad cortex consisting of thin-walled parenchyma cells. The cortex is limited internally
by an endodermis, the cell walls of which are thickened on all but the outer tangential faces.

A definite stele is present, enclosed by a pericycle consisting of a single layer of hexagonal cells. The vascular system consists of four strands. Two of the strands are endarch, each with a large group of collateral phloem. The other two strands are exarch, with radial phloem. The limits of this phloem are difficult to recognize. A pith is present, interrupted by a central cavity. One cortical bundle is present.

Coleoptile

The coleoptile of brome grass has two bundles placed 180 degrees apart and each 90 degrees from the scutellar bundle (Fig. 8). The two bundles arch and converge toward the apex. Occasionally, the basal part of the coleoptile has four bundles but two of these soon terminate. The bundles pass out from the scutellar trace just above the level at which a trace passes into the stele of the radicle.

The phloem is on the dorsal side and consists of approximately twenty sieve tubes and companion cells. The xylem usually consists of three elements placed on the ventral side of the bundle. There is no clear distinction in size between protoxylem and metaxylem. The rest of the coleoptile cells are thin-walled.

The coleoptile has a slit approximately .2 of an inch
from its apex. The opening lies 180 degrees from the scutellar bundle. There is no bud in the axil of the coleoptile.

Culm

The mature culms vary in height from 300-1400 cm. The internodes are solid when young but are hollow at maturity. The schizogenous cavity noted at maturity is produced by a rupturing and collapse of the central parenchyma. The upper internodes are in general longer than the lower ones, the one below the rachis being the longest. The upper internode is thickest in the middle, whereas the lower ones are narrowest at the base.

Occasionally the second internode from the top will be free of the sheath, thus exposing the culm. More than one-half of the highest internode may also be free of the sheath.

The nodes are composed of a solid diaphragm of parenchymatous tissue investing and surrounding numerous vascular bundles. The bundles extend parallel to the internodes, but form an interconnecting network in the nodes. The culm itself is not thickened at the nodes.

More chlorenchyma develops in the upper, exposed parts of the culm than in the lower parts.

The structure of the main part of the culm (Fig. 6) is very similar to that of its upper portion, the rachis. The epidermis is heavily lignified on all but its inner walls. The hypodermis is also lignified, except for small islands
is smooth to the touch and slightly in appearance.

are rare or absent on the inner ventral, the latter layer
sometimes are numerous on the outer dorsal epidermis but
situated in the outer epidermis, the sheath is scabrous.

those on the lowermost leaves are phylloclades. Because of the

At this, in general, the sheath is triangular but occasionally

is present, caused in part by the pressure of the growing

summit but on the side opposite the blade a short slit

shrinkage, or not at all Kept. It is closed above nearly to

The sheath is cuticular in cross-section (fig. 12) and

sheath

is very pronounced (fig. 13).

stratification of cells of the epidermis and leaf primordia
and are characterized by partition walls. Transverse
the corpus, the cells of which are more irregularly polygonal.

or starched nutlets. The central core of cells constitutes
is rectangular, has dense cytoplasm, and a large, spherical

come to two layers of cells with striated walls. Each cell

consists of cells smaller than the broad. The pith in the center of

best studied in young seedlings. It is a compact dome of

The shoot apex, from which the outer differentiates, is

well-defined circles of vascular bundles.

There are two

plates, in the uncovered parts of the stem.

of cells, the walls of which remain thin and develop chlo-
The base of the sheath is swollen near the culm node forming a characteristic thickening at that point. The lower sheaths tend to overlap one another and, unlike the upper sheaths, are often longer than their corresponding internodes.

The upper part of the sheath has its outer epidermis lignified more thickly on the outer wall than on any others. This lignification occurs after the bundle caps have lignified. The cells of the outer epidermis are regular in shape and rather roundish in cross-section unlike those of the inner epidermis. The mesophyll is abundantly supplied with chloroplasts in its outer half. Schizogenous cavities are common between the bundles. The inner epidermis is composed of rectangular cells.

Two types of bundles occur in the sheath. A larger type has protoxylem, metaxylem, tracheids, xylem parenchyma, sieve tubes, companion cells, border parenchyma, bundle sheath, a huge bundle cap on its outer surface (Fig. 16) and a few lignified elements on the inner surface of the bundle. The bundle cap frequently projects over the outer epidermis of the sheath.

The smaller type alternates with the larger ones, is sunken midway into the mesophyll, and is composed only of border parenchyma, bundle sheath, a few xylem elements, and a larger number of phloem cells. Later, a bundle cap
develops but the two types can be readily distinguished.

Basally in the sheath, the outer epidermis is more heavily lignified, chloroplasts are not as plentiful in the mesophyll, and the inner epidermis is more regular. The small bundles are not so different in composition from the larger ones, having usually only a smaller bundle cap. There are no lignified cells along the inner edge of the bundles.

**Blade**

The blade was found to vary from 3.5 mm. to 19 mm. in width and from 100 mm. to 400 mm. in length (Fig. 29). It is convolute in the bud.

When young, the blades as well as the sheaths are purplish at the base. Mature blades are flat, green, taper to a point, diverge at an angle from the stem, and are slightly keeled below and almost ridgeless above. The keels and ridges are external manifestations of the vascular bundles. The leaves are distichous, forming two rows lying in one plane.

Bands of chlorenchyma are situated in the blade. They are wider, greener, but less numerous than those in the sheath.

Stomates are present on both surfaces but they are more numerous on the upper epidermis. There are generally two to three rows of stomates with their long axes parallel with that of the midrib followed by several rows of long cells.
with no stomates. Present on most of the aerial portions of the plant, stomates are similar in appearance throughout. They consist of two narrow guard cells with thickenings on their internal faces. The lumen and nucleus of each guard cell is dumb-bell shaped. The two accessory cells surrounding the guard cells laterally are wider and have large, elliptical nuclei. The stomate is sunken slightly below the epidermal surface. The stomates average 40-41 microns in length and 23-24 microns in width.

All young leaves are pubescent on both surfaces but mature ones are usually glabrous. The edges are scabrous due to the forward-pointing, one-celled, marginal spines. These latter have their walls and apices greatly thickened. The spines vary in length from 58.8 to 64.7 microns. Each spine has one or two short cells with thickened walls near it. The average length of these cells is about 17.6 microns.

A ligule is present at the junction of the blade and sheath. It varies in height from .5 to 2 mm. and is membranous, short, truncate, and lacerate at its summit.

Auricles may be present on young plants but were not seen on mature specimens.

The blade consists of an upper and a lower epidermis, vascular bundles, and mesophyll.

The upper epidermis consists of the common epidermal cells, bulliform cells, stomates and hairs. The unspecialized epidermal cells lie in rows between the bulliform cells and
directly over the vascular bundles. These cells are slightly narrower over the bundles becoming progressively larger until they meet the bulliform cells. In cross-section they are rounded or slightly elliptical and their outer wall is heavily cuticularized.

The bulliform or "motor" cells are in groups of from three to seven rows extending down the length of the blade and lying between the bundles (Fig. 14). They are large and elliptical in cross-section. Reduction of the turgor in the bulliform cells causes their collapse and the consequent rolling of the leaf. Bulliform cells occur only on the upper surface of the blade.

The leaf hairs which originate in epidermal cells are nucleate, single-celled structures.

There is no palisade layer. Some of the sub-epidermal cells may be isodiametric in shape but most of them are irregular in shape, each with several lobes. The term "spongy" mesophyll is applied to this tissue and its cells as well as those of the border parenchyma, to be mentioned later, contain chloroplasts.

The lower epidermal cells are all of equal diameter in cross-section and externally cuticularized. Stomates and hairs similar to those of the upper epidermis are present.

In a leaf fourteen days after germination, only five bundles were found and in one thirty-three days old, five to seven bundles had developed. The mature leaf may have
twenty-seven or more bundles.

The midrib bundle is the largest and the bundles on either side of it are alternately small and large in a definite pattern (Fig. 14). The midrib bundle is distinguished from all others by a large, wedge-shaped mass of sclerenchyma on its lower side, producing the keel of the midrib. The large cap on the upper side is flatter. The outer walls of the superficial sclerenchyma cells are wavy or rippled. Many of the large bundles have sclerenchyma either above or below, or both. This tissue is completely lacking in some bundles. In general, there is more sclerenchyma below the bundle than above. This fact accounts for the prominence of the veins below and their relative obscurity above. The mature fibers in the bundle caps average 11.7 microns in width and range from 936 to 1117 microns in length. Cell walls of the bundle cap become completely lignified shortly after the fifty-ninth day from germination.

Each vascular bundle is enclosed by border parenchyma cells and an endodermis (Fig. 15). The former is composed of a single, continuous layer. Each cell of this layer is elongated with its long diameter parallel with that of the blade. The cells contain chloroplasts, and have large nuclei.

The endodermis is also a single layer of cells. Its thick, inner tangential walls are lignified. The thickenings on the radial walls taper to a point where they meet the
outer tangential walls. No passage cells are found. The endodermis is fully lignified by the thirty-third day after germination.

The leaf has two types of bundles with respect to relative quantities and types of xylem and phloem. The larger bundles contain several protoxylem elements with annular or spiral thickenings, two metaxylem vessels, a small number of tracheids, xylem parenchyma, sieve tubes, and companion cells. The functional phloem is metaphloem.

The smaller bundles are usually made up of phloem with only a few small xylem vessels.

In favorable longitudinal sections, bundle branches can be seen connecting one bundle with another. These branches are not frequent however.

Prophyllum and tiller

The buds in the axils of the lower leaves develop into tillers and rhizomes. Tiller buds are covered by a two-keeled, two-veined protective organ, the prophyllum. Its bundles, like those of the coleoptile, are placed 90 degrees apart. The tillers make their appearance within eight weeks from germination. They emerge by breaking through the sheath in typical extravaginal fashion.

The first leaves of the tillers to emerge are atypical in form and the blade may be extraordinarily short or absent.
Leaves that emerge later have a more characteristic morphology. These peculiarities have little if any counter-part in the development of the main shoot.

The leaves of the tillers in brome grass are placed at right angles to those of the main shoot and similarly, leaves developing from buds in the axils of tiller leaves are oriented at right angles to those of the tiller itself.

**Rhizome**

The rhizome is a subterranean, creeping organ aiding in the lateral expansion of the plant and chiefly responsible for the production of the sod-bound condition so characteristic of this species. Certain strains such as Parkland are non-creeping but they do have short rhizomes.

Potted plants develop short rhizomes after about six months of growth. The internodes on mature rhizomes average 11 mm. in length.

When young, the rhizomes are white but become brown in maturity, covered by brown, papery scales, originating at nodes.

The apex of the rhizome develops leaves which emerge after the rhizome tip has come to the surface. Nodal buds also develop on the rhizome and subsequently become leafy shoots.

Near the distal end of the rhizome, only the protoxylem
elements are lignified but basally, lignification proceeds to a remarkable degree.

In the mature rhizome, the epidermis and one-layered hypodermis are thick-walled and strongly lignified (Figs. 9, 10, 26). The cortex consists of thinner-walled cells. Small cortical bundles are present, each consisting of a broad, bundle sheath, a small number of phloem cells and a lesser number of xylem elements.

The endodermal cells are greatly thickened and lignified on their inner tangential and radial walls. The thickenings appear to be laminated. The endodermis may be double locally.

Great lignification is also apparent in the pericycle. A series of vascular bundles lie in contact with, and partly imbedded in this region, barely discernable as separate bundles.

A small number of bundles lie in the thick-walled pith region. In general, they consist of bundle sheath, two to three protoxylem elements, two metaxylem trachea, xylem parenchyma, tracheids, sieve tubes, and companion cells.

The lignification of the bundle sheath cells in the rhizome scales has been entirely completed before comparable cells in the rhizome itself have lignified.
Cytology and Chromosome Numbers in Strains and Selections

Mitosis

Mitosis is most easily observed in the root tips. In addition to the nuclear reticulum, each prophase nucleus contains one to five nucleoli. The nucleoli are usually spherical and vary in size, ranging from 1.45 microns to 6.80 microns.

Somatic chromosomes at metaphase are predominantly J and V-shaped, with sub-median and median spindle fiber attachment (Fig. 30). They vary in length from 4.41 microns to 6.82 microns and are of a uniform diameter of approximately .65 microns.

Mitosis appears to be rather regular in brome grass. Precise metaphase alignment of the spindle fiber attachments occurs. No evidence of lagging was noted and all of the chromosomes arrive at the poles simultaneously.

Meiosis

The pollen mother cells are favorable for studies of some aspects of meiosis. Early prophases were not emphasized in the present study. Late prophase chromosomes are all straight rods. Previous to diakinesis, the chromosomes range in length from 5.8 microns to 8.3 microns but during
diakinesis they are shorter, measuring from 2.6 microns to 5.2 microns. One nucleolus is present in prophase, persisting up to late diakinesis. Chiasmata are evident but no detailed study was made of them.

At metaphase (Fig. 33) the chromosomes range from 1.3 microns to 2.6 microns in length. Usually the metaphase plates exhibit only bivalents, but occasionally both bivalents and univalents are found on the same plate.

Usually all the pollen mother cells of a field exhibit the same stage of meiosis but occasionally both metaphase and anaphase or even metaphase and telophase figures are found together.

During anaphase, marked irregularity is evident (Fig. 32). In some cells, a few chromosomes reach the polar region well in advance of the majority. More frequently, a few chromosomes lag and reach the poles late. Some bivalents evidently fail to disjoin as quickly as others. An unusual case was noted in which twenty-eight bivalents, the normal number for that plant, separated into two groups of fourteen bivalents each, which moved to opposite poles as bivalents.

Many of the laggards arrive at the poles in time to be included in the telophase nuclei. Frequently, however, one or more chromosomes may be observed lying in the cytoplasm near the reorganized nuclei. These chromosomes probably disintegrate because they are not often seen in the diads.
Occasionally, chromosomes become enmeshed in the partition wall of a diad.

The second division follows the first division quickly. The spindle is oriented at right angles to the spindle of the first division and in the same plane (Fig. 31), resulting in the four microspores lying in one plane. In general, the second division exhibits regularity but precocious as well as lagging anaphase separation may be observed. The four microspores frequently show chromatin material in the cytoplasm left from either the first or second divisions or both.

Chromosome numbers in the strains and selections

The chromosome number was determined in twenty-seven plants belonging to fifteen strains and selections. The numbers by which these strains and selections are designated, and their diploid chromosome count follows:

<table>
<thead>
<tr>
<th>Strain or Selection Number</th>
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DISCUSSION

Morphological Variation

In compiling the known ranges of measurements for eleven characters in *Bromus inermis*, as shown in Table 1, many authors were consulted but no higher or lower limits for the characters were found than those provided by Hegi (42), Hitchcock (44, 45), Shear (82), Waldron (80), Stebler and Schröter (86), Armstrong (6), Beal (12), and Nowosad, Swales, and Dore (71).

It is to be noted that in Table 1, the present author's measurements of height of the culms, condition of the sheath, length of the ligule, length of the lemma, length of the blade, and the number of florets per spikelet, all fall within the previously published ranges.

Blades occur, however, which are 3.5 mm. wide or narrower than any hitherto reported. The shortest rachis measured was 80 mm. or 20 mm. shorter than any measured by the various authorities. Some spikelets and some first and second glumes also fall outside the reported limits.

Waldron (80), Zherebina (104, 105), and Frolich and Newell (34) studied some characters and their variation in smooth brome grass. The present study, however, deals for the most part with characters not studied by the above
writers. These newly-studied characters are: hairiness of the sheaths, height of the ligule, lengths of the rachis, first and second glume, lemma and palea, spikelet, and the number of florets per spikelet. These characters exhibit marked variation between strains and selections and emphasize further the high degree of variability in this species.

In showing great morphological variation, smooth brome grass follows the pattern shown by other grasses such as Anthoxanthum, Triticum, Phleum, Dactylis, Avena, Poa, Lolium, Agrostis, Agropyron, and Bouteloua.

Germination of the Fruit and Development of the Seedling

In smooth brome grass, the coleorhiza emerges before the plumule. Percival (74) found the same course of events in wheat. The emergence of the primary root from the side of the coleorhiza in brome grass finds a counterpart in Holcus Sorghum, as reported by Chi (24). Zinn (106) was of the opinion that this lateral emergence of the primary root is normal for grasses.

The first foliage leaf in brome grass breaks out of the coleoptile on the fourth day as it also frequently does in Bouteloua curtipendula (72). In Holcus Sorghum (24), the first foliage leaf emerges one week after planting. Chi (24) also noted that the first adventitious root from the
scutellar node became evident ten days after planting in the field, whereas in brome grass seedlings, in greenhouse flats, the same organ emerges on the fifth day. The same author found lateral roots on the primary root as early as the second day, but in brome grass this does not occur until the eighth day. In Bouteloua curtipendula, Olmstead (72) noted that the first foliage leaf had grown in length to 90 mm. by the twelfth day but in brome grass this length is not reached until the seventeenth day.

A great difference is to be noted in regard to the functioning of the primary root in Triticum and in Bromus inermis. In the latter plant, the xylem of the primary root develops tyloses as early as the thirty-third day, impairing if not halting entirely the water-conducting power of the root. In Triticum (74), Percival believed that the primary root functions up to harvest time.

In brome grass, the first five leaves die sometime between the seventy-third and the one hundred eleventh day while in Bouteloua curtipendula (72), an equal number are dead between the twenty-eighth and the fifty-sixth day.

There are two main phases in the development of the brome grass plant, as in most grasses. In the first phase, the fruit germinates into a seedling but the growing point or shoot apex remains at or near the ground level. The leaves differentiate and grow and the buds in the axils of
the basal leaves develop into tillers and rhizomes. The adventitious root system assumes dominance over the primary system and the plant stores up quantities of food.

In the second phase, the internodes elongate rather rapidly and the inflorescence differentiates and develops. Pollination and fertilization occur, the embryo develops and the fruit matures. Bonnett (16) and Evans and Grover (30) have noted the same events in other grasses. In the second year, the tillers store up food, develop their root system, and send up the shoot apex rapidly. Shoots develop from the ends of the rhizomes in the first and in succeeding years.

Gross Morphology and Anatomy of the Plant

Anatomical comparison of various organs of smooth brome grass and those of other grasses reveals some striking similarities and differences. Some features of the inflorescence will be discussed first. The restriction of the chlorenchyma in the glumes to the lower half, and to the region of the bundles in the upper half of the glumes resembles the condition found in wheat (74). The enclosure of the entire, undifferentiated spikelet by the glumes in smooth brome grass is also characteristic of oats (41).

Philipson (76) outlines the theories relating to homologies of the lemma. The lemma is inserted on the rachilla
and not on the flower stalk and, therefore, the lemma cannot be homologous with a perianth segment. The lodicules, on the other hand, are regarded as a reduced perianth. Hackel (39) homologizes the awn of the lemma with the blade of the grass leaf. The part of the lemma above the insertion of the awn is the homologue of the ligule and that part below is the homologue of the sheath. According to this view, lemmas of brome grass plants that lack an awn, lack the ancestral blade. In grasses having a number of awns as in Aristida, one must conclude that each lemma had a large number of ancestral blades.

In smooth brome grass, the paleas are longer than the lodicules. The spreading of the lemma and palea in anthesis is caused by the swelling of the lodicules as in other grasses. Annular vessels occur in the tissues of the lodicules. Weatherwax (94) also found vascularization in the lodicules of Zea and Rowlee (80) noted the same condition in other grasses.

Smooth brome grass follows the pattern of other grasses with respect to the insertion of one of its three stamens between the two lodicules. Stebler and Schröter (86) state that the anthers of grasses are versatile whereas Bews (15) considers them to be basifixed. Definitions of versatile are confused in the literature. Lindley (60) defines versatile as being attached near the middle, whereby the two
halves are nearly equally balanced, and can swing freely. If we accept Lindley's definition, then the anthers of smooth brome grass are basifixed. The annular vessels found in the filament have a counterpart in the filament of the wheat anther as noted by Percival (74). This type of thickening is characteristic of tissues undergoing rapid elongation. The tapetum cells of *Bromus inermis* are binucleate at maturity as in *Agropyron repens* (64) and *Triticum vulgare* (74). The pollen grains in *Bromus inermis* contain three nuclei, two sperms and one tube nucleus. Elfving (28) noted the same condition in *Bromus erectus*. Wodehouse (103) characterized the pollen grains of the gramineae and *Bromus inermis* conforms closely to the accepted pattern.

The innermost layer of the ovary wall in *Bromus inermis* appears to be chlorophyllous as in *Poa pratensis* (1). The vascularization of the ovary is simple as Percival (74) also found in *Triticum* and Walker (92) found in *Bromus unioloides*.

Anthesis in smooth brome grass occurs at Ames, Iowa, during the late afternoon. The sequence of events is the same as that described for the species by Beddows (14). In Great Britain, however, the process takes place about 2:00 p.m.

Boyd and Avery (17), Merry (62), and others have discussed the homologies of the embryo of the grasses. The
present writer regards the scutellum as the first leaf or cotyledon and the coleoptile as the second leaf. Both the cotyledon and coleoptile are, therefore, greatly modified leaves. The embryo of *Bromus inermis* has no epiblast, a condition said by Bruns (20) to be characteristic of the genus.

Smooth brome grass has only one seminal root, as also was found in timothy by Evans (29) and sorghum by Chen (23). Oats, according to Hector (41), has from one to five. In the dormant sorghum embryo, the radicle is 1 mm. long, whereas in smooth brome grass it is but .2 mm. long. Numerous laterals develop subsequently on the primary root as in wheat (74) and sorghum (24), originating in the pericycle opposite the phloem. Jeffrey (48) pointed out that the lateral roots of vascular plants originate in the pericycle, opposite the protoxylem points, except in the grasses.

The pericycle consists of both large and small cells. The latter lignify later than do the protoxylem vessels. In barley, Hector (41) designates as protoxylem certain cells that seem to have the position of the small pericycle cells of *Bromus*.

The phloem is similar in origin and appearance to that existing in sorghum (24). Of the three cells of the proto- phloem group, the more peripheral cell is very short-lived, losing its contents and becoming essentially a lysigenous
cavity. Chauveaud (22) recognizes this cell as a sieve tube.

The presence of one or more metaxylem vessels in the center of the primary root is characteristic of grasses, occurring in brome grass, sorghum (24), wheat (74), and rice (41). The expansion of the metaxylem vessels before the maturing of the protoxylem is common in grasses. As Jeffrey (48) pointed out, this sequence is unusual among vascular plants.

In at least one particular, brome grass adventitious roots resemble those of *Bouteloua curtipendula* (72). In both grasses, the adventitious roots become the important absorptive system by the sixth week after germination.

There has been considerable controversy regarding the homologies of the coleoptile. Sargent and Arber, according to Avery (9), believe that the coleoptile represents two fused stipules, because it has two vascular bundles in a number of grasses. *Festuca rubra tenuifolia* (Howarth 47) and *Bromus inermis* generally have two bundles. However, Percival (74) found two to six bundles in the coleoptile of wheat, and Avery (9) found two to five bundles in that of *Zea Mays*. The latter author (10) believes that this variation in the number of bundles indicates that the coleoptile is homologous with a foliage leaf. The anatomy of the bundles in brome grass is very similar to that in wheat (74). Evans (29) prefers to use the term coleophyll (sheath-leaf),
rather than coleoptile (sheath-feather).

An examination of a number of culm apices demonstrates that neither the apical cell theory of Hofmeister and Nägeli nor the histogen theory of Hanstein are applicable in smooth brome grass. The tunica-corpis theory of Buder and Schmidt, as outlined by Foster (33) does seem to be consistent with the observed facts.

The literature on the anatomy of the grass leaf is voluminous. Some of those who have investigated this structure are: Fisher (32), Grob (37), Holm (46), Lewton-Brain (57), Percival (74), Ball (11), Lohauus (61), and Sirrine (83). Arber (2) believes the grass leaf has no lamina, the limb corresponding to the petiole of a dicotyledonous leaf.

Sirrine (83) found as many as thirty-five bundles in the blade of smooth brome grass. The specimens used in the present study showed a maximum of only twenty-seven. Surrounding each bundle is a layer of border parenchyma cells which is said by Lewton-Brain (57) to act as a transfusion tissue. Carleton (21) states that this layer delivers food from the mesophyll cells to those of the bundle.

Directly inside the border parenchyma is an endodermis-like sheath with cell walls thickened on three sides. This same condition was noted by Arber (5) in *Bromus hordeaceus*.

Smooth brome grass ligules are without vascularization as is true of other grasses investigated by Arber (5) and
Percival (74). Philipson (77) investigated the ligule in some grass species and came to the conclusion that the ligule consists of the free, upper portion of the sheath and a median upgrowth of the adaxial epidermis of the leaf. Kennedy (52) believes the ligule to be a double-sheathing axillary stipule.

The prophyllum is variously regarded as a single, modified leaf (2) and as two leaves (27).

Smooth brome grass has well-developed tillers before the eighth week. By way of comparison, Mueller (65) reported that Bouteloua curtipendula, B. gracilis, Andropogon furcatus, and Panicum virgatum tiller in three weeks and Sorghastrum nutans tillers in four weeks.

The internodes on the rhizomes in smooth brome grass average 11 mm. in length. The internodes of Andropogon scoparius and Panicum virgatum are shorter (65). The rhizome scales in smooth brome grass have strong mechanical tissue as was found in other grasses by Hellstroem (43).

Arber (3, 4) believes amphivasal bundles to be common in the rhizomes of the monocotyledons. Lauder-Thompson (56) found this type of bundle in the nodes of Spartina Townsendi. In the stele of Bromus inermis, the bundles are greatly modified by lignification.
Cytology and Chromosome Numbers in Strains and Selections

Müntzing (66) estimates that at least one hundred species of plants are known to have intraspecific races differing in chromosome number. Such races show morphological variation as well. This variation is well illustrated in Phleum pratensis, P. alpinum, Aegilops triaristata, A. crassa, Festuca ovina, F. pratense, Tripsacum dactyloides, and Dactylis glomerata. The same author further states that 50 percent of all known angiosperms are polyploids. Beck and Horton (13) noted that both Bromus villosus and B. marginatus are polyploids and show irregularities in their chromosome behavior.

In the present study, twenty-seven plants belonging to fifteen strains and selections were examined; five of these are octaploids, the diploid number being fifty-six, and twenty-two are hexaploids, the diploid number being forty-two. Avdulov's and Nielsen's count of fifty-six for Bromus inermis and Stählin's count of forty-two are all confirmed. No race with seventy chromosomes such as Nielsen found was noted in this study. It appears that, in common with other grasses, Bromus inermis is variable both morphologically and cytologically. Emphasis is laid on the fact that all the plants used in this study were grown under similar soil and moisture conditions in a relatively uniform breeding nursery.
There seems to be no correlation between the chromosome number and morphological characters. For example, many of the forty-two chromosome plants have longer and wider leaves and taller culms than some of the fifty-six chromosome type plants.

Seeking some cause for variation in the grasses they studied, Hayes and Barker (40), Gregor and Sansome (36), and Peto (73) attributed variation to inheritance. Brown (19, 19) regards variation in *Poa pratensis* to be due to the loss of one genom. Frolich and Newell (34), on the other hand, believe that variation is due largely to environmental factors.

White (98) believes that variability depends upon the gene pattern, gene stability or instability, and the effect of the environment. The gene change may be either chemical or structural.

In view of the fact that *Bromus inermis* varies greatly morphologically and that cross-pollination freely occurs, it seems reasonable to suggest that the natural crossing between plants is responsible for some of the known chromosome irregularities. These irregularities may furnish some basis for the morphological variation in the species. It is also probable that the environment exerts an influence upon the expression of the characters.
SUMMARY

Measurements on eleven morphological characters in *Bromus inermis* revealed five characters which vary to a greater extent than previously reported. These characters are blade width, length of rachis, length of spikelet, length of first glume and length of second glume.

The first foliage leaf appears in the seedling on the fourth day, the second leaf on the nineteenth day, the third leaf about the thirty-sixth day, the fourth on the fortieth day, and the fifth on the forty-eighth day. The first adventitious root emerges from the scutellar node on the fifth day. The first internode appears on the fourteenth day. Tillers emerge on the fifty-fourth day.

Morphological and anatomical investigations were made on the panicle, rachis, secondary branches, spikelet, first glume, second glume, lemma, palea, lodicule, stamen, pistil, caryopsis, embryo, primary root, adventitious root, first internode, coleoptile, culm, sheath, blade, prophyllum, tiller, and rhizome. The structure of the rachis is much like that of the culm itself. The first and second glumes and the lemma have some of the anatomical features of foliage leaves. In the other organs, smooth brome grass resembles other grasses which have been investigated.
Mitosis in the root tip cells is regular. The somatic chromosomes range in length from 4.41 microns to 6.82 microns in length and are approximately .65 microns in diameter.

Metaphase meiotic chromosomes range from 1.3 microns to 2.6 microns in length. Precocious disjunction and lagging were observed in the first and second divisions.

Twenty-seven plants belonging to fifteen strains and selections were examined for chromosome number. Five of the plants have a diploid number of fifty-six and twenty-two plants have a diploid number of forty-two chromosomes.

Natural crossing between the highly variable strains and selections is believed to account for at least some of the chromosome irregularity exhibited by the species. Meiotic irregularities in the pollen mother cells possibly account for some of the morphological variation shown by Bromus inermis. The environment may affect the expression of characters.
LITERATURE CITED


59. ———. Flora Halensis (Editio Altera et Reformata). 1783.


ACKNOWLEDGMENTS

The writer takes this opportunity to express his appreciation to Dr. J. E. Sass for suggesting the problem, and for helpful encouragement and advice throughout the course of the investigation and during the preparation of the manuscript. The writer also wishes to thank Drs. G. J. Goodman and I. J. Johnson for advice during the preparation of the manuscript and to Dr. C. P. Wilsie for the use of brome grass plants in the Iowa Agricultural Experiment Station.
APPENDIX
Table 2. Measurements of Various Characters of Plants of *Bromus inermis* Grown at Ames, Iowa

<table>
<thead>
<tr>
<th>Strain and Plant</th>
<th>Culm mm.</th>
<th>Sheath</th>
<th>Blade mm.</th>
<th>Ligule mm.</th>
<th>Rachis mm.</th>
<th>Spikelet mm.</th>
<th>First Glume mm.</th>
<th>Second Glume mm.</th>
<th>Lemma mm.</th>
<th>Palea mm.</th>
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*f* = fertile, *s* = sterile
Table 2. (Continued)

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PLATE I

Fig. 1. Cross-section of first internode showing relative size and position of stele and cortical bundle. x67.

Fig. 2. Cross-section of mature primary root showing disintegration of the cortex. x200.

Fig. 3. Cross-section of endodermis and stele of old adventitious root showing the extent of lignification. x200.

Fig. 4. Cross-section of endodermis and stele of young adventitious root showing no lignification. x100.

Fig. 5. Stem growing point. Longitudinal section. x200.

Fig. 6. Detail in a section of the culm. Note thick-walled epidermis and hypodermis and thinner-walled chlorenchyma over bundle. x133.

Explanation of Plate: CB, cortical bundle; ST, stele; PH, phloem; MX, metaxylem; PX, protoxylem; EN, endodermis; LF, leaf; TU, tunica; CS, corpus; C, cortex; PE, pericycle; E, epidermis; HY, hypodermis.
PLATE II

Fig. 7. Cross-section of ovary, lodicules, and filaments. Note the one filament placed between two lodicules. The ovary has one ovule. x67.

Fig. 8. Cross-section of embryo through the plumule. Note the position of vascular bundles in scutellum, coleoptile, and leaf. x100.

Fig. 9. Detail of a section of old rhizome. Note extensive lignification especially in endodermis. x233.

Fig. 10. Outline drawing of old rhizome showing position of bundles. x50.

Fig. 11. Cross-section of secondary branch. Chlorenchyma lies under epidermis. Note placing of vascular bundles and large number of fibers. x133.

Explanation of Plate: Fl, filament; OW, ovary wall; OV, ovule; LO, lodicule; SC, scutellum; LF, leaf; CO, coleoptile; MX, metaxylem; EN, endodermis; HY, hypodermis; E, epidermis; BU, bundle; SCL, sclerenchyma; CHL, chlorenchyma; PH, phloem.
PLATE III

Fig. 12. Detail of section of rachis. x233.

Fig. 13. Outline of sheath showing extraordinary development of bundle cap. x27.

Fig. 14. Outline of leaf showing relative position of bundles and bulliform cells. x14.

Fig. 15. Detail of a leaf bundle. Note endodermis-like layer around bundle. x600.

Fig. 16. Detail of a sheath bundle, much cell detail omitted. x135.

Explanation of Plate: E, epidermis; CHL, chlorenchyma; SCL, sclerenchyma; BU, bundle; PX, protoxylem, MX, meta-xylem; PH, phloem; EN, endodermis; XP, xylem parenchyma; TR, tracheid; UE, upper epidermis; BC, bulliform cells.
Fig. 17. Outline of second glume showing three vascular bundles. x67.

Fig. 18. Detail of section of second glume. x300.

Fig. 19. Detail of first glume showing lignified epidermis and hypodermis. x233.

Fig. 20. Detail of lateral tip of first glume. x233.

Fig. 21. Outline of first glume showing one bundle. x100.

Fig. 22. Outline of palea showing a bundle in each keel. x67.

Fig. 23. Detail of a keel of the palea. x300.

Fig. 24. Outline of lemma showing seven bundles. x67.

Fig. 25. Detail of a section of lemma. Note lignified epidermis and hypodermis. x233.

Explanation of Plate: BU, bundle; ST, sieve tube; UE, upper epidermis; CHL, chlorenchyma; LE, lower epidermis; HY, hypodermis; CC, companion cell; X, xylem; SCL, sclerenchyma.
PLATE IV
PLATE V

Fig. 26. Detail of a section of rhizome showing thickened endodermis. x400.

Fig. 27. Cross-section of adventitious root. x184.

Fig. 28. Variation in panicle form of two selections. 1/3 Nat. Size.

Fig. 29. Variation in width of blade of miscellaneous selections. 1/3 Nat. Size.
PLATE VI

Fig. 30. Mitotic metaphase in a root tip cell of a forty-two chromosome plant. x800.

Fig. 31. Metaphases of first and second divisions in pollen mother cells. x800.

Fig. 32. First and second divisions in pollen mother cells. Lower right hand figure is a first division figure with some lagging. Left center figure is a second division with no lagging. x800.

Fig. 33. Meiotic metaphase of first division in a pollen mother cell of a forty-two chromosome plant. x800.