CYTOHISTOLOGICAL STUDIES OF THE OVULE AND ANTHER PRIMORDIA, WITH PARTICULAR EMPHASIS ON MITOTIC BEHAVIOR IN TRITICUM X AGROPYRON HYBRIDS

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INTRODUCTION

Since the first natural hybrids of Triticum spp. x Agropyron intermedium (Host.) Beauv. were found in Russia in 1930, they have received considerable attention in breeding programs throughout the world. The objective in these programs has been the attempt to incorporate into wheat certain Agropyron characters such as winter hardiness, drought resistance, perennial growth habit, rust resistance, and resistance to various other fungus and insect diseases.

Along with these breeding programs, cytological studies have been made in an attempt to determine genome homologies which might be present between the Triticum and Agropyron genera. These studies have resulted in much conflicting evidence as to the chromosome behavior of the hybrids during meiosis of the various individual lines. In spite of the difficulties encountered, there have been successful hybrid lines established in which desirable characters of both Triticum and Agropyron have been combined.

The purpose of this work was to study the ovule and anther development and the mitotic processes involved in the differentiation of the archesporial cells of seventh generation (Triticum spp. x Agropyron elongatum) x Pawnee wheat hybrids. The development of the embryo sac was also examined in the samples which were far enough along to show differentiation.

REVIEW OF LITERATURE

History of *Triticum*-*Agropyron* Hybrids

Research into the development of a perennial wheat by the use of hybrids between *Triticum* spp. and *Agropyron* spp. began in 1930 when N. V. Cicin[1] discovered natural hybrids of these two genera growing in Russia. Cicin's discovery was first referred to by Veruskine and Shechurdine (32)[2].

As a result of these findings, crosses of various species of *Triticum* and *Agropyron* were attempted. Of all the crosses studied, it was found that *Agropyron elongatum* (Host.) Beauv. and *Agropyron intermedium* (Host.) Beauv. showed the greatest promise in producing successful hybrids according to Johnson (15), Lapin (18), Sapegin (25), and Veruskine (31). These two species of *Agropyron* were crossed with the tetraploid and hexaploid wheats with relative ease by Johnson (15, 16). White (35) was successful with many wheat-*Agropyron* crosses with the exception of a cross attempted with *Triticum monococcum*, which failed completely. Veruskine (30) also reported failure in attempted crosses with *T. monococcum*. Sears (26), however, reported that Cicin had been successful with such a cross.

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[1]This name has also been translated as Tzitzin in the literature.

[2]Numbers in parentheses refer to Literature Cited, page 22.

The early hybrids established by Armstrong (2), Johnson (15), Veruskine (31), and White (35) showed strong Agropyron characters and were perennial in the first and second generations. A great deal of sterility was noted, however, and as back crosses were made to wheat, the perennial character was lost or was diminished considerably. Later generations exhibited a more wheat-like appearance. Characters for resistance to rust and other diseases were maintained to a considerable degree, however.

The sterility encountered in the early hybrids was attributed by Armstrong (3) to anthers that failed to dehisce and to empty pollen grains. The possible mechanism behind this has been studied by a number of workers. Sapegin (25) found that there would be from one to six micronuclei formed in the developing pollen grains. These micronuclei being the result of a misdivision of the chromosomes or lack of pairing, due to non-homologous chromosomes, during meiosis. Peto (24), however, found no particular correlation between the number or formation of micronuclei and sterility. Knott (17) suggested a somatic reduction in a pre-meiotic cell of the sporogenous tissue of the anthers of wheat which would account for the formation of microspores having differing chromosome numbers within the same anther.

In line with the research on the Triticum-Agropyron hybrids, studies have also been conducted to determine the phylogenetic relationship of the two genera. Vakar (29) first reported the close relationship of Agropyron elongatum and A. intermedium to the spelta and emmer series of wheat. Armstrong (3) also pointed out the apparent homologies of certain genomes of Triticum and Agropyron. The exact constitution of the genome relationship, if it exists, between Triticum and Agropyron is

still open to question. Matsumara and Sakamoto (20), in comparing the so called homologous "B" genome from Agropyron triticeum, which McFadden and Sears (21) had suggested was responsible for the free threshing character of the hexaploid wheats, found a closer homology to a genome of Agropyron elongatum. Sears (27) has pointed out, however, that such a homology may not exist and the free threshing character may have arisen as a mutation. Jenkins and Mochizuki (14) also established a hybrid between Triticum durum and Agropyron elongatum in an attempt to determine the presence or absence of homologies between the genera. They suggested that the Agropyron genome be called "E".

Developmental Morphology of Floral Primordia

The shoot apex of wheat passes through two stages of development. These were described by Bonnett (8) as the vegetative stage during which only leaves are produced and the reproductive stage during which the floral organs are initiated and developed. The exact time of the transition of the apex from the vegetative to the reproductive stage depends on the environmental conditions. Anderson (1) attempted to apply a scale determining the stages of development in wheat based on the activity of the shoot apex from day to day. His conclusions were that the transformation took place on the 25th to 30th day after the dormant shoot apex began its elongation in the spring.

The order of differentiation of the floral organs in wheat and Agropyron is the same, the order being: glumes, lemma, stamen, palea, lodicule, and pistil. This is true for many of the grasses as described by Artschwager and McGuire (4), Barnard (5, 6), Bonnett (8), Cannon (9), Hayward (11), Holt (12), and Percival (23). Sharman (28) described the

vegetative apex of Agropyron as being more massive than the apex in Triticum. He also described the apex as consisting of an outer layer of dermatogen, a hypodermis, and a sub-hypodermis. This terminology relating to the histogens of the shoot apex has been questioned by some scientists, such as Holt (12), who felt that Schmidt's tunica-corpus theory more closely described the histogens of the shoot apex. Using these terms, the dermatogen and the hypodermis would be the two layered tunica as described by Barnard (5) and Holt (12, 13). The sub-hypodermis would be the outer layer of the corpus. Sharman (28), however, stated that the sub-hypodermis does not persist in Triticum.

Barnard (5) describes the spiklet primordia in wheat as being initiated by periclinal divisions in the outer layer of the corpus. The glumes, and lemma are initiated by periclinal divisions of the two layered tunica. The palea, lodicule, and the carpel are derived by anticlinal divisions of the tunica and corpus in much the same manner as foliage leaves. The ovule is derived directly from the apex of the flower primordium.

Archesporial Development

Due to the order of differentiation of the floral organs, Percival (23) stated that, for a time, the archesporial cells of the stamen are considerably in advance of the archesporial cells of the ovule. When the anther possesses a well defined single row of archesporia surrounded by two parietal and one epidermal zone, the carpillary cavity is open above and there are no integuments formed on the ovule. Archesporia are also absent at this time in the ovule. When the first integument is formed and the megasporocyte is clearly defined, the anther shows a

double row of close fitting microsporocytes.

The megasporocyte has been described by Cannon (9) in Avena fatua, Hair (10) in Agropyron, Percival (23) in Triticum, Walker (33) in Tropaeolum majus L., and Warmke (34) in Taraxacum as being hypodermal in origin.

In most plants, a linear tetrad of megaspores is formed by two succeeding meiotic divisions of the original megasporocyte, according to Artschwager and McGuire (4), Maheshwari (19), and Percival (23). The four megaspores thus formed all have the potential of becoming the functional embryo sac. Usually, however, it is the chalazal megaspore which serves this function while the three remaining megaspores abort. Variations in megasporogenesis are not unusual, however, since Maheshwari (19) has described many types even within the same species. Hair (10), working with Agropyron scabrum, discussed four population types based on megasporogenesis and embryo formation in this single species. Morrison (22), working with monosomics of Triticum vulgare, found instances of the four megaspores forming a "T" shaped tetrad. This was described as being the result of a micropylar diad cell dividing at right angles to the transverse division of the chalazal diad cell. In all cases mentioned, it was found that occasionally the micropylar megaspore would become the functional embryo sac.

MATERIALS AND METHODS

The plant materials used in this study were the seventh generation hybrids of (Triticum spp. x Agropyron elongatum) x Pawnee wheat which were grown in the small grains section of the Agronomy Farm of Oklahoma State University in 1955. No cereal identification numbers were assigned to these plants. The numbers listed below are the head row designations from which the samples were taken:

Head Row Numbers

4687	4700	4713
4688	4701	4714
4689	4702	4715
4690	4703	4716*
4691	4704	4717
4692	4705	4718
4693	4706	4719
4694	4707*	4720
4695	4708	4721
4696	4709	4722
4697*	4710	4723
4698	4711	4724
4699	4712	4725

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* Pawnee check material.

The spikes were still in the boot when the floral samples were taken. This was accomplished by splitting the leaves and excising the spike. At least three samples were taken from each plant and immediately placed in small bottles containing Carnoy's fluid for killing and fixing. The bottles were then placed in a refrigerator for storage.

For analysis and photomicrography, three spiklets were removed from

each head, carried through a dioxane-butyl alcohol series, and embedded in paraffin for sectioning. Sections were cut on a rotary microtome at 8-10 microns, mounted on slides and stained with safranin-O fast green, using iron hemalum as a mordant and contrasting stain.

RESULTS

Spiklet Morphology of the TAP Hybrids

The spiklet of the TAP[1] hybrids is a sessile structure subtended by two sterile glumes with the florets being arranged in an acropetal distichous order. Each floret is subtended by two fertile glumes, the lemma and palea. The lemma is the first floral structure to be initiated. Barnard (5) has stated that in wheat ten lemmas are usually present on the spiklet axis. In most cases, however, in the TAP hybrids there appeared to be only eight lemmas present with the last two or three being only residual structures showing little or no differentiation. Occasionally, a ninth lemma would be present in the form of a slight bulge of tissue near the apex of the spiklet.

In the axil of the lemma, a series of periclinal divisions give rise to an axillary structure which becomes the floral apex. (Figure 1). This development led Barnard (5) to state that the lateral spiklets are homologous to axillary vegetative shoots. From the floral apex, the stamen, the palea, and the lodicule, respectively, are the next structures to be differentiated. (Figures 2, 3, and 4). The carpel which is the last floral organ to be differentiated arises from the floral apex and eventually encloses it. The residual floral apex then becomes the

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[1]The abbreviation TAP is used for hybrids of (*Triticum* spp. x *Agropyron elongatum*) x Pawnee wheat.

ovule with its tunica forming the epidermal layer of the nucellus.

As the development of the spiklet proceeds and the first three or four lower florets reach the stage at which the archesporial cells are differentiated, the development of the remaining florets ceases. This is first evident by the lighter staining of the cells and tissues of these florets, as compared to the fertile members of the spiklet. (Figures 1 and 2). In the older spiklets, it can be observed that many of the cells of the upper florets appear to take no stain at all indicating the complete absence of cytoplasmic material. A number of the cells in the upper florets show the nucleus to be lacking or disintegrated.

Anther Development

Percival (23) has described the stamen, in Triticum, as arising from the floral apex in the form of three rounded papilla. The archesporial cells are set off in these primordia very early in the developmental process. One archesporial cell is differentiated in each lobe of the developing anther.

The archesporial cell undergoes a mitotic division forming one parietal cell and the primary archesporium. Each of these undergoes further divisions with the parietal cell forming the tapetum, the middle layer, and the endothecium. The primary archesporium divides transversally, keeping pace with the elongation of the somatic cells of the anther to form a single row of archesporial cells. Each of the archesporial cells thus formed passes through two or three lateral divisions to form the microspore mother cells.

Although the early stages of the stamen development were not studi-

ed in the TAP hybrids, it is apparent that the stamen formation follows the same developmental pattern. The stamens were observed as being distinctly four lobed and the archesporial cells already formed before the carpel had completely enclosed the floral apex.

In Figure 4, the two lobes of one stamen stand out with a mitotic metaphase present in the apical sporogenous cell. Figure 7 shows a cross section of a fully developed anther in which each locule contains a cylindrical mass of microsporocytes. The tapetal, middle, endothecial, and epidermal zones are also present.

Just prior to the meiotic divisions of the microsporocytes, the zone of cells referred to as the middle layer disentegrates or is destroyed by the outward pressure of the expanding locule. In the tapetum, the cells, as first formed, were uninucleate, but a karyotic division occurs in each tapetal cell resulting in a binucleate condition in this tissue. The two-nucleate condition was quite evident when the microsporocytes were in the metabolic and early prophase stages. (Figure 8).

The expansion of the anther proceeds and the locule becomes an enlarged cavity with the microsporocytes adhering to the walls of the tapetum. As the first division of the microsporocyte takes place forming a diad, it can be seen that the tapetum shows the first signs of becoming disorganized. (Figure 9). It no longer has the close-fitting, compact appearance that was evident in the early stages of development. The proceeding divisions of the microspores show the further breakdown of the tapetal tissue. When the tetrad stage of the microspore is reached, the tapetum shows almost complete disorganization. (Figures 10, and 11).

Ovule Development

The ovule is first observed as a separate structure with the initiation and the subsequent development of the carpel. (Figures 4 and 5). The carpel is initiated by periclinal divisions in the tunica and peripheral layer of the corpus on the distal surface of the floral apex and forms a ring meristem around the floral apex. A series of anticlinal divisions in this tissue extends the carpel above and finally encloses the floral apex with two stigmatic lobes developing from the lateral margins of the carpel. In the young ovary, a cross sectional view will show the provascular tissue leading to the two lateral stigmas. (Figure 14).

With the formation of the complete ovary, the ovule appears as a sessile, semi-ovoid structure approximately .01 mm in length and attached by a broad placenta to the ovary wall. (Figure 6). At this stage, the ovule is an atropus type, but cell divisions and elongation of the tissues in the proximal region of the ovary result in its assuming an anatropus position by the time that the embryo sac is formed. This results in the ovary being rounded along the distal and lateral surfaces and flattened along the proximal surface.

The ovule consists of an outer layer of epidermis, which is the residual tunica layer of the floral apex, and an inner mass of homogenous nucellar tissue. There is no clear hypodermal zone or second tunica layer present.

The integuments are formed in the residual tunica layer by what seems to be a series of anticlinal divisions restricted to a circular zone around the nucellus in the mid-region. These divisions result in

the formation of a fold of tissue two cell layers thick which develops forward and over the nucellus. The second integument develops posterior to the first in the same manner. (Figures 12, 13, and 14). The integuments continue their growth along with the nucellar tissue and in most cases the inner integument will be the one to form the micropylar opening. (Figures 27 and 28). In some instances, however, it appears that the inner integument will completely enclose the tip of the nucellus by the time that the embryo sac is fully formed. (Figures 29 and 30).

Archesporial Development

During the early stages of development of the ovule, the cell which will give rise to the embryo sac cannot be distinguished. Percival (23) stated that the primary archesporium is well defined at the time of the initiation of the first integument. In the TAP hybrids, the archesporium consists of a small group of six or more cells situated in the apex of the ovule. (Figures 4 and 5). In some instances, there would be two or three archesporial cells in a row. (Figures 14 and 15). All of the cells in the archesporial region appear to have very dense cytoplasm and large nuclei. In most cases, however, the apical cell of the group forms the primary archesporium.

In the preliminary observations of the ovule development, the presence of the linear rows of archesporial cells caused some confusion. This arrangement was first interpreted to be the linear tetrad of megasporocytes formed from the meiotic division of the primary archesporium. This misinterpretation was obvious after checking the comparable development of the microsporocytes. This comparison is discussed later.

Once the primary archesporial cell is set off from the other cells

in the nucellus, it undergoes a period of enlargement and elongation. With this increase in size of the megasporocyte, the cells surrounding it can be observed to be under considerable pressure as evidenced by their compressed appearance. (Figures 16 through 23). The secondary archesporial cells are observed to be gradually destroyed by the expansion of the primary archesporium. In Figure 23, one secondary appears as a reduced rectangular cell toward the chalazal end of the primary archesporium.

After an extended period of metabolic activity, the megasporocyte enters the meiotic division which will give rise to the functional embryo sac. Early prophases of this division were quite frequent in the material studied. (Figures 17 through 23). There was a great deal of variation in size of the megasporocyte at the onset of meiosis, as can be seen in the figures.

In three of the hybrids examined, it was found that apparently the archesporial cell had aborted. (Figure 24). In each instance, this had occured in the third floret. The rest of the florets appeared normal and the anthers of the florets containing the aborted megasporocytes were in the normal tetrad stage of development.

Embryo Sac Development

Once the functional embryo sac is differentiated, the subsequent divisions from the one-nucleate condition to the eight-nucleate embryo sac seem to occur rapidly.

Due to the chalazal position of the functional megaspore, (Figure 26), considerable growth pressure is exerted upon the cells separating it from the micropylar end of the ovule. (Figures 27 and 28). The

pressure is such that it causes a marked protrusion of the micropylar end of the embryo sac. Bergman (7) has reported that this condition may even result in a rupturing of the nucellar epidermis.

The appearance of the mature embryo sac shows the egg and synergids occupying their normal positions in the micropylar end. The polar nuclei are located in their normal median position while the antipodals occupy the chalazal end of the embryo sac.

The antipodals undergo a series of cellular divisions to form a complex of as many as thirty-six cells, or more. This antipodal complex seems to spearhead the development of the endosperm by starting the breakdown of the nucellar tissue. Maheshwari (21) has referred to the antipodal cells as acting as an aggressive haustorium. The cells of the nucellus, which are adjacent to the embryo sac, lose their cytoplasmic contents and their structure becomes disorganized as a result of the increased growth of the antipodal cells. (Figures 29 and 30). The antipodal complex persists until after fertilization takes place.

Comparison of Micro-Megasporogenesis

Due to the misinterpretation that was made in the early analysis of the formation of the primary archesporial cell in the ovule, a pattern of development was devised. This consisted of comparing the stages of development of the sporogenous cells in the anther and the ovule. Even though there appears to be very little synchronization between the microsporocytes and the megasporocytes in their relative stages of development, a comparison can be made.

In making this comparison, the anthers and ovules of twenty-five florets, with their sporocytes in various stages of development, were

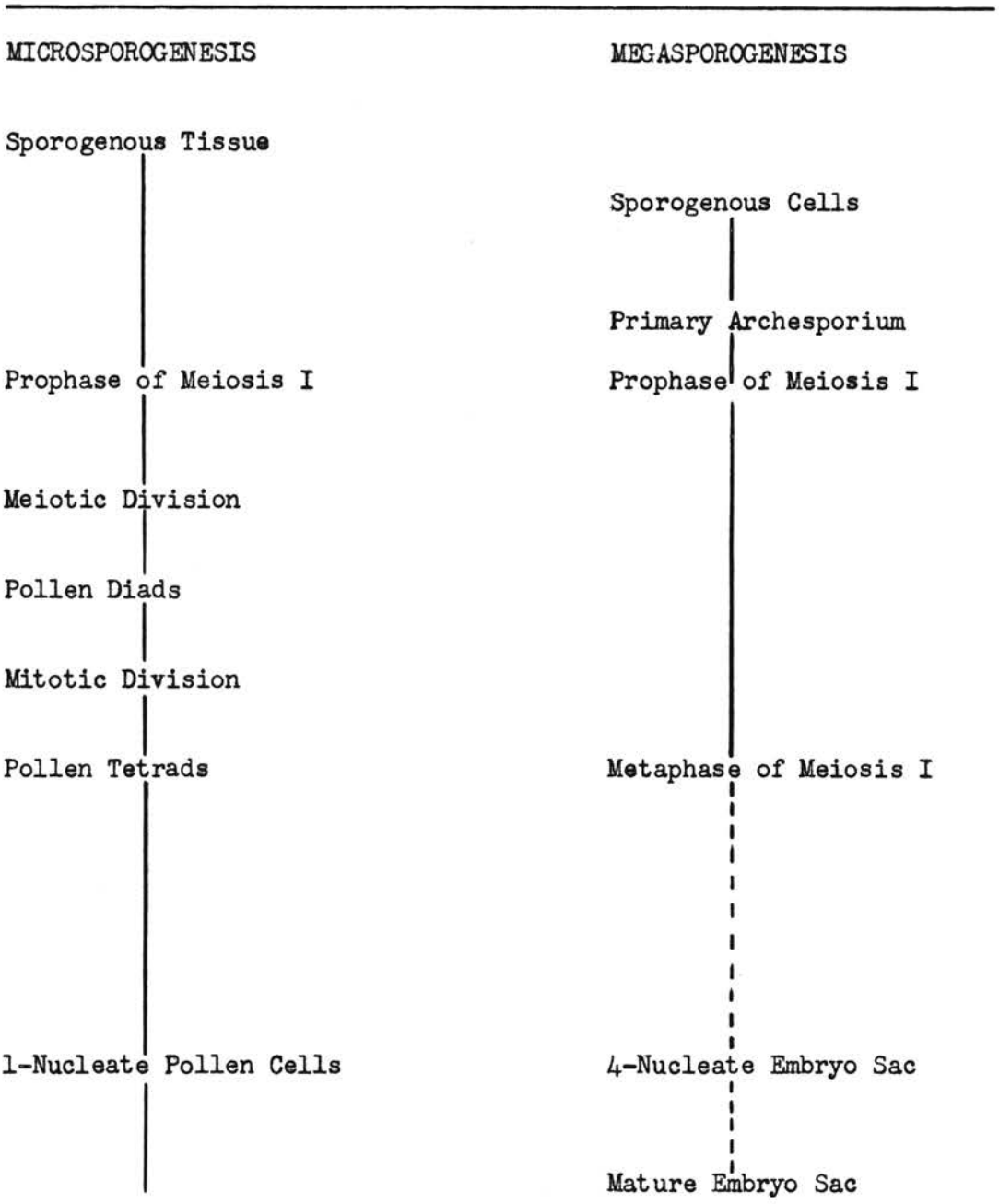
examined. A summary of the results of this examination is given in Table I.

The outline illustrates that in a majority of the samples, the two sporocytes enter prophase I simultaneously, even though the sporogenous cells of the anther are the first to be differentiated. The succeeding divisions of the microsporocytes occur in fairly rapid succession as compared to the megasporocytes. Only one sample, number 4713, showed any marked deviation from this pattern. The ovule of this sample revealed the primary megasporocyte in the prophase stage, while the microsporocytes were still a compact mass of sporogenous tissue. (Figure 20).

At the time the megasporocyte enters metaphase I, (Figure 25), tetrads can be observed in the anthers. With the formation of the four-nucleate and mature embryo sacs, (Figures 27 through 30), the pollen tetrads have separated as one-nucleated pollen cells.

TABLE I

OUTLINE OF SPOROGENESIS



The solid lines represent the periods of build-up or metabolic activity.

The broken lines represent the periods of division which were not observed.

DISCUSSION

Variation resulting from staining intensity of the sporogenous tissue led to difficulties during the reproduction of specific sections in photomicrography. The somatic cells and archesporia of the ovule showed good differential staining as did the somatic cells and archesporia of the anther primordia, but the older anthers did not yield the same results. This was due to the presence of a densely stained extracellular material within the locule. Percival (23) attributed the presence of this material to the breakdown of the middle layer. The tapetum, which acts as the nutritive source for the developing microspores, apparently contributes to this extracellular material, also, according to Artschwager and McGuire (4) and Percival (23).

The phase of this study relating to the mitotic activity in the sporogenous tissues in the ovule and anther primordia met with relatively little success. There were very few of the samples examined which showed any mitotic activity at all. This indicates that the time factors involved in the build up of mitotic activity within these primordia should be taken in to consideration. The mitotic stages which were observed were in the peripheral layers of the sporogenous tissue in the ovule and apparently contributed nothing to the development of the primary archesporium. Those stages found in the sporogenous cells of the anther appeared normal. This was also true of microsporogenesis in which all of the meiotic stages were observed and none of these showed

any abnormal behavior.

Since the mitotic stages leading to the development of the sporocytes of the ovule and the anther were limited, a critical analysis of this process could not be accomplished. Knott (17) has pointed out that chromosome mosaics, occasionally found in the anthers of wheat, might be traced to a somatic reduction in the archesporial tissues. This conclusion illustrates, however, that even though the somatic reduction is strongly indicated, it is still to be demonstrated. The sporogenous tissues of the TAP material were set apart very early in the initiation of the primordia. The formation of the sporocytes, particularly in the ovule, is then a matter of differentiation with no cellular divisions involved.

The development of the ovule and the subsequent differentiation of the primary archesporial cell yielded a partially complete picture of the process of megasporogenesis. The main difficulty in the examination of this process was the absence of the key meiotic divisions in the formation of the functional megaspore. Bergman (7) in studying megasporogenesis in Hieracium, has stated that the analysis of all stages of the process involves the examination of a large number of samples. He contrasted this to the process of microsporogenesis in which a comparatively small number of samples could be studied to form a complete picture of this process. He concluded by saying due to this more desirable factor, most workers restrict themselves to the study of microsporogenesis. Walker (33) and Warmke (34) also discussed the more tedious processes involved in the study of the megaspore development.

During megasporogenesis, a great deal of mitotic activity was observed in the somatic cells of the nucellus and the integuments. This

can be expected, since the ovule is still in the developmental stage and this activity is maintained until the complete embryo sac is formed. This mitotic activity is independent of the divisions of the megasporocyte.

The three instances of the megasporocyte abortion which were found could be the result of an abnormal cell. A more probable explanation lies in the fact that in each instance this abortion had occured in the third floret of the spiklet. Since the first and second florets were normal in every respect, the abortion of the megasporocyte in the third was most likely due to an unbalance in the physiological activity in the spiklet. This is probably the same mechanism which causes the upper florets of the spiklet to cease development.

The outline of the comparisons of microsporogenesis and megasporogenesis lists, in general, the developmental patterns as they occur in the anther and the ovule. Further attempts should be made to correlate the stages of development of the sporocytes since this information would be helpful in future studies of the archesporial development.

Pawnee check material which was processed with the TAP material exhibited the same patterns of development. Differences which were found between the two were not presented since they appeared minor and would probably not exist if an over-all comparison were made.

SUMMARY

A cytohistological study of the ovule and anther primordia was made with seventh generation TAP hybrids. The hybrids exhibited the same growth patterns as wheat.

The sporogenous cells were found to be differentiated very early in both the anther and the ovule. The primary archesporium in the ovule differentiated much later than the sporogenous cells of the anther.

An outline, Table I (page 17), was presented to correlate the various stages of development of the sporocytes. In the outline, it was demonstrated that the meiotic process is synchronized in the initial phase, but the synchronization is not maintained throughout the entire cycle.

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LEGEND FOR PLATE I

Fig. 1 Hybrid 4698. Longitudinal section of the floral primordium. Note the lighter staining of this section and Fig. 2 as compared to Figures 3 and 4. (320X)

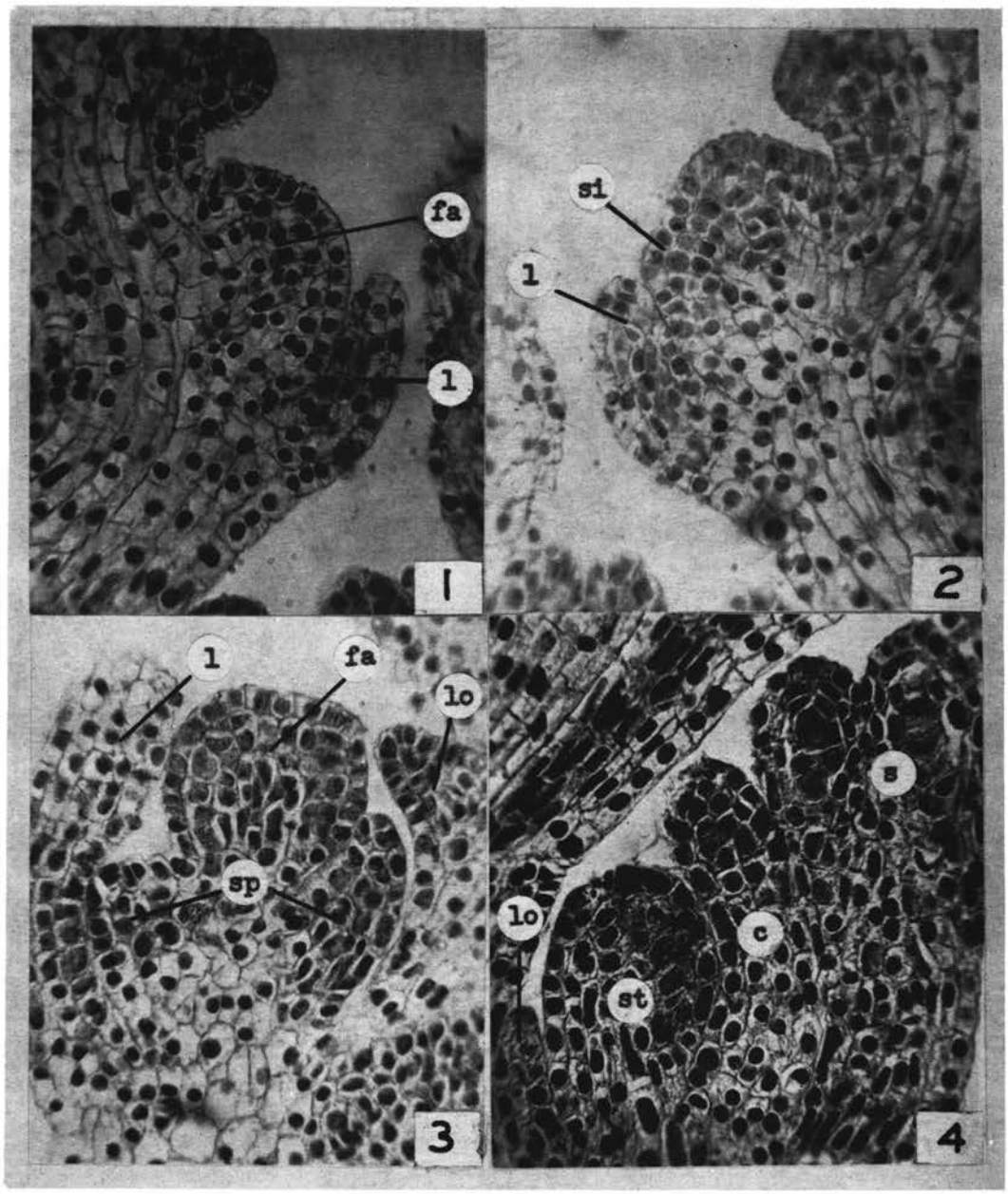
Fig. 2 Hybrid 4713. Longitudinal section of floret number 7. (320X).

Fig. 3 Hybrid 4701. Longitudinal section of the floret showing stamen primordium. (320X).

Fig. 4 Hybrid 4714. Longitudinal section of floret. Note mitotic metaphase in the apical sporogenous cell of the left anther lobe. (320X).

Floral apex (fa); lemma (l); stamen initiation (si); stamen primordia (sp); palea (lo); carpel (c); stamen (s).

PLATE I



LEGEND FOR PLATE II

Fig. 5 Hybrid 4705. Longitudinal section of floret showing carpel development. (320X).

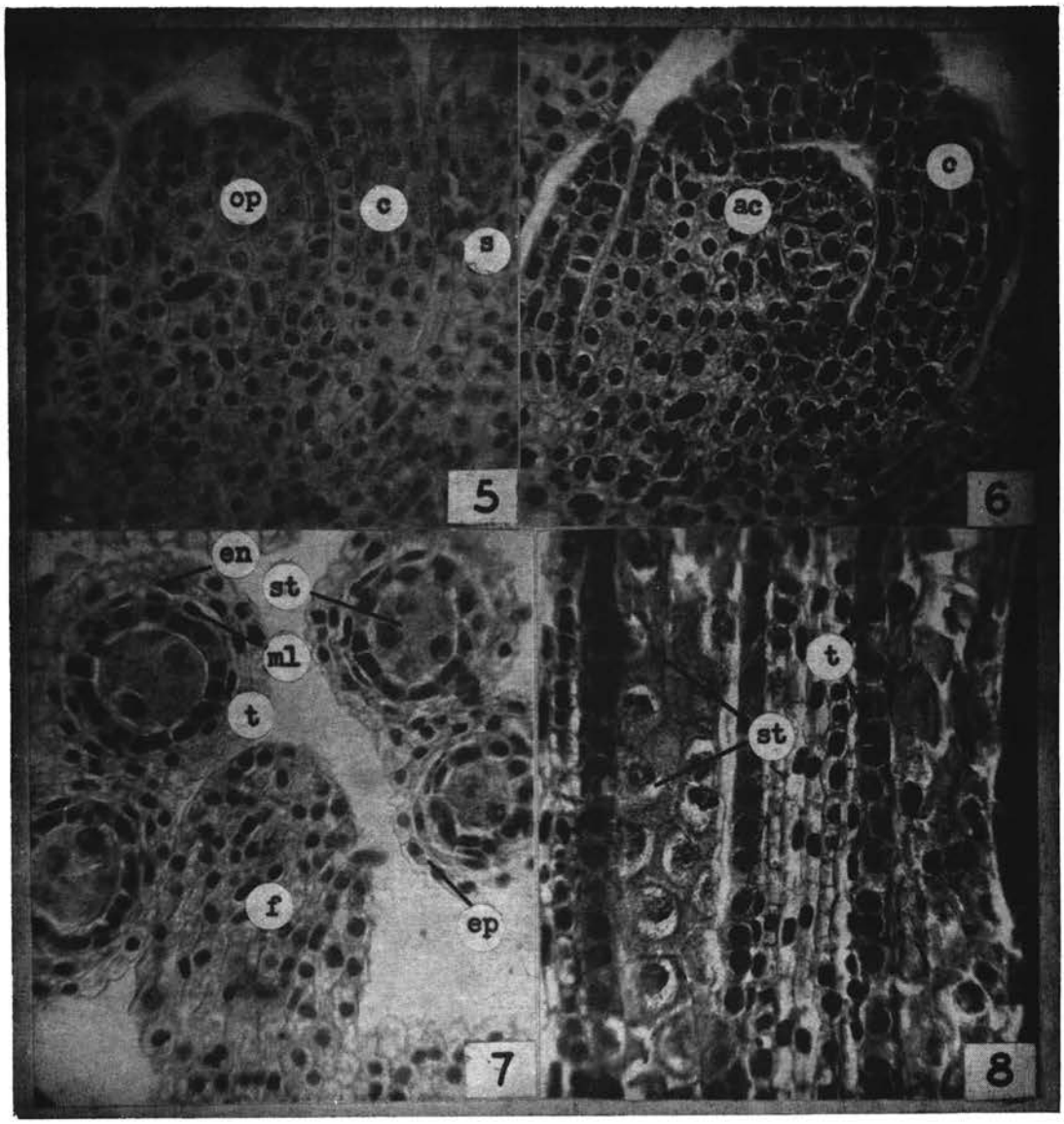
Fig. 6 Hybrid 4701. Longitudinal section of ovary. (320X).

Fig. 7 Hybrid 4698. Transverse section of young stamen. (320X).

Fig. 8 Hybrid 4717. Longitudinal section of anther. Note the two-nucleate tapetum. (320X).

Ovule primordium (op); carpel (c); stamen (s); archesporial cells (ac); filament (f); epidermis (ep); tapetum (t); middle layer (ml); endothecium (en); sporogenous tissue (st).

PLATE II



LEGEND FOR PLATE III

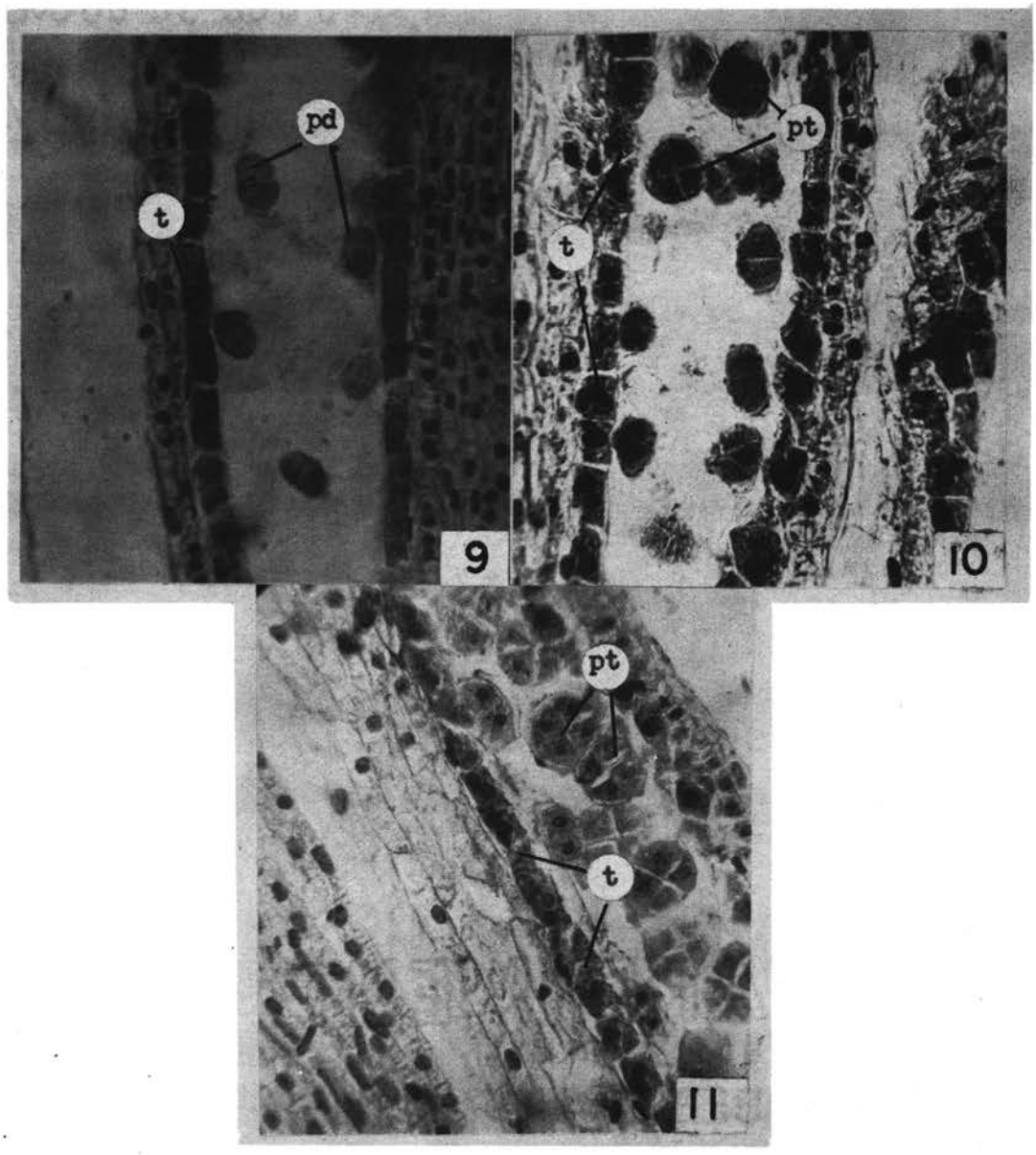
Fig. 9 Hybrid 4696. Longitudinal section of anther. Note the disorganization of the tapetum. (320X).

Fig. 10 Hybrid 4702. Longitudinal section of anther. Note the further disorganization of the tapetum. (320X).

Fig. 11 Hybrid 4707. Longitudinal section of anther. Note the almost complete disorganization of the tapetum. (320X).

Tapetum (t); pollen diads (pd); pollen tetrads (pt).

PLATE III



LEGEND FOR PLATE IV

Fig. 12 Hybrid 4695. Longitudinal section of ovule. Note the compression of cells in the region of the archesporium. (320X).

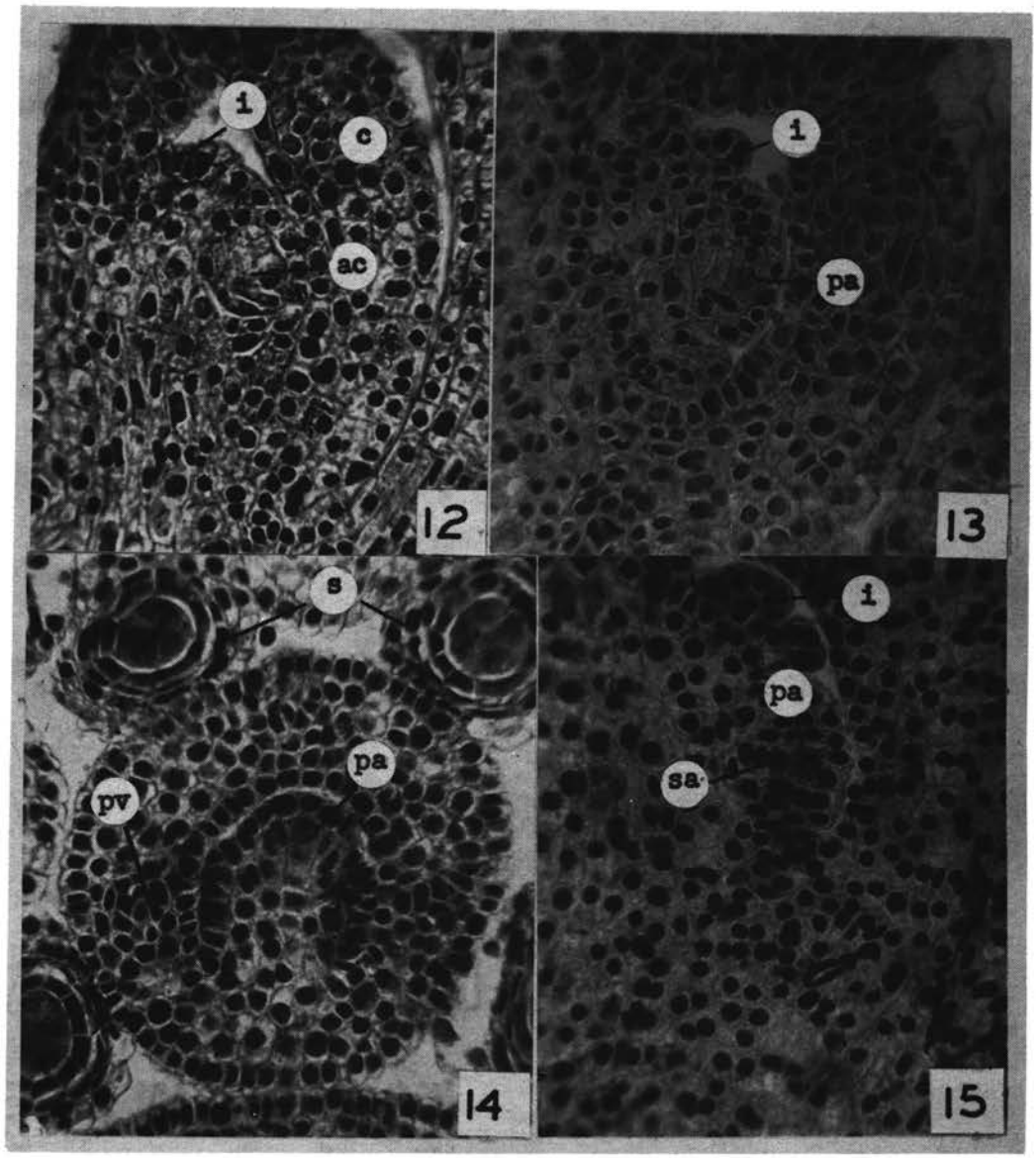
Fig. 13 Pawnee check 4697. Longitudinal section of ovule. Note the large two-nucleolated archesporium with the secondary archesporium. (320X).

Fig. 14 Pawnee check 4707. Transverse section of floret. Note the vascular tissues leading to the stigma. (320X).

Fig. 15 Hybrid 4703. Longitudinal section of ovule showing primary and secondary archesporia formed in a linear row. (320X).

Integument (i); carpel (c); archesporial cells (ac); primary archesporia (pa); stamen (s); secondary archesporium (sa); provascular trace (pv).

PLATE IV



LEGEND FOR PLATE V

Fig. 16 Hybrid 4713. Longitudinal section showing early stage of primary archesporium. (320X).

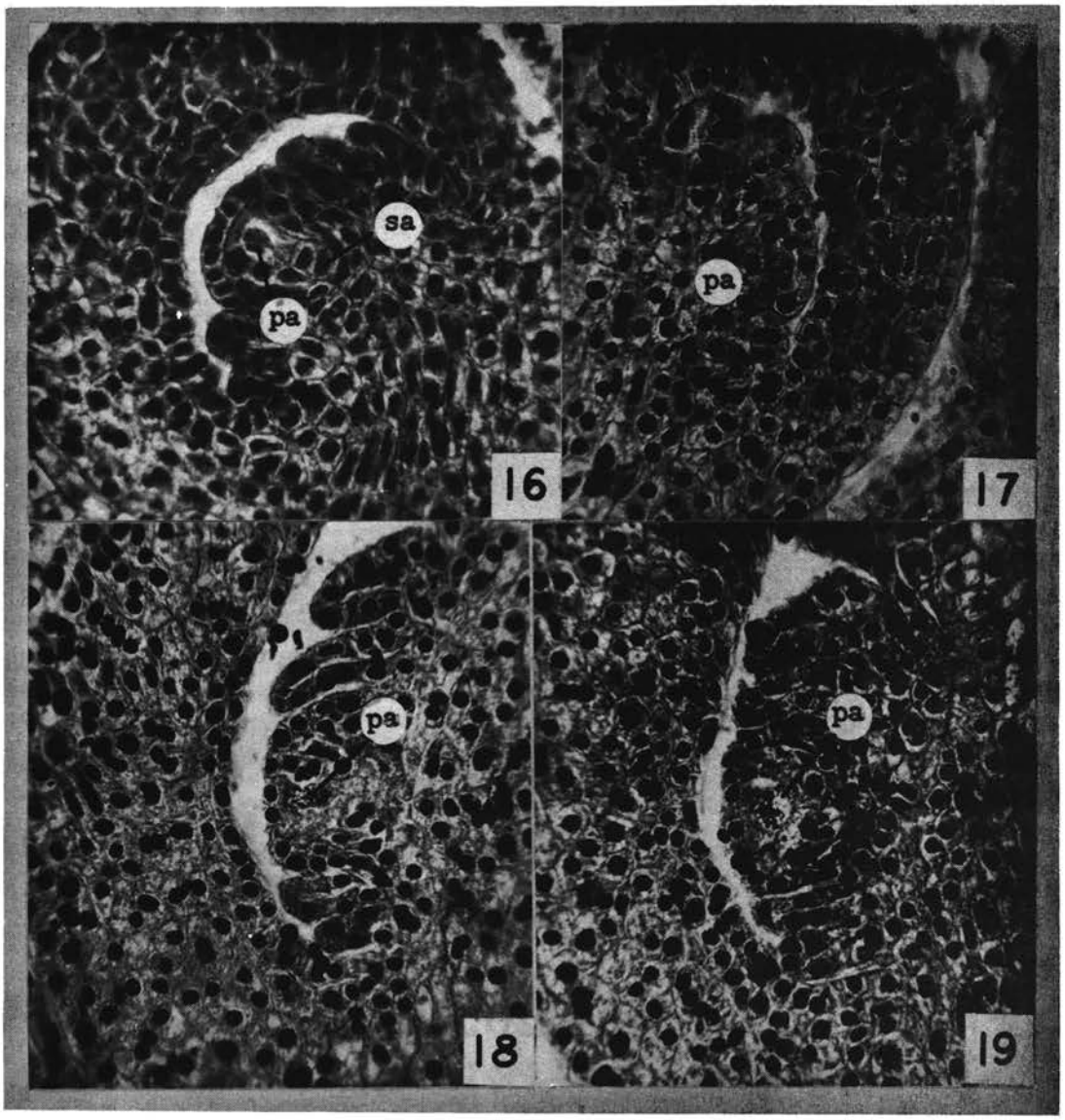
Fig. 17 Hybrid 4712. Longitudinal section of ovule with primary archesporium in early prophase. (320X).

Fig. 18 Hybrid 4710. Longitudinal section of ovule with archesporium in prophase. (320X).

Fig. 19 Hybrid 4706. Longitudinal section of ovule with archesporial cell very prominent. Note the compression of cells around it. (320X).

Primary archesporium (pa); secondary archesporium (sa).

PLATE V



LEGEND FOR PLATE VI

Fig. 20 Hybrid 4713. Longitudinal section of ovule with prophase of primary archesporium. The microsporocytes were still metabolic in this floret. (320X).

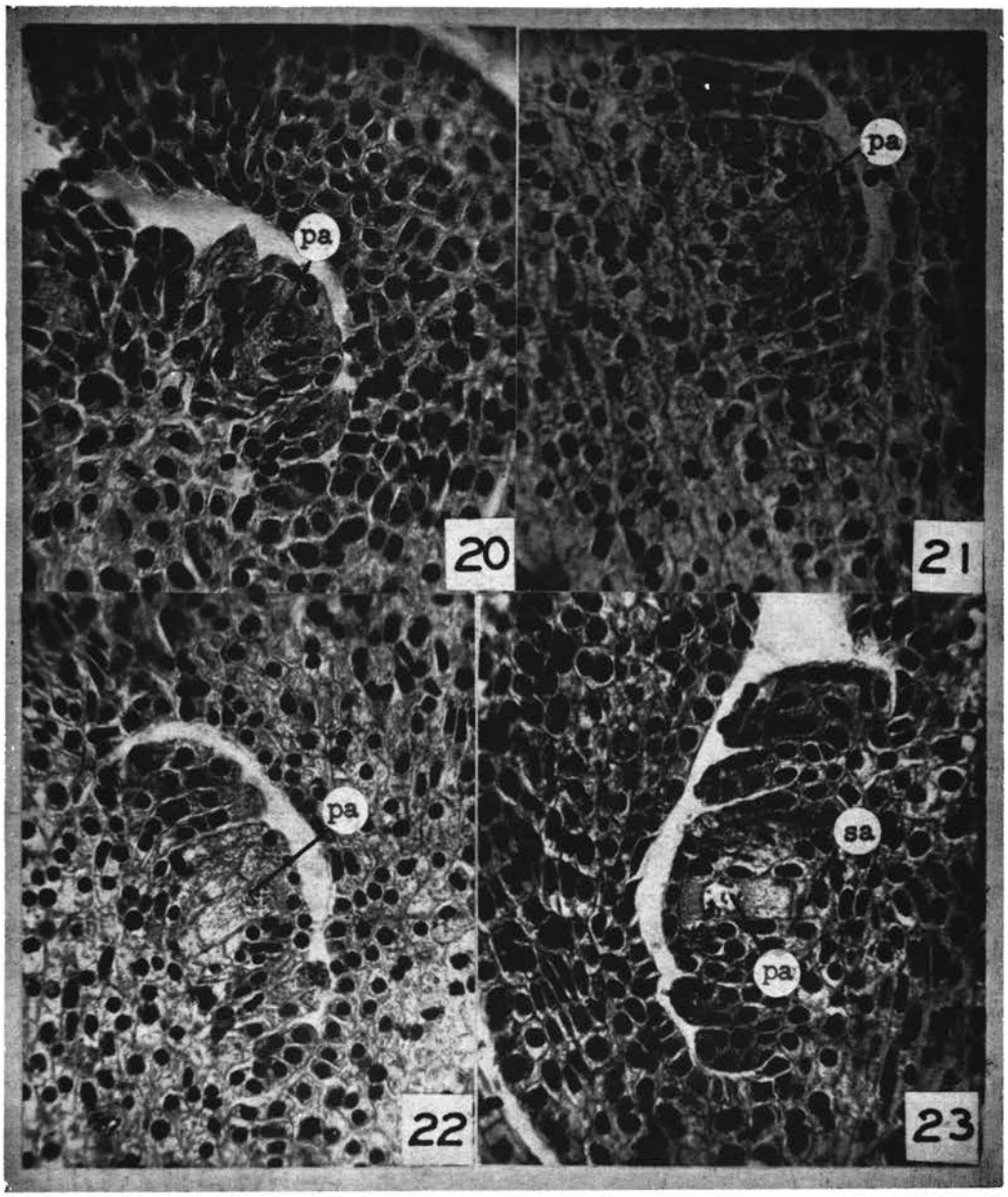
Fig. 21 Pawnee 4707. Longitudinal section of ovule with late stage in development of primary archesporium. (320X).

Fig. 22 Hybrid 4718. Longitudinal section of ovule. Note compression around the primary archesporium. (320X).

Fig. 23 Hybrid 4709. Longitudinal section of ovule. Note the secondary archesporia in the deep chalazal position. (320X).

Primary archesporium (pa); secondary archesporia (sa).

PLATE VI



LEGEND FOR PLATE VII

Fig. 24 Hybrid 4717. Longitudinal section of ovule of the third floret showing the abortion of the archesporium. (320X).

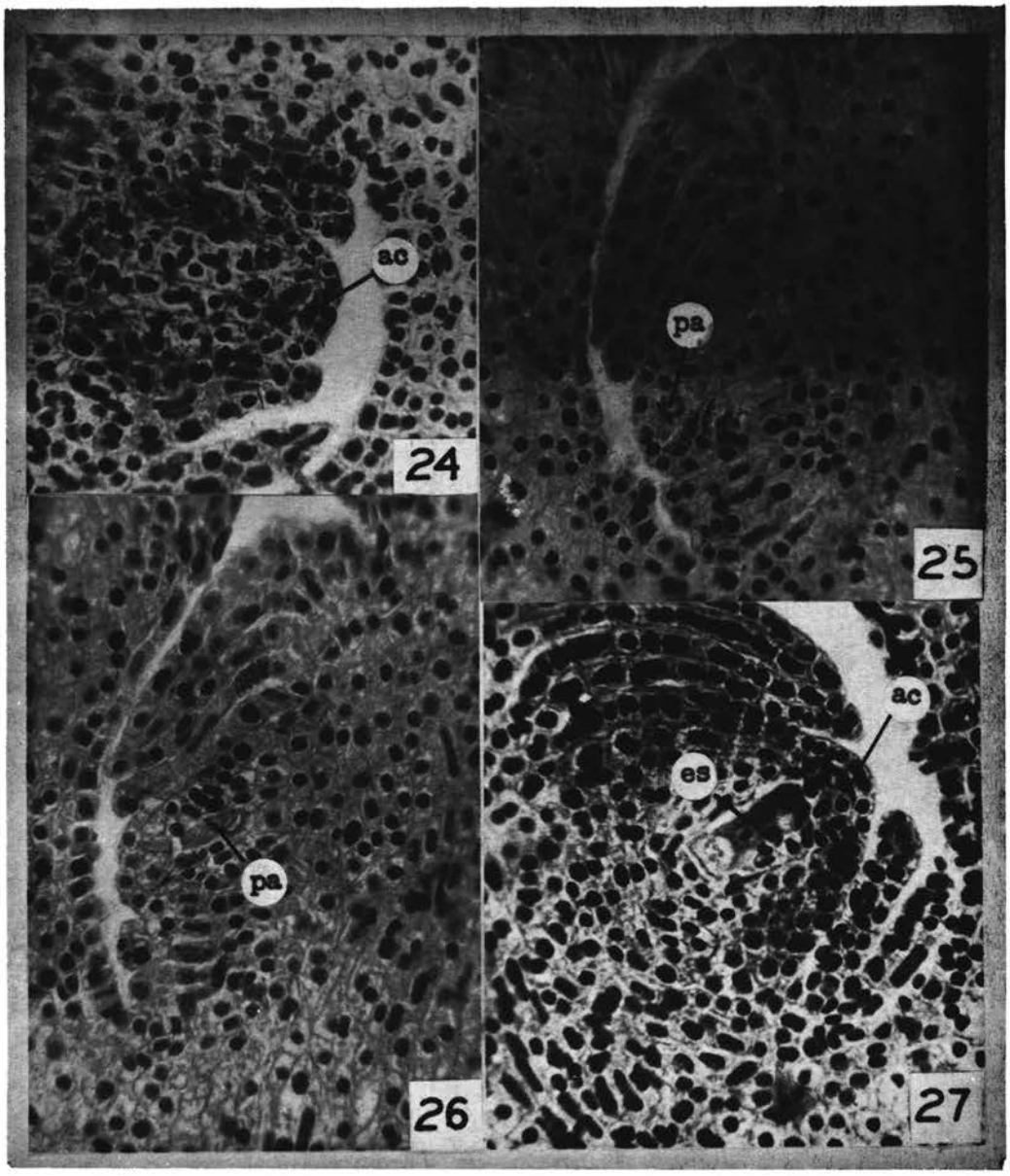
Fig. 25 Hybrid 4721. Longitudinal section of ovule with a metaphase division of the primary archesporium. (320X).

Fig. 26 Hybrid 4725. Longitudinal section of ovule with the metaphase II in the functional megaspore. Note the position of the dividing cell. (320X).

Fig. 27 Hybrid 4717. Longitudinal section of ovule of the first floret with functional 4-nucleate embryo sac. Compare with Fig. 24. (320X).

Aborted cellular material (ac); primary archesporium (pa); embryo sac (es).

PLATE VII



LEGEND FOR PLATE VIII

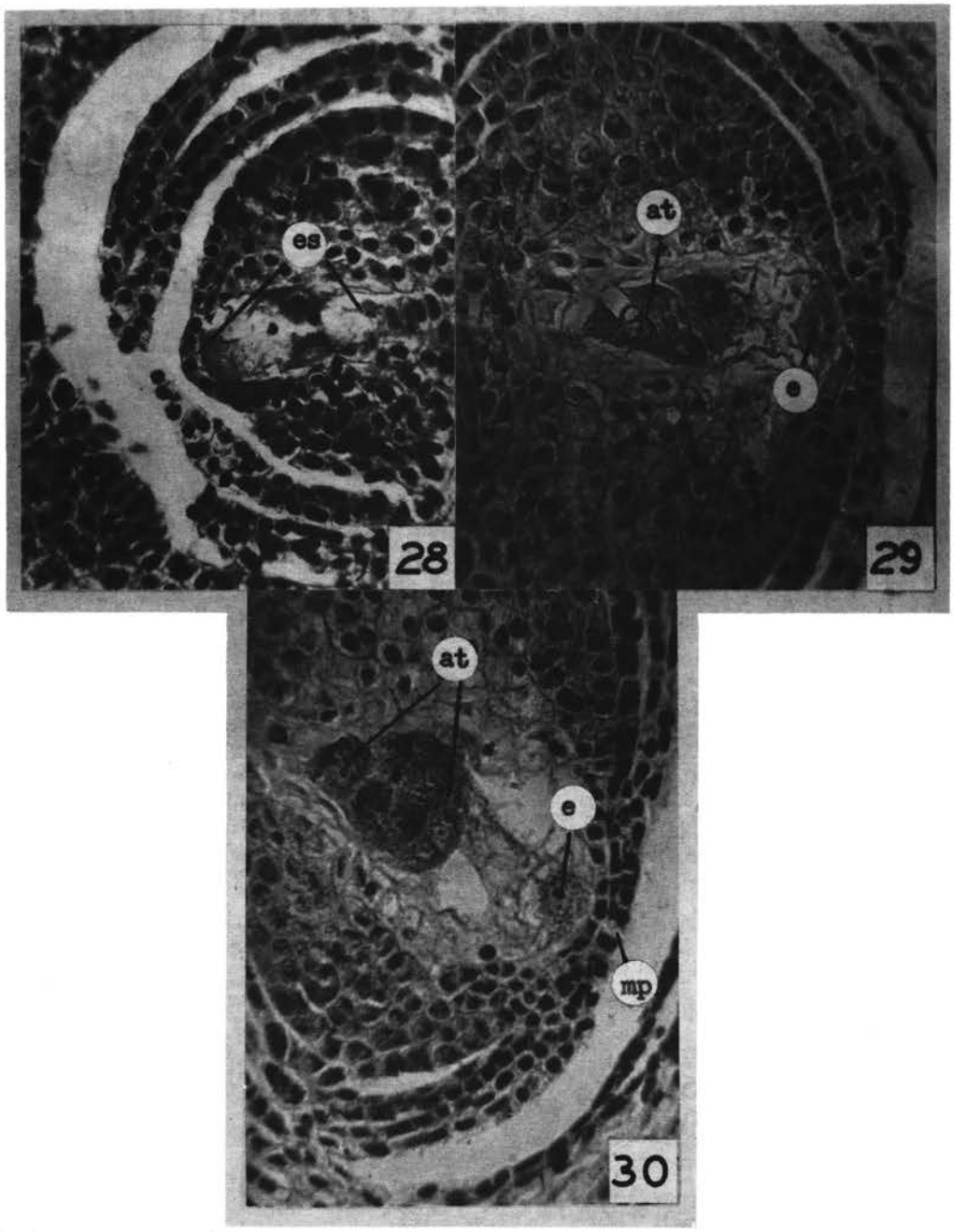
Fig. 28 Hybrid 4717. Longitudinal section of ovule showing protrusion of nucellar epidermis caused by formation of the embryo sac. (320X).

Fig. 29 Hybrid 4718. Transverse section of ovule with mature embryo sac. Note the overgrowth of the inner integument leaving no micropylar opening. (320X).

Fig. 30 Pawnee. Longitudinal section with mature embryo sac. (320X).

Embryo sac (es); antipodals (at); egg cell (e); micropyle (mp).

PLATE VIII



VITA

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Master of Science

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