

Some Notes on Premeiocytes in Wheat

(premeiotic mitosis, premeiotic interphase, archesporial cell, pollen mother cell)

H. A. McQuade and Ann M. Young-Rottler

Department of Radiology
School of Medicine
University of Missouri - Columbia 65212

SUMMARY

Some characteristics of wheat premeiocytes are described as they appear in electron microscopy. These include changes in the endoplasmic reticulum of archesporial cells in premeiotic mitosis (PMM) and some nuclear and cytoplasmic developments in premeiotic interphase (PMI).

INTRODUCTION

This report deals with some observations, gathered by means of transmission electron microscopy (TEM), on premeiocytes of *Triticum aestivum* var. Chinese Spring. The protocols we follow in the preparation of wheat anthers are similar to those used by many investigators and have been reported in detail (MCQUADE & PICKLES, 1980). We are indebted to BENNETT and his colleagues for their fundamental light microscope studies of the premeiotic and meiotic processes in wheat (BENNETT et al., 1973) and their subsequent investigations with EM (1974).

RESULTS AND DISCUSSION

PREMEIOTIC MITOSIS (PMM). Archesporial cells of anther locules at last PMM have remarkably developed ER systems compared to those at earlier PMMs. Archesporial cells in all PMMs are rich in free ribosomes, cell organelles and inclusions. The ER in columns of cells at early PMMs typically occurs in short segments which are relatively few. However, the ER of archesporial cells of columns at last PMM occurs in characteristic stacks of long, rough cisternae. These cisternae are most readily seen at the ends of cells with respect to the cells' long axes. The ER is typically associated with Golgi bodies; ER and Golgi vesicles are

found throughout the cytoplasm adjacent to the primary walls as would be expected in wall development. See FIGURE 1.



FIGURE 1. Cross section of an archesporial cell from a locule at third PMM. ER, endoplasmic reticulum; G, Golgi body; PW, primary wall. There are numerous Golgi and ER vesicles throughout the cytoplasm. Bar equals $0.1 \mu\text{m}$.

In general the amount and array of ER vary with the cell's stage of development and level of activity. The last PMM is the most significant of all in the number of cells produced. From it emerges the number of cells required for PMI and meiosis. That cells of a column at last PMM become extremely active is not surprising. After division they must grow, be maintained and brought into synchrony in order to enter PMI as PMCs with the marked cytological changes this entails.

PREMEIOTIC INTERPHASE (PMI).

Stage 1 (S1). In both light and EM, PMCs in S1 appear strikingly different from archesporial cells which have completed mitosis. S1 nuclei are very large and exhibit diffuse, attenuate chromatin. This condition is illustrated in FIGURE 2. Segments of ER are typically short and often difficult to detect amidst the dense free ribosomes and polyribosomes. See FIGURES 3 and 4. As S1 proceeds, fiber-like profiles, often in contact with or even within the middle lamellae, appear in the primary walls of PMCs to a greater extent than in walls of archesporial cells at PMM. These progressive changes in the primary wall, we think, are likely related to the appearance of callose which becomes visible with light microscopy in S2. The developments within the primary wall at S1 are not visible with light microscopy.

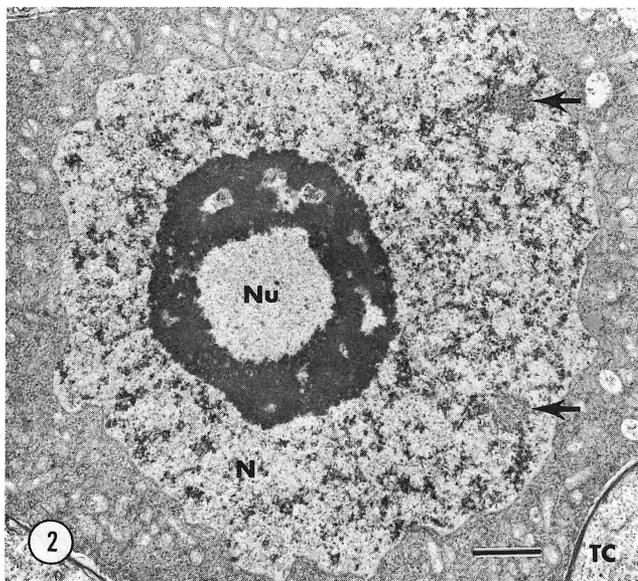


FIGURE 2. A PMC at S1. N, nucleus; Nu, nucleolus; TC, tapetal cell. Arrows point to centromeres. Bar equals 1.0 μ m.

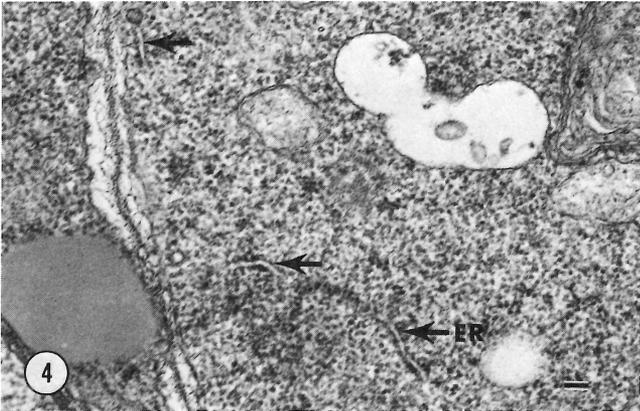
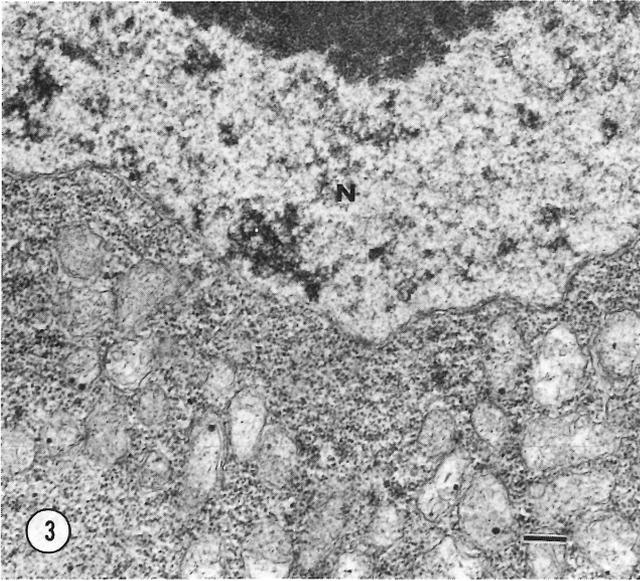


FIGURE 3. Detail of part of an S1 nucleus and adjacent cytoplasm. Bar equals $0.25 \mu\text{m}$.

FIGURE 4. Part of a PMC at S1 near the primary wall. Arrows point to short segments of ER. Bar equals $0.1 \mu\text{m}$.

Stage 2 (S2). In electron micrographs of PMC nuclei at S2, chromatin appears dense and much contracted in contrast to that in S1. There is a zone, described by BENNETT et al (1974), virtually free of chromatin and about $0.2 \mu\text{m}$ wide next to the nuclear envelope. Callose formation, which appears in S2, continues throughout the remainder of PMI and into meiosis. These distinctive markers of S2 are shown in FIGURE 5.

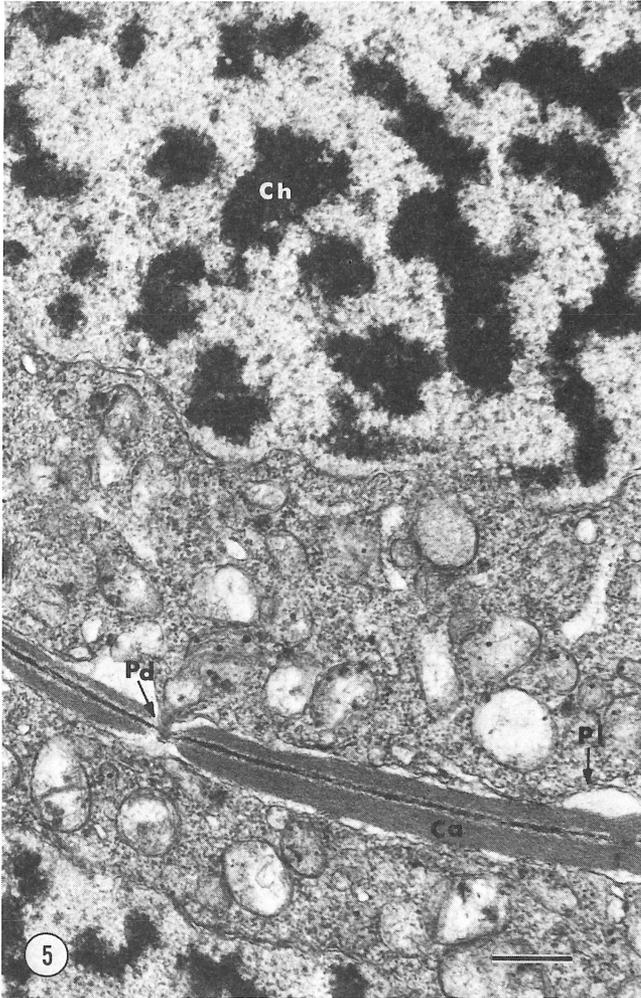


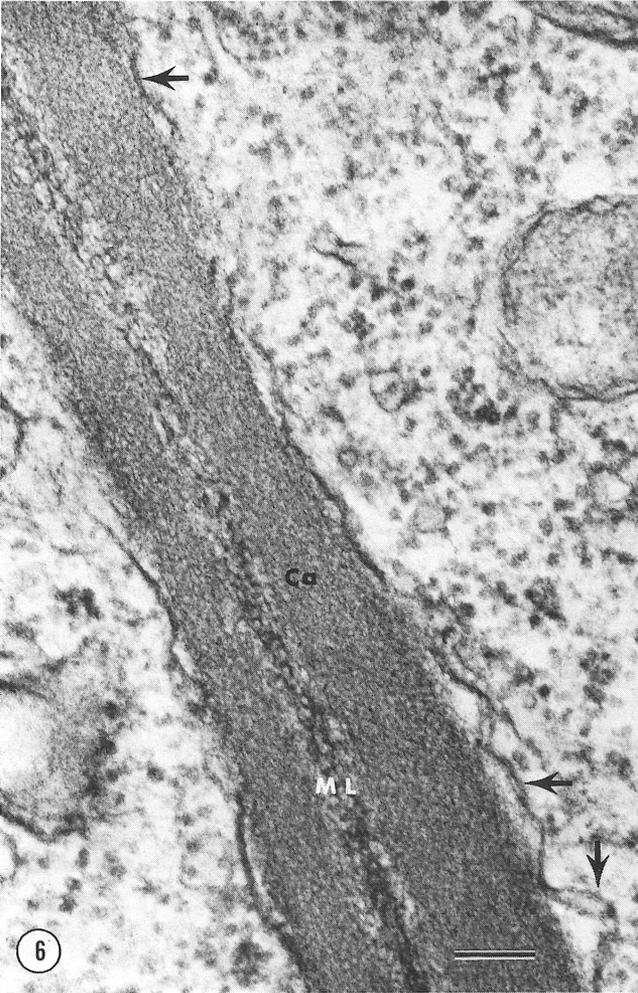
FIGURE 5. Parts of two PMCs at S2 separated by a developing callose special wall. A callose synthetic area in left center of the wall includes the site of a former plasmodesma. Ca, callose; Ch, chromatin; Pd, plasmodesma; Pl, plasmalemma. Bar equals $0.5 \mu\text{m}$.

In general, the progress of callose deposition through the PMC column follows the pattern described in the light microscope studies of *Sorghum* and other *Gramineae* by CHRISTENSEN et al. (1972) and CHRISTENSEN and HORNER (1974). Initially, deposition is central with respect to the long axis of the column, then along radial lines and later in the tapetal aspect of the column. There are very likely some minor differences between *Sorghum* and *Triticum* in this regard. For example in wheat we have observed at various times what appears to be callose synthesis in the tapetal area before synthesis is complete peripherally along radial lines. This might indicate that the flow of synthetic activity could occasionally be in the opposite direction until it meets that radiating from the center of the column.

In wheat callose synthesis appears to begin somewhat earlier than in some other grass species. Cellulose and callose are readily distinguished from each other with EM. Callose is synthesized at the expense of cellulose during PMC development and is in turn destroyed in pollen wall development. ESCHRICH (1964) has commented on the rapidity with which callose can be formed and destroyed.

The behavior of the plasmalemma during callose synthesis resembles that described in *Cucurbita* by ESCHRICH (1964). In brief, the plasmalemma separates from the primary wall at various places and fragments irregularly along its course. Vesicles from nearby ER cisternae and Golgi bodies and other inclusions are introduced to the synthetic area. The plasmalemma is renewed adjacent to the newly synthesized callose. The appearance of the plasmalemma in the development of the callose special wall is shown in FIGURE 6. A more detailed discussion of the EM of callose synthesis will appear elsewhere.

FIGURE 6. A segment of developing callose wall between two PMCs at S2. The plasmalemma has separated from the wall in several places and has broken in others. Arrows point to places in the plasmalemma where its unit membrane structure is revealed. Ca, callose; ML, middle lamella. Note vesicles near the synthetic area. Bar equals 0.1 μ m.



Stage 3 (S3). BENNETT and his associates (1973) have shown that DNA synthesis occurs in PMC nuclei during S3 simultaneously with S in nuclei of tapetal cells. In electron micrographs it can be seen that the chromatin of the PMC nucleus at S3 is no longer as dense as in S2 and is again in contact with the nuclear envelope. See FIGURE 7. MCQUADE and PICKLES (1980) reported small segments of synaptonemal complexes (SCs) in PMC nuclei at S3.

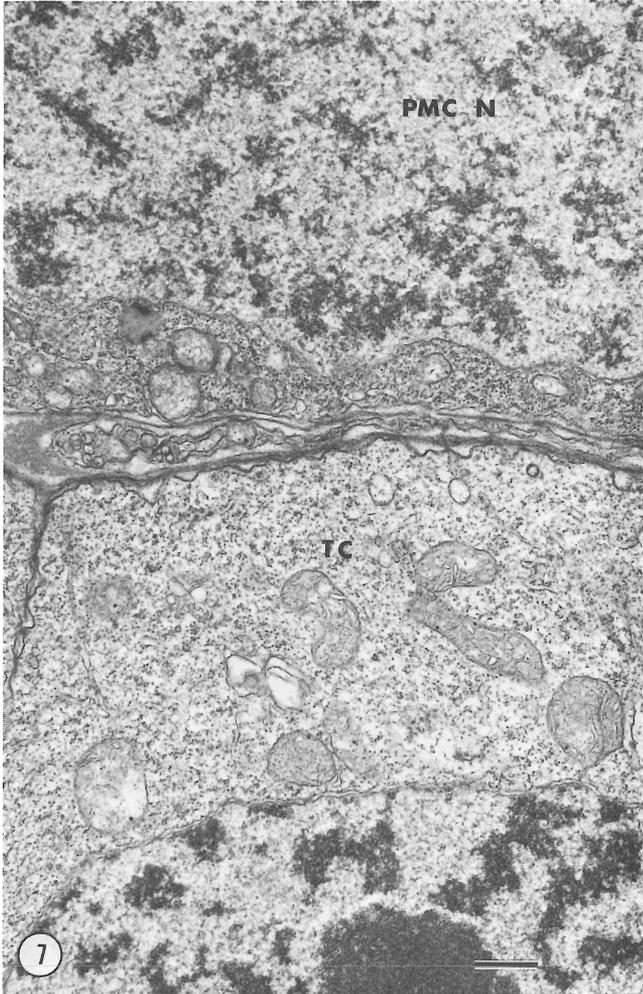


FIGURE 7. A PMC at S3 is shown above; a tapetal cell below. Between the cells callose is being synthesized. Note the difference in the ribosome densities of the two cells. Compare the chromatin of the S3 nucleus with that of the S2 nuclei in FIGURE 5. Bar equals $0.5 \mu m$.

BUTTROSE (1963) reported extensive sac-like proliferations of the outer nuclear membrane accompanied by blebbing of the inner nuclear membrane in endosperm cells of wheat. We have found groups of blebs arising from the inner membrane of the nuclear envelope in the perinuclear spaces of wheat PMCs at S3 and other stages. They may arise in late S2; they are often present in S3. We have seen them in prophase I nuclei through diplotene. We have never seen them in PMM or in S1 of PMI.

These blebs, like those reported by BUTTROSE (1963), give rise to vesicles which appear to carry nuclear material into the cell cytoplasm. In PMCs the blebs arise from what appear to be thickenings or plaques on the inner nuclear membrane. See FIGURES 8 and 9. After enlargement and separation from the inner nuclear membrane, they are released as vesicles from the perinuclear space when the outer nuclear membrane ruptures. As would be expected, the escaping vesicles are characterized by a single outer membrane. A more detailed description and discussion of these blebs will appear elsewhere.

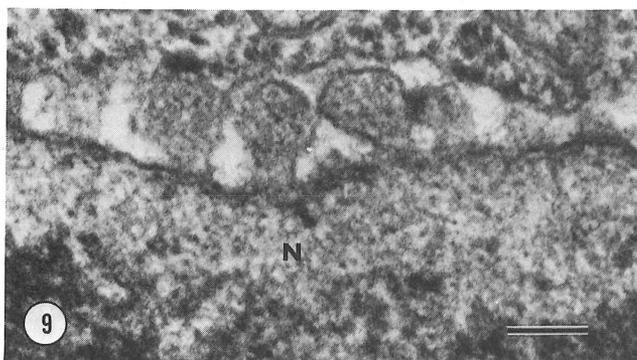
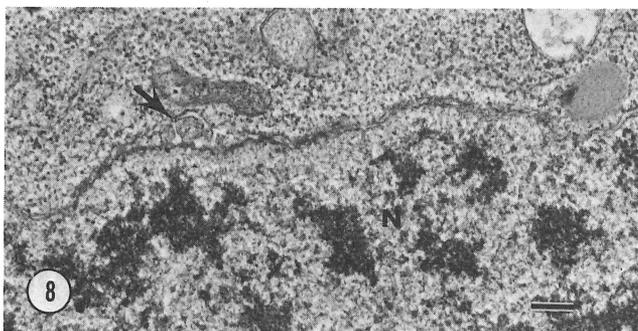


FIGURE 8. Survey micrograph of an S3 nucleus with blebs arising from the inner nuclear membrane within the perinuclear space. Bar equals 0.25 μ m.

FIGURE 9. Detail of a group of blebs arising from the inner nuclear membrane within the perinuclear space of a PMC nucleus at S3. The blebs are filled with material similar to that within the nucleus. Bar equals 0.1 μ m.

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