

MICROSCOPIC REVIEW OF MEIOSIS

INTRODUCTION

Meiosis is the nuclear division in eukaryotic organisms that produces haploid (n) nuclei from diploid (2n) nuclei. In animals, the resulting functional cells are the gametes, egg and sperm. In plants, fungi, and some protists, the resulting functional cells are **spores**.

Regardless of the organism in which meiosis occurs, the overall stages of the process are similar. Details in most of the variations in meiosis are beyond the scope of this general review of meiosis. A **list of references** is provided at the end of this review for the reader interested in more advanced treatments of meiosis.

As you go through the slide show, note that the images selected for this site are to illustrate the generalized, typical view of the represented stages of meiosis. Most of the images have been taken through a compound light microscope with either the 40X objective or the 100X oil immersion objective. The material was prepared by either the Feulgen or orcein methods detailed in the article in *The American Biology Teacher* by Braselton.

Enjoy!

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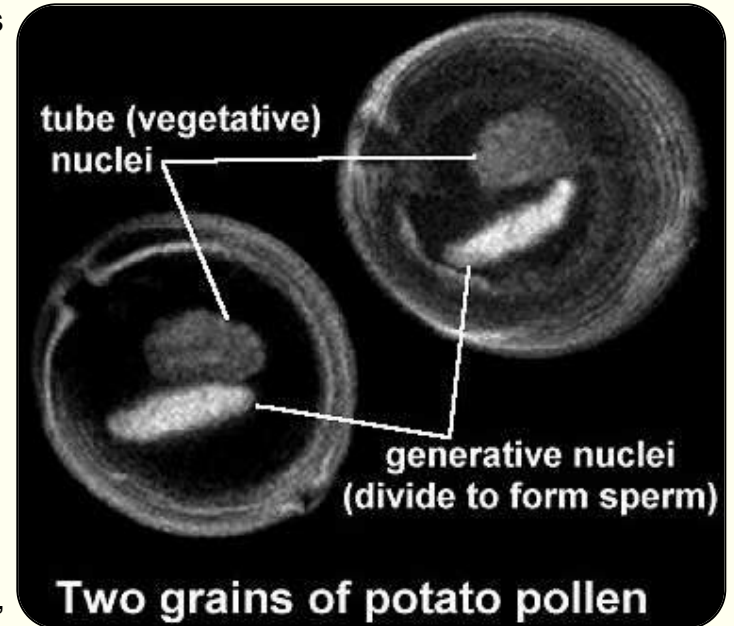
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SPORES

Spores of plants often are incorrectly equated with gametes in treatments of meiosis. Spores upon germination and subsequent development produce gametophytes, the haploid plants that by mitosis produce the gametes, egg and sperm.

In the most common plants, the angiosperms or flowering plants, so-called "male spores" develop into pollen, which is either a two- or three-celled gametophyte when it is shed from the flower. If it is a two-celled gametophyte when it is shed, one of the cells, the generative cell, will divide once to form two sperm when the pollen lands on a receptive flower. In three-celled pollen at shedding, the generative nucleus divided to form the two sperm prior to the pollen being released from the flower.

The egg of angiosperms is produced within an embryo sac (the so-called "female gametophyte"), a structure within the ovule which is contained in the ovary (part of the pistil) of the flower. After pollination (transfer of pollen to the stigma of the pistil) and subsequent fertilization of the egg in the ovule by the sperm from the pollen, the ovule matures to form a seed, which is contained within the fruit (the mature ovary).



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OVERVIEW

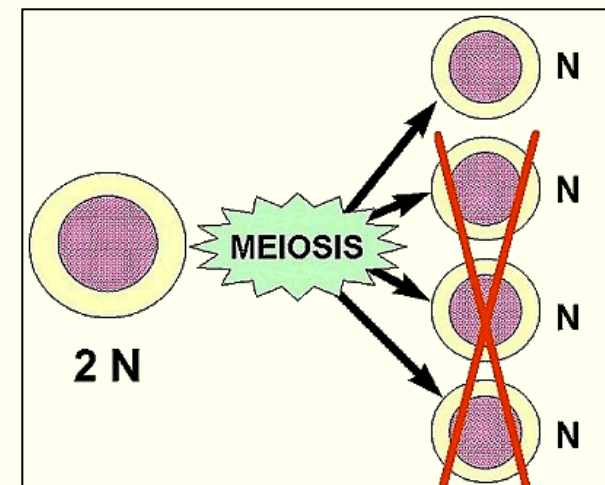
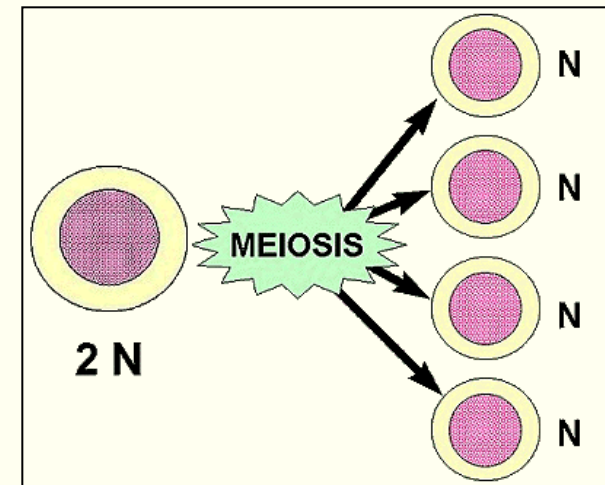
Meiosis consists of two divisions: meiosis I and meiosis II. Prior to meiosis, DNA and the rest of the chromatin are replicated during the S-phase of premeiotic interphase. After replication, each chromosome contains two, identical chromatids. The chromatids will not be visible through light microscopy as structures until midway through prophase I. Most diagrams of meiosis show that each chromosome entering meiosis consists of two, parallel chromatids.

Meiosis I is characterized by a relatively long prophase during which homologous chromosomes pair (synapsis) and exchange DNA (crossing over). In many organisms prophase I may last approximately one day, whereas in some organisms prophase I may last more than a week. Examples: European larch (*Larix*)—prophase I may last over winter; human females—prophase I may last approximately 40 years (from birth to menopause).

Metaphase I, anaphase I, and telophase I occur fairly rapidly, in most cases in less than a few hours. Meiosis II likewise takes a relatively short time to complete, ranging from a few hours to just a little less than a day.

In most cases of meiosis, there are four haploid (n) products from each cell (meiocyte) that enters meiosis.

The most notable exceptions are with females in animals, and in the so-called "female" part of the plant life cycle—three of the meiotic products in these cases degenerate, leaving only one functional egg in animals, or one functional megaspore in plants.



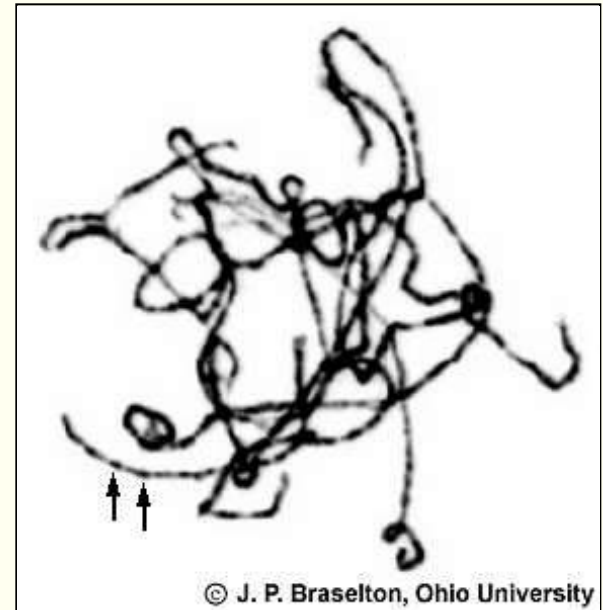
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PACHYNEMA

Pachynema in Mayapple. Leptonema and zygonema occur prior to pachynema. In leptonema, the chromosomes appear as very thin threads. During zygonema, the homologous chromosomes pair (synapsis). Pachynema is characterized by chromosomes having become completely paired. The paired homologues, now called bivalents, are still relatively long and twisted. The homologous chromosomes are so tightly appressed and twisted around each other that at this level of light microscopy the individual homologues and their chromatids cannot be resolved. The arrows in the photograph indicate chromomeres, which are localized compaction of the chromatin. Chromomeres have been used in cytogenetics as markers during mapping of chromosomes. At this stage transmission electron microscopy reveals a structure that occurs between the synapsed homologues—the synaptonemal complex, which is shown on the next page

Some treatments of meiosis refer to the synapsed homologues as "tetrads" instead of bivalents. They do this to emphasize that each pair of homologues consists of four chromatids, two in each of the homologous chromosomes. Use of the term tetrad in place of bivalent should be avoided. The term bivalent fits into an ordered system of names for chromosomes in meiosis. It is possible to have a chromosome that is not paired in meiosis or that has not remained attached to its homologue—such an unpaired chromosome is called a "univalent." In some situations, particularly in plants, it is possible to have three homologous chromosomes present: When they synapse during prophase I, the three homologous attached together form a "trivalent." Similarly, when four homologous chromosomes synapse, together they form a "tetravalent."

Another reason to avoid the use of tetrad for what should be called a bivalent is that the term tetrad is used for the four meiotic products together, particularly when referring to the products in plants. Viz., after meiosis the four spores are in a tetrad.

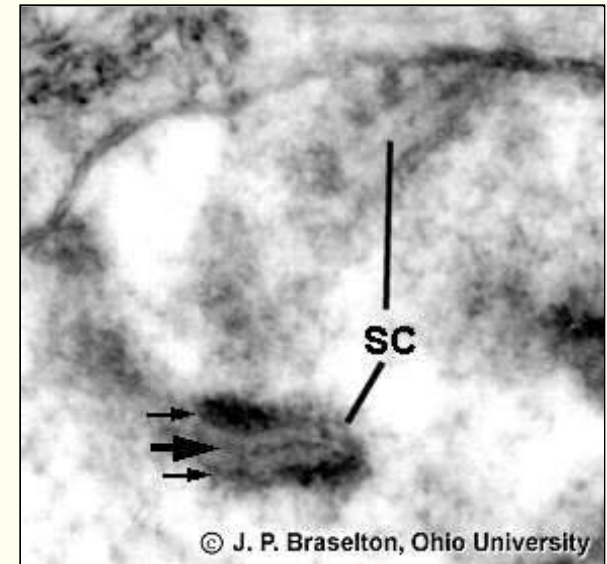


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PACHYNEMA (CONTINUED)

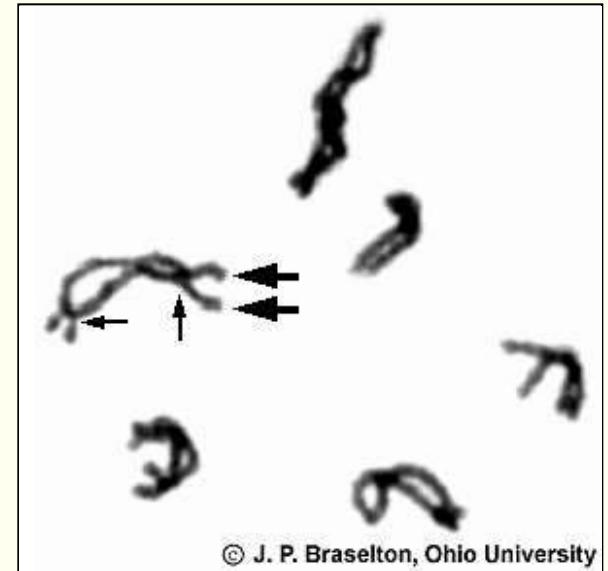
Transmission electron micrograph of synaptonemal complexes (SC) in a pachytene nucleus of a plant parasitic protist, *Polymyxa*. The SC has lateral elements (small arrows) which are separated by a central region (about 200 nm across) which contains a central element (large arrow).



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DIPLONEMA

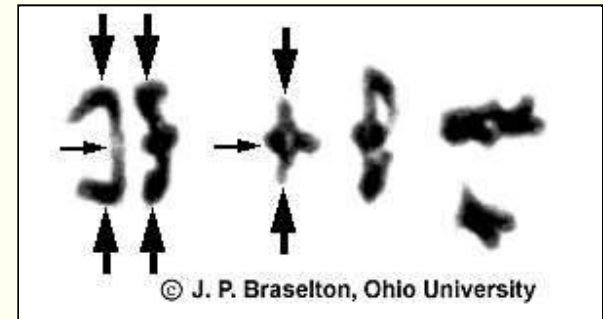
Diplonema in Mayapple. The six bivalents are clearly seen now that they have shortened and thicken after pachynema. The homologous chromosomes (large arrows) appear to be repelling each other—they remain attached at the chiasmata (singular—chiasma, small arrows). Chiasmata are the cytological evidence that crossing over at the molecular level has occurred.



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METAPHASE I

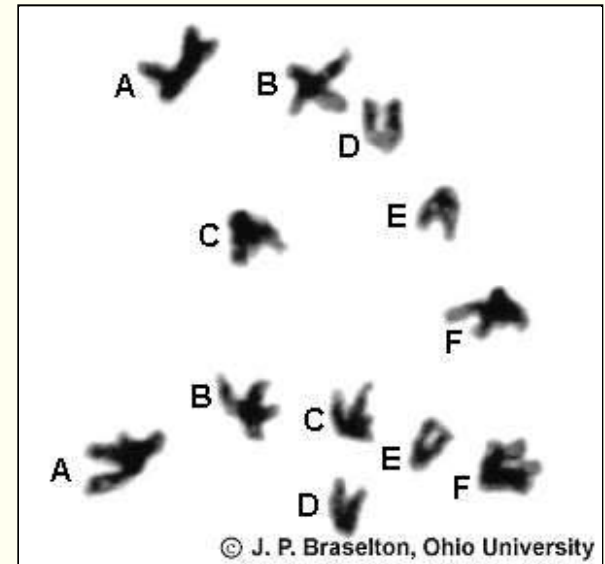
Metaphase I in Mayapple. The six bivalents are aligned on the metaphase plate. The centromeres (large arrows) are pointing toward the poles, whereas the chiasmata (small arrows) are on the metaphase plate.



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ANAPHASE I

Anaphase I in Mayapple. The homologous chromosomes (indicated by the letters) have separated and are progressing toward their respective poles. The chromatids appear to repel each other but remain attached at the centromere so that a chromosome in anaphase I has all of its chromatid arms showing.

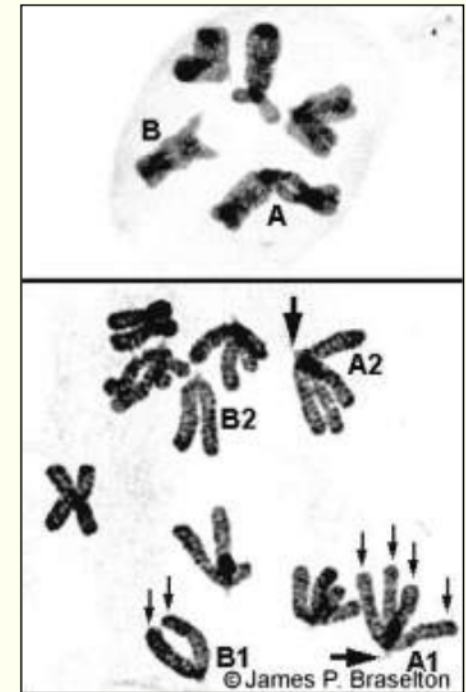


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METAPHASE I AND ANAPHASE I

The metaphase I/anaphase I comparison is made in this pair of images of meiosis in *Trillium grandiflorum* ($n=5$). The top image is of a polar view of metaphase I showing the five bivalents, two of which are labeled A and B respectively for comparison to the bottom image.

The bottom image is of anaphase I and shows the centromeres (large arrows) as well as the chromatid arms (small arrows). Chromosome A1 as well as its homologue (A2) is a metacentric chromosome (i.e., has its centromere located at the midpoint on the chromosome), and shows the four arms of the chromatids joined at the centromeric region. Chromosome B1 as well as its homologue (B2) is a so-called telocentric chromosome (i.e., the centromere is located near the telomere), and thus shows only two chromatid arms.

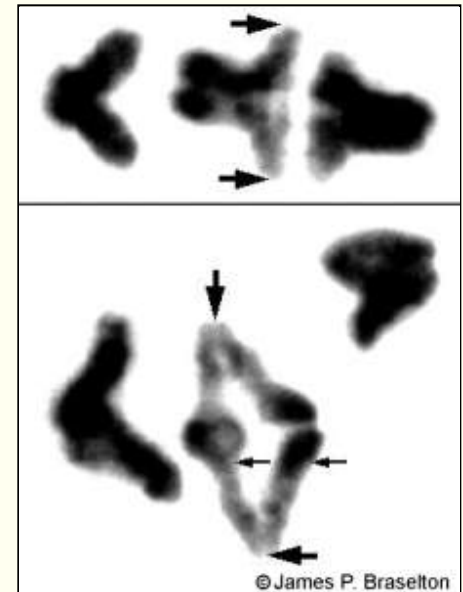


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ANOTHER METAPHASE I AND ANAPHASE I

The metaphase I/anaphase I transition is shown in this pair of images of meiosis in *Ornithogalum* ($n=3$). The top image is of metaphase I showing one telocentric bivalent (large arrows point to the centromeres) just beginning to pull apart.

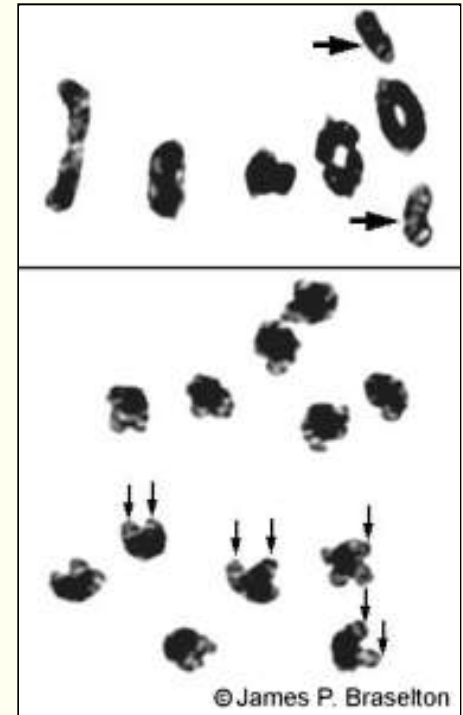
The bottom image is of very early anaphase I and shows the centromeres (large arrows) further toward the poles as well as the two chromatid arms (small arrows) of the telocentric chromosomes.



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ANOTHER METAPHASE I AND ANAPHASE I

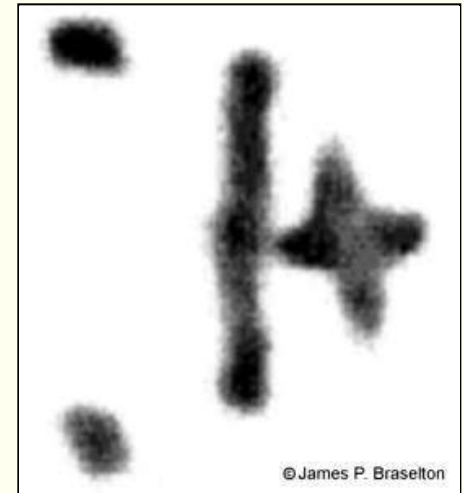
Metaphase I (top) and anaphase I (bottom) in *Tradescantia* ($n=6$). In the top figure, the large arrows point to two unpaired homologues in metaphase I; each is a univalent. The two homologues probably synapsed, but were not held together after pachynema because there was no crossing over between them, thus no formation of chiasmata. We know that the two univalents are still in metaphase I and not in early anaphase I because the chromatids have not begun to repel each other as seen in the anaphase I chromosomes (small arrows) in the bottom figure.



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METAPHASE I (CONTINUED)

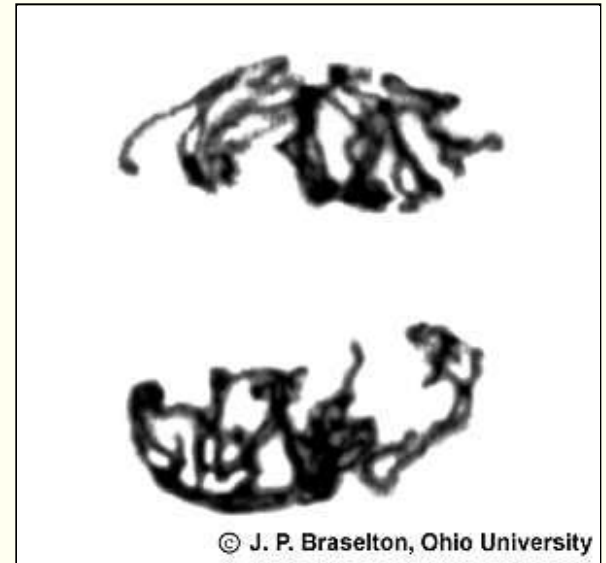
Metaphase I in *Crepis* ($n=3$). This image is here because it shows how to count: 0-1-2. The two univalents on the left represent zero because there was no crossing over, hence no chiasma. The bivalent in the middle has one chiasma. The bivalent on the right has two chiasmata.



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TELOPHASE I

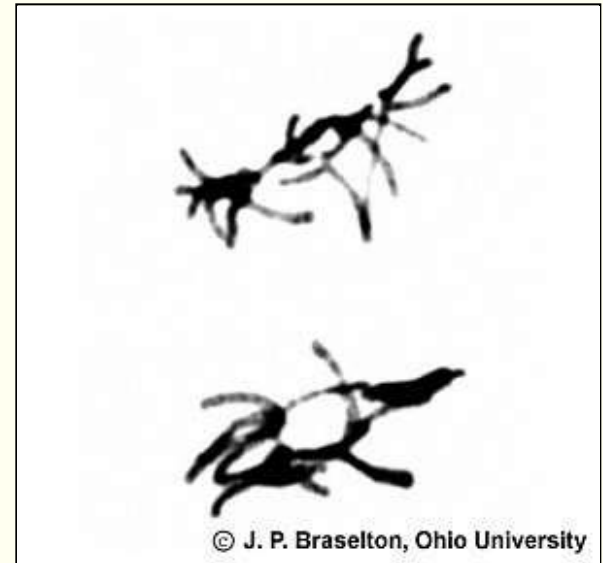
Telophase I/interphase/prophase II in Mayapple. For all practical purposes, telophase I, interphase, and prophase II are the same, particularly from the genetic point-of-view. No DNA synthesis occurs between meiosis I and II, so the nuclei that enter prophase II have the same amount of DNA as they had in anaphase I and telophase I.



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METAPHASE II

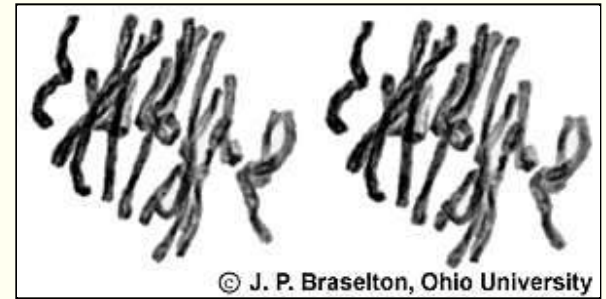
Metaphase II in Mayapple. In meiosis II the chromatids within each chromosome continue to show the appearance of repelling each other as they did in anaphase I. This makes the appearance of metaphase II different from that of a mitotic division. Many textbooks describe meiosis II as being essentially like mitosis. Here are the differences between meiosis II and mitosis. (1) There was no DNA synthesis and chromatin replication in the interphase prior to meiosis II, whereas DNA synthesis and chromatin replication always precede mitosis. (2) Because of crossing over, the chromatids in a chromosome in meiosis II are not genetically identical, but the two chromatids in a mitotic chromosome are genetically identical. (3) The chromatids in a meiotic II chromosome appear to repel each other, whereas in a mitotic chromosome the chromatids are tightly wound around each other as in the image of onion mitosis in the next page.



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METAPHASE IN MITOSIS

Mitosis in onion root tip for comparison to metaphase II on the previous page. The stereo pair was taken with a confocal scanning laser microscope. To see the two images as one 3-D image, you can use a stereo map reader. Or, if you cross your eyes and relax, you can fuse the two images to obtain a 3-D view of the chromosomes and the tightly wound chromatids in each. Otherwise, look closely at one of the images to see the tightly wound chromatids in each chromosome.



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ANAPHASE II

Anaphase II in Mayapple. In this and the image on the next page the chromosomes move to their respective poles and form four haploid nuclei.

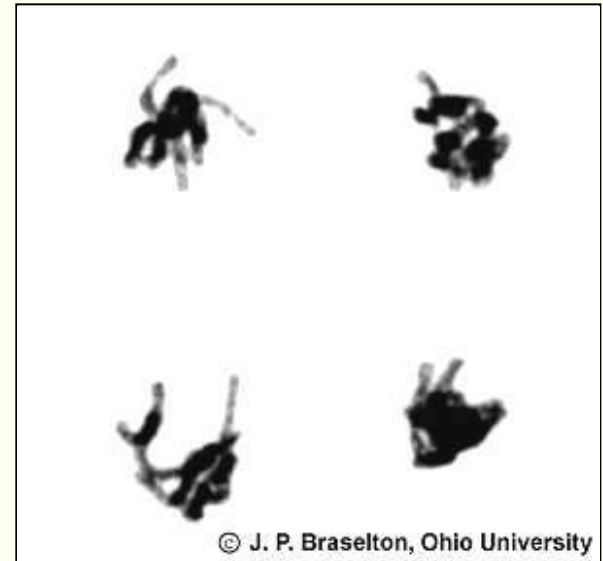


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TELOPHASE II

Telophase II in Mayapple. Cytoplasmic division will occur to form four haploid cells, a tetrad. Since these are in the anthers of Mayapple, the four meiotic products are spores, and will develop into pollen.

That is it for the microscopic review of meiosis. A list of general references is on the next page.



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SELECTED GENERAL REFERENCES FOR MEIOSIS

- **Bennett, M. D. and J. B. Smith. 1972.** The effects of polyploidy on meiotic duration and pollen development in cereal anthers. *Proceedings of the Royal Society of London, Series B* 181: 81-107.
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