Apomixis

III MSc Botany

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- **Apomixis** was defined by Hans Winkler as replacement of the normal sexual reproduction by asexual reproduction, without fertilization.

- plants produced by apomixis are called apomictic which are of two types: obligate, producing only apomictic embryos, and facultative, producing both apomictic and normal embryos.

- This phenomenon where the substitution of sexual process occurs by asexual methods is known as apomixis (apo = away from, mixis = act of mixing), the plants are called apomictic.

Apomixis is the phenomenon where there is no normal fertilisation of the egg cell, hence no normal development of embryo from the egg cell. However, embryo may develop from an un-fertilised egg cell or from a cell other than the egg cell within the embryo sac or from the cell outside the embryo sac

Apomixis is widely distributed among higher plants. More than 300 species belonging to 35 families are apomictic. It is most common in Gramineae, Compositae, Rosaceae and Rutaceae. Among the major cereals maize, wheat, and pearl millet have apomictic relatives.

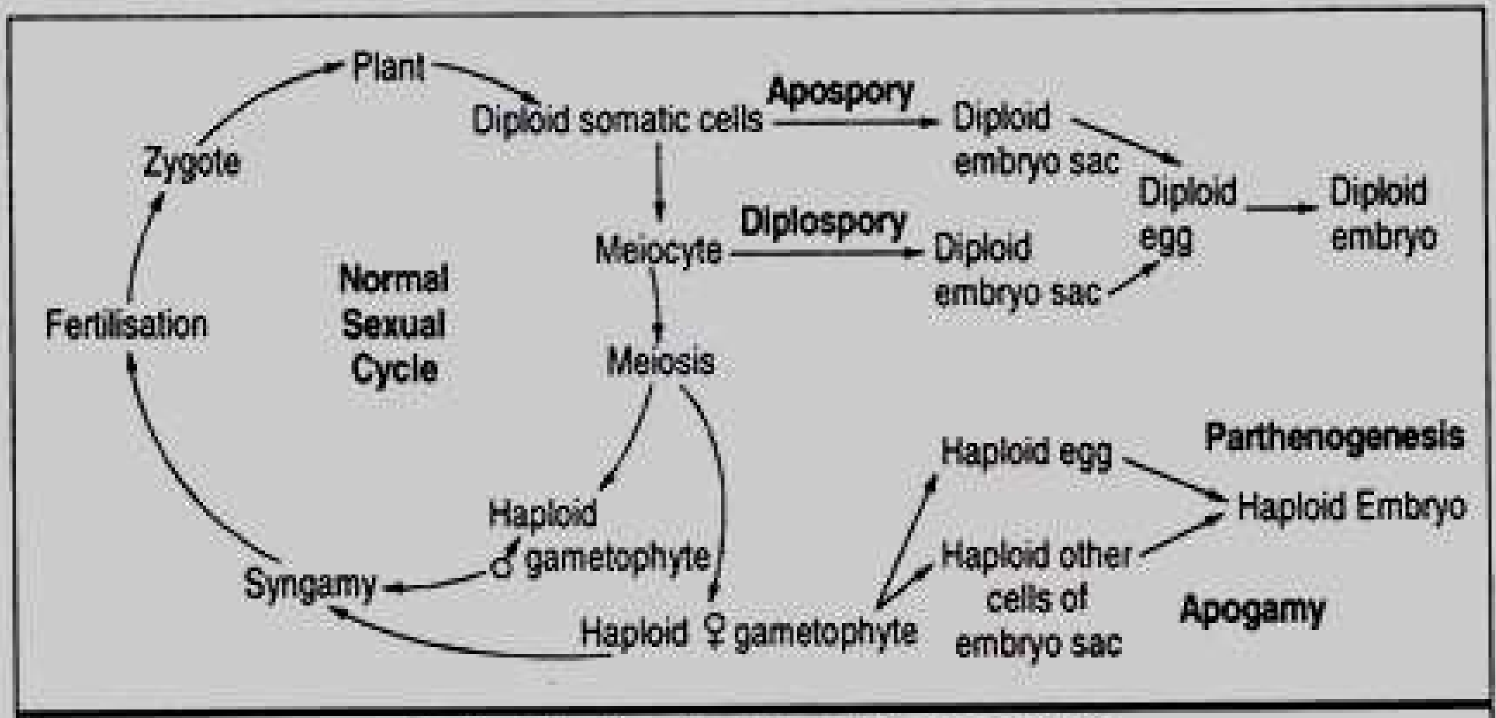


Fig. 2.1: Sexual and apomictic reproduction

Nonrecurrent apomixis:

- "the megaspore mother cell undergoes the usual meiotic divisions and a haploid embryo sac [megagametophyte] is formed.
- The new embryo may then arise either from the egg (haploid parthenogenesis) or from some other cell of the gametophyte (haploid apogamy).“
- The haploid plants have half as many chromosomes as the mother plant, and "the process is not repeated from one generation to another" hence nonrecurrent.

- **Recurrent apomixes** often called as **gametophytic apomixis**:
- In this type, the megagametophyte has the same number of chromosomes as the mother plant because meiosis was not completed.
- It generally arises either from an archesporial cell or from some other part of the nucellus.

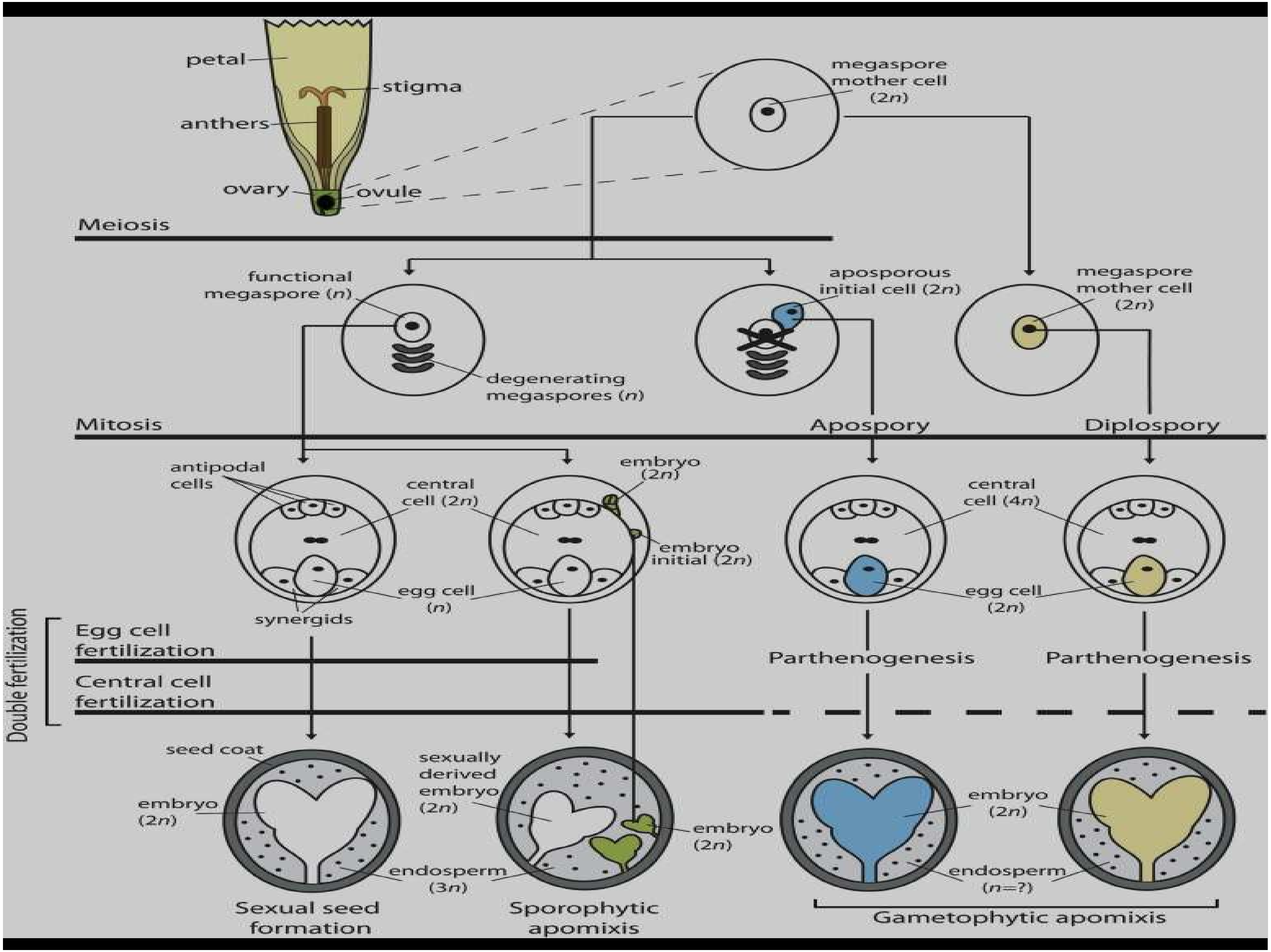
Adventive embryony, also called **sporophytic apomixis**, **sporophytic budding**, or nucellar embryony:

- There may be a megagametophyte in the ovule, but the embryos do not arise from the cells of the gametophyte but arise from cells of nucellus or the integument.
- Adventive embryony is important in several species of *Citrus*, in *Garcinia*, *Euphorbia dulcis*, *Mangifera indica* etc.

Vegetative apomixis:

the flowers are replaced by bulbils or other vegetative propagules which frequently germinate while still on the plant".

Vegetative apomixis is important in *Allium*, *Fragaria*, *Agave*, *Globba* and some grasses, etc.


petal
stigma
anthers
ovary
ovule
megaspore mother cell (2n)
Meiosis
functional megaspore (n)
degenerating megaspores (n)
aposporous initial cell (2n)
megaspore mother cell (2n)
Mitosis
Apospory
Diplospory
antipodal cells
central cell (2n)
embryo (2n)
embryo initial (2n)
central cell (4n)
synergids
egg cell (n)
egg cell (2n)
Double fertilization
Egg cell fertilization
Central cell fertilization
Parthenogenesis
Parthenogenesis
seed coat
embryo (2n)
sexually derived embryo (2n)
embryo (2n)
embryo (2n)
endosperm (3n)
endosperm (n=?)
Sexual seed formation
Sporophytic apomixis
Gametophytic apomixis

sexual seed formation and the apomictic mechanisms of sporophytic and gametophytic apomixis.

Meiosis, mitosis, and double fertilization constitute the major components of the seed formation pathway.

In the process of gametophytic apomixis, embryo sac formation can occur via either apospory or diplospory, which are distinguished by different embyro sac precursor cells.

In gametophytic apomixis, embryo formation is initiated in the absence of fertilization (parthenogenesis); however, endosperm formation can occur either with or without fertilization, which is represented by a dashed line.

The ploidy level of endosperm formed through gametophytic apomixis is variable, depends on a number of factors, and is therefore represented by a question mark (?). In the depicted apospory pathway, the sexual pathway is shown to terminate once the aposporous initial cell undergoes mitosis. Different colors track the precursor cells that form the embryo for each pathway: sexual (white), sporophytic apomixis (green), diplospory (yellow), and apospory (blue). ve

Apomixis can occur by various mechanisms that share three common developmental components:

(i) a bypass of meiosis during embryo sac formation (apomeiosis),

(ii) development of an embryo independent of fertilization (a process known as parthenogenesis), and

(iii) formation of viable endosperm either via fertilization-independent means or following fertilization with a sperm cell (Koltunow and Grossniklaus 2003).

Derivation of the egg from a diploid maternal cell without meiotic reduction, and its subsequent fertilization-independent development into an embryo, means that the progeny derived from apomictic development are clonal and therefore genetically identical to the maternal parent.

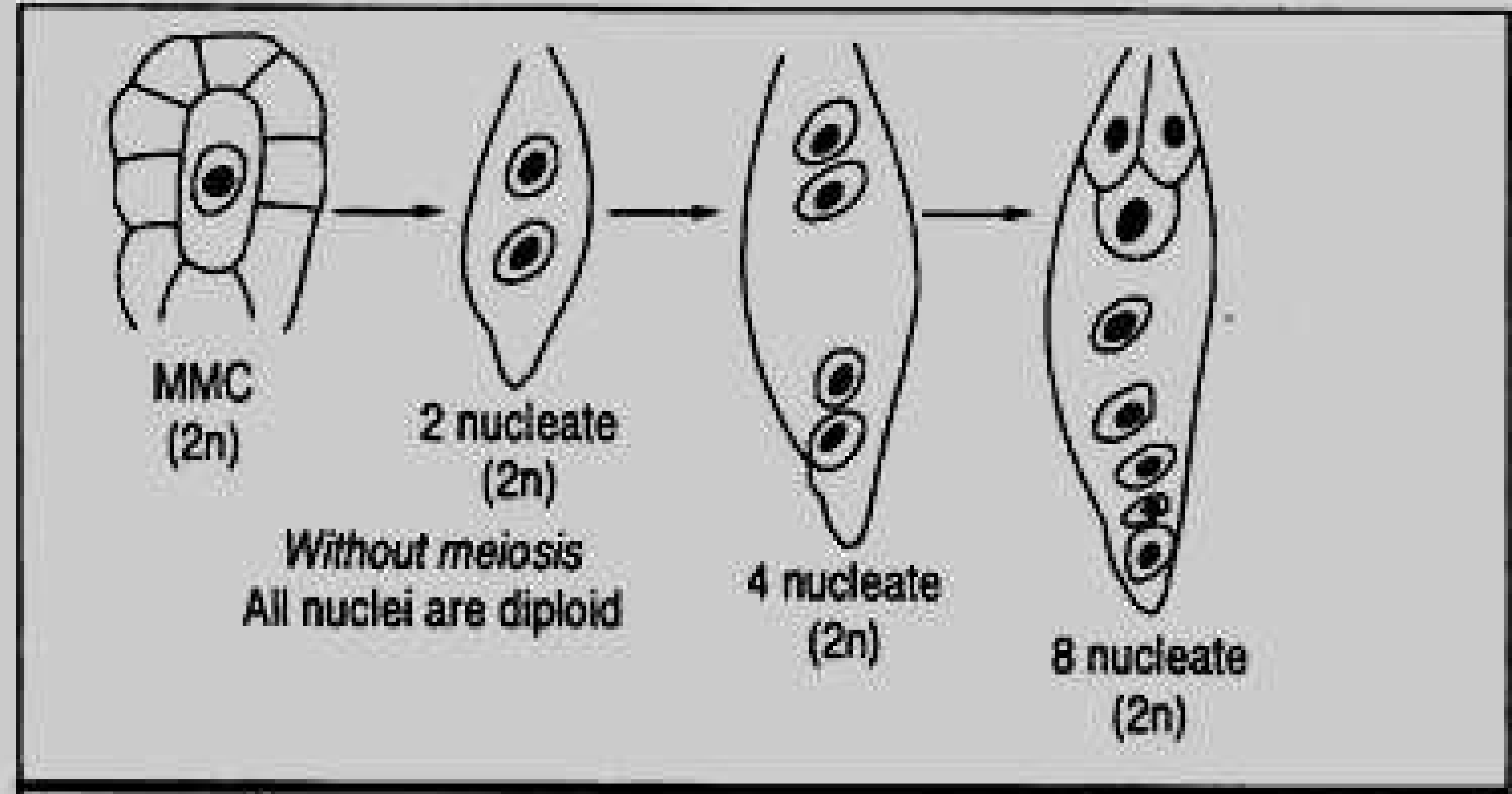


Fig. 2.2a: Aposporous embryo sac in *Eupatorium*

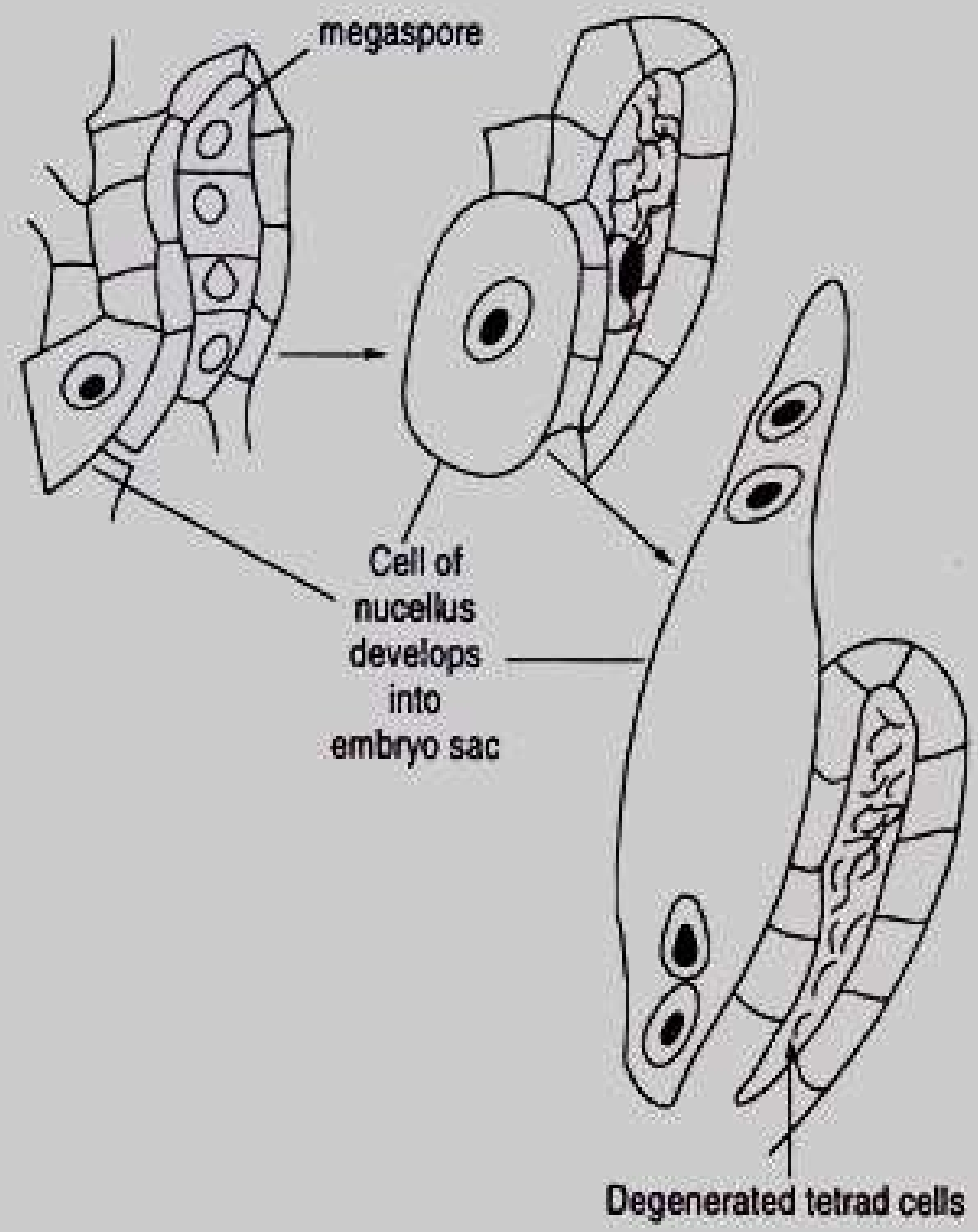


Fig. 2.2b: Aposporous embryo sac in *Hieracium*

Apomixis mechanisms are subdivided into two categories - gametophytic or sporophytic - the embryo develops via a gametophyte (embryo sac) or directly from diploid somatic (sporophytic) cells within the ovule.

During **sporophytic apomixis**, development of an embryo sac following the typical angiosperm sexual pathway.

However, during mitosis of the functional megaspore, diploid somatic ovule cells surrounding the embryo sac differentiate and have an embryogenic cell fate. These embryo initial cells begin mitosis forming multiple globular-shaped embryos that can develop to maturity only if the sexually derived embryo sac is fertilized, as the sexual and asexual embryos share the nutrititive endosperm.

Sporophytic apomixis can therefore lead to a seed containing multiple embryos and is common in *Citrus*. The sexually derived embryo may or may not mature or germinate.

- Gametophytic apomixis relates to mechanisms where an embryo sac is mitotically formed from a diploid cell in the ovule, bypassing meiosis.
- Another term for such mitotic embryo sac development is apomeiosis.
- Embryo development in gametophytic apomixis is fertilization independent whereas endosperm formation may or may not require fertilization.
- Apomeiotic embryo sac development is further subdivided into two types (diplospory and apospory) based upon the origin of the diploid precursor cell that ultimately gives rise to the mitotically derived embryo sac.

- **Diplospory** - the unreduced embryo sac is derived from the megaspore mother cell either directly by mitotic division or by aborted meiotic events.

- This cell may enter meiosis and abort the process or it may immediately begin mitosis.

- Diplospory has been observed in species including *Taraxacum officinale* (dandelion), *Boechera* spp., *Erigeron annuus*, and *Tripsacum dactyloides*.

In the Taraxacumtype, meiotic prophase is initiated but then the process is aborted resulting in two unreduced dyads one of which gives rise to the embryo sac by mitotic division. In the Ixeris type, two further mitotic divisions of the nuclei to give rise to an eight-nucleate embryo sac follow equational division following meiotic prophase. The Taraxacum and Ixeris types are known as meiotic diplospory because they involve modifications of meiosis.

- **Apospory** involves development of the embryo sac via mitosis not from the megaspore mother cell, but from a diploid somatic cell positioned adjacent to the megaspore mother cell.

- This cell, termed the aposporous initial cell, undergoes mitosis and the nuclei cellularize.

- The mitotic events of diplospory and apospory may or may not make a seven-nucleate *Polygonum*-type embryo sac; however, an egg, a central cell, and synergids are typically formed.

Apospory

Some ovules can contain multiple embryo sacs and, depending on the species, the structure of the embryo sac may be quite different from that seen in the sexual process. The initiation of the apospory embryo sac can occur together with a sexual one or it can display or inhibit sexual embryo sac formation.

Depending on the species, both sexually derived and aposporous embryo sacs can coexist within the one ovule, as occurs in *Brachiaria* species.

Alternatively, development of the aposporous embryo sac may lead to the demise of the sexually derived embryo sac or pathway as occurs in aposporous *Hieracium* and *Pennisetum* species.

Embryo development from the diploid egg formed in aposporous and diplosporous embryo sacs occurs without fertilization and the term parthenogenesis is used to describe this process.

Endosperm development can occur without fertilization of the central cell (rare) occure predominantly in Asteraceae family.

Apomicts that require fertilization to produce endosperm have disturbed maternal and paternal genome contributions in the endosperm.

Those apomicts that require fertilization to develop endosperm have therefore developed multiple strategies to ensure seed viability.

•*Allium odorum–A. nutans* type. The chromosomes double (endomitosis) and then meiosis proceeds in an unusual way, with the chromosome copies pairing up (rather than the original maternal and paternal copies pairing up).

•*Taraxacum* type: Meiosis I fails to complete, meiosis II creates two cells, one of which degenerates; three mitotic divisions form the megagametophyte.

•*Ixeris* type: Meiosis I fails to complete; three rounds of nuclear division occur without cell-wall formation; wall formation then occurs.

•*Blumea*–*Elymus* types: A mitotic division is followed by degeneration of one cell; three mitotic divisions form the megagametophyte.

•*Antennaria*–*Hieracium* types: three mitotic divisions form the megagametophyte.

•*Eragrostis*–*Panicum* types: Two mitotic division give a 4-nucleate megagametophyte, with cell walls to form either three or four cells.

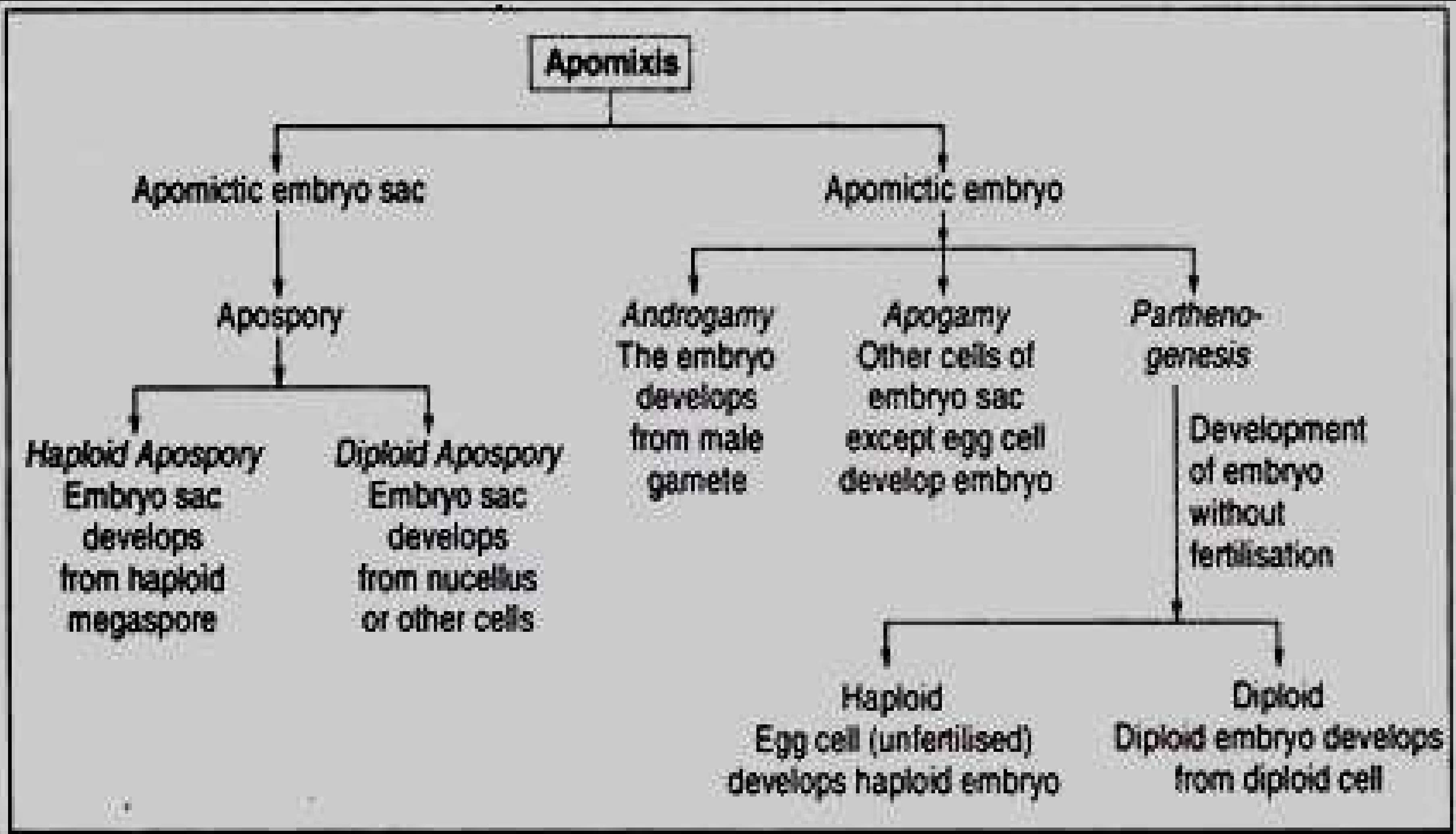


Fig. 2.3: Classification of apomixis

Potential for Apomixis in Plant Breeding:

Fixation of genotype (hybrid vigour) –
Nawaschin and Karpachenko (1930)

- Reduced cost of hybrid seed production
- Successive progagation of hybrids
- Accelerated breeding
- Encourage “risk” in breeding practice