

Fundamentals of the morphology of generative organs. The structure and functions of the flower. Inflorescences.

Part 1

Plan.

Angiosperms division. Their origin.

Flower. Concept and functions. Flower Parts

Flower formula and diagram

Inflorescence. Classification of inflorescences

Biology of Angiosperm reproduction.

Microsporogenesis and male gametophyte

Megasporogenesis and female gametophyte

Flowering and pollination of plants

Seed development

Reproductive (generative) organs are intended for sexual or asexual reproduction itself. The reproductive organs of plants include sporangia and organs of sexual reproduction: archegonia and antheridia. In angiosperms, the reproductive organs include a flower and its derivatives - a seed and a fruit.

We'll look more closely at reproduction in angiosperms, which are unique among plants for three defining features: they have flowers, they have fruit-covered seeds, and they reproduce via a process called double fertilization.

Angiosperms or flowering plants (Magnoliophyta or Angiospermae) are a group of higher plants that dominate the modern flora of the Earth. It includes 165 orders, 540 families, about 13,000 genera, 250,000 species, grouped into 2 classes and 12 subclasses. The prosperity of this group is currently due to the appearance of a flower that combines the structures of sexual and asexual reproduction and attracting insects as an active pollination agent. The main feature of angiosperms is that

their ovules are enclosed in the ovary cavity formed by a once open carpel, the edges of which are fused together. Seeds are formed inside the fruit.

Flower.

The flower is a modified shortened shoot adapted to produce spores for asexual reproduction as well as gametes for the sexual process that results in seeds and fruit.

In its origin, the flower is related to the strobilus of the gymnosperms. Like the strobilus, a flower is a compressed stem, with crowded spore-bearing appendages. The occurrence of coloured petals and attractive scents is not essential and is by no means characteristic of all flowers. This has led to the fact that the true nature of the flower organs is difficult to recognize and often leads to various interpretations.

In the flower, the sporogenesis, the gametogenesis and the sexual process take place. After pollination and fertilization, the flowers turn into fruits and the ovules into seeds. The fruit cannot arise independently of the flower, but is always formed from it.

Flowers arise from the apical and axillary meristems of shoots. The leaf in the axils of which the flower is formed is called **the bract**. It may be modified or normal.

Symmetry divides flowers into **actinomorphic** or regular flowers, which have radial symmetry, or several symmetry planes, and **zygomorphic** or irregular flowers, with one symmetry plane. If no symmetry plane can be drawn through the flower, and the perianth leaves are of different sizes, it is an **asymmetrical flower**.

The pedicel and receptacle are the stem parts of the flower. If the pedicel is absent, the flower is called **sessile**.

The leafy parts of the flower are the **perianth leaflets**, **stamens** (microsporophylls), and **carpels** (megasporophylls). All flower elements sit on the axis, the receptacle. The receptacle may be convex, flat or concave.

Leaf parts of the flower are arranged on the receptacle either in a circle (**cyclic flowers**), or spirally (**acyclic or spiral flowers**), or perianth leaflets are arranged in circles, while stamens and pistils are arranged in spirals (**hemicyclic**).

The leafy parts of a flower are divided into sterile parts - perianth (sepals, petals, tepals), and fertile (reproductive) parts - androecium (stamens) and gynoecium (pistils). The male sphere in the flower is represented by the stamens and the female by the pistil.

A "perfect" flower has both stamens and carpels, and may be described as "bisexual" or "hermaphroditic". A "unisexual" flower is one in which either the stamens or the carpels are missing, vestigial or otherwise non-functional. Each flower is either "staminate" (having only functional stamens) and thus "male", or "carpellate" (or "pistillate") (having only functional carpels) and thus "female". If separate staminate and carpellate flowers are always found on the same plant, the species is called monoecious. If separate staminate and carpellate flowers are always found on different plants, the species is called dioecious.

Floral diversity is achieved by numerous variation patterns resulting from changes in 1) symmetry, 2) numbers of each floral part, and 3) degree of fusion of the parts. If like parts are fused, they are connate; if unlike parts are fused, they are adnate. Prefixes such as gamo-, sym-, and syn- denote connation, as in gamopetaly and sympetaly (fusion of petals to each other) and syncarpy (fusion of carpels). The prefix epi- refers to adnation, as in epipetalous stamens (stamens fused to the petals). In floral morphology, the prefixes poly- and apo- represent the lack of fusion, as in polypetaly (separate petals) and apocarpy (separate carpels).

Flower parts.

The perianth. - the sterile part of the flower, which performs the functions of protecting and attracting pollinating insects. The perianth can be differentiated into a calyx and a corolla, in this case it is called double, or consist only of a calyx or only of a corolla and is called simple. The leflets of simple perianth is called tepals.

The calyx usually consists of small green leaflets - sepals, but sometimes are brightly colored. The sepals form only one circle most often. Sometimes another or several circles of sepals are formed under the calyx, such sepals are called a podchash. The sepals can be free or fused bases. Sometimes the sepals are fused together, forming calyx, in which a tube and teeth are distinguished. If the sepals are free (not fused) then the calyx is called free.

The corolla consists of larger and, as a rule, brightly colored leaflets – petals. The main function of the petals is to attract pollinators and promote successful pollination. The petals can fuse together at least partially or be free.

The androecium is a collection of stamens of one flower. The number of stamens varies widely from one to several hundred. The stamens can be free or fused to varying degrees.

The stamen consists of a filament and anther. Filaments in most plants are simple and unbranched, but sometimes they have lateral outgrowths of various shapes. If there is no stamen filaments, the stamen is called sessile.

It consists of one or two anther lobes and accordingly, anthers are called monothecous or ditheous. The two anther lobes are separated in the anterior region by a deep groove but are attached to each other on the back side by a sterile parenchymatous tissue called connective. Connective possesses a vascular strand. Connective is absent in monothecous stamen.

Each anther lobe contains two long and cylindrical pollen sacs or microsporangia. Thus a ditheous anther is tetrasporangiate while monothecous stamen is bisporangiate. Rarely, an anther lobe has only one microsporangium. The four microsporangia of an anther lie at its four comers.

Inside each nest there is a sporogenic tissue, from the cells of which microspores are formed, and then pollen.

In some plant species, part of the stamens does not have anthers and is represented only by staminate filaments. Such infertile stamens are called staminodes.

The gynoecium is a set of carpels (megasporophylls) of one flower that form one or many pistils.

The pistil is a closed receptacle for ovules, consisting of ovary, style and stigma. The ovary forms a fruit, the stigma receives pollen, and the style carries the stigma closer to pollinators. Sometimes the style is absent, and then the stigma will be sessile. A pistil with a single carpel is called a simple pistil. Pistil with two or more carpels is called compound.

The ovary is the swollen part of the pistil that contains the ovules. The position of the ovary in relation to the other floral parts is often used as a character to distinguish taxa, especially families. If the ovary is borne above the insertion of the sepals, petals, and stamens, the ovary is superior. If the ovary is borne below the attachment of the other floral parts, it is inferior. If the sepals, petals, and stamens are borne on a hypanthium or floral cup around the ovary, the ovary position can be either superior or half-inferior or inferior. Flowers may be described as hypogynous (with a superior ovary), epigynous (with an inferior ovary), or perigynous (with a basal disk or hypanthium distinct from the ovary).

The hypanthium is a floral cup or ring formed usually from the fusion of the lower parts of the calyx, corolla, and androecium. In some instances, the hypanthium may be derived from the receptacle.

Depending on the number of non-communicating chambers, ovaries can be unilocular, bilocular and trilocular, tetralocular, pentalocular and multilocular.

There are three evolutionarily related **types of gynoecium**

- **monocarpel or unicarpel gynoecium** is represented in the flower by one simple pistil;

- **apocarpic gynoecium**, consisting of two or more simple pistils (have two or more definite individualized carpels);

- **syncarpic gynoecium** or cenocarpic consists of several fused carpels forming a single pistil. The fusion of the carpels can be complete or partial. The cenocarpic gynoecium consists of as many carpels as there are individual styles carried by the ovary or lobes - the stigma.

Sometimes a **pseudomonocarpic gynoecium** is differentiated, which developed from a cenocarpic gynoecium. It is formed by one compound pistil, but inside there is one ovulus.

Floral formula

Floral formula is a means to represent the structure of a flower using numbers, letters and various symbols, presenting substantial information about the flower in a compact form. It can represent particular species, or can be generalized to characterize higher taxa, usually giving ranges of organ numbers. Floral formulae are one of the two ways of describing flower structure developed during the 19th century, the other being floral diagrams.

A floral formula consists of five symbols indicating from left to right:

Floral Symmetry: * - Actinomorphic; ↑ - zygomorphic; ↯ - Asymmetry flower

Number of Tepal - P

Number of Sepals - Ca

Number of Petals - Co

Number of Stamens - A

Number of Carpels - G

The number of members of each part of the flower is indicated by numbers in the subscript. The parts of the flower are described according to their arrangement from the outside to the inside of the flower. If an organ type is arranged in more whorls, the outermost is denoted first, and the whorls are separated by "+". If the

organ number is large or fluctuating, is denoted as “ ∞ ”. In the case of fusion of parts of the flower, the fused parts are taken in parentheses.

When describing the gynoecium, the formula should reflect the number of carpels that formed it, as well as the position of the ovary. The position of the ovary is indicated by a line above the numerical index of the gynoecium if it is lower, under the numerical index - if it is upper.

Floral Diagram.

It sometimes becomes very lucid if the ground plan of a flower be represented in the form of a floral diagram, in a floral diagram the position of the inflorescence axis or stem is shown by a dot or a small circle while the sepals, petals and stamens are put in concentric circles (or spirals when the floral phyllotaxy is spiral), the gynoecium being put at the centre.

It has become customary to represent petals by thick first brackets (representing t.s. of petals), sepals by the same symbol but showing the midrib, stamens by anthers and carpels by placentation.

The median, lateral or diagonal planes may be shown as straight lines. The bract may be shown by a second bracket. Thus, the orientation and symmetry of the flower and its different members may be shown very clearly. Adhesion and cohesion are shown by connecting lines.

The floral diagrams of some common flowers illustrating their constructions are shown.

Inflorescence.

An inflorescence is a shoot or a system of shoots bearing flowers. At the nodes of the inflorescence axes there are leaves called bracts.

The biological advantage of inflorescences over single flowers is to increase the guarantee of pollination, to reduce the likelihood of flowers being damaged by adverse environmental factors due to their gradual blooming. Inflorescences have most plants.

The stem holding the whole inflorescence is called a peduncle. The major axis (incorrectly referred to as the main stem) above the peduncle bearing the flowers or secondary branches is called the rachis. The stalk of each flower in the inflorescence is called a pedicel. A flower that is not part of an inflorescence is called a solitary flower and its stalk is also referred to as a peduncle. Any flower in an inflorescence may be referred to as a floret, especially when the individual flowers.

Inflorescences are described by many different characteristics including how the flowers are arranged on the peduncle, the blooming order of the flowers and how different clusters of flowers are grouped within it. These terms are general representations as plants in nature can have a combination of types. These structural types are largely based on natural selection.

Classification of inflorescences.

The modifications can involve the length and the nature of the internodes and the phyllotaxis, as well as variations in the proportions, compressions, swellings, adnations, connations and reduction of main and secondary axes.

Inflorescences may be **simple (single)** or **complex (panicle)**. The rachis may be one of several types, including single, composite, umbel, spike or raceme.

Complex inflorescences – when the flowers are located on the branches of the main axis.

Simple inflorescences - directly on the main axis.

Inflorescences usually have modified foliage different from the vegetative part of the plant. Considering the broadest meaning of the term, any leaf associated with an inflorescence is called a bract. A bract is usually located at the node where the main stem of the inflorescence forms, joined to the rachis of the plant, but other bracts can exist within the inflorescence itself. They serve a variety of functions which include attracting pollinators and protecting young flowers. According to the presence or absence of bracts and their characteristics we can distinguish:

Ebracteate inflorescences: No bracts in the inflorescence.

Bracteate inflorescences: The bracts in the inflorescence are very specialised, sometimes reduced to small scales, divided or dissected.

Leafy inflorescences: Though often reduced in size, the bracts are unspecialised and look like the typical leaves of the plant, so that the term flowering stem is usually applied instead of inflorescence. This use is not technically correct, as, despite their 'normal' appearance, these leaves are considered, in fact, bracts, so that 'leafy inflorescence' is preferable.

Leafy-bracted inflorescences: Intermediate between bracteate and leafy inflorescence.

If many bracts are present and they are strictly connected to the stem, like in the family Asteraceae, the bracts might collectively be called an involucre. If the inflorescence has a second unit of bracts further up the stem, they might be called an involucl.

If the inflorescence ends with a flower, it is called determined. If the inflorescence ends with the bud is called indetermined. The growth of the main axis of the indetermined inflorescence is unlimited. The growth of the main axis of the determined one is finite.

Plant organs can grow according to two different schemes, namely monopodial or racemose and sympodial or cymose. In inflorescences these two different growth patterns are called indeterminate and determinate respectively, and indicate whether a terminal flower is formed and where flowering starts within the inflorescence.

Indeterminate inflorescence: Monopodial (racemose) growth. The terminal bud keeps growing and forming lateral flowers. A terminal flower is never formed.

Determinate inflorescence: Sympodial (cymose) growth. The terminal bud forms a terminal flower and then dies out. Other flowers then grow from lateral buds.

Indeterminate simple inflorescences are generally called racemose /'ræsimous/. The main kind of racemose inflorescence is the raceme (/ 'ræsi:m/, from

classical Latin racemus, cluster of grapes).[5] The other kind of racemose inflorescences can all be derived from this one by dilation, compression, swelling or reduction of the different axes. Some passage forms between the obvious ones are commonly admitted.

A **raceme** is an unbranched, indeterminate inflorescence with pedicellate (having short floral stalks) flowers along the axis.

A **spike** is a type of raceme with flowers that do not have a pedicel.

A **racemose corymb** is an unbranched, indeterminate inflorescence that is flat-topped or convex due to their outer pedicels which are progressively longer than inner ones.

An **umbel** is a type of raceme with a short axis and multiple floral pedicels of equal length that appear to arise from a common point. It is characteristic of Umbelliferae.

A **spadix** is a spike of flowers densely arranged around it, enclosed or accompanied by a highly specialised bract called a spathe. It is characteristic of the family Araceae.

A **flower head or capitulum** is a very contracted raceme in which the single sessile flowers share are borne on an enlarged stem. It is characteristic of Dipsacaceae.

A **catkin or ament** is a scaly, generally drooping spike or raceme.

Cymose or other complex inflorescences that are superficially similar are also generally called thus.

Determinate simple inflorescences are generally called **cymose**. The main kind of cymose inflorescence is the cyme (pronounced 'saim', from the Latin cyma in the sense 'cabbage sprout', from Greek kuma 'anything swollen').[6][7] Cymes are further divided according to this scheme:

Only one secondary axis: **monochasium**

Secondary buds always develop on the same side of the stem the successive pedicels are aligned on the same plane: **drepanium**

Secondary buds develop alternately on the stem, the successive pedicels follow a zig-zag path on the same plane: **rhipidium** (many Iridaceae)

Two secondary axes, secondary axis still dichasial: **dichasium** (characteristic of Caryophyllaceae)

More than two secondary axes: **pleiochasium** (characteristic of Euphorbiaceae)

Thyrus is a **mixed inflorescence**. In this type, the peduncle grows indefinitely. Upon the peduncle clusters of flowers are arranged in acropetal sequence. These are racemose characters.

At each node of the peduncle bracts are present. In the axils of bracts simple cymes appear in false whorl. It is a cymose character. It is described as a mixed type because of indefinite growth of the peduncle bearing cymose clusters, for example, *Ocimum*.

Biology of Angiosperm reproduction. Double fertilization.

<https://www.youtube.com/watch?v=AykzPemLs7Q>

<https://www.youtube.com/watch?v=l5dEgwTdBok>

https://www.youtube.com/watch?v=0UEpq1W9C_E

MICROSPOROGENESIS AND MALE GAMETOPHYTE

The anther and microsporangium. The anther is the apex of a microsporophyll in which the leaf part is reduced and bears fused microsporangia.

In the early stages of ontogenesis, anther consists of homogeneous cells surrounded by epidermis. Later, under the epidermis, strands of the so-called archesporial tissue are differenti-

ated. As a result of archesporial cell division, the outer layer of cells and the inner layer of sporogenic cells of microsporangium appear. The cells of the wall layer divide, resulting in the formation of 3-4 concentrically arranged layers that are part of the wall of the microsporangium. The sporogenic cells are transformed either directly into mother cells of spores or previously undergo a series of divisions.

The layer of cells, which is located directly under epidermis, i.e. the outermost layer resulting from division, forms endothecia, which reaches its maximum development when pollen is ready for sowing. Endothecium is the outermost layer of microsporangium wall while epidermis belongs to microsporophyll; thus, microsporangium of flowering plants is submerged under microsporophyll epidermis. Endothecium cells lose their living contents early and contribute to the opening of anther as they rapidly contract when drying; in this case a crack appears which opens both sockets at once. Other ways of opening the anther are also known.

The innermost layer of anther wall, the tapetum, or covering layer, plays an important physiological role, since all the nutrients supplying sporogenic tissue must pass through it. Tapetum has a number of functions: 1 Nourishment of the developing microspore mother cells and pollen grains, 2 It produces lipid rich granules containing sporopollenin for exine formation, pollenkit (oily, sticky covering of lipids and carotenoids) in case of entomophilous pollen grains, special proteins for the pollen grains to recognise compatibility and hormones. 3 It secretes enzymes like callase responsible for the degradation of callose wall around pollen tetrad.

By the time the microspores begin to separate from each other, the tapetum cells are usually destroyed.

The sporogenic cells form the mother cells of the microspores, most often after several divisions. As noted above, 4 nests of continuous sporogenic tissue are usually formed in the anther.

Sporogenous tissue fills the whole interior of a microsporangium. Its cells divide with the growth of anther and increase their number. Ultimately they are transformed into microspore or pollen mother cells. The latter are diploid, that is, they possess two genomes or sets of chromosomes.

The microspore mother cells or microsporocytes develop an internal layer of callose which breaks the plasmodesmal connections among themselves. The separated mother cells round off and undergo meiosis to produce tetrads of haploid microspores or pollen grains.

Microspores. Microspores arise from the mother cells of microspores as a result of meiosis. Maternal microspore cells divide in two stages to produce microspore tetrads. In most cases the tetrad stage is short-lived and the microspores separate from each other very soon.

Male gametophyte. The development of the male gametophyte reduced to a single division. By the time the microspore germinates, a large vacuole is developed in the microspore and the

division occurs in the wall layer of cytoplasm. This results in a small generative cell and a large cell, the "pollen tube cell". This cell is often referred to as a vegetative cell. Prothallial cells are completely lost in the axillarians. The entire male gametophyte consists of only 2 (!) cells.

The generative cell initially adjoins the microspore sheath, but then more and more recedes into the tube cell, subsequently the generative cell lies free inside the latter's cytoplasm. Often, the generative cell produces two sperm cells even before the beginning of pollen seeding. The tube cell is further transformed into a pollen tube.

Flowers have many adaptations to protect pollen from rain. Many plants have drooping flowers (lily of the valley, lingonberry) or inflorescences; others have flowers or inflorescences-baskets being closed when it rains; some plants have flowers under leaf protection (linden, prickly Pear). In irises stamens are hidden under the petal-like lobes of stigmas, etc.

The pollen in fact, is a male gametophyte of the angiosperms. After the above mentioned divisions, the microspore shell turns out to be a dustwort wall. However, only at the pollen stage (otherwise pollen grain) rather than the microspore stage does the shell reach its full development.

Pollen grain protoplast is uni-nucleate in the beginning but at the time of liberation it becomes 2-3 celled. Wall or covering of pollen grain is called sporoderm. It has two layers, outer exine and inner intine. Intine is pecto-cellulosic in nature. Exine is made of a highly resistant fatty substance called sporopollenin. Sporopollenin is not degraded by any enzyme.

The shape, size of pollen grains and structure of their shells are strikingly diverse. There is a certain dependence of pollen grain size on the size of a flower. However, the most important factor related to pollen size is, apparently, the distance a pollen tube should pass, i.e. column length. Pollen grains can be spherical, ellipsoidal, filiform, etc.

An amazing variety of sporoderm structure and at the same time its constancy and stability led to the foundation of a special field of botany, palynology, which allows to establish the systematic composition of flora of previous periods and explain the climate changes in the cases when other data are completely inadequate. Our information about climate and vegetation of Quaternary period is based first of all on the spore-pollen analysis.

Structure of Ovule

The ovule is a multicellular oval-shaped structure which originates from the placenta and lies inside the chamber of the ovary. Each chamber may consist of one or more number of ovules. A fully mature ovule consists of the stalk or funicle and the body. One end of the funicle is attached to the placenta and the other end to the body of the ovule. The point of attachment of the funicle with the body is called hilum. Funicle sometimes extends up to the base of the ovule and the ridge thus formed is called raphe.

The body of the ovule shows two ends – the basal end often called, the chalaza and the

upper end, known as the micropylar end. The main body of the ovule is covered with one or two envelopes called the integument. In some cases, however, there may be a single layer of integument. Accordingly, the ovules are referred to as unitegmic or bitegmic. The integument gives protection to the internal tissues.

There is a small opening at the apex of the integument called the micropyle. The integument encloses a large parenchymatous tissue known as nucellus. In center of the nucellus is situated the female gametophyte known as embryo-sac which develops from a functional megaspore. The embryo sac bears the embryo and is the most important part of the ovule.

Embryo Sac

The embryo sac is the female gametophyte. It is oval in shape and lies within the nucellus of the ovule. A mature embryo sac consists of a group of three cells at each of its ends, lying on either side of a big centrally placed nucleus. These cells are thin-walled. The group of three cells lying towards the micropylar end is called the egg-apparatus. The central cell of the egg-apparatus is known as the egg cell or ovum. It forms the female gamete. The other two cells, one on each side of the egg cell are called the synergids. The egg cell after fusion with the male gamete, i.e., after fertilization, gives rise to the embryo. The synergids are nonfunctional, short-lived and disintegrate soon after the fertilization.

The group of three cells at the chalazal end and lying opposite to the egg-apparatus are called the antipodal cells. The antipodal cells have no definite function and they disintegrate after the fertilization of the ovum. The large nucleus lying somewhat at the center of the embryo sac is called the definitive nucleus. It is the fused product of the two polar nuclei, contributed one each from the two poles or ends of the embryo-sac. The definitive nucleus fuses with one of the male gametes to form the endosperm nucleus, which later grows into the endosperm of the seed.

Development of the embryo sac: The embryo sac develops from a single cell of the hypodermal layer of the nucellus. This cell is called the embryo-sac mother cell or megaspore mother cell. It divides twice to produce a row of four embryo-sac cells or megaspores. The upper three cells degenerate and form dark patches or caps, while the lowermost cell becomes functional. It enlarges to form the embryo sac. The nucleus of the embryo sac divides thrice to give rise to eight nuclei, four at each end or pole. One nucleus from each pole migrates to the center of the embryo-sac. These are called the polar nuclei, which fuse together to give rise to definitive nucleus or fusion nucleus. The other six nuclei three at each pole enclose themselves by their walls and form the egg-apparatus and antipodal cells.

FLOWERING AND POLLINATION OF PLANTS

Introduction to flowering. The essence of flowering consists in opening of anthers and

functioning of pistils as organs perceiving pollen. Pre-blooming of flowers, that is, the proper transition from budding to flowering, especially noticeable in flowers with bright corolla, takes place in most plants. The end of flowering is accompanied by fading of the corolla (or the entire perianth).

Blooming time of individual flowers varies greatly - from a few hours or less to several weeks (some tropical orchids).

Pollination is the actual transfer of pollen from stamens to stigmas of pistils. A distinction is made between self-pollination (autogamy: Greek auto - self) and cross-pollination (allogamy: Greek allos - other). In the first case, pollen pollinates the stigmas of the same flower, and in the second, pollinators pollinate other flowers of the same or different specimens.

Cross-pollination is the process of applying pollen from one flower to the pistils of another flower. Cross-pollination is biologically more advantageous first of all because it increases the possibility of recombination of genetic material and promotes the increase of intraspecific diversity and further adaptive evolution. However, self-pollination is also important for the stabilization of species traits, in breeding - when breeding pure lines, etc.

Flowers often have some kind of adaptations that prevent self-pollination.

Dichogamy is very common. This term is used to refer to the maturation of anthers and stigma at different times. It is widespread in angiosperms and mainly divided into two main types; proterandry and proterogyny. When anthers mature before stigma it is called proterandry. While earlier maturation of stigmas is called proterogyny. In degree it may be partial (incomplete) or complete. Proterandry and proterogyny are safeguards against self-pollination.

Heterostyly. Some plants have some specimens with long columns, others with short ones, and sometimes there are even third ones with intermediate length columns. Accordingly, anthers are lower on some plants, higher on others, and at the level of the stigma on others. The flower morphs differ in the lengths of the pistil and stamens, and these traits are not continuous. The morph phenotype is genetically linked to genes responsible for a unique system of self-incompatibility, termed heteromorphic self-incompatibility, that is, the pollen from a flower on one morph cannot fertilize another flower of the same morph.

Entomophilia. The agents of cross-pollination (pollen carriers) are most often insects. This method of pollination is called entomophilia (Greek entomos - insect). Many species of flowering plants are visited and pollinated by insects. The evolution of many families of flowers and certain groups of insects was carried out jointly and very often by the way of narrow specialization, close adaptations of the flower and the insect to each other.

Entomophilous plants have brightly colored corolla or corolla-like perianth and often large flowers. Many entomophilous plants have small flowers. However, they are arranged in large,

conspicuous inflorescences. Marginal flowers of umbellates, compositae and some other families are often enlarged, in particular those parts of their corolla directed to the periphery. Even more important are the scents of flowers, which are extremely diverse and attract the most diverse insects. Besides such pleasant smells for us as lilac, tobacco, rose (or rosehip), clove, night violet (*Platanthera*, of the orchids) and others, there are flowers with the smell of vanilla, ginger, rotten fish, dung and so on. This is due to the fact that these often unpleasant smells attract appropriate insects, and not only flies and beetles, but also certain butterflies. For many insects, it is established that they find their way to flowers mainly by smell; optical means of attraction play a secondary role for them.

Some entomophilous plants are visited by insects for pollen. Among such plants in our flora are hellebores, rose hips, and poppies in more southern areas; their flowers are large, open, not drooping, with many (up to 100 or more) stamens, often (but not always) unscented.

Other types of zoophilia. Pollination of flowers by various vertebrates, especially by birds and bats which visit flowers mainly for nectar in the tropics is prevalent in the tropics.

Hydrophilia. Water acts as pollinating agent not only for plants whose flowers are entirely submerged in water, but also for those whose flowers are located above the water surface.

Anemophilia. Approximately 20% of all species of temperate forests are anemophilous (Greek *anemos* means wind). Their flowers are usually small, plain, naked or with calyx-like simple perianth, unscented. Pollen is very small and develops in great quantities. All these features are certain adaptations to wind pollination. Anemophilous plants often have separate inflorescences. Pollen sits on long, easily swinging staminate filaments. Very characteristic are long hairy pinnate stigmas. The light pollen of anemophilous plants can be carried by the wind for distances up to several hundred kilometers.

Peculiarities and significance of autogamy (self-pollination). Despite the fact that autogamy has no possibility of new gene recombinations, its importance in nature is quite high. The principle "better self-pollination than no pollination" is implemented. Many plants develop special adaptations to retain the possibility of autogamy. It should be emphasized that the vast majority of wild species do not have autogamy exclusively, but are combined with cross-pollination, and the relative role of each is very different for various species or under various conditions.

Rainy weather, when flowers of some species do not open at all, greatly promotes autogamy. But even in open flowers of many species of *Ranunculus*, rainwater favors self-pollination, since pollen floating in the flower easily reaches stigmas. More or less accidental self-fertilization is occasionally carried out by small insects having little flight. Sometimes self-pollination occurs by chance. In other cases, there are special reserve devices associated with the growth of staminate filaments or styles during flowering. For example, some crucifers and carnations have anthers

initially located under stigmas, which contributes to allogamy, but then, due to the growth of staminate filaments, they come into contact with the latter.

Finally, some plants, along with normal flowers, produce closed, cleistogamous (Greek *cleistos* means closed) flowers, which are mainly located near the soil surface and bear seeds, of course, only by self-fertilization. Cleistogamy is found in a variety of systematic groups.

FERTILIZATION AND DEVELOPMENT OF THE SEED

Development of the pollen tube. A pollen falling on the stigma of a pistil germinates in the absence of inhibitory factors (see above); its contents, dressed with intina, protrudes through pores in the exine and forms a pollen tube.

The time between pollination and fertilization varies greatly from plant to plant. Some oaks have a pollination period of 12-14 months, alder and hazel-3-4 months, and kok-sagyz - 15-45 months. The pollen tube growth rate is 35 mm/h. An increase in temperature usually accelerates growth.

The cell nucleus of the pollen tube and the generative nucleus (or 2 sperms formed from it) are located at the growing end of the pollen tube. Having reached the ovary, the pollen tube heads towards the ovary and enters it, most often through the micropyle. The ruff of the germ sac is dissolved, coming into contact with the tip of the pollen tube. In the germ sac, the pollen tube grows towards the egg. The membrane at the tip of the pollen tube breaks and two sperms emerge, one of which fuses with the oocyte and the other with the secondary nucleus of the germ sac or with one of the central nuclei. The so-called double fertilization is a characteristic feature of the angiosperms that is not encountered in the gymnosperms.

Double fertilization was discovered in 1898 by the Russian botanist S.G. Navashin on two plants of the lily family: *Lilium martagon* and *Fritillaria tenella*. Subsequently, an embryo develops from a fertilized egg cell, and an endosperm develops from a cell with a fertilized second nucleus. Endosperm of angiosperms is triploid and, contrary to the gymnosperms, it appears only after fertilization. This is one of the fundamental differences between the holosperms and the pseudosperms.

After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. In the meantime, if the generative cell has not already split into two cells,

it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac, and it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei, forming a triploid cell that develops into the endosperm. Together, these two fertilization events in angiosperms are known as double fertilization (Figure 1). After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.

Conclusion. After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. In the meantime, if the generative cell has not already split into two cells, it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac, and it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei, forming a triploid cell that develops into the endosperm. Together, these two fertilization events in angiosperms are known as double fertilization. After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.

Embryo formation.

A fertilized egg passes into a dormant state, which varies greatly in time and depends partly on external conditions. In obsoletus and cereals this period is the shortest (a few hours). The first division is accompanied by setting of the transverse septum. Cell, separated towards the middle of the embryo sac, is called terminal, the other is called basal. Further division in different plants is different.

In dicotyledons, a formed embryo has two cotyledons, a hypocotyl, a primary root and a cone of apex of the primary shoot. The latter sometimes, together with several rudimentary leaves, forms a kidney.

In monocotyledons, only one cotyledon at the apex of embryo is formed and the growing apex of the shoot occupies the lateral position.

In many orchids as well as in parasitic and saprophytic plants, the embryo is very small and consists of a group of identical cells.

The endosperm is very important for embryo development, as it often serves as the main source of nutrients for the embryo.

The ovule gradually transforms into a seed. The cortex is formed from the integumentes, partly from the nucellus. From nucellus in some cases so-called external protein, perisperm, is formed.

After fertilization the ovary wall produces a pericarp surrounding the developing seeds in the ovary. The whole ovary becomes a fruit. Other parts of the flower are also involved in the formation of the fruit very many plants.

Apomixis in flowering plants is defined as the asexual formation of a seed from the maternal tissues of the ovule, avoiding the processes of meiosis and fertilization, leading to embryo development.

There are quite a few different variants of apomixis.

In so-called regular apomixis, the germ sac is diploid and can arise from the nucellus or archesporium cell. In this case there is no reductive division and the megaspore stage, the so-called aposporium, is bypassed. Apospore germ sacks, similarly to normal germ sacks, are usually 8-core, but often with impaired polarity and various abnormalities.

Sometimes apomixis also includes replacement of flowers with bulbs or other formations intended for vegetative reproduction.

Apomictic plants often have morphological abnormalities as well. Pollen degenerates and anthers are reduced.

Nonrecurrent apomixis: In this type "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" (which is why it is called nonrecurrent). See also parthenogenesis and apogamy below.

Recurrent apomixis, is now more often called 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: Here there may be a megagametophyte in the ovule, but the embryos do not arise from

the cells of the gametophyte; they 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: In this type "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, and some grasses, among others.

Thus "normal asexual reproduction" of plants, such as propagation from cuttings or leaves, has never been considered to be apomixis, but replacement of the seed by a plantlet or replacement of the flower by bulbils were categorized as types of apomixis. Apomictically produced offspring are genetically identical to the parent plant.

Zemlyansraya I.V.