STRUCTURE OF PLANTS AND FUNGI

Edited by: Zoltán Kristóf

Pál Vági
Éva Preininger
Gábor M. Kovács
Zoltán Kristóf
Károly Bóka
Béla Böddi

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Chapter 1. INTRODUCTION

(Béla Böddi)

The general introduction to plant properties should follow the principle of functional anatomy. We are over the "classic" view, which was satisfied with the only morphological, anatomical or cell biological description of an organism; we must raise questions how does function a given structure, what kind of environmental effects caused its differentiation or what environmental conditions can tolerate a given structure. Other interesting question is the direction of differentiation, in which the evolution of a complicated structure from a simple one can be observed but the opposite process is also possible, i.e. a complex structure can be reduced during the acclimatization to given environmental properties.

The anatomy as well as the physiology of plants is strongly affected by the sessile mode of life of plants, especially of land plants. This means that a sessile organism has to develop organs which allow survival and utilization of much less variable environmental conditions than the organism with locomotory organs. Unfortunately, lots of people less educated in biology connect the locomotory motion to life phenomena, thus they may look at plants as non-living objects what we must consider as an extremity.

This chapter presents important plant properties which should be kept in mind. Many of the general biological rules created mainly on the basis of animal or microbial examples, cannot be directly applied for plants. When raising a question what kind of living creature is a plant, we have to think about the subjects discussed below.

1.1. Organization levels

Basically, three levels of plant body organization can be distinguished; unicellulars, thallophytes and cormophytes. The definition of unicellulars is simple but the sharp distinction of the latter two is not always easy. According to the general view, the basic difference is the lack of tissue differentiation in thallophytes and the organization of tissue systems in cormophytes. The three dimensional thalli provide sometimes problems; in these organs, certain steps of tissue-like differentiation appears. Cells or cell groups can differentiate to serve certain functions; however, they do not build up well-defined tissues or tissue systems.

It is obvious that a unicellular plant completes all functions of the organism. This however does not mean that no differentiation can be observed in unicellulars: certain parts of the cell can differentiate for given functions. The giant cell of *Acetabularia* can have a cap, a stalk and a rhizoid part or two poles can be found in the single cell of flagellates.

A next level of differentiation is when cells in variable number form cell-groups kept together by mechanical (connections of cell wall projections) or chemical (common slime coat) tools. However, these cells are independent, metabolically and energetically, no or minimal differentiation can be observed between the members of these cell groups. The number of the joint cells cannot be arbitrary because the physical forces of the environment have strong effect on it. Such force can be water movement, after reaching a certain size the cell group falls into parts under simple mechanical forces. A next developmental step is when the number of cells is strictly defined in the cell groups. This lead to the appearance of thalli with constant thallus shapes. Although the functional independence of the cells is still unaffected (the cells of these thalli do not function as a complete organism) partial differentiation can appear; causing the characteristic and constant shape.

An interesting association of independent cells can be observed in *Volvox* spheres: metabolically independent flagellated cells (upto 50 000 can be their number) form a one cell layer hollow sphere containing extracellular glycoproteins. The flagella movement of the cells can be synchronized and move this way the whole colony towards the light. The synchronization is done via thin strands interconnecting the cells and forming this way network.

Certainly, the filamentous structure is the simplest thallus structure. The growth direction is determined by the tip cell of the thallus, which divides in the plane perpendicular to the axis of the filament. The cells form simple or branching filament. The cell on the opposite pole of the thallus can differentiate into holdfast cell, fixing the filament to a substrate. Studying the metabolism of this thallus, we can conclude that the cells are equal, i.e. with the exception of the tip and holdfast cells all other cells are uniform. (Certain cells, however can transform into gametangia forming gametes.)

The lamellar structures form a new form of thallus. The tip cells of these thalli divide into two directions within the same plane. This way the daughter cells are produced alternatively towards left or right side and the thallus growth happens to the margin. At the base of the thallus holdfast cells can differentiate; gametangia appear at the margin of the thallus. The thallus can be dioecious, for example, int he case of *Ulva* (sea lettuce) female and male thalli develop which are morphologically identical. In this case, a further interesting property of t5his plant is, that the diploid thallus developing from the zygote (as a result of the fertilization of sperms), forms also a lamellar thallus which is morphologically identical to the haploid female and male thalli. Anatomic difference is that certain cells in the margin of the diploid thallus develop spores via meiotic divisions. Since all cells of this two dimensional thallus (in case of all three forms) are in direct connection with the environment in similar way, there is no remarkable labour distribution between them.

A new phenomenon appears in the three dimensional thallus, considering its connection to the environment. In this case, the tip cells defining the growth way of the thallus, can produce daughter cells towards three coordinates of space, i.e. the division plane can be x, y, or z. Consequently, “internal” and “external” cells can be distinguished. The external cell layer or layers contain chloroplasts and run thus photosynthesis. Since the basis of photosynthesis is the absorption of light, these layers behave as optical filters at the same time. Thus the light cannot reach the internal cells at all or the light intensity is negligible in the axial cells. This labour distribution became the reason of the differentiation of conductive (transport) cells. Also the biochemistry of the photosynthetic and non-photosynthetic cells is different. The cytoplasm of the photosynthetic cells use as substrate organic compounds exported from the chloroplasts, while the internal, medulla cells utilize hexoses originating from sucrose transported from the photosynthesising cells. The three dimensional thalli can be giant algae called kelp. Kelps can contain specialized cell groups resembling organs; these can be considered as “primitive organs”. Root-like – holdfast structure, axis, leaf like flat blades, gas filled bladders develop.

The Briophytes are three dimensional thalli, too, most of which adapted to the terrestrial conditions and thus further differentiation processes evolved. Epidermis like cell layer containing ventilation pores appeared on their surface, photosynthesising cell layer(s) are arranged under this epidermal cell layer, medulla cell fill in the space, holdfast rhizoid cells are there on the soil side of the thallus. Supporting stereid and water conducting hydroid cells differentiated or special water storing hyaline cells can be found in the *Sphagnum*.

All of these cell differentiation phenomena show an evolutionary process: the labour distribution in the three dimensional thallus is an intermediary stage towards the tissue organization.

1.2. Autotrophy and body structure

Photoautotrophy is the basic property of plant metabolism. This means that plants synthesize their own organic compounds from inorganic material using light energy. The anatomic consequence of this is the presence of photosynthesizing ground tissue, named chlorenhcyma in all plant organisms (with the exception of a few parasite and saprophyte species). (This tissue is referred sometimes as „assimilating ground tissue” but this expression is not accurate: the process of assimilation is the property of heterotrophic organisms – it means only the synthesis of own compounds.) So, a plant can function only if at least a part of its body is illuminated. In the three dimensional organisms, especially in the terrestrial plants, organs, tissues, or cells develop which are covered by external tissue layers. Thus their energy and row material supply depend on the function of photosynthesizing organs. A developed organism has two types of organs, tissues and cells: the photoautotrophic and the heterotrophic ones. Obviously, a transport system must connect the two systems. A special plant strategy has evolved for the transport of organic compounds. The cells of the tissue transporting organic compounds are connected to each other with cytoplasm bridges (plasmodesmata) creating this way the phloem system. This system is connected to an uploading system (a system of the companion cells and the photosynthesising chlorenchyma cells) as well as in the sink (the target – often parenchyma cells of a storage organ - of the organic compound transport) to an unloading system. The connection is ensured also with plasmodesmata.

1.3. The role of water

Water has special physiological and structural role in plants. According to the role of osmosis, the direction of water movement is determined by the concentration difference between the plant cell and its environment. If the external medium is more diluted than the cell, the water diffuses into the cell, the vacuole and the cytoplasm will be saturated with water and its volume increases, i.e. the cell swells. The cytoplasm will be pressed towards the

cell wall which, depending on its elasticity constant, resists the volume increase. A hydrostatic pressure is generated between the cytoplasm and the cell wall, this is determined as turgor pressure. The sum of the turgor pressure on the organism level provides a hydrostatic „skeleton" for the plant. However, in case if the medium is more concentrated than the cell, water diffuses towards the medium. The vacuole and the cytoplasm shrink and plasmolysis occur. In this stage, the value of turgor pressure is zero; the plant first reversibly then irreversibly wilts.

Concerning their water relations, great differences are between aquatic and terrestrial plants. The osmotic concentration of the medium is usually smaller than that of most aquatic plant cells, in case of terrestrial plants however, the water relation is basically different. The direct water source of the above soil shoot is the moisture in air or the rain water and indirect source is water transported from the root. The direct water source of the root and under-soil shoot parts is the soil water, the availability of which depends on the soil quality. Therefore, water transport oriented from the root towards the shoot, as well as the formation of tissues regulating water evaporation and transpiration are of basic importance.

In addition to the formation of the hydrostatic skeleton, water has essential role in the transport processes. Uptake and transport of minerals, i.e. mineral nutrition of plants is associated to water uptake and transport. The majority of minerals is absorbed by roots in case of terrestrial plants. This mineral solution must reach each living cell of the plant. This transport process can proceed within the cell wall (apoplastic transport) under certain conditions, however, the minerals enter the parenchyma cells (symplastic transport which ensures the regulation of the mineral ratios of the organism) and finally the solution is transferred into the xylary elements. The root pressure (the sum of the turgor of the root cells) and/or the negative pressure of transpiration guarantee a water movement directed from the root towards the shoot tip. The direction of this movement is opposite to the direction of organic material transport. Interesting phenomenon is the cooperation of the water and organic transport within a bundle where the xylem and phloem elements are arranged in direct connection. The calculated osmotic potential, water potential and partial pressure values show that these two systems help each other's function.

1.4. The transport process and the possibility of regulation on organism level

Plants have one way water and one way organic material transport systems. No extracellular space exists which could be an "inner environment" – similar to those of animals. Therefore, the organism level regulation of plants is basically differs from that of plants. There is no possibility for and organism level homeostatic regulation which gives special principles for the hormonal regulation of plants. There is no way to form a more or less standard hormone level because the structural conditions for a feed back control are not given. There are no regulatory control systems (feedback loops) with regulatory centre, effectors and receptor s neither connections between them. Therefore, the general theory of "regulation" cannot be applied for plants. Hormone producing cells can be distinguished but the productivity of these cells is regulated by the environmental conditions and not by the hormone concentration. In case of auxin (IAA), hormone producing cell groups can be identified in the shoot apex, but the direction of hormone transport, the hormone distribution is determined by special transport proteins. These form a special hormone gradient along the vertical axis of the plant. The auxin interacting with other hormones have a basic role in the tissue differentiation and the formation of the organs.

1.5. Specialities of plant secretion

Due to the above described absence of the internal environment, the plant secretion should be interpreted in a different way than in the case of animals. Plant secretion not necessarily means the removal or isolation of harmful or useless compounds from the metabolism, thus it cannot be connected to any, organism-level homeostatic regulation. Plant often produce, accumulate and excrete into the environment special compounds, which are indirectly beneficial for it. Production of secondary metabolites is example for this; such volatile compounds can be attractive for an insect and motivate the pollination or the opposite, certain compound are poisons for the animals and protect the plant from herbivores. Anatomically more forms of the excretion can be identified in plants than in animals. In plants, two main categories can be distinguished, the secretion into the environment completed by the external secretory structures and the secretion into the plant body completed by the internal secretory structures. Examples for the former are structures differentiated in the epidermis (glandular trichomes, nectarines, osmophores) or a whole organ can modify for secretaion (for nectar production): a stamen transforms into staminodium. Even the

rhyzodermis (the epidermis of the root) can complete secretory function: chelate forming molecules are secreted into the environment and the chelate-metal complex is absorbed by the root. Plant property is the secretion into the plant body which may be intracellular or extracellular. Vacuoles are good targets for the intracellular secretion. Through their tonoplast (the membrane surrounding the vacuole), accumulation of compounds, even more crystal formation can proceed. Crystal holding cells develop which may contain single crystals, raphids or club-shaped complex structures. The whole cell can also modify; oil cells, mucilage containing cells. In other cases cell groups or cell lines modify for secretion; articulated or non-articulated laticifers differentiate. These laticifers, i.e. this form of secretion provide important industrial row material (for example for the pharmaceutical or rubber industry). The extracellular (but internal) secretion means material accumulation in the intracellular cavities. Perenchyma cells, i.e. their cell walls can split away from each other; this way, schizogenic cavities are formed: resin ducts of pines are examples for this. The resin ducts contain not only resin but volatile oils; their mixture is called balsam. Secretory cavities can be formed also via enzymatic cell lysis; the pericarpium of citruses can have such oil containing cavities. These examples show that the plant secretion has many different forms; its research has remarkable practical relations.

1.6. Morphological and anatomical polarity of plants

Morphological and/or anatomical polarity can be detected in most of plant organisms. Certain form of polarity is present already in thallophytes: a dividing cell is present on one (apical) pole of the thallus which determines the direction and the way of growth and a holdfast cell or cell group on the other pole (at the base) of the thallus. In case of terrestrial plants, the polarity is connected to very complex phenomena. One pole is the apex of the photosynthesising shoot, the meristem cells of which control the growth direction to reach light. The negative geotropism or gravitropism and the phototropism regulate it. The other pole is the root apex, the growth of which is under the control of positive gravitropism and ensures the attachment of the plant in the soil. (It is worth mentioning that the growth direction is controlled by various chemotropic and hydrotopic stimuli, too.) All of the external effects combined with the internal genetic program affect in combination on the shape, the size, the zonation (vertical histological arrangement) and histology of the whole plant.

1.7. Stem cells and cell plasticity in plants

An important characteristics of the Cormophytes is the presence and function of promeristems in the shoot and root apexes a group of which can be considered as special “plant stem cells”. These cells are defined to be stem cells in the embryo, and they maintain their stem cell property during the whole life of the given plant: via their slow division, the genom structure does not alter or its alteration is non-significant. The differentiation pathway of their daughter cells is determined by the surrounding cells. In an ephemeric (short life span) or annual plant their function is limited for a single vegetation period only, but a giant sequoia (*Sequoiadendron giganteum*) living even for several thousand of years, has these cells in its each shoot or root apex theoretically fo forever.

Plant property is the high extent of cell plasticity. This means that determined cells, for example differentiated to parenchyma, can regain their ability for division and even a whole organ or a whole plant organism can be regenerated from them. Such processes are known from the everyday life: for example, if we want to propagate a plant vegetatively and initiate the root production on a shoot cutting. The cells of the cut shoot develop adventitious roots. In this process, the determined cells of the cutting turn pluripotent and produce all cell types of the adventitious root. In addition, these adventitious roots have their own root apex meristem (promeristem) cells, a group of which can be taken as stem cells. It is interesting to analyze the differentiation processes during lateral root formation. The lateral root formation starts from certain (usually above the xylem bundles) cells of the pericycle, the external cell layer of the central cylinder of young roots. Via regular differentiation processes, the whole lateral root is formed, including all cell and tissue types; also the cells of the root apex meristem (promeristem).

Thanks to this plasticity, the tissue culturing became a basic method int he modern agriculture and horticulture. Tissue cultures are prepared from hybrid plants which are results of long and complex genetical work. Undifferentiated cell mass – called callus is grown on special medium. Plenty of genetically identical individual plants can be produced from the pieces of the callus. Studies on plant plasticity gave surprising results: tissue cultures, somatic embryos and whole plants were grown from haploid cells. In other works, the chromosome number of haploid

cells was doubled and then dihaploid plants were regenerated from these cells. These plants were homozygous for their all alleles. In other plants, the differentiation processes were artificially modified, the promeristem cells of lateral roots were transformed into somatic embryos or embryos were forced to flower – skipping the rigorous steps of ontogeny.

The one directional determination is present in the plants, too. The differentiation of tracheids or vessel members from the living cambium daughter cells is a well-konwn example for this: this process means the decomposition of the whole cytoplasma; practically only the thickened cell walls represent the formerly living cell. In case of phloem, only the nuclei of sieve tube members are decomposed, consequently these cells cannot divide but they function as living cells. There are plant cells living only for several days: root hair cells or cells of the root cap (calyptra) belong to this category. The programmed cell death is also known in plants: certain cells die and important regulatory compounds are produced in this process.

1.8. The anatomical and physiological role of storage

Having special modified organs, certain plant species can temporally cut themselves from extreme conditions. Interesting examples are plants having storage organs. They accumulate storage material during the vegetation period; this is the period of the development of the storage organ. These organs survive for example the winter of the temperate zone; during this dormancy period some or all above soil shoot parts are decomposed. Next spring they can start the new vegetation period using the storage material very early in the spring. Certain species grow twin corms: the older is used for the flower formation, the younger develops in the recent vegetation period and accumulates storage material for the next year. This way, both, the storage organ and the above soil part of the plant can renew.

Not only special storage organs help the survival of plants. The living parenchyma of tree trunks or younger twigs store starch. During winter dormancy, these cells run only minimal metabolism but in the next spring, the opening and bud development the utilization of the stored materials is needed. Only the stored materials are used when cut twigs are dark-forced.

The utilization of storage material is necessary for the germination. The seeds usually start their germination in various depths of the soil. The development of radicle and plumule starts with the help of the storage materials of the seed; the cotyledons, endospermium or perispermium can contain starch, proteins or lipids. This heterotrophic metabolism runs until the shoot reaches the soil surface, the chlorenchyma differentiates and the photosynthsis starts.

A unique for of storage was observed in several desert plant species. At the start of a dry period, the chlorophyll is decomposed in their leaves, storage materials are accumulated the transforming chloroplasts. Finally a desiccoplast is formed, which, after re-wetting restarts chlorophyll biosynthesis, chloroplast formation and photosynthesis within a couple of hours. This high efficiency of the revival is due to the effective utilization of the stored materials.

1.9. Basic rules of plant reproduction

The reproduction of thallophyte water plants is obviously connected to the water environment which transports the gametes and spores. In case of lower plants, the gametes have the ability of active locomotory movement; both the males and females. During the evolution, the female gametes loose this ability, the accumulate storage material and develop in the archegonia as special protecting organs. The male sperm cells have flagellar movement in algae, mosses and in seedless vascular plants (pteridophytes) ; water environment is essential for the fertilization. Interesting ancient relict property of the ginkgo is the ciliary movement of the sperm, which is possible in internal fluid of the plant. In case of other plants, the sperm cell moves in pollen tube with the help of motor proteins.

Spores as asexual reproductory cells have flagellar movement in case of lower plants; however, the spores lost this property during the evolution: zoospores evolve into sessile spores. In case of water plants water, in case of terrestrial plants the air or animals transport the spores. In case of seed plants (Gymnosperms and Angiosperms) not the spores themselves but the whole male gametophyte (i.e. the pollen grain) is transported to the female gametophyte which developed from the sessile megaspore protected by the sporophyte and containing the egg cell. The pollen

can be transported by air; the air pollination needs adequate morphology. The male flowers are arranged into inflorescence, each flower contains plenty of stamina, the filaments of which are elongated and thus the stamina bend out from the flower, the sepals and petals (or tepals) are reduced, vast amount of pollen is produced. Even more, the pollen can have air sacks (see pine pollen) to help its transport. The female flower is modified accordingly. Great number of flowers are arranged into inflorescence, the stigma surface increases (feather like stigma appears at Graminae) and the lengths of the style increases which ensures the availability of the embryo sack of flowers even at the base of a spadix (for example at maize). The perianth leaves are reduced also in the female flowers.

If animal play a role in the pollination, the flower structure modifies accordingly to guarantee attractivity for the flower. Optical properties can be important such the great size of the flower, the shape, the colour, special figures or the fine structure of their surface (causing interference or polarisation – the structure of the cuticle or wax) of the perianth leaves. In addition, chemical compounds can increase the attractivity: nectar producing nectarines, or odor (smell) producing osmophores develop in the flower. Insect traps are known in some flowers which lock the insects into the flower until the pollination is completed. Other flowers have special tools which can move under tigmonastic stimulus and fix pollen grains in the hairs of the insects.

1.10. Alternation of generations in the plant kingdom

Although the “alternation of generation” is a widely used term in botany, the correct interpretation of this term is very important. It is known also as “alternation of phases” which means that the a haploid and a diploid phase can be generally distinguished in the life cycles of plants. These “generations” consequently do not correspond to the “generation” used in genetics. The plants’ diploid spore mother cells produce haploid spores via meiotic cell division. The haploid spores divide mitotically; this way a haploid organism develops from them. This haploid organism contains the sexual organs, in which gametes are produced via mitotic division. Since this haploid organism produces the gametes, this organism is called gametophyte (and the haploid phase is called gametophyte phase). The fusion of the gametes results in the production of zygote, which dividing with mitotic cell divisions produces a diploid organism. This diploid organism contains diploid spore mother cells which produce spores via meiotic divisions. This is the origin of the name of the diploid organism: it is called sporophyte (and the diploid phase sporophyte phase). The ratio of the gametophyte to the sporophyte is variable. The gametophyte can be very simple, it can contain only a few cells; in this case the sporophyte is dominant but we can find the opposite phenomenon: the sporophyton is represented only by the single cell of the zygote and the gametophyte is dominant in the life cycle of a given plant. There are examples for the intermediary stage, too, when the gametophyte and sporophyte organisms are morphologically similar (they are izomorph). On the basis of the ratio of the gametophyte and sporophyte , the life cycles are categorized into haplontic, diplontic, haplodiplontic or diplohaplontic types. Despite the evolutionary trends in the ratio of gametophyte to the sporophyte (i.e. the cell number and the importance of gametophyte gradually decrease and those of the sporophyte gradually increase) there is no absolute rule for the dominance of gametophyte in primitive plants and for the dominance of the sporophyte in developed plants. We can find unicellular and diploid diatoms (*Bacillariophyceae)* and giant diploid brown alga kelps (Phaeophyceae).

1.11. Genetic interpretation of the alternation phases

Sexual reproduction ensures the genetic variability. The gametes of animals are produced in meiotic cell division. In the process of meiosis, an enormous number of allele combination arises. The crossing over proceeding during the pairing of homologous chromosomes, then the random and independent segregation the chromosomes into the gametes (the recombination processes), furthermore, the random combination of gametes at fertilization, all these together ensure the great variability. Interesting subject to be discussed is that spores (considered as asexual reproductive cells) are produced with meiosis in plants. Thus all genetic variability linked to meiosis appears in spores. Consequently, the gametophyte developing from spores is genetically heterogeneous. This is striking at heterosporeous plants which have male and female prothallia or thally (i.e. they are dioecious) which are different not only in their sexual properties but in other characteristics, too. The gametophyte produces gametes via mitosis. Consequently, gametes produced on a given gametophyte are genetically uniform. The gametes randomly meet at fertilization, thus at this step, the genetical recombination is ensured in the sexual reproduction. When compared

to animals, the great difference is, that the animal gametes never divide; their only function is the fertilization, i.e. the production of the diploid zygote. In plants, however, the meiotically produced haploid spore can divide mitotically. In this process, prothallium or thallium, sexual organs and gametes are produced; all with mitosis. The gametes will then fertilize each other and produce the zygote.

The above described characteristics are only examples to show several plant specialities but many other plant specialities exist. These examples, however, demonstrate that despite their special characteristics, the basic biological features are similar to those of other living organisms.

Chapter 2. MORPHOLOGY

(Károly Bóka)

Morphology of flowering plants: description of plant body with characteristics perceptible to the naked eyes or visible at low magnification. The report on the characteristics ought to be correct, unequivocally typifying the appearance of plant body. It makes the plants recognizable and identifies it unmistakably.

Features of plants develop during morphogenesis which is under tight genetic control; however, environmental factors influence also their coming out. According to this fact, genotype should be distinguished from phenotype, a possible manifestation of genetic background. Information coded in genetic material offer principles of the "body plan" while the phenotype represents their way of materialization affected by environmental circumstances.

At the appreciation of morphological features there are a few viewpoints worth to keep in mind:

Specialized organs with peculiar anatomy indicate that they have specific functions as a result of adaptation. Identical environmental cues may cause similarity of organs even at not related species.

The more a plant is specialized, the more its appearance differs from the average.

An organ has not only one function, although one of them seems to dominate. But among highly extreme conditions a special function has priority.

Similar extremity causes analogy even between different organs with comparable functions, so in their morphology there are also similarities.

Because of the abovementioned tendencies morphology may be used widely but one should be aware of its possibilities and limits.

Plant organs can be categorized as:

Vegetative organs: important in self-preservation.

Reproductive organs: relevant for sexual reproduction.

2.1. Seed and seedling

Seed, present in the gymnosperms and angiosperms (*Spermatophyta* - seed-bearing plants), has been evolved for survival of the new sporophyte (as an organ of perennation) and dispersal of the species. Its abstraction is being an embryo supplied with food and protected by a seed-coat. The embryo, a new sporophyte, persists in a dormancy period among unfavourable conditions and it can bypass at the same time for long distances from its production site.

Development of the seed and its parts are discussed in details in a chapter on sexual reproduction. Here some morphological aspects are only debated. The ovule is joined to placental tissue by means of the funiculus (funicle). Integument(s) and nucellus (in which megaspore, and later the embryo sac is formed) belong to the old sporophyte and are connected to the chalaza. There is a small opening on the integument, the micropyle. These 2n sporophytic parts transforms fundamentally during maturation of the ovule. Integuments develop into the seed-coat. Anticlinal walls of the columnar coat cells become strongly thickened while their outer periclinar walls remain thin and during seed dehydratation might come to be deflated. Cells of the coat are tightly attached, often pavement-cell like in shape and can hold protrusions or hairs. If the ovule is an anatropous type, the remnant of funiculus joint to the integument is visible as a longitudinal ridge (raphe). Although the seed-coat is often sclerenchymatic (sclerotesta), the outer layer of the coat may be fleshy (sarcotesta) in peculiar cases. Caruncle, elaiosome and aril are special appendages of the seed-coat- The last one is a coloured and fleshy outgrowth of the funiculus.

Nucellus might develop into nutritive perisperm or may be reabsorbed as the embryo develops. One product of the double fertilization characteristic for angiosperms is the triploid endosperm. It might be present in the fully

matured seed but its reabsorption is also possible during embryo development. If perisperm and endosperm are extint, the food supply is stored in the embryo, largely in its cotyledons.

Developmental stage of the embryo in the seed is different in the distinct families but it has usually initials of some organs yet: radicle with root apical meristem, embryonic stem with shoot apical meristem, cotyledon(s) and primordial foliar leaves (seed leaves). The embryonic stem is divided into epicotyl, mesocotyl and hypocotyl according to their position compared to the cotyledon insertion.

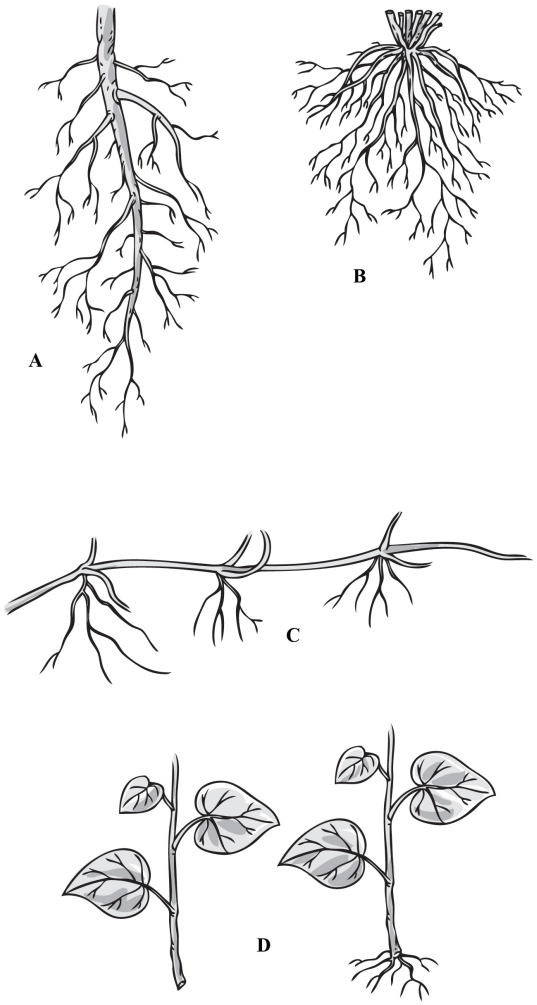
Over germination there are two possible scenarios if the seed germinate in the soil: 1. Cotyledons remain in the soil (hypogeal germination) when the epicotyl elongates and leaves emerge from the soil because of it. 2. Cotyledons are raised above the soil surface by the considerable elongation of the hypocotyl.

Expanded radicle forms the root and plumule develops into a shoot emerging from the soil slightly later. It holds the young leaves which enlarge, expand and start photosynthesis. During this process, the new sporophyte changes to an autotrophic organism. Role, position, shape and greening of cotyledons and seed leaves are so characteristic over germination that there are special seedling keys (eg. for weeds, trees) important in agriculture and forestry. Quick detection and control of young weeds and protection of tree seedlings has great economic impact decreasing costs.

From morphological point of view another uncommon feature is also worth to mention. In some cases, not the seed but the whole fruit or parts of it behave as a seed-equivalent structure. The seed-coat covered by the whole (caryopsis, achene) or part/segment (mericarps/shizocarps of *Apiaceae* or *Malvaceae*) of pericarp is thin. The main protective structure is the pericarp itself.

2.2. Root

Radicle develops first, it break through the seed-coat and forms the first organ of the plant, the root. The embryonic root grows into root system which may include a main root branching repeatedly (taproot) and/or adventitious roots arising from the stem (fibrous root system). Roots anchor plant and absorb water and nutrients dissolved in it to transport them to other organs. Adventitious roots are underground or aerial organs that arise regularly from the base or the upper part of the stem but they might be induced irregularly in unexpected positions by external factors (eg. loss of radication, cuttings). They are of endogenous origin, from the endodermis or starch sheet of the stem, and pass the cortex to achieve its surface. Adventitious roots may supplement primary root system for absorption or specify for other functions.



Roots of plants A. Taproot. B. Fibrous root. C. Adventitious root. D. Adventitious roots of cuts (cut on left, cut with roots after a few weeks on right).

The growth of primary root is generally orthotropic while lateral roots grow plagiotropically. Geotropism of adventitious roots depends on their function.

In connection with extreme conditions, appearance and structure of roots might be changed and their basic functions strongly altered. They often become a thickened storage organ. Though almost all roots store some starch and other stored material, habit of roots modified for storage is typical with enlarged diameter because of the large amount of parenchymatic ground tissue composed of thin walled cells filled with storage material. These storage roots (swollen root, root tuber, taproot, etc.) may function for long time ensuring survival. Water content of these organs is essential at dry conditions (hot summer of continental climate; dry season of subtropical areas; semi-arid environment) to survive. Geophytes of the temperate zone have similar roots (eg. *Ficaria verna*) not because of the dry conditions but to grow quickly in springtime to avoid shade of other species of the vegetation. Apart of storage stem tubers and cereals, storage roots are elementary part of human diet in many countries.

Contractile roots help to achieve the proper positioning of underground bulbs and corms (eg. *Lilium*). Plants are able to regulate in this manner their depth according to the season.

Roots of some species can serve for vegetative reproduction (*Robinia*, *Cerasus*) especially in case of shoot loss or mechanical injury of root. From the adventitious buds initiated on the root complete plants regenerate.

Roots with haustorial function (suckers) enable parasites and hemi-parasites to use substances of the host plant. Haustoria of the parasitic partner (*Cuscuta*, *Orobanche*) enter in the root or stem of host and reaching its phloem

they take organic compounds from there. Hemi-parasite plants (*Viscum*, *Loranthus*) contain chloroplasts and they are able to photosynthesize, so these plants transport water from the xylem of host.

Beside roots growing in the soil a ray of modified roots are aerial roots specialized for different functions.

Aerial roots can improve the water and nutrient supply of a tall plant. This type of root arises from the upper nodal or internodial parts of the climbing stem. They reach the soil and are thin to prop the stem but rooting in the soil they transfer water for transpiration (*Monstera*).

Climbing roots arise from the stem and allow the plant with (at least at the beginning) feeble and thin stem to grow high to reach more light. These plants use supports or other plants in a non-invasive manner; they do not injure them directly (*Hedera*).

Tall plants should have additional support to guarantee the proper position of their body. Stilt roots arise from the lower nodes, get to the soil and anchor the shoot (*Zea*). Pop roots arise from the upper part of shoot, often from branches, and support the shoot standing against the ground usually rooting in it later (*Pandanus*, *Ficus bengaliensis*). A special kind of support is provided by buttresses for the tropic giant trees (kapok tree). These roots grow in different directions on the soil surface and form high, vertically flattened mechanical support to prevent to come down the high and heavy trunk.

Root thorns are strongly sclerenchymatized roots arising on the stem above the ground to save the plant against herbivores. The hard and sharp thorns may also save properties effectively if the plants are grown by people as a hedge. Thorns were used also for other purposes in different tools.

In swamps and marches soil is flooded and oxygen content is very low in it. Respiratory roots grow upward and has specialized root epidermis allowing gas exchange (*Taxodium*, *Rhizophora)*. Large intercellular spaces and ducts form channels to ventilate the internal space. It permits to conduct oxygen to the cells of the underground parts.

Epiphytes (eg. epiphytic orchids) are usually completely separated from the ground and live in ”nests” fare above the soil surface. Their hygroscopic roots absorb water from the atmosphere (moisture, rain) with their specialized dermal tissue (velamen). Specialized and died cells (in fully differentiated stage) of velamen with reticulate cell wall thickening absorb the water and transmit it to the cells of cortex. From there it is transported to other organs. Cortex is also important in photosynthesis of the epiphytic orchid plant. Its living cells contain chloroplasts and they are active in synthesis. They also store part of the synthetized organic material in starch.

Roots have got in touch with microorganisms living in the soil evolutionary very early. Fungi and bacteria formed different interrelations with their plant partners and some of these interactions were conserved as a stabile morphological formation. (Close ties with algae, liverworts and mosses were assembled before the history of vascular plants: lichens, mycothallic forms, cyanobacteria and liverwort connections.) The main types of symbiotic relations between microorganisms and roots are the next:

Mycorrhiza: Tight metabolic and structural interrelation (thought to be mutualistic) between hyphae and roots, especially the tip part of the last one. Plant is able to absorb more efficiently the water and nutrients (eg. phosphorus) through the fungal partner from the soil while fungus gets organic compounds from the root. There are different types of mycorhhizal interaction but here only two of them, the ecto- and the endomycorrhiza will be mentioned. In case of ectomycorhhiza, hyphae grow on the surface of the root (mantle) and between the cortical cells (Hartig-net) but do not enter into the cells. Elongation and ramification pattern of root is changed. Strategy of endomycorrhizal fungus is quite different. Hyphae break through the wall of the cortex cells and grow into them pushing the plasma membrane inside. Important to see, that the entity of cell is not diminished by the fungus. There is an interface created by the partners located between the fungal wall and plasma membrane of plant but cellular integrity of plant cell is not destroyed.

Nitrogen is essential for plants and its availability is fundamental. The best solution is to be near to organisms which are able to fix the atmospheric nitrogen. Some prokaryotes form morphologically stable structures with roots for nitrogen fixation.

Rhizobium bacteria induce cell divisions in the cortex of leguminosae roots and as a result of it, root nodules develop on them. Bacteria are engulfed into the plant cells and become bacteroids. In this form they coexist with the plant, they get sugars from the plant partner and transport fixed nitrogen into it.

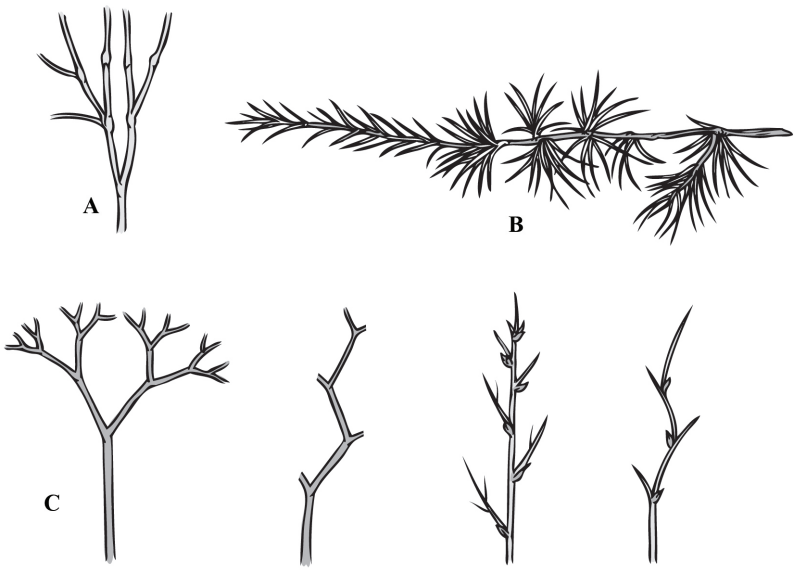
Actinorrhiza is similar in its metabolism and structure but the partners are *Frankia* (*Actinobacteria*) and plants from other families (eg. *Ulmus*).

Cycads live together with photosynthetic cyanobacteria. The metabolic scenario is very similar as above but there is a big difference: cyanobacteria need light for their photosynthesis. Coralloid roots of cycads grow upward and cyanobacteria living in the cortex of the root can get light.

2.3. Stem

The root system joins the aerial part of plant axis, the stem, which bears the leaves and reproductive organs. Appearance and morphology of stem is variable because it has several features to point to its specific attributes and accurate to describe its physiognomy. Nodes and internodes form a developmental and functional unit. Length of internodes is considerable on long shoots but dwarf shoots have very short internodes. Long and short sections may be combined at different parts of the shoot. Apical meristem of a long shoot is active for an extended period while meristemic activity of apex of dwarf shoots decline shortly. Long and dwarf shoot parts may build up together a shoot and there are several dwarf shoots on a long shoot (eg. *Ginkgo*, *Larix*).

Ramification of shoot system has three basic forms: 1. Dichotomy: Axis of shoot is split regularly into two equal parts. A special form of dichotomous shoot is unequal dichotomy (overtopping) when one of the two branches dominate and the other one become weak and shorter. 2. Monopodial: Long-lasting activity of shoot apical meristem produces the whole main axis of the shoot system. All other stems (of lateral shoots) originate from the main one with activity of axillary buds. 3. Sympodial: Growth of the main axis is ceased soon but lateral branches from axillary buds continue the growth of the shoot which become similar to a main axis. All segments produced after stop of the relative axis growth arise from a new apical meristem.



Shoots A. Shoot with long internodes and well developed nodes. B. Long shoot and dwarf shoots of *Larix*. C. Ramification of shoot: dichotomic, overtopping, monopodial, sympodial (from left to right).

There are several basic shoot forms distinguished on the base of their construction characteristic for a taxon or a group of plants. 1. Herbaceous stem is representative for non-woody annual plants. It is soft, green and slightly woody only at its base if at all. 2. Woody stem: Lignified, highly branched, perennial stem. It is produced by long-lasting secondary growth. 3. Scape: Soft, non woody, not branched stem without leaves and with a long internode bearing flower or inflorescence at the top. 4. Caudex (trunk of palms): Not branched, slim, woody but rather spongy stem produced by specific (not secondary) thickening process. Crown of leaves is at the top of the trunk. This type

is characteristic for palms. 5. Calm (wheat stalk): Herbaceous, weakly lignified stem with well-developed nodes and long and hollow internodes. In wheat, it consists of cellulose while in reed it is strongly lignified. 7. Rush stem: Base part of it is with short internodes but the upper last one is extremely long and its central part is filled with soft aerenchymatic tissue. At the top there is a bract.

Colour, type and number of hairs, emergences and epicuticular wax influence the appearance of stem. Shape of cross-section is also characteristic (round, semi-round, oval, triangular, square, grooved, furrowed, winged etc.) and the centre of it may be filled with pith or empty having diaphragm at the nodes.

Apart from „regular" aerial stem there are different modified forms of aerial and underground stems alike.

Modified aerial stems: 1. Succulent stem: Water storing and photosynthetic stem of cacti. It is not dissected into cladodial parts (Cereus). 2. Cladode: Green, photosynthetic stem composed of flattened units also with water storage function. Its growth is not terminated, foliage leaves are reduced and modified into spines (Opuntia). 3. Phylloclade: Phylloclade is a flattened, leaf-like, green organ. Its growth is terminated and in this feature phylloclade is also similar to a leaf. Foliage leaves are reduced into scales. Flower develops on the surface or at the base of phylloclade and it has bracts (Ruscus). 4. Shoot tendril: There are several types of tendrils. In this peculiar case, the whole lateral shoot is changed into a tendril (Vitis). 5. Thorn: Some of lateral shoots is modified into thorns to protect the plant. Thorn may bear leaves or flowers (Prunus). 6. Runner: This type of shoot is for vegetative propagation and spread on the surface of soil. It grows with long internodes and at the nodes shoots are induced at the upper surface while at the lower side roots are produced. The new unit separates easily and becomes a new plant soon (eg. creepers: Fragaria).

Modified underground stems: 1. Stem tuber: The end or the whole underground stem becomes a swollen storage organ. There are buds on it (Solanum tuberosum). 2. Rhizome: Storage organ for survival among unfavourable conditions. It may have long or short internodes and generally it grows horizontally in the soil. It serves also as a vegetative propagative organ. 3. Corm: Its axis is vertical and condensed (with short internodes), often bulb-like in its appearance. Cataphylls protect the corm in the soil. 4. Bulb: Its stem is reduced to a disc-like structure bearing flashy modified leaves. The whole organ is protected with scale leaves.

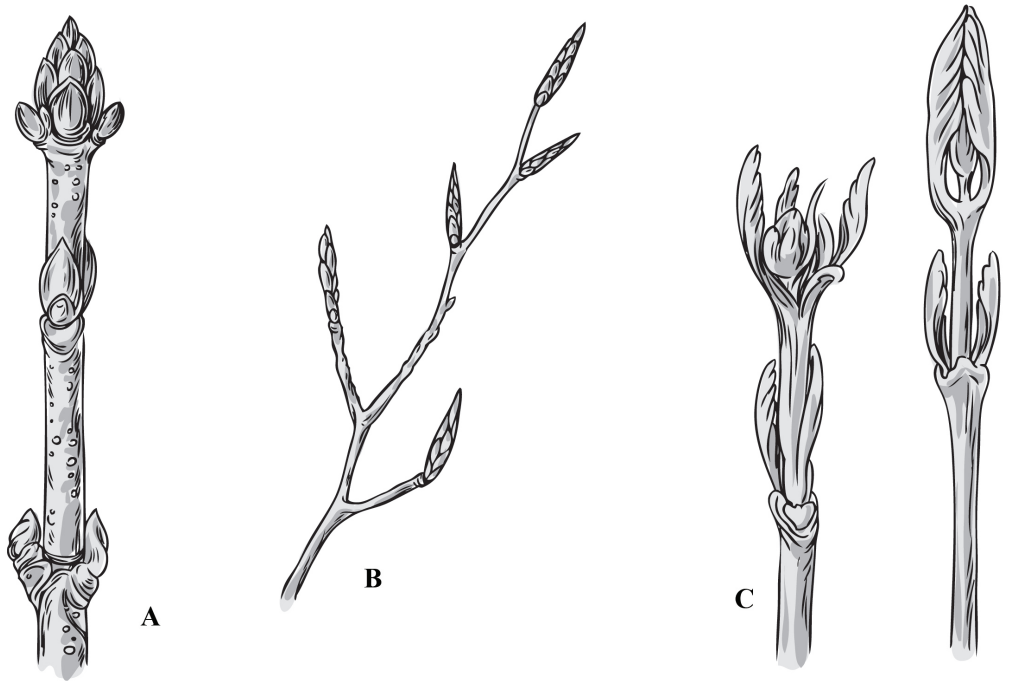
Structures specially produced for symbiotic relations are also formed from stem and shoot, eg. *Myrmecodia*, *Acacia*. In the cavities of tem or specialized stipular spines ants have their nests. Ants protect the plant against pathogens and herbivores. *Gunnera* has special glands on its stem and petiols for the nitrogen fixing cyanobacteria.

2.4. Buds

All developing shoots are buds, but axillary buds of overwintering woody plants are special forms of leafy shoots. The shoots overwinter on the twigs in embryonic state covered and protected by bud scales and grow into new shoots in the springtime. The new buds develop to the end of summer and they have a dormancy period up to the next spring. Features of buds and bud bearing twigs are characteristic for species and they are valuable for identification. Buds are grouped according to their different features. Buds may be free, semi-hidden, or hidden depending on their access. If there are bud scales and they fully cover the undeveloped shoot, the bud is covered. From this point of view bud may be semi-covered and naked as well. At the last one, bud scales are absent, the shoot apex and young primordia are protected by the older primordia and young leaves. Bud may have a holder or it may be sessile. Position of bud (erected, appressed, terminal, lateral, etc.) and its shape (rounded, conical, elongated, etc.) are also important for their characterization. Colour, resin coat, and hairs of the bud scales are also features usable for identification. Buds may stay separately or in groups (clustered buds, buds in groups, buds in pairs). During bud break, leafy shoot, flowers or both these types of organs may develop from the bud (leaf bud, flower bud, mixed bud, respectively). An interesting, functionally unique type is the dormant bud. It may exist in its latent state for years. Their bud break is initiated by unusual events like loss of shoot.

The undeveloped shoot part in a bud bears leaf primordia and young leaves. Aestivation and vernation types describe their position, order, folding and rolling in the bud. These features may be studied on cross-section of a bud or in dissected and disassembled buds.

Apart from characteristics of buds, features of twigs are also useful. Colour of their periderm, their waxy surface layer, hairs, pattern and number, position, shape and size of lenticels are also necessary for full description. Shape and size of leaf scars and number and position of leaf traces may be also distinctive.



Buds of trees. A. Buds on monopodial shoot, apical and lateral buds with bud scales. B. Buds on a sympodial shoot with seemingly apical and lateral buds (buds with bud scales). C. Naked buds. From the apical bud of left shoot develops an inflorescence while from the apical bud of the right shoot a new shoot develops.

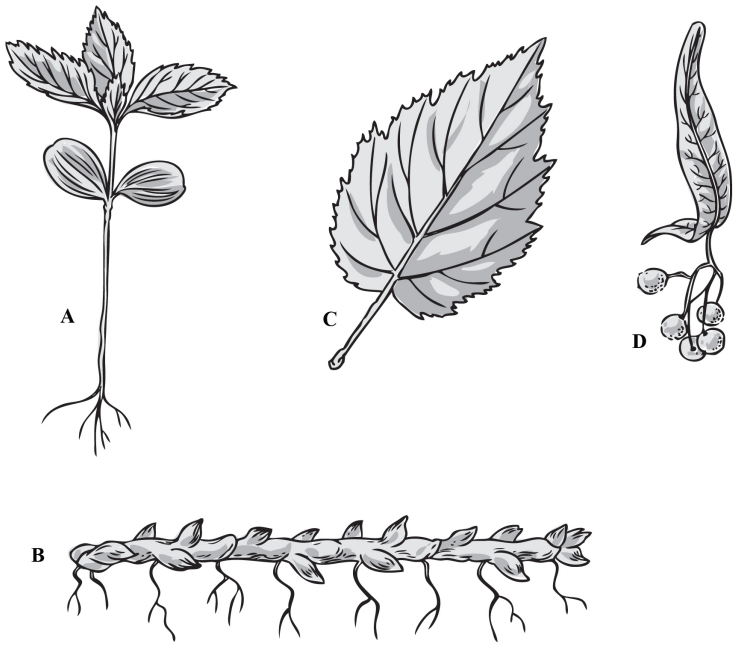
2.5. Leaf

Leaf is generally a flat, green photosynthetic organ on the stem. This type is the foliage leaf. There are other leaves alike: cotyledons (cotyledonary leaf), leaves at the base of the stem, below the level of foliage leaves (scaly leaf), and leaves at the upper region of the stem, above the level of foliage leaves (bract leaf). The last two types are difficult to delimit from the foliage leaves. Floral leaves are specialized leaves of flowers.

Cotyledons store and/or absorb nutrients for germination and transmit them to other parts of the embryo. Generally, it dies soon (*Phaseolus*) or can serve as the first photosynthetic organ of the seedling (*Ricinus*) but exceptionally it may remain and photosynthesize for long time, eg. some *Streptocarpus* species do not have true foliage leaves at all. They have one enlarged cotyledon photosynthesizing during their life.

Scales (scaly leaves) develop often on the underground stems or at the base part of shoot. They are difficult to observe because of their short lifetime or hidden position. On modified underground shoots (bulb, corm, rhizome) as protecting or storing organs are important.

Morphology of bracts, leaves in an upper position, is rather simple but they colour, size and shape may be characteristic. They are present or absent at flowers in inflorescences. Bracts may have protective function eg. husk, pseudocalyx, spathe, etc.

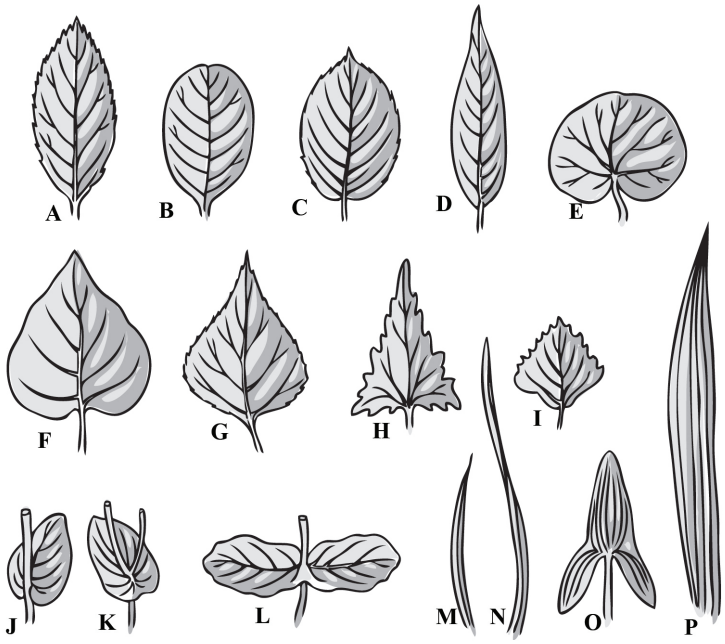


Types of leaves A. Cotyledons (and first foliage leaves). B. Scaly leaves. C. Foliage leaf. D. Bract leaf (bract of *Tilia* inflorescence).

The most prominent type and most often described morphologically is the foliage leaf. It has three main parts: leaf base, petiole and lamina (blade). Some of them (or even all of them) might be reduced (eg. needle, where lamina is reduced while the two other parts are indistinct.

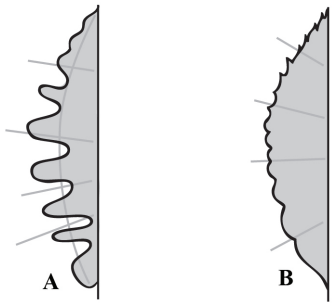
Leaf base is more or less developed; however, at certain species (eg. *Ailanthus*) it is strongly developed while at others (eg. *Vallisneria*) almost lacking, at least morphologically. Stipules are modified parts of the leaf base. The stipular spines are formed from the leaf base (*Robinia*) and protect plant against herbivores. Leaf base may also specify into ochrate, vaginate form, tendril or photosynthetic organ.

Petiole keeps lamina in proper position to collect light optimally (leaf mosaic). Shape of its cross-section is often rounded, elliptical or grooved on the top side. Number of vascular bundles in it or its other features (swollen, tendril-like, flat and photosynthetic form, etc.) may be characteristic.



Characterization of leaf shape is composed of a few features (shape of lamina, leaf apex, form of basal part of lamina, leaf margin, etc.). A. Elliptic. B. Obovate. C. Ovate. D. Lanceolate. E. Reniform. F. Cordate. G. Trullate. H. Deltoid. I. Rhomboid. J. Amplexicaul. K. Perfoliate. L. Connate-perfoliate. M. Ensiform. N. Ligulate. O. Sagittate. P. Plated.

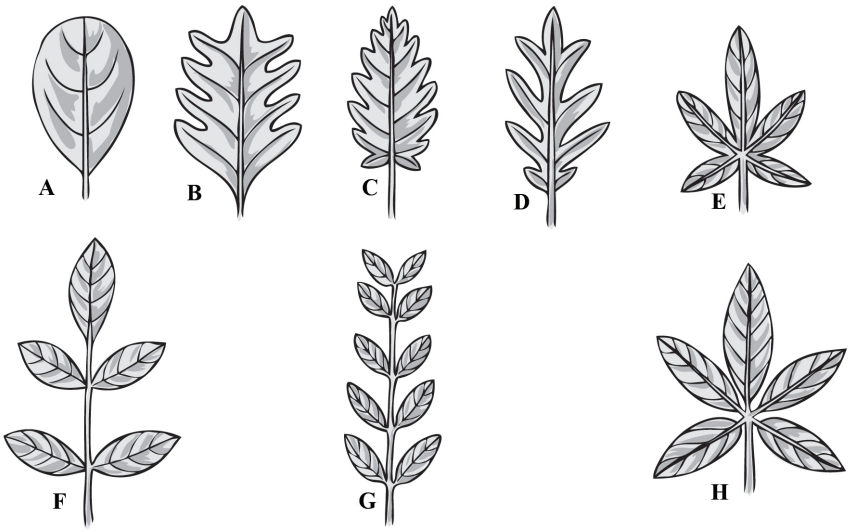
Epidermis, hairs on it (their shape, density, function, form, etc.) and venation are also good morphological and taxonomical features. Shape of lamina (oval, lanceolate, ensiform, ovate, obovate, elliptic, triangular, trullate, reniform, cordate, etc.) is basic information on the leaf. Description of the basal part of lamina and apex of leaf gives additional information on leaf blade. Morphology of leaf margin is also a well-known hallmark to describe (entire, sinuate, crenate, serrate, undulate, etc.), it shows the type of smaller or bigger incisions of leaf blade. The deeper incisions dissect the lamina into more or less separated segments in pinnate (odd-pinnate or even-pinnate) or palmate form.



Smaller or deeper incisions of lamina and leaf margin A. Lamina entire, repand, sinuate, lacerate, laciniate (from top to dawn). B. Margin: serrate, dentate, crenate, undulate, entire (from top to dawn).

The previously described features show morphological characteristics of simple leaves with more or less whole blade formed from one primordium. If during the earliest phase of leaf primordium development, a series of new primordia are initiated and leaflets evolve from them, the leaf become compound.

Compound leaf may be composed of one or more series of simple elements (eg. pinnate, bipinnate, tripinnate). Leaflets form the lamina in pinnate or palmate order (pinnately or palmately compound leaves).



Simple and compound leaves A. Obovate with entire lamina. B. Pinnatipartite. C. Pinnatifid. D. Pinnatisect. E. Palmatisect. F. Odd-pinnate (imparipinnate). G. Even-pinnate (paripinnate). H. Palmate (digitate).

Phyllotaxy describes position of leaves on the stem. Point of leaf insertion is the node. Number of leaves per node is various. Leaves may stay singularly at the node (alternate/spiral phyllotaxy). Each subsequent leaf emerges in a different position than the previous one, and the angle of divergence measured between them is characteristic. If it is 180^{o} , the leaves are in two rows (alternate distichous). Leaves may also stay in two rows if two leaves are inserted to each node and the leaves are in one plane (opposite phyllotaxy). If the planes of subsequent leaf pairs are perpendicular, the phyllotaxy is decussate. Phyllotaxy is circular if three or more leaves are at one node, in one whorl. In pseudo-whorls there are leaf-like organs (eg. stipules) apart from true leaves and phyllotaxy is whorled only seemingly.

Plasticity of leaf is high and this organ has the biggest variability in structure, function and morphology. Beside the photosynthetic function, leaf may be modified for other purposes changing its basic form and structure. There are several possible functions like: 1. Leaf or leaflet modified into tendrils (*Pisum*). 2. Leaf is modified into spine (*Opuntia*). 3. Leaf serves for water or nutrient storage (*Allium*). 4. Leaf is changed into bladder-like or other type of trap for insects (*Utricularia*). 5. Leaf becomes similar to roots and its function is absorption of water and nutrients (*Salvinia*). 6. Leaf develops into a scale (*Juniperus*, *Thuja*). 7. Leaves are involved in vegetative propagation with their residual meristemoids (*Bryophyllum*).

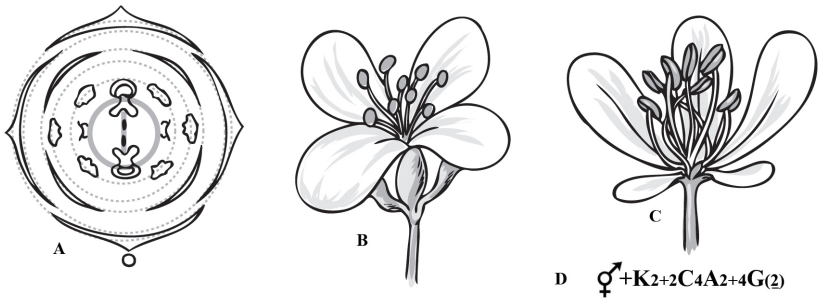
Leaves (even foliage leaves) differ in their form and function in case of heterophylly (*Hedera*, *Sagittaria*) or they have altered size as in case of anisophylly (*Selaginella*).

2.6. Flower, inflorescence

In spite of vegetative shoots which photosynthesize and produce organic compounds, flower's function is the reproduction. According to its definition, flower is a modified dwarf shoot built up from modified leaves which serve for sexual reproduction. Its growth is terminated when gynoecium is initiated, so no other parts are produced by the reproductive shoot apical meristem after pistil formation. Observation of flower development (and defects caused by mutations) pointed to the fact that homeobox genes are also present in plants and they govern development of flower. Flower induction and development is a rigorous morphogenetic advance, in which number, position of flower parts and timing of their development is a highly ordered, regulated process. It makes obvious that structure of the flower characteristic for a plant species is a result of a long-lasting evolutionary progression.

Parts of the flower are joined to the upper part of pedicel called receptacle. Basically, there are two categories of the modified leaves in the flower: 1. parts of perianth and 2. essential flower parts involved in sexual reproduction sensu stricto (stamens and carpel(s)). Parts in the perianth may be uniform (homochlamydeous /monochlamydeous/) or different (heterochlamydeous). The homochlamydeous perianth is composed of tepals. They are green at first

and later they become coloured, attractive for pollinators. In the flower with heterochlamydeous perianth there is a separate calyx whorl and inside of it the corolla whorl develops. Sepals are usually green and protect the younger parts of the flower, while petals are coloured and attractive. It should be emphasized that this tendencies are visible in animal (eg. insect) pollinated flowers where size and colour have great importance. But a large portion of plant species is pollinated in other way (eg. by wind). At these species flowers are numerous, small, very simple, often with reduced perianth. If some of the flower parts are absent, the flower is incomplete.



Brassicaceae flower Characteristic structure of the *Brassicaceae* flower. A. Floral diagram: floral parts, their number and position, are drawn on concentric circles. B. Picture of the whole flower. C. Picture of the dissected flower. D. Description of floral structure with symbols.

Inside the perianth are the stamens and the pistil(s).

The flower of ancient angiosperms had its components in unidentified number and spiral arrangement. From that developmental stage the evolutional tendency was to form them in whorls and in defined numbers per whorl (cyclic). Hemi-cyclic arrangement, when parts of the perianth are in whorls while stamens and carpels are spirally arranged, is a transition between them. If the number of parts in a whorl is 3, 4, 5 etc., the flower is trimerous, tetramerous, pentamerous, etc. If the number of whorls is 3, 4, 5, etc., the flower is tricyclic, tetracyclic, pentacyclic, etc. In some special cases, number of parts in a whorl may be reduced or they might divide into more parts. Pentamerous pentacyclic flower is one of the basic types. Number of whorls and parts in them is strictly regulated and stable in a species. Of course, exceptions are always found.

Examples for flowers Perianth is determining on flower appearance but it provides also other information (pollination, evolution development, relationship, etc.). A. Heterochlamydeous flower, parts of perianth are free, insect pollination (entomophily), eg. *Brassicaceae*. B. Heterochlamydeous flower, parts of perianth are fused, insect pollination (entomophily), eg. *Solanaceae*. C. Homochlamydeous flower, parts of perianth are free, insect pollination (entomophily), eg. *Liliaceae*. D. Flower with reduced homochlamydeous perianth, pollinated by wind (anemophily), eg. *Poaceae*.

Calyx is a whorl of sepals, the green, protecting parts of the outer whorl of a heterochlamydeous perianth. Sepals are initiated first on the reproductive shoot apex and the other, developing parts are enclosed in the calyx up to the flowering. After pollination, sepals are usually detached; however, they may stay to protect young fruit(s) or to form the false fruit together with the ovary/pistil. Sepals are separated or fused. Apart from true calyx, in some families a false calyx (pseudocalyx) is formed from bracts.

Corolla is composed of petals and it is the inner whorl of the heterochlamydeous perianth. Number, size, colour of petals determines flower's morphology. Cells of corolla contain pigments and between the cells extended inter-

cellular space is found which is filled with air. This air-filled space and projections of epidermal cells (mamillae or papillae) disperse the sunlight and change optical features of petals. Petals function short and after flowering fall down. In case of their reduction, coloured bracts or filaments of stamens can attract the pollinators. Petals may be connate and in this case corolla tube is formed.

If the corolla is homochlamydeous (perigonium), sepals and petals are not produced but in the perianth there are uniform tepals. Tepals are green at the beginning of flower development but later, just before flowering, they turn into coloured parts and make the flower attractive for the pollinators. In flowers with reduced perigonium, tepals are small and green or lacking at all.

In the case of extreme reduction of perianth, stamens and pistil(s) remain only in the flower.

One of the morphological features is the symmetry of flower, that is, how many planes divide the flower into symmetrical halves. If there are three or more, the flower is actinomorphic. In case of two planes, the flower is bisymmetric. One plane divides the flower into two symmetrical halves, the flower is zygomorphic. Asymmetric flower does not have such a plane. Additionally to symmetry, there are often extra characteristics according to the corolla structure, eg. exceptional forms of petals or tepals (*Lamiaceae*, *Fabaceae*, *Orchidaceae*, etc.).

Stamens develop on the androecium, inside of the corolla/perigonium. Number and position of stamens may characterize the plant family. If there are no divisions or reductions, stamens stay in whorls (one or two, sometimes more), while in more primitive forms they arrangement is spiral. Generally, they number per whorl agrees with the number of parts in corolla. High number of stamens is characteristic for some families but in others number of stamens may be reduced up to one. If stamens are not in whorls but in groups, androecium is monodelphous, diadelphous, pentadelphous, polydelphous, depending on the number of groups.

The ancient type of stamen is almost phyllous, flat (eg. *Nymphaeaceae*) but most of the angiosperms have simplified stamen composed of filament and anther on the top of it. In the filament there is a central vascular bundle which runs up to the connective part of the anther and transports nutrients for microspore development. Usually, anter contains two halves and in each halves there are two pollen sacs (loculus). Archesporial tissue develops in the loculi and microspore mother cells differentiate from is central cells. Microspores are formed by meiotic cell division. During pollen cell wall development and subsequent mitotic cell divisions the pollen grain gets ready for discharge. Loculus opens with longitudinal dehiscence, pores or unregularly.

Gynoecium develops from the central primordia of the reproductive shoot apex. At angiosperms, carpels are fused and form a pistil. Usually, carpels are in one whorl but in primitive families they have spiral arrangement. Exceptionally, they may stay in more than one whorl. Number of carpels changes from one to numerous depending on the family. Number of carpels may correspond with the number of parts of corolla but very often differs from it. According to fusion of carpels, there are two possibilities: 1. Margins of each carpel fuse with its own margin, so each carpel forms a pistil equivalent structure (apocarpous gynoecium). 2. The carpels fuse together and form one pistil (syncarpous gynoecium). The united carpels of syncarpous gynoecium may form ovary with septa (coenocarpous gynoecium) or ovary with partially or totally reduced septa (paracarpous gynoecium). Lysicarpous gynoecium is similar to the paracarpous but it has basal placentation. Ovary is the lower part of the pistil, style is attached to its top part and stigma is at the upper end of the style. Stigma has a central role in pollen adhesion, rehydratation of pollen grain and initiation of pollen tube growth. Style provides pollen tubes in direction of ovules in the ovary. Structure, form, size of stigma and length of the style depends on the mode of pollination.

Placentation is the pattern of ovule connection to the carpels (in the ovary). Placentation is marginal if ovules are attached to the margins of carpels. Parietal placentation is when ovules are on the wall (surface) of carpels. Ovules are sitting on the central protrusion of receptacle in case of axial/central free placentation. Basal placentation differs from it. Ovules are joint to the short protrusion of receptacle at the basal part of ovary. Number of ovules is various, from one up to several thousand, depending on the species.

The outer layer of ovule is the integument which may have one or two layers and it protects the nucellus inside. There is a small pore on the integument(s), the micropyle. Structure of the ovule is anatropous, orthotropous or campyllotropous depending on the micropyle-chalaza-placenta position and embryo sac location. Structure of ovule influences seed morphology (see seed and seedling morphology).

The flower is hypogynous if insertion of the perianth is lower than ovary is. In epigynous flower insertion of the perianth is above the level of ovary. In case if perigynous flower ovary is more or less at the height of perianth insertion. Ovary can be adnate to the hypanthial part.

Unisexual (diclinous) flowers contain only one of the sexes. In a bisexual (monoclinous) flower both sexes are present. If stamens and carpels lack in the flower, it is asexual. It is worth to add that in most of unisexual flowers both sexual organs start to develop but one of them stops in its development and abort soon. In this way one sex develops fully only in the flower.

Generally, one type of flowers is present in a plant species. If the plant is dioecious, the two types of flowers are on separate male and female plants. In case of monoecism, the main and female flowers are on the same individual.

Size and length of stamens and styles are variable in certain species. Heterodistyly (eg. *Primula*) appears in different length of filament/anther position and style: short filament/anther at lower position - longer style, and vice versa. Three types of filament and style lengths are combined in the flower population in case of heterotristyly (eg. *Lithrum*). These features promote the allogamy which raises genetic variability and is positive evolutionarily. However, this mechanism is only one from the possible strategies evolved by angiosperms to avoid self-pollination.

Similarly to the connations in the perianth whorls, fusion of stamens and part of gynoecium is also possible. Filaments may fuse with the corolla, especially with corolla tube, and filaments can be connate. Anthers together may form a tube-like structure (eg. *Campanulaceae*, *Asteraceae*), the synandrium. Stamen adnate pistil and form gynostemium, a compact columnar union of all sexual parts. These structural changes enhance the effectiveness of pollination, mainly allogamy.

Pollination is facilitated by nectaries in the animal pollinated flowers. Nectaries secrete nectar, a sweet, sugar containing fluid and during collection of nectar the animal (insect, bird or mammal) transmits the pollen from flower to flower. According to the position of the nectary, intrafloral, circumfloral and extanuptial nectaries are distinguished. Apart from sweet nectar, nectaries may secret scent as an additional attractant. Beside nectar, the pollen may also attract pollinators as a food. In this special case, strategy of plant is that consumption of a certain portion of pollen by the pollinators ensures the pollination with the rest of it. Pollination is also helped with different scents secreted by various parts of flower or inflorescent. A special case is when the flower exudes feromones and animals pollinate the flower seeking for a sexual partner. Evolution of angiosperms sets a bunch of examples for flower and pollinator co-evolution. In some extreme instances, the partners are unable to live and propagate separately, and in this way, to survive. Air-pollinated plants have quite different mode of pollination and it meets with their flowers' morphological appearance. Pollen grains are produced in a vast amount in the numerous but small and reduced flowers.

Evolutionary changes of flower structure can be monitored with investigation of fossil forms or less developed species from related groups. Atavistic features help to enlighten the way of modification. The typical reduced flower of *Poaceae* is a good example. In the ancient flower there was a two whorled perigonium (3+3), three stamens per whorl in two whorls and pistil composed of united three carpels. From the two-whorled perianth three parts remained but with non-tepal looks (from the outer whorl one part /palea/, from the inner whorl two lodicules remain). One whorl of the androecium is reduced, so the number of stamens is reduced to three. From the three carpels remained only one.

Flowers may develop separately but they can grow in inflorescences.

Development of the inflorescence starts from the reproductive shoot apex but its growth is not terminated as in the flower. It produces new meristems which become the parts of inflorescence. The innate genetic program terminates the growth and the lastly produced meristems develop into flowers. Inflorescence is a specialized shoot system and the sort of ramification (at least partly) characterizes the morphogenetic processes. This fact enables botanists to use the mode of ramification for inflorescence classification.

To distinguish the types of simple inflorescences the next features were taken into consideration: ramification of the main axis of inflorescence and pedicels, the length of pedicels, direction and quality of main axis. Existence or reduction of bracts does not pay respect. On the basis of the abovementioned facts, two main groups are distinct: the racemose and cymose types. Several subtypes are in these two categories:

Racemose: Monopodial ramification, flowering direction from down to upwards or from the periphery to the centre characterize this type. 1. Raceme: Main axis is elongated, erected or hanging. Flowers have pedicels. 2. Spike: Main axis is elongated, erected, flowers are sessile. 3. Catkin: Main axis is elongated, soft and hanging. Flowers are small and unisexual. After the overblown catkin falls down in one piece. 4. Spadix: Main axis is thick and fleshy. Flowers are sessile. A special bract, the spathe protects the young inflorescence and makes it attractive. 5. Corymb: Main axis is shortened at the top of it. Pedicels of older flowers are more elongated. As a result, flowers are at the same level. 6. Umbel: Internodes of the main axis are short, pedicels arise from the same level. Pedicels of flowers have more or less equal length, so flowers are at the same level. 8. Capitulum: The thick and flattened, conical or broad main axis bears sessile flowers. Young inflorescence is protected by involucres composed of involucral bracts. A special form of capitulum is the head when flowers together shape a globe. 9. Cone: Woody female inflorescence of gymnosperms composed of carpels and their bracts.

Cymose: Ramification is sympodial. The main axis terminates in a flower and a lateral shoot continue the growth of inflorescence. All the relative main parts end in a flower and grow from a new axillary meristem. Direction of flowering is from the centre to the periphery. 1. Cyme: Main axis and lateral shoots end in flower, main axis holds the oldest flower. Number of shoots may be one, two or more. 2. Cicinnus (helicoid cyme): Flowers with gradually shortened pedicels are in one plane. 3. Bostryx (scorpioid cyme): Flowers with gradually shortened pedicels alternately develop in left and right from a plane. 4. Drepanium: Flowers with gradually shortening pedicels are arranged in one plane and one direction. Flowers are almost at the same level. 5. Rhipidium: Flowers with gradually shortening pedicels are in one plane and arranged alternatively. Flowers are almost at the same level. 6. Coenanthium: The flattened and fleshy main axis bears sessile flowers. 7. Hypanthodium: As coenanthodium, but it is a cup-like structure. Flowers are in an almost closed space inside.

Beside simple inflorescences, compound inflorescences are also distinguished. If the compound inflorescence contains the same units, it is a homotactic one. If different types of simple inflorescences are combined in the compound inflorescence, it is a heterotactic type.

2.7. Fruit

Seed is present at the gymnosperms and angiosperms. It contains the new sporophyte. Evolutionarily seed appeared earlier than the fruit because seeds were produced on the carpels while fruit developed from the pistil, which arise from the fused carpels. Inasmuch as gymnosperms possess free carpels, they do not have fruits.

Apart from the true fruits formed from the ovary of pistil or the whole pistil, there are also false fruits developed from the pistil and some other parts of the flower (receptacle, sepal, etc.).

Pericarp evolves from the wall of ovary and during this process its structure changes significantly, meanwhile ovules become seeds. Structure of the pericarp facilitates dissemination of seeds and they are released from the fruit. Middle layer of pericarp, the mesocarp, is decisive; however, thickness and structure of other layers may also have remarkable influence (eg. sclerenchymatized endocarp of drupe). According to the differentiation of mesocarp there are two basic types of fruits: 1: Mesocarp is sclerenchymatized, sclereids and fibers dominate in it. Fruit becomes dry. 2. Mesocarp is fleshy, soft parenchymatic tissue dominate in it. In both cases fruits may be dehiscent or indehiscent.

The position of ovary, its construction, number of carpels, fusions, type of differentiation and note on special structures (eg. pappus) is added in the description of fruit type. Exceptions are always found but they do not query the trends (eg. legume is a dry, dehiscent type, but there are indehiscent and fleshy forms as well, eg. *Sophora*).

Dry, dehiscent fruits: 1. Capsule: Usually dry, unichambered or multichambered, from multicarpellary and syncarpous ovary, hypogynous flower. Dehiscent with pores, apical teeth, valves, or loculicidic, septicidic, septifragal ways. It might also develop from epigynous flower (*Amaryllidaceae*) or could contain only one seed (*Luzula*). 2. Follicle: Multiseeded, monocarpellary ovary, hypogynous flower, apocarpous gynoecium. Dehiscent on one side (ventral). Often as aggregate fruits. 3. Legume/pod: Monocarpellary (from monomerous gynoecium), generally multiseeded, hypogynous flower, marginal placentation. Dehiscence is on two sides (ventral and dorsal) from the apex of the fruit. Characteristic for *Fabaceae*. 4. Siliqua: Bicarpellary, syncarpous ovary, hypogynous flower, parietal placentation, replum. Dehiscence is in two sides, in direction of upper part. Characteristic for *Brassicaceae*. 5. Siliqula: As siliqua but shorter and wider. Also in *Brassicaceae*. 6. Utricle: Single seeded, mono- or bicarpellary, syncarpous ovary, hypogynous flower. Dehiscence is with a cap or unregularly.

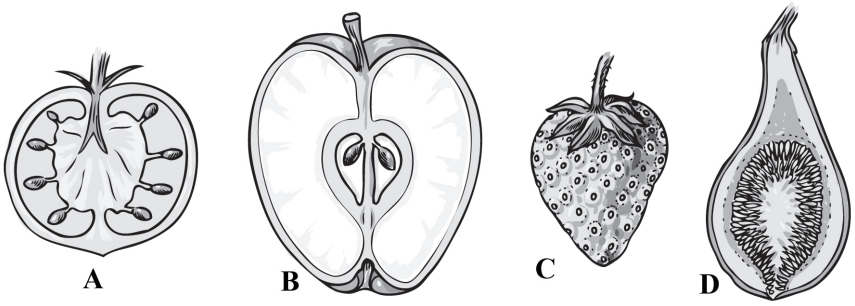
Dry, indehiscent fruits and false fruits: 1. Nut: Single seeded, mono- or multicarpellary, unichambered, syncarpous ovary, hypogynous flower, woody pericarp, membranous testa, often cupule from bracts. 2. Cypsela: Single seeded, bicarpellary, syncarpous ovary, epigynous flower, slightly woody pericarp and membranous testa separated, often pappus from hairs or remnants of calyx. 3. Caryopsis: Single seeded, monocarpellary, hypogynous flower, pericarp and testa fused. Characteristic for *Poaceae*. 4. Achene: Single seeded, monocarpellary ovary, from apocarpous gynoecium, hypogynous flower, pericarp slightly woody. Often in aggregate fruits. 5. Samara: Single seeded, bi- or tricarpellary, syncarpous ovary, hypogynous flower. Wing from the pericarp.

Mericarps: Fruit falls into uniseeded parts. Seeds are covered with a segment of pericarp. They are seed-equivalent, dispersal structures: cremocarp, double samara, carcerulus, lomentum, etc.

Fleshy fruits and false fruits: 1. Berry: Multiseeded, mono- or multicarpellary, syncarpous ovary, flower hypogynous, mesocarp fleshy and seeds are embedded in it, epicarp and endocarp thin. 2. False berry: As berry but from epigynous flower. 3. Pepo: Multiseeded, tricarpellary, syncarpous ovary, epigynous flower, unichambered but filled with soft paremchymatic tissue. Epicarp becomes hard. Characteristic for *Cucurbitaceae*. 4. Drupe: Mono-or multicarpellary, syncarpous ovary, hypogynous flower. Epicarp thin, mesocarp fleshy, endocarp hard and stony. Single seeded. In some case dehiscent (almond) or mesocarp becomes fibrous (coconut). 5. Hesperidium: Multiseeded, multicarpellary, syncarpous ovary, hypogynous flower, mesocarp spongy, fleshy hairs on the endocarp. Characteristic for *Rutaceae*. 6. Pome: Multiseeded, bi- or multicarpellary (typically pentacarpellary), partly syncarpous or apocarpous gynoecium, epigynous flower. Like follicles embedded in fleshy tissue from receptacle and basal part of sepals, real ovary walls become hard (pergamenous in *Malus*, stony in *Mespilus*). 7. Balausta: Multiseeded, multicarpellary, syncarpous ovary, epigynous flower. Pericarp (partly from receptacle and sepals) hard, testa fleshy.

From one flower not only one fruit might develop. If several fruits are formed on the apocarpic gynoecium of a flower than it is called aggregate fruit like etaerio of follicles, etaerio of achenes, etaerio of berries, etaerio of drupes, etc.

If the whole inflorescence grows into a fruit like structure where seeds are in the fruits and simple fruits are embedded into the fruit like structure developed from the axis, bracts, etc. of inflorescence, it is called composite fruit (*Ananas*, *Ficus*, *Morus* etc.)



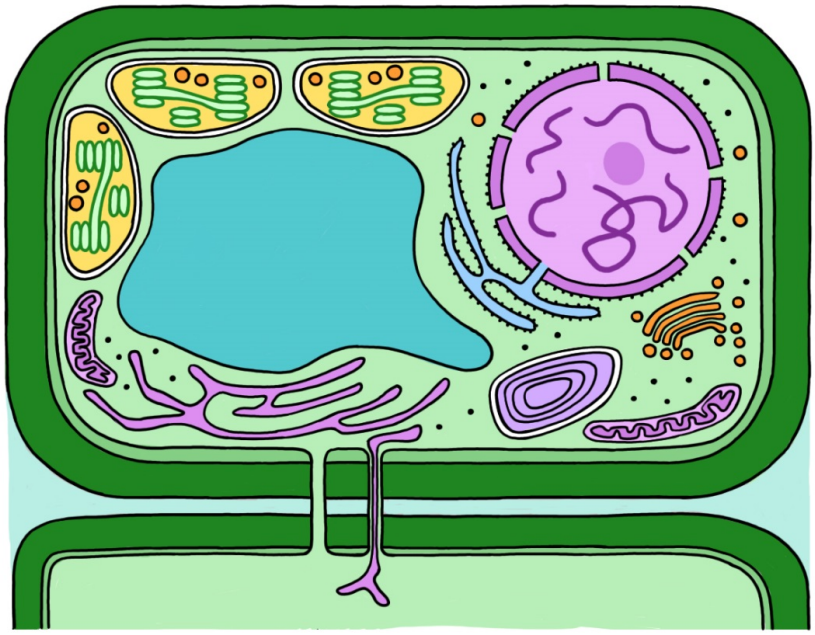
True fruits and fruit-like structures. A. True fruit: from ovary or the whole pistil (berry). B. False fruit: apart of pistil other parts of flower (eg. receptacle, sepals) take part in fruit formation (pome). C. Etaerio: several fruits develop in one flower from its apocarpic gynoecium (etaerio of achenes). D. Syncarp: the whole inflorescence developes into a fruit-like structure (sycamore of *Ficus*).

Chapter 3. CYTOLOGY

(Zoltán Kristóf)

3.1. Characteristics of the plant cell

The typical plant cell shows many similarities to the animal cell, although there are many dissimilarities between them as well. The plant cells are limited by the cell wall, which restricts the movement and growth, and determines the shape of the cells, while taking place in cell differentiation and function. Plant cells may contain a large vacuole fulfilling multiple functions and occupying up to 90% of the volume of the cell. The cells of higher plants (conifers and angiosperms) lack centrioles, and for this reason they lack motile (flagellate or ciliate) cell types. In comparison with the animal cells, they contain more Golgi stacks of undefined location. Plant cells possess plastids, and due to their chloroplasts they are characterized by photosynthetic autotrophy. Compared to the animal cells, plant cells differentiate into less, and less differentiated cell types. Due to their interconnections via plasmodesmata, they are less separated, as their membranes and to some extent also their cytoplasm are continuous with those of the neighbouring cells.



Plant cell

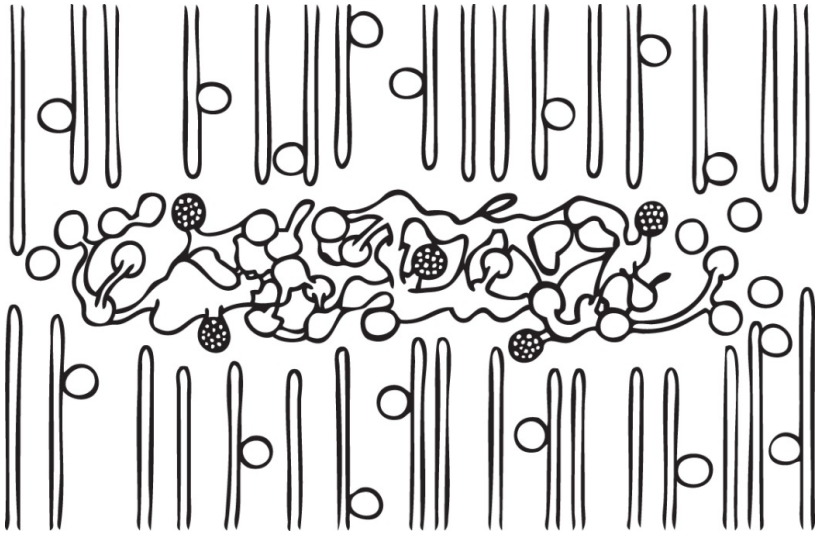
3.2. The cell wall

Plant cells are surrounded by the cell wall. Exceptions of this rule are the sperm cells and their precursor, the generative cell in the pollen grain. The cell wall belongs to the extracellular space (apoplast). It fulfills multiple functions, among others:

- giving mechanical support
- resisting turgor pressure
- determining the growth and shape of the cell
- strengthening the plant

- influencing the apoplast transport
- due to its certain components serving as nutritive depot
- protecting the cell from mechanical and chemical influences
- yielding signal molecules for itself and for interacting organisms
- participating in cell-to-cell connections.

The cell wall starts to form at the end of the cell division, when daughter cells separate. By the aid of the remnants of the mitotic spindle Golgi-vesicles are transported into the equatorial plane, where they coalesce forming a flattened sack-like structure. Their pectin content unites giving rise to the **cell plate** covered on both sides by the former vesicle membranes, now the new plasma membranes.



Phragmoplast

During the fusion of the vesicles, holes remain leaving space to the endoplasmic reticulum (ER) extending from one daughter cell into the other. These structures are the **plasmodesmata,** which retain the membranous and cytoplasmic connection between the daughter cells. The ER traversing the plasmodesmata forms a tubule (desmotubule) and is anchored by proteins to the wall of the plasmodesmata. Plasmodesmata let pass through substances below a certain size limit, but viruses can utilize plasmodesmata for spreading from cell to cell. Plasmodesmata may be formed through pre-existing cell walls, also they can be tightened or closed by callose synthesized around their neck regions.

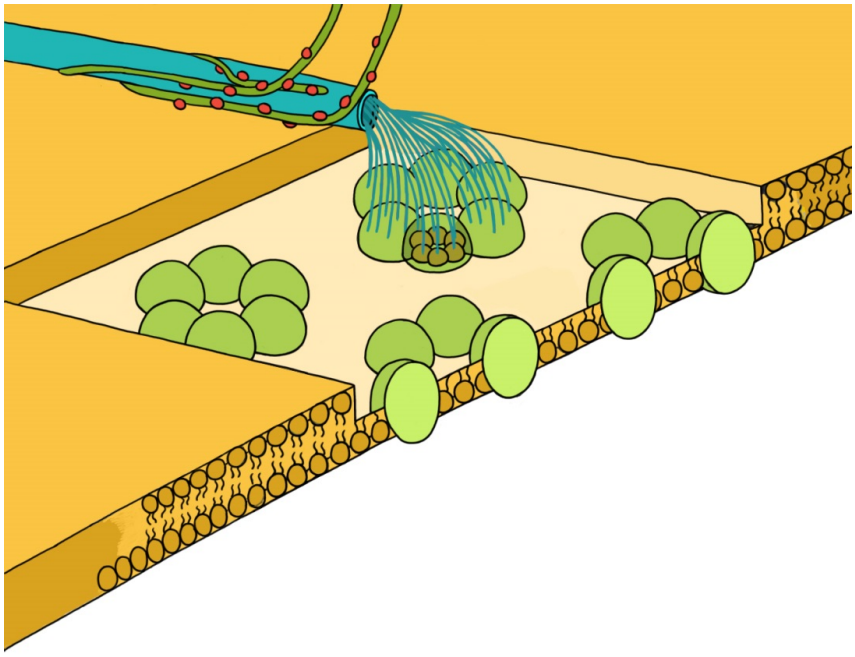
With the formation of the cell plate the daughter cells are separated, and the synthesis of the primary cell wall commences. This means that on both sides of the pectinic cell plate (now becoming middle lamella) cellulose will be synthesized. The newer wall lamellae are deposited on the older ones, so the newest layer is found immediately below the cell membrane. So the thickening of the cell wall is **centripetal.** The **primary cell wall** consists of mostly cellulose and pectin, and is capable to extension, coping with the growth of the cell. The wall of the differentiated, nongrowing cells is the **secondary cell wall**, which contains various kinds of deposits. It may reach a considerable thickness, so it is not able to expand, or change shape. The secondary cell wall consists of some (generally 3) layers, these contain different arrays of cellulose microfibrils. Deposits onto and into the secondary wall (adcrustations and incrustations) participate in the special functions of the differentiated cells. Such deposits are the woody substance lignin, the hydrophobic suberin, cutin, or wax, etc.

The cell wall substances are generally classified into:

- skeletal substances
- matrix substances

- incrustations and adcrustations.

The most important skeletal substance is the **cellulose**. It is a 1-4 linked β-D glucose polymer, synthesized by the **rosette enzymes** in the cell membrane (in a well-studied object 36 chain molecules per each rosette). These cellulose molecules held together by H-bonds form the **microfibril** with repeated crystalline parts called micelles.



Cellulose synthesis and rosette complexes

A rather rare skeletal substance is the **callose**. This is a 1-3 linked β-D glucose polymer with a spiral structure consisting of two or three twisted molecules. It is characteristic of the wall of the pollen tubes, the sieve plates of the sieve tubes, the common wall of the microspores, and appears in places where a pore or wound in the cell wall has to be plugged (see plasmodesmata).

Into the **matrix substances** hemicellulose, pectin and the glycoproteins of the cell wall are classified.

The **hemicelluloses** are similar in structure to the cellulose molecules, containing glucose 1-4, or xylose 1-4 linked backbone and side chains joining with 1-6 links to it (consisting of other sugars). These are mentioned also as **cross-linking glycanes**. In dicots and some monocots the hemicellulose is the xyloglucan (XyG), i.e. glucose polymer with xylose side chains. The other part of monocots (grasses) contains glucurono-arabinoxylanes (GAX), which are xylose polymers with glucuronic acid and arabinose side chains. As the name cross-linking glycanes shows, these polysaccharides join to the cellulose microfibrils with H-bonds and maintain cross-links between them either directly, or via pectins.

The **pectins** are also polysaccharides, they are well hydrated and by binding Ca^{2+} ions occur as Ca pectate in the cell walls. They can be extracted from the wall easily by Ca chelators (e.g. EDTA, EGTA, ammonium oxalate), or by boiling. Their main building block is the galacturonic acid constituting the polysaccharide backbone either alone as a homopolymer, or alternating with rhamnose (another hexose). Side-chains of various sugars join to this backbone, so a variety of molecules may be formed.

The cell wall contains proteins, glycoproteins and proteinoglycanes (the term refers to the protein – carbohydrate ratio), the significance of these are not fully understood. The proteins are partly enzymes responsible for the splitting of the bonds during the extension of the cell wall, while others are structural proteins.

The incrustations and adcrustations in the secondary cell wall are different, depending on the differentiation of the cell.

In the largest amount **lignin** is deposited in the secondary cell wall, which causes the hardening of the wall. It is synthesized by the oxidative polymerization of monolignols (coumaryl, coniferyl and sinapyl alcohols), which are the products of the phenylpropane pathway. The lignified cell walls are hard, they are characteristic of the mechanical and conductive tissues.

Suberin (cork) is deposited into cell walls for water or heat insulation. Suberin consists of long fatty acid molecules of 20-30 carbon atoms and polyphenols. Corky cell walls in general are tightly anchored to the plasma membrane assuring total water insulation, so the water can get neither through the cell wall, nor between the wall and the cell membrane. Such a structure occurs in the root endodermis, where suberinization inhibits the movement of water in the apoplast.

Cutin and **wax** occur on the plant surfaces and are primarily water insulators. These are deposited on the outer wall of the epidermal cells known as **cuticle**, which is wax secreted into and onto the cutin matrix. Mainly the wax (consisting of fatty acids of 16-18 carbon atoms) is responsible for the hydrophobic character of the cuticle. The appearance of the cuticle is a precondition of living on the land, as it hinders the evaporation of water from the plant surface.

The **sporopollenin** in the outer exine of the pollen grains is perhaps the most resistant substance in nature. No known organism or enzyme is capable of disassembling it. For this reason its chemical composition is not fully known, but it has much in common with the structure of cork.

In most cells the thickening of cell walls progresses toward the plasmalemma (**centripetal cell wall thickening**), as the wall substances are synthesized either in the plasma membrane (cellulose, callose), or are transported in vesicles to the cell surface, then get into the cell wall by exocytosis. The hemicellulose and pectin molecules are synthesized in the Golgi apparatus, while the glycoproteins and proteoglycans receive here their carbohydrate moieties. In contrast to the centripetal thickening the walls of spores and pollen grains are thickened partly **centrifugally**, as sporopollenin is the product of the tapetal cells, and is deposited on the walls from outside.

3.3. The vacuolar system

A considerable part of the volume of plant cells is filled by the vacuolar system. It may consist of one large central vacuole, or a few smaller vacuoles. The young meristem cells contain tiny vacuoles, while in certain differentiated cells the large central vacuole may occupy up to 90% of cell volume. In such cells the cytoplasm forms a thin layer along the wall. The vacuole generally contains a watery solution, and is separated from the cytoplasm by a membrane, the tonoplast. The vacuole is a multifunctional compartment, increasing the cell size, storing nutritive substances (e.g. proteins), pigments, secretions, xenobiotics, also plays a role in maintaining the ionic homeostasis and in generating the turgor pressure. Here take place the lytic processes of the cell, and some protective mechanisms of the plant.

The **origin of the vacuoles** may be various. They can be derived from Golgi vesicles, or from subdomains of the smooth endoplasmic reticulum. These parts of SER show a characteristic accumulation of vacuolar proton ATPase (V-type H^+ ATPase) and certain aquaporin (alpha-TIP). Later these SER subdomains are separated and inflated. Alternatively, the vacuole may be formed by SER such a way, that its protrusions surround a part of the cytoplasm, the membranes fuse, then the inner membrane and the included cytoplasm will be lysed, so the vacuole will be formed (autophagosome).

If the cell contains more than one vacuole, these may fall into two types. One is **protein storing**, while the other is the **lytic vacuole**. The storing vacuoles have an approximately neutral pH and contain stored proteins, while the lytic vacuoles have an acidic pH and harbor lytic processes.

The **stored proteins** are primarily amino acid reserves, and frequently occur in the endosperm of the seeds. Proteins can reach the storing vacuoles in two ways. The easily soluble albumins and globulins having a simple structure get from the rough endoplasmic reticulum (RER) into the Golgi apparatus, then via the Golgi vesicles are transported to the storing vacuole with which they fuse. The prolamins soluble in alcohol, and the gluteins stabilized by disulphide linkages are transported from RER directly to the stores omitting the Golgi apparatus. The storing vacuole engulfs the vesicles by a mechanism similar to phagocytosis.

The **aleuron grains** are small protein storing vacuoles. They may be homogeneous, containing proteins of the same physical state, or may be heterogeneous with dissolved and unsolved, membrane-bound proteins. These latters form the crystalloid. In the heterogeneous aleuron grain of castor bean there is also a third component, the globoid. It consists of phytic acid, i.e. inositol hexaphosphate (IP_6).

The lytic vacuole is the disassembling compartment of the plant cell. The lytic vesicles are produced by the Golgi apparatus in the area of the trans-Golgi network. They contain lytic enzymes, and their pH becomes acidic due to the activity of the proton pumps bound to their membrane. The lytic vesicles fuse with other vesicles or larger vacuoles forming the lytic vacuole. This compartment disassembles the cell organelles, proteins or other substances which underwent autophagy or endocytosis. Lytic vesicles or vacuoles may fuse with protein storing vacuoles starting the degradation of stored proteins.

The vacuole may contain **crystals**. Certain cells are specialized for crystal formation, these are **idioblasts**. Generally crystals consist of calcium oxalate, but also other salt may be crystallized. Crystal forms are manifold, from tiny particles to needle-like raphids, rosettes, etc. Crystal formation has a role in the ionic homeostasis, but needle crystals may protect the plant against herbivores. Crystal formation depends on environmental factors; plants can produce or dissolve crystals rather quickly.

Many kinds of plant cells may contain **lipid bodies**, which are abundant in oily seeds and fruits. The lipid bodies are not vacuoles, their content is not bound by an entire membrane. Lipids are synthesized in between the two lipid layers of the endoplasmic reticulum, the dilated membrane domain will be pinched off as a lipid body having a half-membrane on its surface.

The vacuole has a fundamental role in maintaining the **turgor**. The solved vacuolar substances have a relatively high osmotic concentration causing water uptake from the cytoplasm. The cytoplasm will retrieve its lost water from the extracellular space. As a consequence, the vacuole increases its volume, and presses the cytoplasm against the cell wall. The intracellular pressure on the wall is the turgor. Water uptake lasts until the increased internal pressure stops it. The turgor has a major role in strengthening the plant body, the decreasing turgor during water loss leads to wilting of the soft tissues.

If plant cells are incubated with a medium of relatively high osmotic concentration, they lose water, and the vacuolar volume starts to decrease, which process is termed plasmolysis. During convex plasmolysis the plasma membrane separates from the wall, and the protoplast rounds up. During concave plasmolysis the plasma membrane is anchored at some points to the cell wall, so it forms bulges. Finally just narrow connections, the Hechtian strands remain between the body of the cell and the wall. These are not related to plasmodesmata, as they occur in epidermal cells also toward the outer tangential wall, where there are no plasmodesmata. Plasmolysis is reversible within a time period, transferring the cells into a more dilute medium; the cells will take up water and will fill the volume within the walls. This is **deplasmolysis**.

The vacuoles may contain **pigments**, mainly **anthocyanins**. These compounds change their color as indicators, according to the pH of the vacuole. These are frequently found in epidermal cells of petals, leaves, or fruits. The change of color in petals may inform the pollinating insects about the pollinated or unpollinated state of the flower.

The vacuolar pH may change according to the stored acids. During the **Crassulacean-type of photosynthesis** (CAM) the cells store the CO_2 fixed at night in the form of malic acid, prior to further processing, which takes place daytime.

3.4. Plastids

The photosynthesis of the plant relies on chloroplasts in the cell. The cyanobacterial ancestors of the plastids established endosymbiosis with the ancient eukaryotic host cell, in which they work now as semi-autonomous organelles. Alike mitochondria, they have circular DNA and bacterial type of ribosomes, although most of their genes were transferred to the nucleus. So they can synthesize just a part of their own proteins, while the others are produced by cytoplasmic ribosomes using mRNAs exported by the nucleus. During photosynthesis the chloroplasts reduce carbon dioxide with electrons originating from water splitting, by the energy of light. Plants release oxygen and synthesize carbohydrates during photosynthesis, therefore they are considered as photoautotrophic organisms.

The plastids (as their name shows) have widely variable appearance, which may change, so the plastids differentiate for fulfilling various tasks (storing, accumulation of pigments, etc.). Being semi-autonomous endosymbionts, they multiply exclusively by division, rather than appearing de novo. Their least differentiated form is the **proplastid**, giving rise to any other plastid types. This kind of plastids is typical for meristematic cells, although similar plastids may occur in roots, or in epidermal cells. It is small (generally less than 1 micrometer) spherical or lens shaped organelle with rudimentary thylakoid membranes. In their stroma little starch grains, lipid droplets or vesicles containing stored proteins may occur.

Chloroplasts are the most important plastids, performing photosynthesis. They can develop directly from proplastids, if these are kept in light. In their interior an extensive thylakoid membrane system develops, containing the pigments and members of the electron transport chain of photosynthesis. The sack-like thylakoids can be layered upon each other forming grana, while their parts extending freely into the stroma are named stroma thylakoids. The space limited by the thylakoid membrane is the lumen. Chloroplasts are generally lens shaped with a diameter of 5-8 micrometer and thickness of 3-4 micrometer. They are abundant in leaf mesophyll, here their number per cell may exceed 100.

Etioplasts are formed when the development of chloroplasts is inhibited in the absence of light. Such a way thylakoids cannot develop, as they would require chlorophyll-protein complexes, but chlorophyll biosynthesis includes a light dependent step. So it stops at the protochlorophyllide level, and a quasi-crystalline three-dimensional tubular system is formed instead of thylakoids. Upon illumination this **prolamellar body** (PLB) quickly rearranges into thylakoids, and the etioplast transforms into chloroplast.

The **chromoplasts** are yellow, orange, or red plastids according to the ratio of the carotenes and xanthophylls in them. These give the color of certain fruits (tomato, red pepper), flowers (Calendula, Tagetes), or roots (carrot, sweet potato). The chromoplasts may develop directly from proplastids, or from chloroplasts. In the latter case the green fruits turn yellow or red. Sometimes this development may be reverted, e.g. in the aerial, greening part of carrot the chromoplasts can give rise to chloroplasts. Carotenoid synthesis may be conspicuous in chromoplasts, sometimes these pigments form crystals in them.

Amyloplasts are starch storing plastids. They contain starch grains in the stroma, accompanied by a few thylakoids. Starch is formed always in plastids (mostly in amyloplasts) in plants, never in the cytoplasm. Amyloplasts are abundant in cells of the storing organs, e.g. in potato tuber. Special amyloplasts acting as statoliths in certain cells of the root apex are responsible for the gravitropism of the roots.

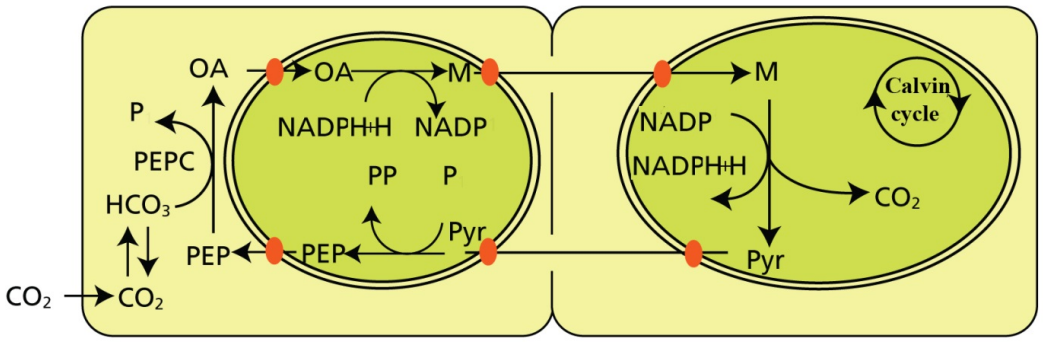
Amyloplasts are generally considered as a type of the **leucoplasts** storing different nutritives. **Proteinoplasts** store proteins, **elaioplasts** accumulate lipids.

The coloration of autumn leaves is the consequence of the transformation of chloroplasts into **gerontoplasts.** These senescent chloroplasts cease photosynthesis and partly disassemble, their components being transformed and transported into the surviving parts of the plant. As the disorganisation of the electron transport chain while collecting light would lead to the formation of very harmful free radicals, the degradation of the chlorophyll is not accompanied by that of the carotenoid pigments, which can protect plastids as antioxidants.

The light phase of **photosynthesis** is coupled to the thylakoid membranes of chloroplasts. Granum thylakoids contain the second photosystem (PS II), which utilises light energy for channeling electrons originating from water splitting into the electron transport chain. Another product of water splitting is oxygen; it diffuses out of the plastids and gets from the plant into the atmosphere. The third product of water splitting is a number of protons increasing proton concentration in the thylakoid lumen. Electrons proceed via the electron transport chain to the first photosystem (PS I), then into the stroma. The proton gradient is equilibrated toward the stroma via proton ATPases synthesizing ATP. In the stroma the protons and electrons reduce NADP to NADPH+H. So both NADPH+H and ATP will be available for the Calvin cycle in the stroma. Carbon dioxide is fixed by the enzyme **rubisco** (ribulose 1, 5 bisphosphate carboxylase-oxigenase). Fixation of 6 carbon dioxide molecules during 6 turns of the cycle yields in synthesis of one glucose molecule.

The concentration of carbon dioxide fixed during photosynthesis has also a regulatory role. Leaf cells access to carbon dioxide by opening the stomata, this increases, however, also transpiration, which may be dangerous in an arid environment. A group of plants circumvents this by a mechanism maintaining the operation of Calvin cycle even at low carbon dioxide concentration. The problem is caused by the poor fixing activity of rubisco below a threshold concentration of carbon dioxide. Moreover, in this situation the enzyme catalyses oxidation, rather than

fixation, which leads to a loss of carbon dioxide (**photorespiration**). For maintaining the minimal carbon dioxide concentration required, the plant either should open stomata (which might cause a fatal water loss under dry circumstances), or should concentrate carbon dioxide for rubisco. For this latter option the so called **C4 plants** developed a specific carbon dioxide fixation mechanism. (The term shows that the fixed carbon dioxide first appears in a molecule of 4 carbon atoms, in contrast to the molecule of 3 carbons appearing in Calvin cycle, or C3 carbon dioxide assimilation pathway). This is hallmarked by the so called **Kranz syndrome**, the leaf structure of some C4 plants, where two groups of photosynthesizing cells can be clearly distinguished. The large bundle sheath (BS) cells around the bundles belong to one cell type, while the mesophyll (M) cells surrounding these in a radial arrangement constitute the other type of cells. Also the chloroplasts differ in BS and M cells, in BS they store starch but their thylakoids do not develop grana, while in M they have grana but no starch grains. These latter cells transport carbon dioxide to the BS cells, where its concentration will be enough for the Calvin cycle, namely to the rubisco enzyme. The way, how they do it is that they couple carbon dioxide to a molecule of 3-carbon atoms (phosphoenol pyruvic acid), forming a 4 carbon molecule (oxaloacetic acid). This is transformed by oxidizing NADPH into malic acid, which is transmitted via plasmodesmata to the BS cells. In these cells the carbon dioxide is released by reducing NADP, and the malic acid is reverted to a 3-carbon molecule (pyruvic acid). This is transported back to the M cells, where it transforms into phosphoenol pyruvic acid for binding carbon dioxide again. The concentration of carbon dioxide released in the BS cells is high enough for the operation of the Calvin cycle. The ATP needed for the cycle can be synthesized by the agranal plastids containing only PS I, by the **cyclic photophosphorylation,** these plastids, however, cannot produce NADPH in lack of PS II which splits water generating electrons. However, the necessary NADPH is available in them by decomposition of malic acid concomitantly producing also carbon dioxide. This explains why these plastids contain much starch, the end product of the Calvin cycle, without having grana. In contrast to this, the M cells are able to generate NADPH needed for the primary fixation of carbon dioxide, by their granum thylakoids containing PS II. As they do not run Calvin cycle, do not store starch either. Such a way C4 plants need to open stomata much less frequently, which decreases transpiration, still permitting carbon dioxide fixation while limiting photorespiration.



C4 carbon dioxide fixation pathway

3.5. Cell division

Dividing plant cells, like animal cells, are involved in a cell cycle. Cell division is similar in these organisms, although showing considerable differences as well. These are the consequences of the presence of the plant cell wall, the absence of the centrioles in higher plants, or are connected to other properties. The two principal forms of the cell division are the mitosis and meiosis, maintaining or halving chromosome number, respectively. In plants only the spores are generated by meiosis, while the cells of the sporophyte and the reduced gametophyte undergo mitosis and this holds true also for the formation of the gametes. Before both kinds of division the interphase involves G_1, S, and G_2 phases. During the S phase (synthesis) the DNA is doubled, so in a diploid cell its quantity increasesfrom 2C to 4C before division.

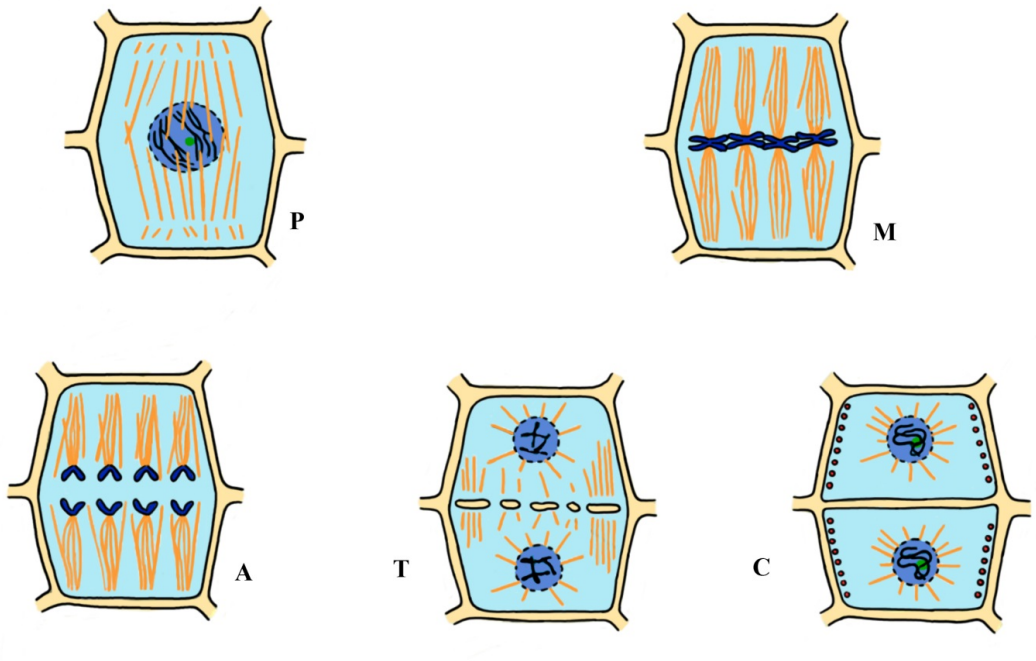
Division may be equal or unequal. This does not concern the distribution of the DNA – it is always equal – rather the distribution of the cytoplasmic constituents is concerned. Unequal division yields in two cells of different composition and frequently of different size. These cells follow altered differentiation pathways, which may include in an extreme case the quick degeneration of one of them.

It may occur that during division only the nuclei divide (karyokinesis), without the division of the cells (cytokinesis). In this case dikaryotic, or further multikaryotic cells (syntitia) may develop. It is common that later such syntitia are fragmented into cells simultaneously. In angiosperms one type of the endosperm develops this way.

A special case of the division is the endomitosis, when chromosomes segregate within the nucleus. By this mechanism haploid cells may develop into autodiploid homozygous cells.

3.5.1. Mitosis

It occurs in both diploid and haploid cells, partitioning the genetic material and the cytoplasm, and leading to the separation of the daughter cells. The process can be divided into phases.



Mitosis P= prophase, M= metaphase, A= anaphase, T= telophase, C= cytokinesis

In the **prophase** the doubled DNA strands are condensing. Before condensation, in interphase, they are 1-2 m in length. During transcription the DNA must be decondensed, to be accessible for the enzymes. In this state the DNA is less stainable, and forms the euchromatic region of the nucleus. The inactive, more condensed DNA is staining more intensively, and forms the heterochromatic region. During prophase the DNA has to be packed into chromosomes, which makes possible their transport to the poles. The process can be monitored easily by light microscopy, due to the staining of the DNA. At the beginning of the phase the thin chromosomes seem to form a reel, then they are shortened and thickened all the more the DNA is wound up. Before prophase the microtubules form a ring in the equatorial plane of the cell (preprophase band), which disappears by the end of the phase. This is characteristic of the plant cells, but its function is not exactly known. Even if higher plants lack centrioles, they have cytocenters, which organize microtubules at the poles of the cell. The cytoplasmic organelles are distributed into the two halves of the cell.

Between prophase and metaphase (in the **prometaphase**) the nuclear envelope is fragmented, and the forming vesicles are dispersed in the cytoplasm. The mitotic spindle consisting of microtubules is formed from the two cytocenters; the elongating microtubules grow toward the chromosomes or toward the antipodal cytocenters. The former ones move chromosomes into the equatorial plane by joining to the kinetochore in the centromere region of the chromosome.

During **metaphase** the chromosomes are aligned by the kinetochore fibers such a way that each chromosome is connected to both cytocenters, one kinetochore being connected to one of the centers. The disjunction of chromosomes is halted until these conditions are fulfilled. The chromosomes can be investigated at the very most in this

phase. Each chromosome consists of two sister chromatids, which are equal due to the doubling of the DNA in the S phase of the cell cycle.

In the **anaphase** the sister chromatids segregate, and move toward the poles. This is the result of their interaction with the kinetochore fibers.

In the t**elophase** the nuclear envelope is formed again around the decondensing chromosomes at the poles, partly from the fragments of the former envelope, and partly from the rough endoplasmic reticulum. The mitotic spindle is disassembled, although a part of it remains in the mid-zone. These fibers together with the joined actin filaments will move the pectin containing vesicles from the Golgi apparatus to the equatorial plane. This cytoskeletal-vesicular complex is termed phragmoplast.

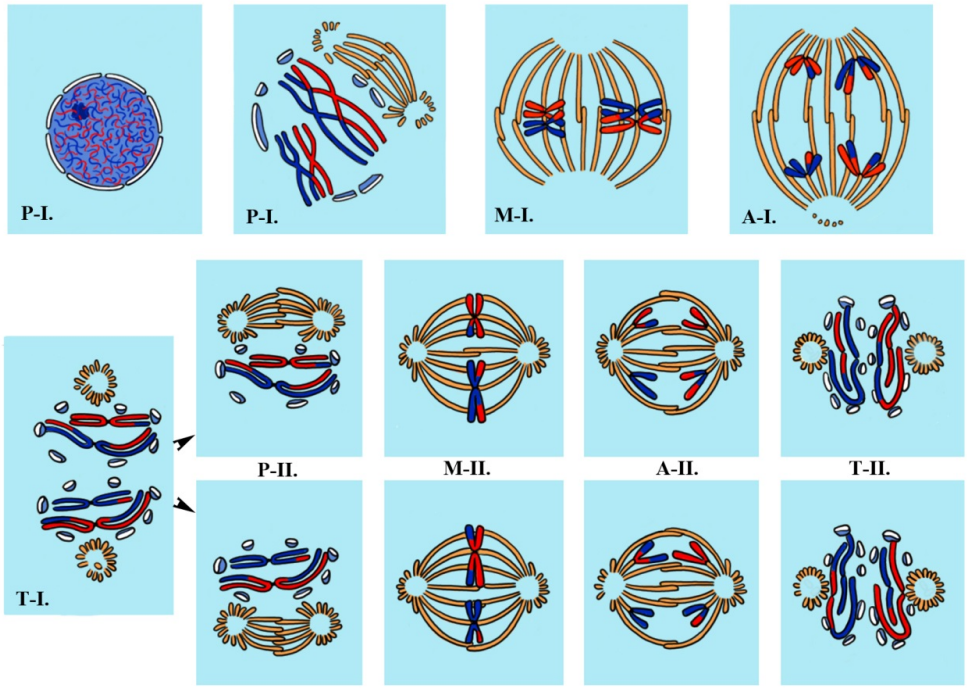
During **cytokinesis** the vesicles coalesce, their pectinic content will form the cell plate, while their membrane will yield the new cell membranes of the daughter cells. At certain points the fusion is not complete; here develop the plasmodesmata connecting the cells.

3.5.2. Meiosis

During meiosis four haploid cells originate from one diploid cell. The process involves two consecutive divisions, the second one being mitosis. The essential events belong to the first stage. Compared this to the mitosis, the important difference is that the paternal and maternal chromosomes are paired, and these will segregate, rather than the chromatids, during division. This way one daughter cell will receive either the paternal or the maternal variant of the chromosome. Before disjunction certain alleles are exchanged between the paired chromosomes by crossing over, which yields in recombination i.e. a limited mixing of the maternal and paternal properties. Apart from this the phases of the process are similar to those of mitosis, except prophase, which is longer and more complex (involving also pairing of chromosomes); therefore it is divided into further phases.

Meiosis I

The first stage of **prophase I** is **leptotene**, when the partially condensed chromosomes seem as thin threads with two chromatids. Paternal and maternal chromosomes are paired in the **zygotene** stage. Bivalents consisting of four chromatids are formed and are interconnected by special proteins, the **synaptonemal complex**. Chromosomes are further shortened and thickened in the **pachytene** stage. In the synaptonemal complex nodules are visible, which are probably enzyme complexes active in recombination. In the **diplotene** stage the connection between the paired chromosomes is loosened, although they remain coupled at several sites. These points are the **chiasmata**, the morphological appearance of **crossing over**. In the **diakinesis** stage the chiasmata are sliding toward the terminal parts of the chromosomes.



Meiosis P= prophase, M= metaphase, A= anaphase, T= telophase, I.= meiosis I., II.= meiosis II.

About the end of prophase I the nuclear envelope is disintegrated, which corresponds to the **prometaphase**. In **metaphase I** the bivalents are arranged into the equatorial plane, but the chromosomal fibers join either to paternal or maternal chromosomes, as these have one common kinetochore, rather than one per each chromatid. Consequently in **anaphase I** the parental chromosomes with two chromatids migrate toward the poles. Such a way the nuclei forming in **telophase** contain half as many chromosomes as the nucleus of the mother cell had. The two cells do not always separate, nuclei may undergo the second division without cytokinesis, and the partitioning may happen at the end. In case of the tetrasporic embryo sac development, cellularization commences after further mitotic divisions.

Meiosis II

During the second main stage of meiosis, the haploid daughter cells divide mitotically, i.e. the chromatids will segregate. Such a way four haploid cells will be formed, two-two of them being equal.

Chapter 4. PLANT TISSUES

(Éva Preininger)

According to the traditional concept, plant tissues are determined as aggregations of morphologically, ontogenetically and functionally similar cells. Nevertheless, today we use the term in a rather broad sense, i.e. for cells possibly of different shapes and function yet of the same origin. Earlier, this latter was the definition of the 'tissue system'. Plant tissues are classified based on various aspects. They are primarily grouped according to the stage of their development into meristems and differentiated tissues. Besides, on the grounds of their function we distinguish e.g. dividing, storage, conductive or secretory tissues. Composition of tissues may be simple or complex, the latter category including the dermal, the ground and the conductive tissue systems. The process through which tissue cells gain their final form and function is called differentiation.

4.1. Meristems

In plants, dividing, undifferentiated cells are called meristematic. They chiefly occur in clusters of various sizes comprising the meristems. The most important feature of meristematic cells is their capability of division. Initials (promeristems) retain their mitotic activity through the whole life of the plant. These cells are present already in the embryo, and later they divide continuously within the shoot tip and the root tip. The daughter cells produced by the meristems begin to differentiate. Meristematic cells are mostly isodiamteric in shape, bear dens cytoplasm and few, small vacuoles. Their plastids are proplastids and they possess primary cell wall.

Meristems are grouped according to different criteria, for instance 1) origin, 2) position, 3) angle of the cell division plane etc. Due to the limited length of the present material, classification based on the origin is reviewed here in details; further ones are just briefly discussed.

4.1.1. Classification of meristems according to their origin

Based on their origin, meristems are classified into promeristems, primary meristems and secondary meristems. Continuously dividing cells of the shoot tip and the root tip comprise the promeristem. Their function is to produce the cells of the primary meristems. Promeristem is composed of the initials and the quiescent centre. Actually, continuous division is the characteristic of the initials, thus all cells of the plant can be traced back to these cells. The number of the initials ranges from 1 to 20; higher number of initials being more secure is typical of the higher plants. These cells are of direct embryonic origin. They are present already in the globular stage, yet they become discernible in the heart-shaped embryo. In the mature embryo, the function of the initials (and the whole promeristem) is restricted to the plumule and the radicle. Later, they are present only in the shoot and the root tips of the mature plant. Surrounded by the initials is the quiescent centre (zone of central mother cells). These cells divide rather slowly, their mitotic cycle lasts for 200-400 hours. Their role is to preserve the genetic material within the promeristem. Cells of the promeristem are characteristically totipotent; they are also called the stem cells of the plants. (Some authors regard only the cells of the quiescent center as stem cells.)

Daughter cells produced by the division of the promeritematic cells comprise the primary meristems (or histogens) that give rise to the primary tissue systems. Cells of the primary meristems have determined faith, i.e. a cell of a certain primary meristem cannot change into another type. They are more differentiated than the cells of the promeristem, and are more heterogeneous from any aspects. Both their shape and their division plane vary depending on the primary tissue they produce. In the shoot tip, three different types of primary meristems are distinguished: the dermatogen (or protoderm) producing the epidermis, the ground meristem giving rise to the ground tissue system and the procambium that cuts off the vascular tissues. However, the root tip contains four different primary meristems: the dermatogen producing the rhizodermis, the periblem forming the primary cortex, the plerome giving rise to the stele and the calyptrogen that produces the calyptra.

Secondary meristems arise by the dedifferentiation of primary tissue cells. Such meristems are the vascular cambium responsible for the secondary thickening of the plant organs and the cork cambium (phellogen) producing the periderm (secondary dermal tissue). Nevertheless, this categorization is too general and not always accurate. For

example, certain strands of the vascular cambium are of primary, others of secondary origin (both in the root and the shoot); however, it is regarded as a secondary meristem. The formation of the cambium is discussed later in the chapter on the secondary thickening of the root and the shoot, while the cork cambium is presented in the paragraph on the periderm.

4.1.2. Classification of meristems according to position

On the grounds of their position, 1) apical, 2) lateral and 3) intercalary meristems are distinguished.

- Apical meristems are present in the shoot and the root tips.
- Lateral meristems are responsible for the thickening of vascular bundles of the root and the shoot.
- Intercalary meristems are interposed between differentiated tissues. They serve the elongation of certain organs being positioned in their basal region. For instance, their characteristic role is the extension of leaf petioles or the internodes.

4.1.3. Classification of meristems according to the cell division plane

As a quite different aspect, meristems can also be classified according to the angle of the cell division planes. This classification refers only to the meristems of the shoot tip, and not applied for the root tip. The apical zone of the shoot, being composed of the promeristem and certain cells of the primary meristems, is divided into the regions of the tunica and the corpus. The outer cell layers comprise the tunica, the cells of which divide anticlinally, i.e. with cell division planes perpendicular to the surface. Consequently, the walls between the cells are also perpendicular to the surface of the organ. Tunica chiefly contains a single cell layer, yet it may be composed of several (up to 8) cell rows. On the average, it consists of 1-3 layers. The region covered by the tunica is the corpus. Its cells divide both anticlinally and periclinally, thus they are easily discernible from those of the tunica.

4.2. Dermal tissue system

The surface of the plant is covered by the dermal tissue system. It principally protects the inner tissues if the plant, but also connects them to the outer world. A distinct outer cell layer giving rise to the later epidermis is well discernible already on the globular embryo.

4.2.1. Epidermis

Epidermis is a protective tissue, formed by the dermatogen or the protoderm. It covers the young stems and the generative organs. Epidermal cells are of diverse functions and various levels of differentiation.

Epidermal cells

Epidermal cells are the least differentiated cells of the epidermis. Their shapes depend on the plant organ they cover, thus they may be e.g. elongated (monocot leaves) or of sinuous cell wall (abaxial epidermis of dicot leaves). They usually contain no chloroplasts, only leucoplasts. They possess a large central vacuole. The outer surface of the epidermis is covered with the cuticle. Its main constituent, cutin is secreted from the epidermal cells into their outer and radial cell walls. Cuticle plays a significant role in the water household of the plant, thus its thickness varies depending on the humidity of the environment. Thick cuticle is the characteristic feature of xerophytes. Cutin consists of polyester derivatives of C14-18 hydroxy-fatty acids. The cuticle is multilayered. In the lower layers, cell wall constituents intermingle with those of the cuticle, whilst the upper layers compose the cuticle proper. Cuticle is often covered also with a hydrophobic layer of epicuticular waxes.

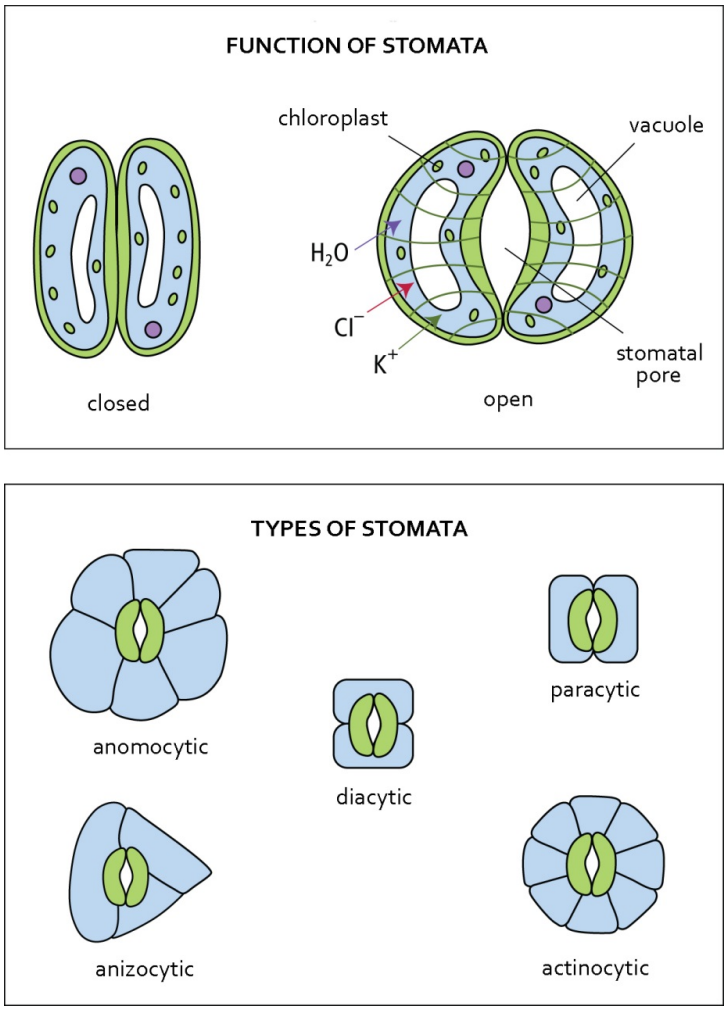
Stomata

Stomata are composed of the most differentiated cells of the epidermis. They serve the function of transpiration and the exchange of gases used in photosynthesis and respiration. The stomatal complex is the unity of the guard cells and the subsidiary cells. On the basis of their ontogeny three different types of stomata are recognized. In case of perigenous stomata, guard cells and subsidiary cells derive from different mother cells, because guard cells are produced by the equal division of a young epidermal cell. During the ontogeny of mesogenous stomata, the dermatogen cell divides unequally to produce a smaller daughter cell with dense cytoplasm and a larger, highly vacuolised cell. The latter give rise to the subsidiary cell, while the other divides equally into the guard cells. The development of the mesoperigenous stoma is the mixture of the previous two ontogenetic processes.

The shapes of the guard cells are manifold. They are mostly bean- or kidney-shaped, but for example in grasses (Poaceae) they resemble dumb-bells. They contain chloroplasts. Their cell wall is unevenly thickened: its inner region, adjacent to the stomatal pore is thicker and highly cutinized. The stomatal pore usually opens into a substomatal cavity within the ground tissue below the stoma. Guard cells open and close the stomatal pore with the aid of the surrounding cells, which movements are driven by the changing turgidity of the cells. When opening, the potassium- and sugar-content of the guard cells increase, what results osmotic water uptake and so the swelling of the cells. Owing to the uneven cell wall thickening, the swelling causes the opening of the stomatal pore. The process also requires the presence of radially oriented cellulose microfibrils. Closure is the result of the reverse processes. Subsidiary cells also play important roles in both the opening and the closure of the pore.

Different configurations of stomata

On the bases of the number and position of subsidiary cells, various types of stomata are distinguished. If the subsidiary cells cannot be distinguished from the ordinary epidermal cells, the stoma is called anomocytic. If two subsidiary cells are born in the complex, the stoma is either paracytic (the longitudinal axis of subsidiary cells is parallel with those of the guard cells) or diacytic (the longitudinal axis and the common wall of subsidiary cells is perpendicular to those of the guard cells). Besides, the stoma may be of tetracytic (four subsidiary cells, two of them in polar, the other ones in lateral position), anisocytic (three subsidiary cells, one being smaller or larger than the other ones) or any further types.



Function and different types of stomata

Plant hairs (trichomes)

Trichomes are unicellular or multicellular derivatives of the protoderm. The latter ones are initiated by an unequal division and derive from the smaller daughter cell called trichoblast. Trichomes may serve a variety of functions; they may form a pubescence on the surface or serve the function of secretion (glandular hairs).

Papillae are not individual structures, but the mere outgrowths of the epidermal cells that increasing the surface. Papillae cause for example the velvety touch of the petals. Real trichomes are protective structures against too intense transpiration, UV radiation, the chewing of herbivores etc. Their form and size are manifold. Bristle hairs are rigid structures protecting the stem against herbivores. Drought resistance is aided for instance by the squamiform hairs (silver berry) arranged parallel to the shoot surface, interlacing each other, or by the long candelabriform hairs (mullein) giving a felted cover of the shoot. Hooked trichomes (clinging hairs) fasten the plant on their support (hop).

Glandular hairs are epidermal secretory structures. The secreted material is often accumulated between the cell wall and the cuticle, and released when the cuticle ruptures. glandular trichomes are composed of a stalk and a head region, both may be uni- or multicellular. The cells of the glandular hair are connected to each other via several plasmodesmata. During intense secretion, the cells contain high amount of dictiosomes and ER. The secreted material is various (e.g. volatile oils, flavonoids etc.). Unique are the glandular hairs of the carnivorous plants being responsible for both prey attraction and digestion, since they also produce proteolytic enzymes.

Through the **hydatodes** water droplets are exuded, a phenomenon called guttation. The droplets are formed on the edge of the leaves, at the termination of the vascular bundles. Actually, hydatodes are permanently open stomata. Guttated water principally contains inorganic salts.

Salt and chalk glands are typical structures of salt resistant plants. In structure, they resemble the hydatodes. They serve the discharge of excess salt.

Nectaries, present usually on entomophilous species, produce a sugary solution to attract the insects. They are principally occur in the flowers (floral nectaries), but they are also found outside of flowers (extrafloral nectaries), e.g. on the stem or the leaf. The nectar secreted by the nectary contains various sugars and amino acids in high concentration.

Further cell types of the epidermis

Beside the above mentioned types, cells of further functions may also be present in the epidermis. Some examples are the silica cells causing the roughness of the grass leaves, the crystal containing idioblasts (*Ficus* leaf) or the bulliform cells of some xerophytes that cause the curling up of the leaves.

4.2.2. Rhizodermis

In contrast with the epidermis, rhizodermis contains no stomata and it is not covered by cuticle, either. Its unique feature is the presence of root hairs. Root hair is the outgrowth of a single rhizodermal cell. They occur in high frequency in the adsorptive zone of the root. Root hair derives from a trichoblast as a result of an unequal division. It contains a large vacuole; its cytoplasm and nucleus is superceded to the apical region of the outgrowth. Although it does not divide, its DNA replicates so the nucleus is polyploid. Root hairs live only for few days, they die off in 1-2 days due to mechanical damages.

4.2.3. Secondary and tertiary dermal tissues

As a result of secondary thickening, the epidermis, incapable of expanding with the increasing circumference, splits from the surface. Since the inner tissues should not remain unprotected, a secondary dermal tissue develops. The outermost cell layer of the cortical parenchyma, adjacent to the epidermis, regains its mitotic ability. This secondary meristem is the phellogen or cork cambium. The periclinal divisions of the phellogen cells produce the phellem (cork) toward the outside, and the phelloderm toward the cortex. If cells are cut off in both directions, the phellogen is bipleuric, whilst when only cork cells are produced outwards, the phellogen is called monopleuric. The unity of the three tissue layers (i.e. the phellem, the phellogen and the phelloderm respectively) comprise the secondary dermal tissue (periderm). In the cell walls of the phellem suberin is deposited, so these cells die off after a while and form some kind of insulating layer. Cork is often of several cell rows. Phelloderm consists of alive parenchymatic cells.

During the several-year-long thickening of the stem the established periderm is also sloughed away, and further parenchyma cells dedifferentiate into a cork cambium to produce a new periderm. Thus year-by-year, the phellogen is initiated in deeper and deeper layers and it gives rise to regular secondary dermal tissue till there is any cell layer left in the primary cortex. Afterwards, only phloem elements (phloem parenchyma cells) can dedifferentiate into the phellogen. From this very moment, phloem elements are also present in the produced dermal tissue, which is now called tertiary dermal tissue or rhytidome. Rhytidome is the characteristic surface tissue of perennial woody plants; it comprises the bark of the trees. Its outer layers are gradually sloughed away.

Among the suberised cells of the phellem comprising an impenetrable surface layer, clusters of living cells are formed to permit gas exchange and transpiration through the periderm. These protruding structures are the lenticels or cork warts being composed of loosely packed, living parenchyma cells. They are usually established above previous stomata. The shape, size and the density of lenticels are characteristic features of the plant species. Two main types are recognized, the *Sambucus* type lenticel that is filled homogeneously with parenchyma cells (filling tissue), and the *Gleditsia* type lenticel, when layers of the filling tissue alternate with closing layers of thick-walled cells. Closing layers are successively broken due to the tension of the filling tissue that is continuously produced by the phellogen.

The ontogeny of the secondary dermal tissue covering the roots is discussed below, in the chapter on the root.

4.3. Ground tissue system

Ground tissues are produced by the ground meristems. This tissue type comprises the majority of the plant body. Ground tissue system includes three cell typeys of different functions: parenchyma, collenchyma and sclerenchyma.

4.3.1. Parenchyma

Parenchyma cells are slightly differentiated cells, still being capable of dividing. Among certain circumstances they can dedifferentiate into dividing tissues (secondary meristems). Out of these cells the whole plant may be regenerated; this process is called redifferentiation. Parenchyma cells are characterized by complete plasticity. They are large, usually isodiamteric cells. Nevertheless, lobed or branched parenchyma cells also occur in some plants. Large central vacuole is also a typical feature of the parenchyma cell, thus its cytoplasm forms a thin layer adjacent to the cell wall. Its cell wall is composed of cellulose, mostly without any other deposited material. Its secondary cell wall is typically pitted, which indicates plasmodesmal connections between the neighboring cells.

Functional classification of parenchyma

Assimilatory parenchyma or chlorenchyma: parenchyma, containing chloroplasts, adapted for photosynthesis. Most typically, it constitutes the mesophyll of the leaf, yet it is also present in any other green plant organs (e.g. stems, unripe fruits).

Storage parenchyma: this tissue type is characteristic of storage organs, so it occurs principally in roots, rhizomes, bulbs, tubers, seeds or cotyledons. The accumulated compound is chiefly starch. Sugars may also be stored as sucrose accumulated in the vacuole, as in the sugar beet.

Proteins are stored in protein vacuoles; in seeds, they are present as solid aleurone grains. Lipids are accumulated in the elaioplasts or as lipid bodies in the cytoplasm.

Aerenchyma: The typical parenchyma of water plants and species living in moist habitats. It may occur in the root, stem and leaf as well. It has typically enlarged intercellular cavities, what is often due to the characteristically branched or lobed cell forms. It is of crucial importance for the oxygen supply and gas exchange of these plants.

Water storage parenchyma: The characteristic ground tissue of succulent plants living in arid habitats. This strategy of drought adaptation is achieved by storing the rare but periodically high precipitation either in the stem or in the leaves. Water is absorbed in the form of mucilage.

Secretory parenchyma: Plant secretion may occur both via external, epidermal structures (e.g. glandular trichomes) and within internal tissues. Internal secretion is served by specialized parenchyma cells, that sometimes observed individually or even in clusters. Secreted material gathers within internal cavities or secretory canals. The inner cavity may be formed lysigenously, that is the result of cell lysis (e.g. secretion of volatile oils in the pericarp of citrus species), or schizogenously, which means the separation of the cell walls along the middle lamella. In the latter case, the cavity is lined with epithel cells (e.g. resin ducts of pines). Sometimes secretory cells are scattered among other cell types. Often these cells also store the secreted material (e.g. tannin cells). Further characteristic secretory structures are the laticifers producing a fluid called latex. Laticifers may be articulated or nonarticulated.

4.3.2. Supporting or mechanical ground tissues

Collenchyma

Together with sclerenchyma, collenchyma belongs to supporting ground tissues. It is mostly found in leaves and stems. In leaves, it forms strands usually found above and below the midrib and within the petiole. In stems it forms a closed cylinder right beneath the epidermis or under the outer parenchyma layers. It is observed less frequently in roots. It is a characteristic supporting tissue of the dicots.

Collenchyma derives from the ground meristem, and differentiates usually from parenchyma cells. These cells are elongated and contain living cytoplasm. The long collenchyma cells are oriented parallel to the longitudinal axis of the organ. Their cell wall is composed of cellulose, hemicellulose and pectin. They typically contain a high

amount of pectin, the proportion of which component may reach up to 40%. This tissue type of high tearing resistance provides flexibility.

The cell walls of collenchyma cells is considerably but unevenly thickened. On the basis of the thickening pattern, 4 main types are distinguished, among which the first two ones are the most frequent ones:

- angular: cell walls are most intensely thickened at the corners
- lamellar: tangential cell walls are considerably, radial walls only slightly thickened (thus the thickened cell walls are visible as lamellar structures under the microscope)
- lacunar: cell walls adjacent to intercellular cavities are thickened
- annular: thickened cell walls are ring-like in cross section

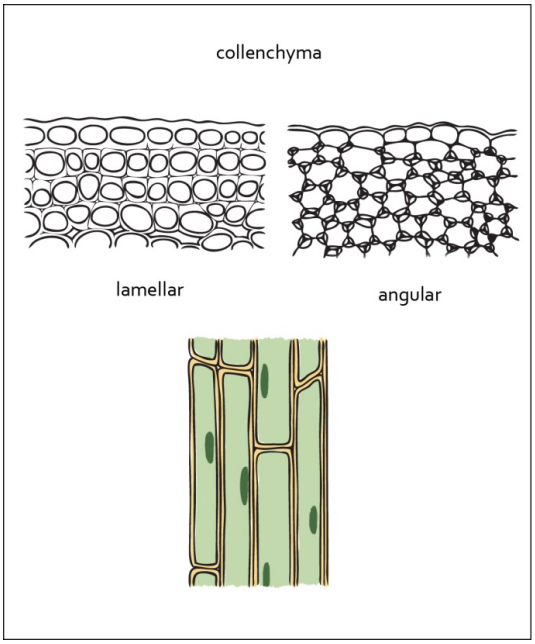
Sclerenchyma

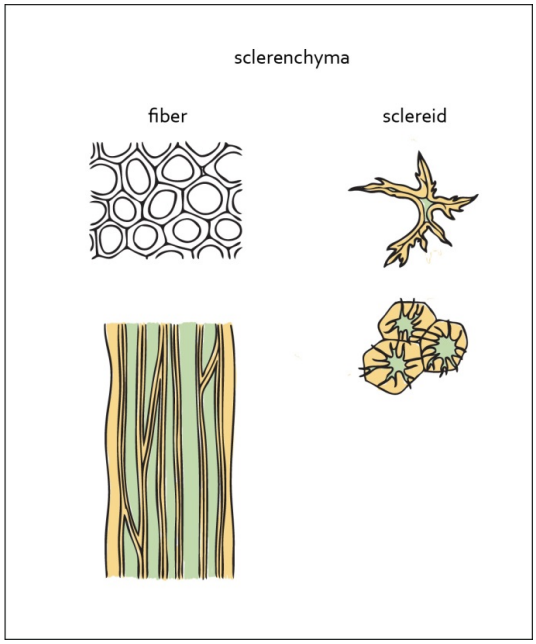
Sclerenchyma is another type of mechanical ground tissues. It is present in all parts of the plant. It is a long, elongated cell with admirably and evenly thickened cell wall. Into the walls lignin is deposited, what causes the death of the cells. Due to the composition and structure of the cell walls, sclerenchyma provides an inflexible support. These cells may occur individually, scattered among other tissues, but more typically they form strands. It is usually the derivative of parenchyma. Depending on its position, it may be produced by different meristems. Its two main types are the sclerenchyma fiber and the sclereid.

Sclereids are non-elongated, rather isodiametric cells. They occur scattered or in clusters, mostly embedded in ground tissues. These cells differentiate from parenchyma and have very thick cell walls. Certain sclereid types are named after their shape, e.g. brachisclereids or stone cells are round cells often present in the flesh of fruits. Asterosclereids are star-shaped cells occurring in leaves.

Sclerenchyma fibers are long, extended cells often with tapering ends. They possess rather small cell lumen and thick wall. Based on their position xilary fibers (within the xylem) and extraxylary fibers (outside the xylem) are distinguished. Xylary fibers develop among the xylem elements and derive from either the procambium or the cambium. Fibers located in any other position are called extraxylary fibers, e.g. the phloem fibers, that are also the products of the procambium or the cambium, but the hypodermal sclerenchyma layers, the sclerenchymatic vascular bundles and the sclerenchyma cap over the phloem are all consist of extraxylary fibers. Sclerenchyma fibers outside the vascular tissues originate from ground meristems.

Fibers of fiber crops (e.g. flax or hemp) are quite elongate, reaching a length up to several cm.





Supporting ground tissues (cross- and longitudinal section)

4.4. Vascular tissue system

In plants, long-distant transportation is provided by the xylem (water and ions taken up from the soil) and the phloem (principally organic nutrients).

Primary vascular elements derive from the procambium, while secondary vascular elements are produced by the cambium during the process of secondary thickening. For the first time, procambium gives rise to the protoxylem and the protophloem, later it cuts off the elements of the metaxylem and the metaphloem. Cambium of thickened organs produces exclusively meta elements. Proto elements are established during the elongation of the respective organ, so they are also capable of elongation for a certain period. That is why protophloem cells have typically thin cellulose walls, whilst protoxylem elements bear annular and spiral secondary cell wall thickenings enabling the extension.

4.4.1. Xylem

Xylem is composed of the tracheary (conducting) elements together with the associated parenchyma cells and fibers.

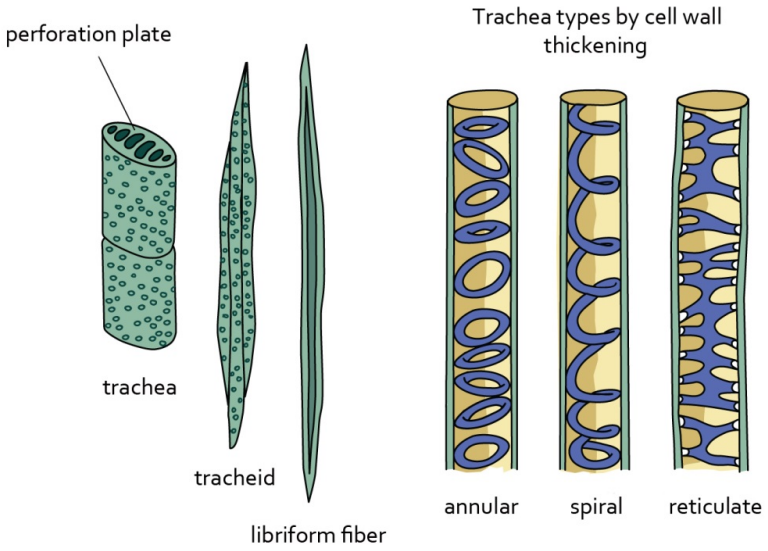
Tracheids Tracheids are the more ancient tracheary elements, the main water conductive cells of the pteridiophytes and the gymnosperms. They are elongate cells with tapering ends. Their cell walls characteristically bear spiral (pteridiophytes), pitted or bordered-pitted (gymnosperms) thickening. Water moves from cell to cell through the side walls.

Tracheas Tracheas are advanced water conductive elements, which occur typically in angiosperms being their main tracheary elements. Besides, they are also present in later gymnosperms (*Gnetophyta*) and even some pteridiophytes (*Selaginella*, ferns). These long, nonliving tubes develop from vessel elements by apoptosis. The oblique cell wall between the adjacent vessel members becomes partially or completely perforated; this is the perforation plate. If perforation is partial, various patterns are observed on the plate (e.g. reticulate, foraminate). The wall of the trachea is considerably thickened and lignified. Metaxylem elements have reticulate secondary walls. The characteristic thickening pattern, the thickness and the lignin content of the cell wall provide the vessel rigidity and make it resistant against the collapsing effect of the intense transpiration of the leaves.

Wood parenchyma Wood parenchyma cells are the sole living cells of the xylem. Their roles are storage (e.g. starch, crystals) and secretion (e.g. resin). Secondary xylem contains radially oriented parenchyma cells, as well, which comprise the rays.

Libriform fiber. Libriform fibers are elongate cells with thick, lignified cell walls. Their general features resemble to those of the sclerenchymatic cells. Their cell walls are pitted.

Fiber-tracheid Fiber-tracheids comprise a transitional state between tracheids and libriform fibers. In gymnosperms, the narrow-lumened and quite thick-walled tracheids of the latewood are regarded as fiber-tracheids. Their role is support.



Elements of the xylem

4.4.2. Phloem

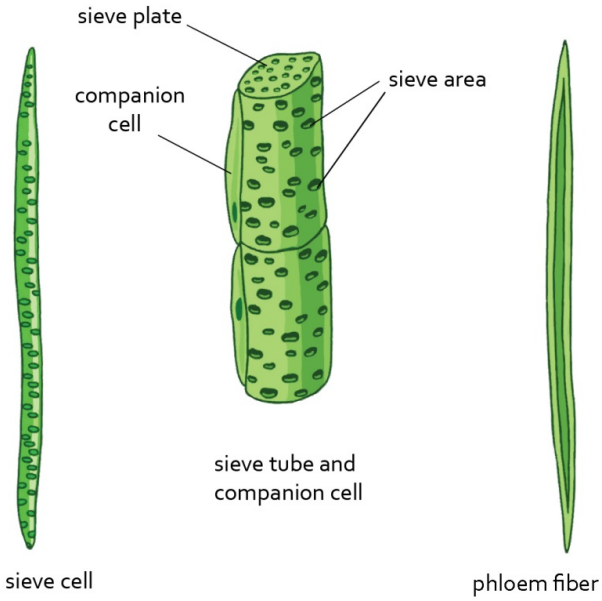
Phloem principally conducts sugars, yet a small amount of hormones and amino acids, as well. Moreover, plant viruses also move along in the phloem.

Sieve cell Similarly to tracheids, sieve cells are the sole conductive elements of the phloem of pteridiophytes and gymnosperms, but they are also present in angiosperms. They are living, elongated cells. They connect to each other via cytoplasmatic strands through the pits of the side walls. Pits constitute sieve areas on the lateral walls of the sieve cells.

Sieve tube Sieve tube parallels to the trachea of the xylem, both occurring only in angiosperms. It is a vessel consisting of a series of sieve-tube elements. The oblique cell wall between the adjacent elements is the sieve plate. Sieve plate is penetrated by pores, through which plasmodesmata connect the neighboring elements to each other. Differentiation of the pores begins with the formation of paired callose deposits around the plasmodesmata, on the two sides of the wall. Later, the cell wall degrades and callose lined pores remain on the place of the deposits. Through the pores strands of P-protein extends, which may even jam the pores. In non-functioning sieve tubes, pores are blocked by callose plugs. The sieve tube has unique plasma. In the course of time, the tonoplast breaks down and thus the vacuolar content mixes with the cytoplasm (mictoplasm). The nucleus degrades, as well.

Phloem parenchyma Concerning their function and position, phloem parenchyma cells resemble to the wood parenchyma. Additionally, they also take part in the formation of the tertiary dermal tissue, the rhytidome.

Phloem fibers Long cells with lignified cell walls, reminiscent of the libriform fibers. Industrial fibers (flax, hemp) are phloem fibers.



Elements of the phloem

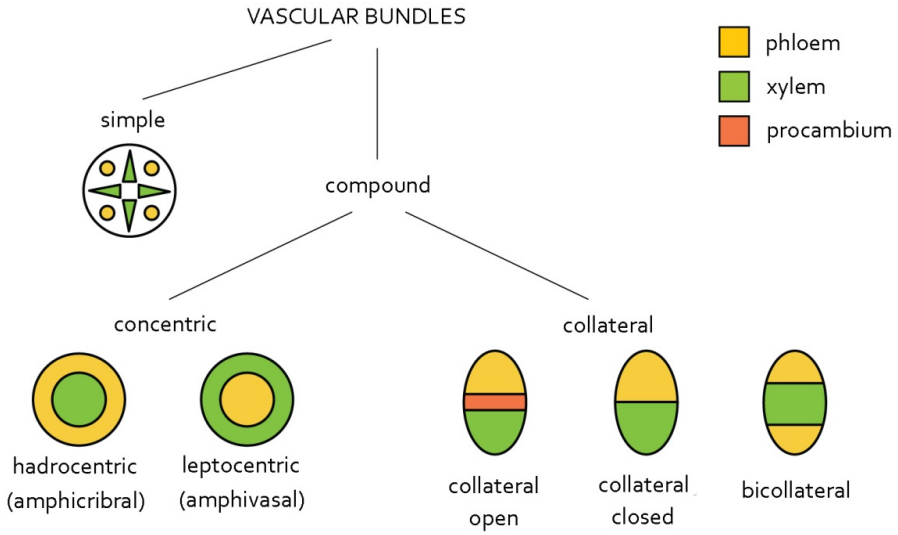
4.4.3. Vascular bundles

In the majority of plants, vascular elements cluster into bundles. Exceptional is the vascular tissue of the trees, where both xylem and phloem are arranged as close, concentric rings (xylem to the interior and phloem to the exterior of the stem). This arrangement is the consequence of the closed procambium cylinder in these stems.

Simple bundles: xylem and phloem elements constitute separate bundles. This is the characteristic bundle type of young roots.

Compound bundles: bundles are composed of both xylem and phloem elements.

- **Concentric**: xylem and phloem elements form concentric rings in cross section. In hadrocentric (amphicribral) bundles phloem surrounds the ring of the xylem (ferns). The leptocentric (amphivasal) bundle contains xylem and phloem elements in a reverse order (*Convallaria majalis*).
- **Collateral**: bundles containing xylem and phloem adjoining each other side by side, xylem facing to the centre of the organ, phloem facing outwards. In case of the collateral closed bundle, procambium completely differentiated into xylem or phloem, so no dividing cell remains in the bundle. This bundle is incapable of secondary thickening (monocots). Differentiation in collateral open bundles is not complete, thus a thin layer of dividing procambium remains between the xylem and the phloem. These bundles may take part in secondary thickening (dicots). In bicollateral bundles, phloem is set between two layers of xylems (*Cucurbitaceae*).

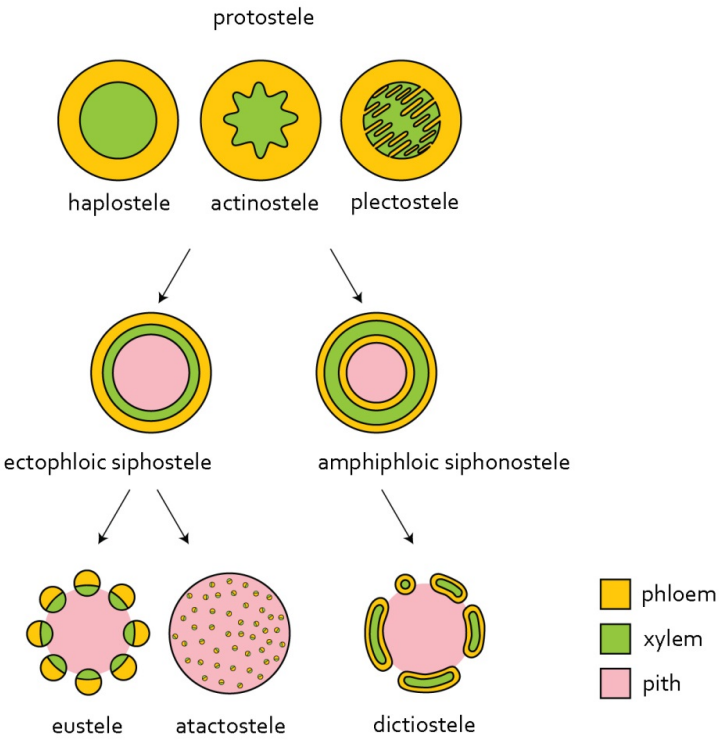


Types of vascular bundles

4.4.4. Different types of stele

The most ancient type is protostele. In the centre of the stem, vascular tissues form a compact cylinder; the phloem surrounds the interior xylem in a ring-like manner. According to the shape of the xylem in cross section, three subtypes are distinguished: halpostele (circular), actinostele (star-shaped) and plectostele (xylem forming plates).

With the appearance of the central pith, **siphonostele** evolved and the xylem also became ring-like in section. The siphonostele is called **amphiphloic** if the phloem is present both on the outside and the inside of the xylem, and it is ectophloic, if the phloem is only external. Dissecting of the siphonostele and thus the appearance of vascular bundles resulted from the evolution of the megaphyll. Splitting of the siphonostele gave rise to the **dictiostele**, whilst that separation of the **ectophloic siphonostele** led to the appearance of **eustele** and **atactostele**.



Different stele types

Chapter 5. PLANT ORGANS (ORGANOGRAPHY)

(Éva Preininger)

5.1. Root

Root provides the anchorage of the plant, as well as the adsorption of water and dissolved nutrients.

5.1.1. Longitudinal zonation pattern of the root

In longitudinal section, root can be separated into well discernible zones.

Root cap (calyptra) Its primary function is to protect the delicate apical region containing dividing cells. Besides, its outermost cell layer becomes slimy and is sloughed off, what eases the movement of the root within the soil. The mucigel is produced in the dictyosomes, and the decaying cells are continuously replaced. The third important function of the calyptra is enabling the geotropic growth of the root. Its youngest part is the inner axis called columella. These cells contain special amyloplasts (statoliths), which are interestingly always observed at the lower part of the cells. Statoliths serve as sensors.

Zone of cell division The promeristematic region of the root is within the root tip protected by the calyptra. As we mentioned previously, in the chapter on the meristems, in the centre of this zone is the quiescent center of slowly dividing cells surrounded by the initials. Mitoses of the latter cells produce the primary meristems called histogens. Primary meristems have determined positions, i.e. their position depends on the tissues they give rise to. Root contains four different primary meristems. The calyptra produces the root cap, the dermatogen gives rise to the rhizodermis (dicotyledonous plants have a common meristem called dermocalyptrogen, instead), the periblem differentiates into the primary cortex, and the plerome forms the stele.

Zone of elongation Above the meristematic zone of the root, discernible is a region with cells that do not divide but elongate. As a first step of differentiation, they lengthen considerably due to intense vacuolisation.

Zone of differentiated tissues Above the zone of elongation, differentiation of the derivatives of the primary meristems continues. So the main regions and tissue systems of the root become discernible here. This zone contains the primary tissues of the young root. For water is intensely absorbed here, in this region root hairs are born, as well (and so it is called the ‘zone of absorption’). Development and dying of the root hairs are continuous and acropetal: they are initiated close to the tip from young rhizodermal cells and within 1-2 days they decay in the uppermost area of the zone.

Zone of transportation and lateral root initiation After the decay of root hairs, above the zone of differentiated tissues, no water uptake occurs. The main functions of this region are transportation and storage. Lateral roots are also initiated here.

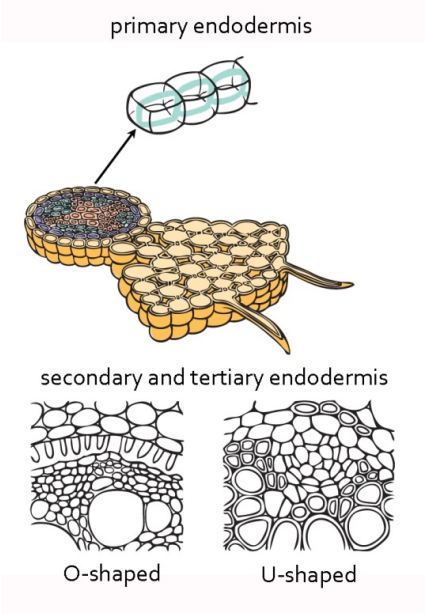
Zone of secondary thickening In plants undergoing secondary thickening, above the zone of transportation secondary tissues are produced by the cambium.

5.1.2. Primary tissues of the root

Primary tissues of the root are well discernible on cross sections made from the zone of absorbtion. It is covered by the **rhizodermis** discussed in details in the chapter on Plant tissues. A particular, rhizodermis-like structure is the multilayered velamen, which is the typical dermal tissue covering the aerial roots of epiphytic orchids. This envelope is also the derivative of the dermatogen. It consists of nonliving cells of suberised cell walls being capable of absorbing the condensed vapor out of the air.

The outermost layer of the cortex, adjacent to the rhizodermis, is the **exodermis**. It may consist of a single or several cell rows. It contains dead cells of suberised cell wall. The size, wall thickness and shape of these cells differ from those of the parenchyma cells underneath. As root hairs are continuously torn off due to friction and so the rhizodermis dies, exodermis becomes the outermost protective tissue of the root. Inner parts of the cortex are usually composed of storage parenchyma. In water plants, aerenchyma constitutes the primary cortex.

The innermost layer of the cortex is the **endodermis** that surrounds the stele takes part in transmitting the water absorbed by the root hairs into the vascular tissues. The zone of absorption contains primary or Casparian endodermis. Its thickness is a single cell row. In these cells a band-like suberin deposition is present in the second third of the radial walls. In this stripe, cell membrane (plasmalemma) closely attaches to the cell wall. Consequently, water that is transported apoplastically (i.e. intercellularly and within the cell walls) from the root hairs to the endodermis, here must cross the cell membrane to enter the stele. Since water passes through the membrane and enters the cell, water transport becomes symplastic and thus controllable here. Above the zone of differentiated tissues, suberin is also deposited in the tangential walls of the endodermal cells, so the cells have U- or O-shaped cell wall thickening. This blocks the transport through the cells. Consequently, endodermis completely isolates the primary cortex and the stele, which would cause the death of the stele. Nutrient exchange between the two regions is maintained via the passage cells interposed between the cells of O- and U-shaped thickenings. These cells remain in the primary endodermis condition. In plants of no secondary thickening (monocots), lignin is also deposited into the O- or U-shaped cell walls of the endodermal cells beside suberin.



Different types of endodermis

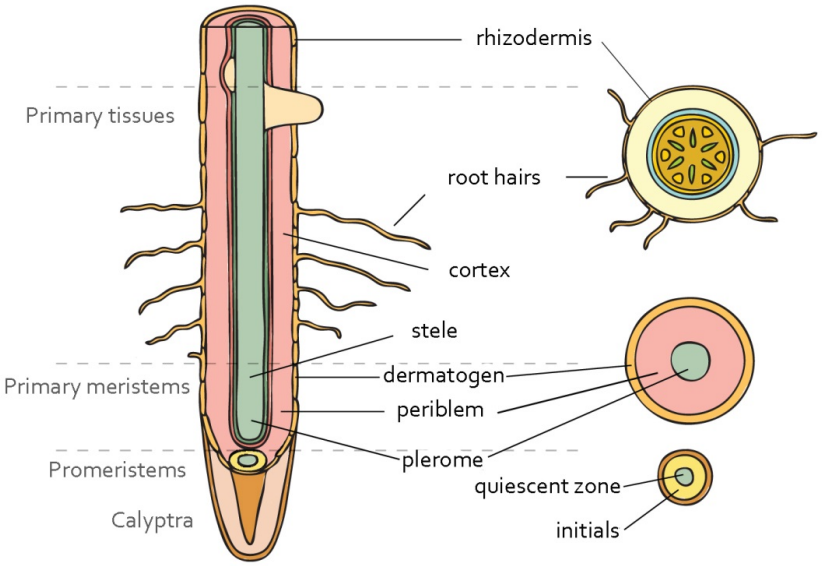
The outmost cell row of the stele is the **pericycle**. This layer of primary meristematic origin derives from the plerome. It maintains its mitotic capacity and has three main functions. 1: formation of the vascular cambium in the root during secondary thickening, 2: giving rise to the phellogen (cork cambium) producing the secondary dermal tissue in the same process and 3: initiation of lateral roots.

Vascular tissues of the root are clustered into simple bundles, that is, xylem and phloem elements group separately. Phloem and xylem bundles of equal number are arranged alternately, isolated from each other by parenchyma cells. Based on the number of xylem bundles, diarch, triarch, tetrarch, polyarch etc. roots are distinguished. Dicotyledonous plants possess oligarch (2-8), monocots bear polyarch (several bundles) roots. Xylem bundles extend into the center of the root, often adjoining each other. Pith tissue is principally observed in polyarch roots. Conductive elements of both the xylem and the phloem differentiate centripetally from the plerome, so both the xylem and the phloem is exarch. Firstly initiated protoelements face the pericycle within the bundles, while metaelements are on the inner side facing the axis of the stele.

Formation of lateral roots. Lateral roots are initiated by divisions of the pericycle cells, thus they are of endogenous origin. At the beginning, cells of the pericycle divide periclinally, then both periclinally and anticlinally to produce

a new root tip that entirely resembles the apical meristematic region of the taproot. For a certain period, the endodermis expands with the growth of the root primordium, yet later it ruptures and the growing lateral root breaks through the cortex and the epidermis, and then it emerges finally.

Modified roots are discussed in details in the chapter on Morphology.



Longitudinal zonation of the root and cross section of most important zones

5.1.3. Secondary thickening of the root

Secondary thickening of stem and root is characteristic in gymnosperms and angiosperms. Secondary xylem and phloem is cut off by a secondary meristem called vascular cambium. Actually, cambium is a meristem of heterogeneous origin. Its strands outside the xylem derive from the pericycle bearing meristematic activity also within the zone of differentiated tissues. These strands can be regarded as primary meristems. Nevertheless, cambial regions positioned between xylem and phloem bundles are composed of dedifferentiated parenchyma cells, what is the criterion of secondary meristems. Consequently, the vascular cambium of the root is wawy at the beginning. Subsequent to its initiation, cells of the cambium divide periclinally to produce secondary xylem outwards and secondary phloem toward the interior. At first, cambial regions around the phloem divide more intensely, thus the cambium becomes ring-shaped in cross section. The continuously dividing cylinder forms a contiguous secondary xylem inwards and a ring-like secondary phloem to the outside. Primary bundles are discernible for a while: xylem bundles in the centre of the root, whilst phloem bundles outside the secondary phloem. Owing to the thickening of the root, not only the rhizodermis, but also the whole cortex, as well as the endodermis ruptures and is sloughed off. A new protective tissue (the secondary and then the tertiary dermal tissue) develops. Phellogen producing the secondary dermal tissue (periderm) originates from the meristematic pericycle, which is now exposed on the surface. Its divisions form the cork tissue (phellem) to the outside and the phelloderm to the interior. Ontogeny of the tertiary dermal tissue is introduced in details in the chapter on Plant tissues.

5.2. Stem

Stem is the axis of the shoot. Its growth is provided by the meristems of the shoot tip. Structure and function of the shoot tip is discussed in details in the chapter on Plant tissues. Under the meristematic region, a zone of elongating cells is present also in the stem similarly to the root. Below the zone of elongation, daughter cells of the primary meristems differentiate into the respective tissue systems. Branching of the shoot, modified epigeous and hypogeous stems, as well as buds (undeveloped, embryonic form of the shoot) are introduced in the Morphology chapter. Leaf primordia and buds develop on the nodes of the shoot tip. At first they are quite alike, but after a while leaves become flattened and their apical growth ceases (determined lateral organ), whilst buds giving rise

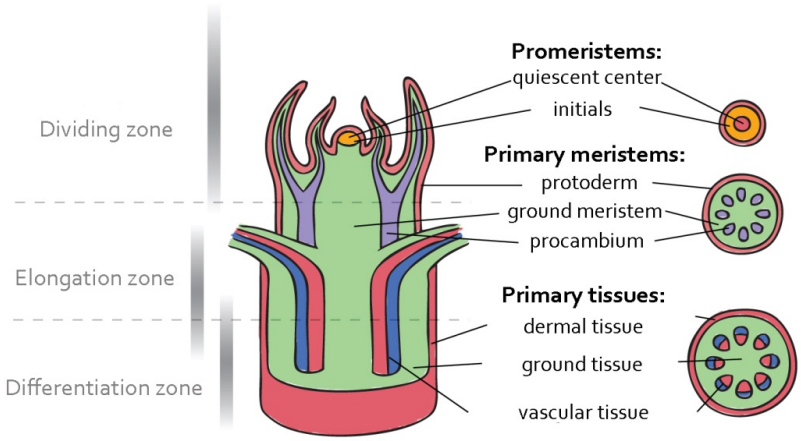
to lateral branches retain their radial symmetry and the activity of their apical meristems (indeterminate lateral organ). In the axil of each leaf a bud develops. Obviously, not all the buds give rise to mature stems. The elongation of the internodes is provided by intercalary meristems.

5.2.1. Primary tissues of the stem

Stem is covered by the **epidermis**. Its characteristic structures are the stomata, the trichomes and the glandular hairs (chapter Plant tissues). In contrast with the root, in the 'ordinary' stem the proportion of the cortex is lower than that of the stele. However, the two regions are not clearly discernible, because usually no borderline separates them from each other. **Primary cortex** consists of ground tissues, mostly parenchyma, but in young, green stems it is chlorenchyma. Besides, storage or secretory parenchyma (e.g. laticifers) may also occur here. Storage parenchyma is typical in hypogeous stems (bulb, rhizome, tuber etc.). The stem is supported by mechanical ground tissues. If this tissue forms a closed cylinder right beneath the epidermis, it is called **hypodermis**. In dicots it is principally collenchyma, yet rather sclerenchyma in monocots. Protrusions of ribbed stems contain strands of collenchyma or sclerenchyma. Discernible endodermis is just rarely present in the innermost cell layer of the cortex; it occurs only in hypogeous stems or in the shoot axis of aquatic plants. The primary cortex of some plants has an innermost layer of starch accumulating parenchyma cells; this is called **starch sheath**.

The **stele** is just rarely separated with an obvious borderline from the cortex. Unlike in roots, meristematic pericycle never occurs in the stem. If, however, the two regions are distinct, it is due to the presence of a multistratose sclerenchyma in the outermost layers of the stele. Vascular bundles of the stem are always compound. In angiosperms, they are collateral, being open in dicots and closed in monocots. In the majority of woody plants, vascular elements do not form any bundles but a continuous cylinder of xylem and another of phloem. Dicotyledonous stem has eustele, while that of the monocots bears atactostele. Bundles of the eustele are typically arranged in one, or rarely two rings, whilst those of the atactostele are scattered. Xylem elements of the stem differentiate centrifugally, thus protoxylem, produced first by the procambium, face the axis of the stem, so the xylem is endarch. In contrast, differentiation of phloem elements is centripetal (i.e. inside out), thus the youngest protophloem elements are in the outermost region of the phloem (exarch phloem). Metaxylem and metaphloem elements produced later are set in the central region of the bundle. In open bundles, meristematic procambium remains between the xylem and the phloem. In closed bundles, procambium completely differentiates into other tissues.

The inner, central region of the stele is the pith that consists of ground tissues. In plants with hollow stems, the pith tissue is torn to form a pith cavity.



Longitudinal zonation of the stem and cross section of most important zones

5.2.2. Secondary thickening of the stem

Development of the stem of perennial plants do not terminate when primary tissues are produced. This is the process of secondary thickening provided by the initiation and functioning of a secondary meristem, the cambium. Dicoty-

ledonous plants containing open collateral bundles are capable of thickening, because procambium remains in their bundles. The mitotic activity of the procambium does not cease, so its cells continuously divide. Cambium is a meristem of complex origin. Its strands within the bundles (fascicular cambium) are direct derivatives of the procambium. Fascicular regions are connected to each other via the stripes of interfascicular cambium, which originate from dedifferentiated parenchyma cells. Thus, cambium is observed as an uninterrupted ring in cross section. Consequently, fascicular cambium is considered as primary, interfascicular cambium as secondary meristem. Nevertheless, the complete cambium ring is regarded as a secondary meristem.

Similarly to those of the procambium, cambial cells are elongate, but unlike other meristematic cells they are highly vacuolated. Cambium consists of two types of meristematic cells: fusiform initials and ray initials. Periclinal divisions of fusiform initials cut off phloem elements to the outside and xylem elements inwards. The intensity of divisions is not the same in the two directions: always more xylem elements are produced than phloem constituents. Ray initials form the parenchyma cells comprising the rays. Rays are discussed in details in the chapter on “Secondary xylem”.

In plants with bundled vascular tissue, three main types of secondary thickening are distinguished. The first step of all the three different processes is the same, i.e. the formation of the continuous cambium ring.

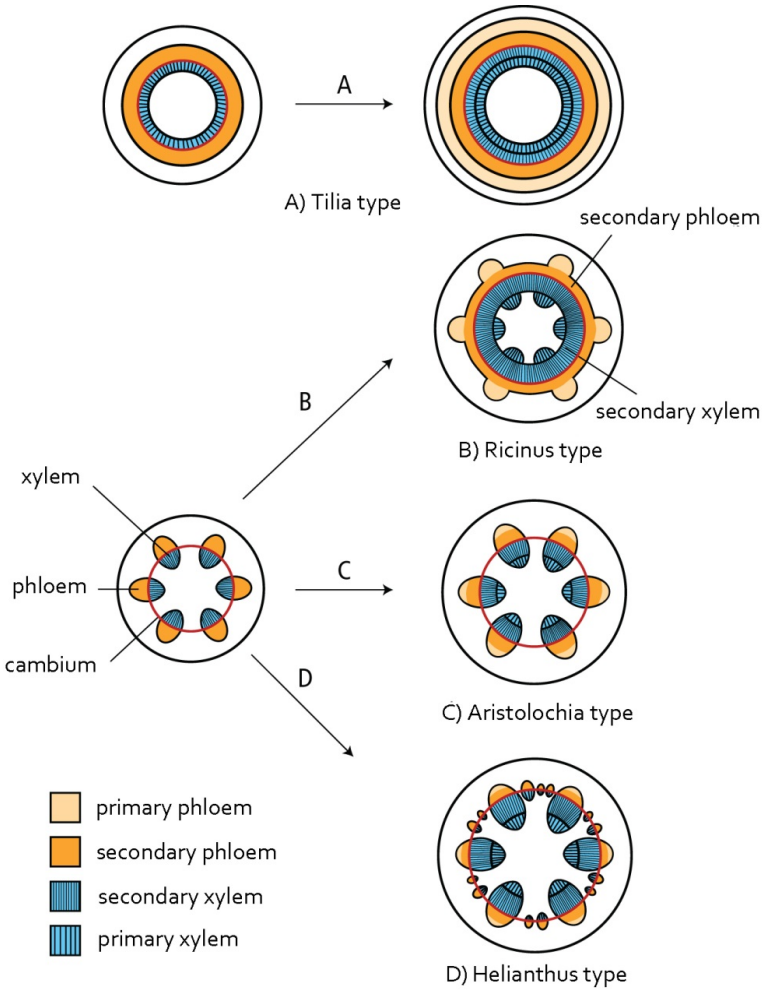
- In case of ***Ricinus*** **type** thickening, both fascicular and interfascicular cambium give rise to secondary vascular elements. Thus, the thickened stem contains uninterrupted rings of secondary xylem and secondary phloem. Original bundles are parted and their primary xylem is separated from the primary phloem.

- In the course of ***Aristolochia*** **(birthwort) type** thickening, fascicular cambium produces secondary vascular elements, while interfascicular strands cut off parenchyma cells. Thus, the bundled structure remains, together with the original number of bundles. Just the bundles enlarge continuously. Parenchyma cells formed by the interfascicular cambium comprise rays between the bundles. This type is also called ‘liana-type thickening’ being typical of the creeping and winding stems of lianas.

- In stems of ***Helianthus*** **(sunflower) type** thickening, fascicular cambium forms secondary vascular tissues, interfascicular cambium produces both vascular elements and parenchyma cells. New bundles appeare continuously between the original ones. Consequently, the thickened stem of sunflower contains bundles of various sizes. The largest ones are the original bundles bearing primary xylem and phloem elements on their edges, while secondary elements produced by the cambium are in the center of them. The youngest bundles are the smallest ones being composed merely of secondary xylem and secondary phloem.

To sum up, the three types differ in the function of the interfascicular cambium, i.e. whether it cuts off vascular elements, parenchyma cells or both.

- The fourth, ***Tilia*** **(lime) type** thickening, is the typical process of secondary thickening in woody plants. In these stems, procambium remains ring-like in cross section, so both primary xylem and primary phloem occur as continuous rings on the two sides of the procambium. Thus, the whole cambium is the direct derivative of the procambium and it resumes the meristematic function to produce uninterrupted rings of secondary xylem to the interior and secondary phloem outwards.



Secondary thickening of the stem

As a result of the secondary thickening of the stem, the primary dermal tissue (epidermis) tears off, and it is substituted by the secondary dermal tissue, the periderm. (This process is described in details in the chapter on Plant tissues.)

5.3. Secondary xylem (wood)

The secondary thickening of woody plants is provided by continuous divisions of the cambium – as we mentioned in the previous chapter. The stem of woods enlarges by *Tilia* or *Ricinus* type thickening. However, the two types cannot be distinguished after a while. Wood is the entirety of the secondary xylem produced by the cambium throughout the life of the tree and which accumulates till the death of the plant. Nevertheless, not the same is the faith of the secondary phloem formed outwards by the cambium. It does not include all the phloem elements produce during the life of the plant, for the outer, older parts continuously split, develop into the rhytidome and finally are sloughed away due to the intense dilatation growth. Thus, secondary phloem is only a thin stripe in the outer region of the woody stem containing only the youngest annual rings.

In the temperate climatic zone, cambium has a seasonal activity. In the vegetation period (spring and summer) it functions and produces xylem and phloem elements, yet it does not divide in autumn and winter. This activity results the formation of annual rings. Xylem elements cut off in spring comprise the earlywood onto which latewood is deposited during the summer. At the end of autumn, the cambium cease to divide and it stops to widen the respective annual ring. Thus, in a single year the wood is thickened with a stripe of earlywood and another of latewood. In next spring, the cambium begins to divide and a new earlywood starts to deposit onto the latewood of the previous year. Between them a distinct borderline is discernible. The presence of these borderlines makes the annual ringed structure discernible for the unaided eye. The width of tree rings is variable and depends on weather conditions.

Among extreme circumstances false rings may also be produced. The oldest tree rings are in the center of the wood, while the youngest ones are in the outermost region, adjacent to the cambium. Naturally, growth rings are also present in the secondary phloem, but they are less clearly visible.

The structure of the secondary wood is characterized by three different sections. In cross section, discernible are the annual rings and vascular elements are observed in cross section. The radial longitudinal section is made through the central axis of the wood. Vascular elements are visible in longitudinal section, perpendicular to the horizontal bands of the xylem rays. The plane of tangential longitudinal section is perpendicular to that of the radial section and it is tangential to the rings. Vascular elements are parallel to the plane, but rays appear in cross section as typical spindle-shaped structures.

Wood of angiosperms contains of all the xylem elements (trachea, tracheid, libriform fiber, xylem parenchyma) and it is called heteroxylous wood. However, gymnosperm wood is homoxylous, because tracheas and fibers are absent.

In the **heteroxylous wood** of certain trees, the diameters of the tracheas of the earlywood do not differ remarkably from those of the latewood, so no obvious dissimilarity occurs between the two stripes. These are the **diffuse-porous woods** (e.g. *Tilia*). In **ring-porous woods** (e.g. *Fraxinus*) tracheas produced in spring has a wider lumen and thinner walls due to the intense water uptake. In summer, the intensity of water uptake decreases, so tracheas of smaller lumen and thicker cell wall are cut off. Thus, large tracheas (‘pores’) of the earlywood are visible in concentric rings on the cross section; that is why this wood type is termed ‘ring-porous’.

Water is not conducted in all the annual rings of the wood, but only in the outermost, youngest rings. This functioning area consists usually of only 2-5 rings (less rings transport water in ring-porous woods). The water column in the rest of the rings is sooner-or-later broken, what means the cessation of water conduction. The surrounding parenchyma cells penetrate into the lumen of the tracheas through the pits of the cell walls and form balloon-like protrusions (tyloses) here, a phenomenon called tylosis. The emanating parenchymatic tyloses, being alive for a while, block the vessels so hindering further water transport. Tyloses finally die. Into the inner, non-functioning annual rings special meatabolites are deposited. These materials are produced, stored and transported here by the parenchyma cells. The special compounds (e.g. tannins, resin, pigments) imbue and impregnate the cell walls and color the inner tree rings, what is noticeable also to the naked eye. This inner, darker and more colorful area is the heartwood, while the outer, lighter ring is the sapwood. Heartwood is not conspicuous in all the trees. Woods with distinct heartwood do not decay in hollows, for they are more resistant to saprotrophic microorganisms owing to the impregnating compounds. These trees are more valuable, as well.

The majority of parenchyma cells of the secondary wood comprise the rays. Their main role is radial transportation and so the interconnection of the annual rings. Some of them are primary rays stretching through the whole secondary xylem and phloem. These are present also in stems of primary tissues, between the bundles, so they are produced by primary meristems. These primary parenchymatic strands are later extended by the ray initials of the cambium. Secondary rays are cut off by the cambium. They are much shorter than the primary ones and stretch through few annual rings. Homogenous rays are constituted only from ray parenchyma cells. Heterogenous rays contain other cell types (e.g. oblique resin ducts), as well.

From the industrial aspect, woods are divided into hardwoods and softwoods. Hardness of the wood depends on the lignin content of the cell walls. In hardwoods, high is the proportion of the highly lignified libriform fibers (e.g. oak). Obviously, the wood of gymnosperms is soft, but some heteroxylous woods are also considered as softwood (e.g. poplar).

5.4. Leaf

5.4.1. Ontogeny of the leaf

Leaves are initiated as primordia in the shoot tip, at the height of the procambium. Leaf is an organ of exogenous origin: it derives from the outer cells of the corpus and those of the tunica. At the beginning, periclinal divisions produce a small, cylindrical protrusion by apical growth. However, apical divisions cease soon, thus the growth of leaf is determined. Then the primordium flattens and several meristems occurring only in the leaf continue the elaboration of the organ. Marginal meristem produces the adaxial and abaxial epidermises, while submarginal

meristem gives rise to the ground tissues of the leaf (mesophyll). The vascular tissue system is the derivative of the procambium. At first the midrib is produced, and then with the further expansion of the leaf do the lateral veins of the dicots and the parallel veins of monocots develop. The petiole of the dicotyledonous leaf is formed by intercalary meristem, but an intercalary meristem is present at the leaf base of grasses, as well.

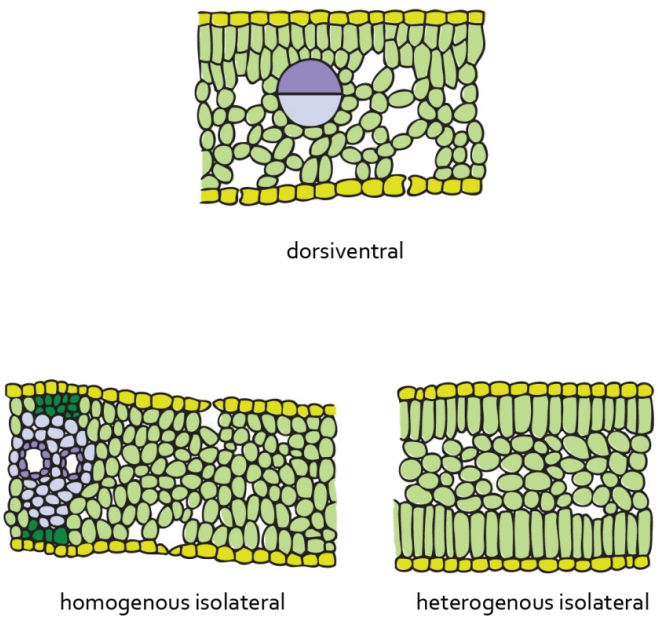
In case of the megaphylls of horsetails, ferns, gymnosperms and angiosperms the vascular tissue of the stem departs into the leaf. However, the vascular tissues of microphylls of lower plants simply connects to those of the stem. As a consequence, the continuous stele of the stem bearing megaphylls is separated into bundles that run into the leaves. Moreover, above the departing leaf traces the continuity of the vascular cylinder is disrupted by a small opening, the leaf gap. The gap is filled with parenchyma cells. In the leaf trace, the (originally interior) xylem is adaxial and the (previously exterior) phloem becomes abaxial in position.

5.4.2. Leaf anatomy

The leaf is covered by epidermis. Between the epidermises are the vascular bundles (nerves) embedded in the ground tissues (mesophyll) of the leaf. The usually unilayered epidermis rarely may consist of several (2-6) cell rows. In this case, even the protoderm is multistratose. Stomata may be born on both sides of the leaf (amphistomatous) or only on one of them (epistomatous or hypostomatous).

Leaves are classified according to several aspects. One of these is the symmetry of the mesophyll. Most dicots have dorsiventral leaves containing two types of parenchyma. On the adaxial side these leaves contain elongate, columnar cells rich in chloroplasts (palisade parenchyma), while on the abaxial side spongy parenchyma occurs. The structure of isolateral leaf is symmetric. In one subtype, the interior of the leaf is filled with a single cell type resembling that of the spongy parenchyma. This homogenous isolateral leaf is the common type of the monocots. Below both epidermises of the heterogeneous isolateral leaf palisade parenchyma is observed and the interior is filled with spongy parenchyma.

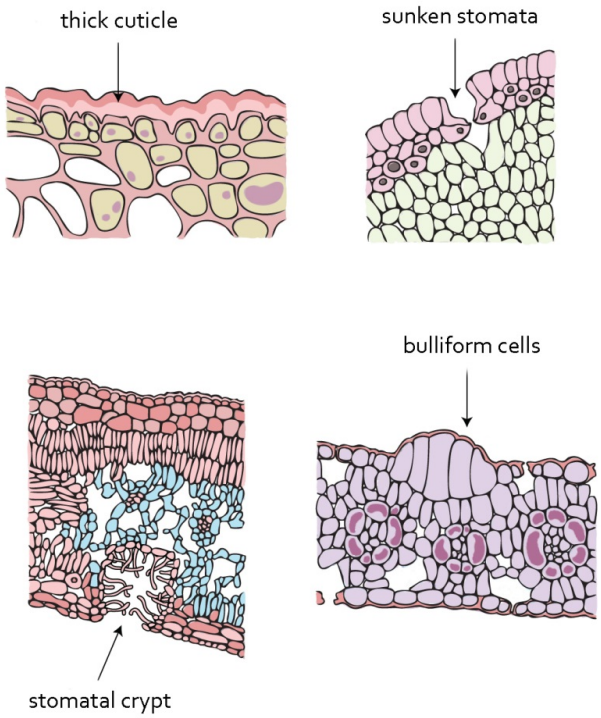
Another way of classification is based on the epidermal tissues covering the leaf. Leaf types of this system can be related to each other concerning their evolution. The most ancient type is the bifacial leaf of dicots, which possess an upper epidermis above the palisade and a distinct lower epidermis over the spongy parenchyma. This gave rise to the quite rare inverse bifacial leaf, in which the two epidermises are in the reverse position. From the inverse bifacial leaf derive the unifacial type that is covered only by a uniform, lower epidermis. This is achieved by the folding of the leaf margins towards the upper side that results the disappearance of the adaxial epidermis. One subtype is the cylindrical or radial unifacial leaf (e.g. onion), the other is the flattened ensiform unifacial leaf (*Iris*) that develops with the compression of the previous subtype. In the outer region of the cylindrical leaf, adjacent to the epidermis palisade parenchyma occurs and the interior is filled with the spongy parenchyma. Bundles are arranged like in the stem, i.e. with their xylem facing inwards. The unique feature of the ensiform unifacial leaf is the fact that bundles are not in the same orientation. They may form two rows facing each other, or a single row with bundles in alternating orientation. Equifacial leaf derives from the bifacial one. The needles of most pines belong to this category. Its structure resembles rather that of the stem: its two surfaces are covered by identical epidermises and the mesophyll is also the same on the two sides, as well. The central region containing the vascular bundles is separated from the parenchymatic outer region by endodermis.



Classification of leaves by the symmetry of the mesophyll

5.4.3. Leaf and environment

The morphology and anatomy of the leaf is considerably influenced by environmental factors, principally light intensity (sun leaves and shade leaves) and the available amount of water. Here we discuss the consequences of various water supplies in details. Among balanced water conditions mesomorphic leaves develop. Hygrophytes living in moist or marshy habitats have thin hygromorphic leaves with loosely packed mesophyll cells. They are usually shade-tolerant plants, as well. Water plants are called hydromorphic. Natant leaves floating on the water surface are thick and bear aerenchymatic spongy parenchyma. They are often supported by sclereids. Stomata are born on the adaxial surface and they elevate from the plane of the epidermis. In contrast, submersed leaves are remarkably thin. They possess no stomata, and their epidermal cells often contain chloroplasts. Their vascular and supporting tissues are less developed. Drought-resistant plants are termed xerophytes. The main strategy of these plants is to minimize the intensity of transpiration. Their leaves are often of restricted surface area. Stomata are sunken, sometimes set in deep, cavern-like cavities called stomatal crypts. Leave surface is covered with thick cuticle, sometimes also with a wax layer and often bears trichomes. The supporting tissue is well-developed. Succulent plants have a quite dissimilar strategy to survive drought periods: they accumulate water within their tissues. Some species store the moisture in the leaves (e.g. houseleek, stonecrop) others in the stem (cacti). Water is absorbed as mucilage.



Strategies of drought tolerant plants

5.4.4. Abscission

Perennial, deciduous plants drop their leaves each year, at the end of the vegetation period, in autumn. Evergreens also abscise their leaves, yet continuously, throughout the whole year and never at the same time. Prior to abscission, leaves undergo the process of ageing (senescence). The decrease of photosynthetic activity coincides with other metabolic changes, like the remarkable decrease of protein, RNA and carbohydrate content as a result of catabolic processes. Finally, due to the degradation of chlorophyll and the presence of carotenoids the leaves turn yellow. Breakdown products are quickly withdrawn from the leaf. Senescence is a process of hormonal control. It is accelerated by abscisic acid and chiefly ethylene, but it is impeded by gibberelin, cytokinin and principally auxin.

At the base of the petiole, a multistratose abscission zone develops. In the proximal layers cells begin to enlarge, what exerts pressure on the outer cell rows. In the distal region cell wall decaying enzymes are synthesized and a separation layer forms. Finally, the distal portion of the petiole detaches from the proximal one along the separation layer, and the leaf drops. The walls of the lower cells are impregnated with suberin and they comprise a protective barrier.

Chapter 6. Anatomy and reproduction of lower plants

(Pál Vági)

6.1. Mosses

The mosses form a paraphyletic group but they share some common features:

-The dominant generation is the gametophyte and it usually bears the developing sporophyte.

-They lack of real tissues but the leafy mosses differentiate certain cell groups which perform different tasks.

-The regulation of water supply is very feeble, it strongly depends on their environment; sexual reproduction occurs only in humid areas.

Their three main groups are:

6.1.1. Hornworts (Anthocerophyta)

The multistratose and homogen gametophyte gives place to nitrogen-fixing cyanobacteria. It is stabilized by rhizoids. Asexual reproduction is carried out by exfoliated thallus particles and gemmae.

The sex organs are located inside the gametophyte and the biflagellate sperms become released by the opening of the surface. Usually the gametophyte is monoicious.

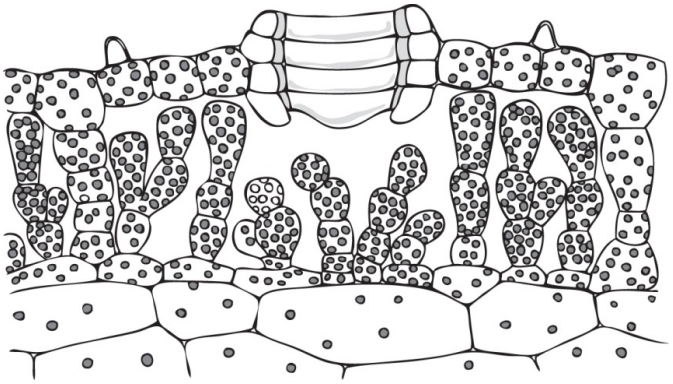
The development of the sporophyte starts in the female sex organ than it breaks through its calyptra-like apical part. The sporophyte forms a cylindrical capsule which has a multistratose, photosynthesizing wall. The surface bears stomata and a columella extends inside surrounded by developing spores and pseudoelaters. The pseudoelaters are haploids and they help the spore dispersal by their hygroscopic movement. The capsule dehisces longitudinally at the top and it grows continuously by a meristem located at the base. The foot which is the widened, basal part of the capsule is anchored to the gametophyte. Under adequate circumstances an intercalary meristem above the foot replaces the apical, degenerating part of the capsule.

Laminate gametophyte of hornworts bearing developing, cylindrical sporophytes

6.1.2. Liverworts (Hepatophyta)

Simple thalloid liverworts

The morphology of thalloid liverworts will be presented by the Marchantia genus. The gametophyte is a ribbon-shaped, dichotomous, relatively differentiated thallus. The upper surface of the plant is divided into polygonal air chambers with each one having a pore. The surface is covered by cuticle which inhibits the water uptake. The arch height of the chambers changes with the water content of the cells: water loss results in the closing of the cruciform cuticle pore; when the chamber bulks, the gap widens. The bottom and the sides of the air chambers contain assimilative cells and under them reserving parenchyma cells form a layer containing a few plastids.



Cross section of the gametophyte of thalloid liverworts with an air chamber near to the surface

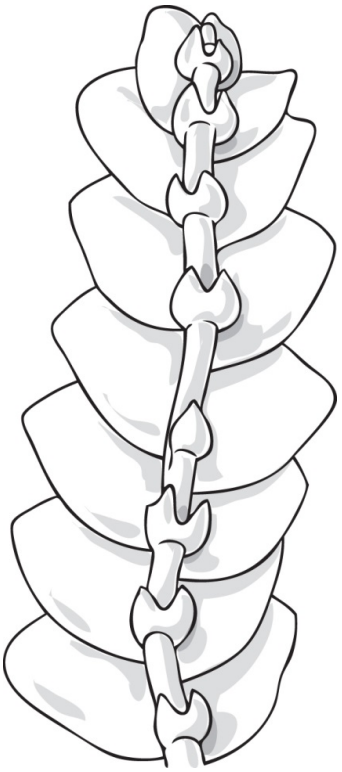
Rhizoids develop on the ventral side of the thallus; they either have simple or pitted cell wall. The rhizoids with simple cell wall penetrate into the soil and stabilize the thallus, the pitted rhizoids create a parallel jacket on the

underside. These parallel rhizoids are fixed by the ventral scales and together they conduct the water based on capillary force through the underside of the thallus. The gametophyte of the liverworts is able to reproduce asexually by gemmae which develop in gemma cups on the uppermost layer of the thallus. The lenticular gemmae are connected to the thallus by a short stalk. When the cups are filled with water the gemmae are washed out or water drops spread them even to a distance of one meter far. Each gemma has two apices which results in a bipolar growth. Marchantia liverworts are dioecious; the male and female sex organs appear on separate plants. The sex organs are situated on gametangiophor which are column-like emersions from the ventral side of the thallus. The male antheridiophor has a shape of an inverted umbrella and the female archegoniophor is similar to a palm tree. The antheridia sink into chambers on the upper side of the antheridiophor with the oldest ones at the bottom and the latest ones on the sides. When water is collected on the surface of the gametangiophor the sperms are able to leave the chamber through a pore. The archegonia are situated at the base of the archegoniophor lobes and are covered by sterile filaments. The necks of the bottle-shaped archegonia contain six rows of cells and each archegonium is opened by a pore toward the ground. The relatively big distance between the two sex organs presumes that the sperms are long-lived and they approach the archegonia by swimming in a liquid film on the surface of the thallus or through the spraying effect of water drops.

Gametophyte of Marchantia liverworts with emerging female gametangiophors; sporophyte with developing and already opened capsule; spores dispersed by elaters

Leafy liverworts

The gametophyte is dorsi-ventral with a hyaline axis and two rows of unistratose leaves; a ventral row of leaves are also common (amphigastria) but these underleaves are different in shape and size. On the ventral side of the shoot rhizoids can appear with simple cell wall. In rare cases the shoot is upstanding showing radial symmetry and isophylly. The leaves lack of veins and supporting tissues. The absence of cuticle gives rise to a water uptake throughout the whole plant body and the flattened thallus and the overlapping leaves also help to reserve humidity. Vegetative reproduction can happen by exfoliated leaves and gemmae.



Ventral view of leafy liverworts showing the underleaves

The leafy liverworts are dioicious and morphological differences can be observed between the two sexes. The antheridia are bud or cone-like structures which appear at the leaf base on the lateral branches. The thin-stalked antheridium produces many biflagellate sperms. Under adequate circumstances the jacket cells of the mature antheridium disintegrate and turn back toward the stalk. The released sperms reach the archegonia actively by swimming in a liquid film layer.

The archegonia are developed from the apical cells of the lateral branches thus the growth of these branches are limited. The neck of the bottle-shaped archegonium contains five rows of cells which form a canal. After fertilization the surrounding leaves enlarge and form a special structure called perichaetium. One side branch can bear 8-10 archegonia and most of them become fertilized but usually only one sporophyte develops from one perichaetium.

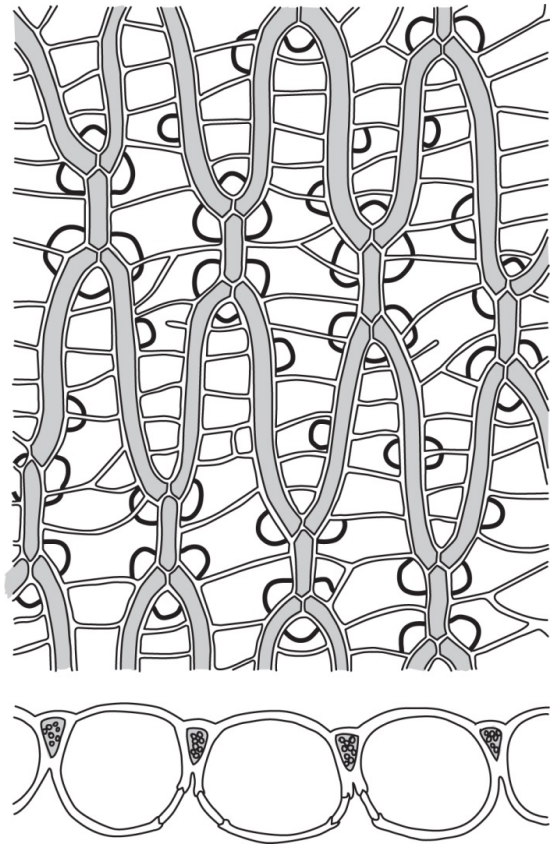
The partially autotrophic sporophyte is capable of photosynthesis. The foot of the sporophyte is anchored into the calyptra which is formed by the archegonium and is surrounded by the leaves of the perichaetium. The sporophyte has a stalk (seta) which is short and dense and a capsule where spores and elaters are formed under a 2-4 cell layers thick jacket. During maturation the seta elongates about 40-50 fold and raises the capsule above the perichaetium. The capsule dehisces along 4 longitudinal lines where the cells have thinner walls. By their hygroscopic movement the elaters help to disrupt the aggregated spores. In some cases the spores go under division before dispersal; when they reach the soil a spherical thallus is formed than a tetrahedral apical cell develops the axis. The morphology of the prothallus is very much diverse among the leafy liverworts.

Bryophyta

6.1.3. Peat mosses (Sphagnopsida)

The gametophyte is very characteristic with a quite complex branching system. The upstanding main axis has unlimited growth by a triangular apical cell. At the top the short lateral branches are closely packed and create a head (capitulum). The main axis bears two kinds of side branches: one is hanging down and attached to the stem, the other is protruding and connected to other plants. Therefore the mosses create a continuous layer which has an outstanding water-retaining capacity. The peat mosses lack of rhizoids, the underside of the main axis constantly dies away. The water uptake happens throughout the whole plant body. In the stem a central cylinder-like part can

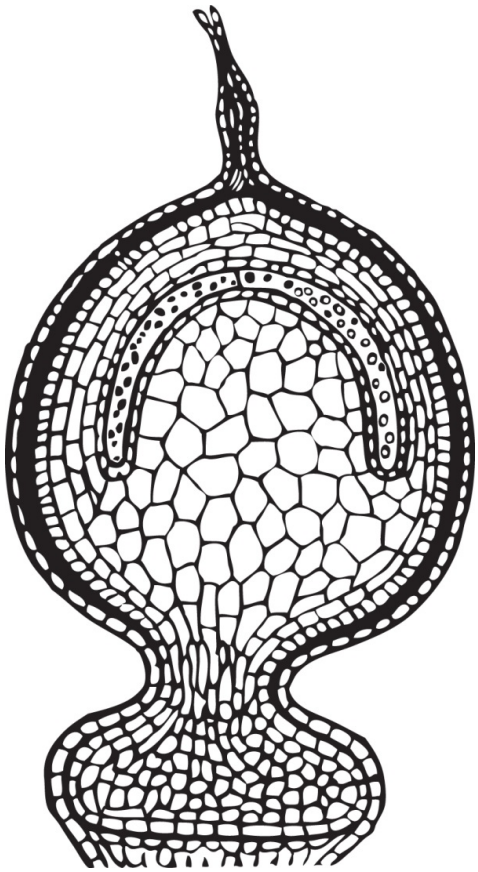
be distinguished containing cells with thick walls and it is surrounded by a cortex made up of 4-5 rows of hyaline cells. These cortical cells function as water storages. The central cylinder is unlikely to conduct water; it is more feasible that passive water transport is carried out by a capillary system which is evolved on the surface of the plant and between the mosses. The leaves initially contain uniform cells which later transform into either barrel-shaped, dead hyalines or narrow, green, photosynthesizing cells. Pores with thickened edge are located on the wall of the hyalines and the cells have annular secondary wall thickenings to expand their inner surfaces. These cells are able to store water in quantity. The few assimilative cells give a characteristic light green color to the peat mosses.



Plan view and cross section of assimilative and hyalin cells from peat mosses

There are mono- and dioicious peat mosses. The reddish or purple antheridia are developed in the axils of the leaves on the side branches near to the capitulum. Leaves cover the antheridia like in the case of the leafy liverworts. The sperms are biflagellate. The archegonia appear in the middle of the capitulum on short lateral branches whose growth become limited and similarly to the male sex organs covering leaves can be observed. The female gametangia have a stalk and are bottle-shaped; the neck contains 5-6 rows of cells. During maturation 8-9 canal cells degenerate in the archegonium.

The archegonium stays on the sporophyte as a calyptra until the spores mature. The sporophyte is anchored to the gametophyte by a haustorium-like foot. The seta is very short; the capsule differentiates into an endothecium and an amphithecium early in the ontogeny. The endothecium rises up as an arch and forms the columella. The 4-5 inner layers of the amphithecium develop a sporogenous tissue, the outer sterile cells form the capsule wall covered by the epidermis. No sterile cells and elaters are produced among the spores. When the spores mature a pseudopodium - a stalk of gametophyte origin - heighten the sporophyte. During maturation the wall of the spores and the capsule itself get pigmented and the capsule wall becomes dehydrated. The shedding is a bursting-like process triggered by inner pressure. The apical part of the capsule contains cells with thin walls in a ring called annulus. The capsule dehisces along this line and the apical lid or operculum loudly comes off spreading the spores even to a distance of 15-20 cm far. The spores develop either a filamentous prothallus or a flattened unistratose disc but both of them form only one gametophyte.

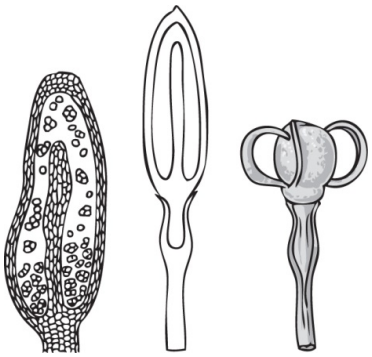


Developing sporophyte of peat mosses: short seta, columella and sporogenous tissue inside the calyptra

6.1.4. Granite mosses (Andreaeopsida)

The granite mosses are dark green, dichotomous mosses with rhizoids. The leaves lack of main veins and are arranged into three overlapping rows. The leaf cells accumulate oils. The stem lacks of central cylinder, the cells have thick secondary walls. There are mono- and dioicious granite mosses and the sex organs appear on separate branches on the former ones. The stalked antheridia are elongated and finger-like, the archegonia are bottle-shaped.

The absorbing foot of the sporophyte intrudes into the gametophytic tissue. The sporogenous tissue is developed from the outer layer of the endothecium, the remaining tissue creates the columella; no gap appears between the capsule wall and the columella. The wall contains 4-5 cell layers and they form a photosynthetic tissue. During spore maturation the capsule wall become thickened except four longitudinal lines. The capsule dehisces along them and the evolving four lobes stays connected to each other at the top thus the operculum and the peristome are absent. The capsule is raised by the gametophytic pseudopodium because the stalk of the sporophyte is extremely short. It is common that the spores germinate before dispersal; they develop a ribbon-like or flat prothallus where several buds form the gametophytes.



Longitudinal section of the sporophyte of granite mosses; view of a dehiscing sporophyte

6.1.5. True mosses (Bryopsida)

Most of the protonemas of true mosses are branching and filamentous. The apical growth results in a prothallus which could cover a surface of even 30 cm diameter. The prothallus develops partially under the soil surface; the undersoil parts become brown and the upper segments are green, the plastids are lenticular. Many leafy buds appear on the prothallus and they form many gametophytes. During the long life of the photosynthetic protonema several plants can develop. The gametophytes use the prothalloid filaments for absorbing nutrients but later transparent or brown rhizoids appear at the bottom of the axis. Usually three layers can be distinguished in the stem: an outermost dermal layer followed by a dense cortex and an innermost, thin central cylinder. In the Polytrichum genus and related genera the central cylinder is formed by dead hydroids and living leptoids similar to phloem elements. The cross walls of the leptoids contain plasmodesmata; the nucleus eventually vanishes from these cells. Water transport in the central cylinder was demonstrated in some mosses but it is always supplemented by the fluid movement evolved on the surface of the plant. The central cylinder and the main veins of the leaves are connected but no transport was detected. The main water source is the rain adsorbed by the whole plant body. The leaf of Polytrichum species has a complex structure. The midrib is formed by highly thickened stereids. On the adaxial surface photosynthesizing cells create parallel lamellae and between them small ducts are formed which adsorb and store water by capillary force. During dry periods the membranous margin of the leaf leans back on the lamellae protecting them from dehydration. The rhizoids occasionally form secondary protonemas which evolve new plants. Asexual reproduction is carried out by fragmentation of leaves, stems and protonemas and some true mosses are able to produce gemmae as well. The sex organs can be localized on the top of the non-branching gametophyte; it characterizes the acrocarpous mosses. In other cases the gametangia appear at the end of the side branches; these are called the pleurocarpous mosses. Both mono- and dioicy are characteristic for true mosses. The arrangement and the time of development of the sex organs vary greatly among the monoicious plants. On the acrocarpous mosses the apex usually widens and densely packed, sometimes colorful leaves create a plate-like perichaetium commonly known as the moss flower. Sterile filaments, the paraphyses, can be found among the gametangia. The leaves of the perichaetium form a cup which keeps the water inside; when the cup becomes full the sperms swim out and the falling raindrops splash them away. This kind of dispersal is characteristic for the mosses whose sex organs are located quite far from each other; otherwise the sperms reach the archegonia by swimming in a liquid film layer on the surface. Both of the gametangia are stalked. The relatively big, visible archegonium has a long, twisted neck made up of 6 layers and the egg cell is locked deep in the archegonial tissue. The chloroplasts transform into chromoplasts at maturity turning the antheridium to orange color. The antheridium dehisces at the top by inner liquid pressure which releases the sperms in a column at once. Each curled, biflagellate sperm is covered by a membrane which later disrupts by the movement of the cell.

Gametophyte of true mosses with developing sporopyhtes and detailed drawing of the perichaetium

The fusiform sporophyte is located inside the archegonium early in the ontogeny. The foot is haustorium-like and anchored into the archegonial stalk then into the stem of the gametophyte. The jacket of the gametangium, the calyptra, follows the sporophytic growth with constant cell divisions but after a while the sporophyte grows out of the archegonium. The calyptra partially splits but still covers the top of the sporophyte; it falls down only at maturity. In Polytrichum species the top of the calyptra splits into protonema-like filaments. The seta grows continuously by an intercalary meristem. The capsule differentiates into an endo- and an amphithecium, the arched top forms the operculum, the peristome and the annulus. The endothecium develops the columella and a sporogenous tissue surrounded by the tapetum; there is a gap held by trabeculae between them. The base of the capsule enlarges and its sterile tissue is called apophysis. The stomata of this area are controlled only by turgor pressure; light intensity and concentration of carbon dioxide have no effect on the closing mechanism. Despite the fact that the sporophyte is able to photosynthesize, nutrients are supplied by the gametophyte through the foot. Pronounced thickening is typical of cells located under the jacket of the capsule in a depth of 4-6 layers and they form a lobed peristome. The cells are partially degraded around it creating a line, the annulus, where the operculum dehisces. Diurnal changes in humidity are accounted for the hygroscopic movement of the peristome teeth: they remove the apical lid from the capsule in a dried state by bending out and they curve back and close the operculum under aqueous conditions thus the spore dispersal is a gradual and sustained process.

6.2. Pteridophytes

The sporophyte is the dominant generation in all groups of vascular plants thus the plant morphology primarily refers to the anatomy of the sporophyte.

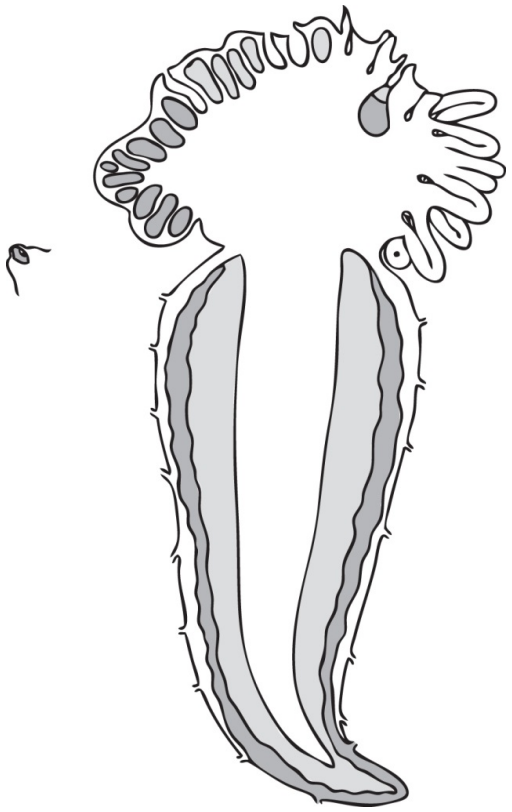
6.2.1. Club mosses

Most of the club mosses are perennial geophytes but some tropical epiphytes are also included. They are herbaceous and the shoot branches dichotomously or pseudomonopodially. In the case of the latter one the main axis evolves side branches but one of them remains undeveloped. The microphylls are arranged into a spiral or rows. They develop a fascicle of procambium which later differentiates a vein containing tracheids, sieve and parenchymatic

cells. The homogenous mesophyll is made up of uniform assimilative cells with small intercellular spaces between them. The leaf vein is connected to the vascular tissue of the central cylinder through a leaf trace and no leaf gap is associated with it. This is the main distinguishing feature between the micro- and macrophylls. The location of the stomata is species-specific: hypostomic, epistomic and amphistomic leaves are also common. The club mosses evolve a branching, horizontal rhizome which develops upright stems. The base of the shoot bears adventitious roots emerging from inside and they break through the cortex as they grow toward the soil. The shoot and root apex has undifferentiated promeristem and procambium which later evolves an exarch protostele. The stem contains laminate stele (plectostele) surrounded by a few layers thick pericycle and a developed endodermis. The xylem is only made up of tracheids and the phloem contains sieve cells bearing plasmodesmata and pores at both ends. The stele of roots shows great variety in size and structure between and within species. The xylem forms bundles which are embedded into a radially separated phloem in the plectostele of roots. The roots are protected by calyptra and the rhizodermal cells bear double root hairs.

Vegetative reproduction is carried out by bulblets or gemmae which are leafy side branches with wide base and develop new sporophytes after falling out. The sporophylls are either located randomly or arranged into compact groups. The reniform sporangia sit on short stalks at the corner of the stem and the leaves. The sporangium-bearing microphyll is very similar to a sterile leaf considering the morphology. The sporophylls usually transform into unphotosynthesizing scales and they create a cone-like stobilus at the top of the shoot. The internodes are very short in the stobilus. The sporangia are developed from protodermal cells near to the base of the embryonic microphyll and in some species they are moved to the stem. The sporangia contain tapetum and sporogenous tissue covered by a few layers thick wall. The tapetum surrounds the sporogenous cells entirely and supplies the developing spores as it degenerates during the ontogeny. The sporogenous cells become separated and each one produces a spore tetrad which later disintegrates. The spores develop a bistratose wall with an inner intine and an outer exine. The mature spores have yellow color. The wall dehisces along a line perpendicular to the axis of the sporophyll. Prior dispersal the internodes become elongated and the sporophylls shrink.

The germinating spores evolve a green, lobed prothallus. Only the gametophytes of a few species were observed in the nature. Their undersoil parts are covered by rhizoids and the upper surfaces form disc-like structures. Mycorrhiza formations with symbiotic fungi are common but entirely mycoheterotrophic gametophytes exist as well. The gametophytes are monoecious, they bear both sex organs. The large antheridia produce large number of sperms and are submerged into the gametophytic tissue. The sperms become released by the burst of the apical cells. The bottle-shaped archegonia are located deeply and their necks contain 4-5 rows of cells. The sporophytes are at different developmental stages thus the gametophyte is long-lived and supplies the sporophytes. The sex organs either functions for a long time or they are developed continuously. The zygote goes under transversal division and produces an outer suspensor and an inner cell which later forms the embryo. The embryo lacks of radicle, the first root is adventitious and appears at the base of the first leaf. When the sporophytes reach full development the gametophyte degenerates.



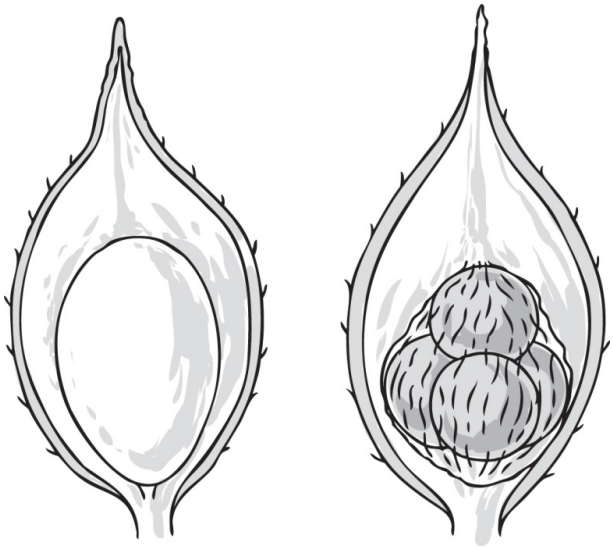
Longitudinal section of the gametophyte of clubmosses and a biflagellate sperm. The sex organs are sunk into the wide, apical part.

6.2.2. Spike mosses

The shoot develops several branches creating a dense, planar structure and it gives the plant a characteristic shape of a fan. The branching type is dichotomous, pseudodichotomous or sympodial. The growth is either carried out by one apical cell or differentiated meristems. The elder branches become hollow and the formed cavity separates the cortex from the central cylinder, only few columns of endodermis cells called trabecules connect the cortex and the stele. The structure of the stele is species-specific; it can be cylindrical or ribbon-like. The branching of the central cylinder precedes the actual separation of the stem thus two or sometimes even more steles can be observed in certain sections; it is called polystele. Each stele is surrounded by pericycle. The sieve cells bear pores on their entire surface. The xylem has a simple, cylindrical structure and in some species it contains not only tracheids but elongated, multicellular vessels. The thin cortex is made up of photosynthetic parenchyma. The epidermis covering the shoot lacks of stomata. The stem evolves adventitious roots on the ventral side near to the branches. These exogenous roots have dichotomous branching and lack of calyptra until they emerge above the soil surface and develop root hairs. The roots have protostele. The spike mosses with dorsiventral symmetry bear 2 dorsal rows of small and 2 lateral or ventral rows of bigger leaves. These plants are anisophyllous but some species have radial symmetry and uniform leaves thus they are isophyllous. The sessile leaves contain one non-branching vein which is connected to the central cylinder by a leaf trace without gap. These microphylls bear stomata on the abaxial or on both surfaces.

The spike mosses are eusporangiate plants. The sporophylls are very similar to the vegetative, sterile leaves and arranged into loose rows thus the strobili are hidden. They bear stalked sporangia at the base on the upper surface. The sporangium wall is bistratose, the sporogenous tissue is formed inside and tapetum is differentiated between them. There are two types of sporangia. The microsporangium contains many sporocytes which produce spore tetrads by meiosis and these tetrads stay together during maturation. The macrosporangium contains only one functioning sporocyte which goes under meiotic division creating a tetrad. The four megaspores enlarge as they take up the materials of the other, already degenerated sporocytes. The nutrients are stored as lipid and protein grains. The spores fill the sporangium and bulk the wall thus the macrosporangium can be recognized easily. The microsporophylls bear the microsporangia containing the microspores and the macrosporangia are located on the

macrosporophylls. Heterospory is characteristic which means that the spores differ in size and function. The microsporangia are developed near to the top of the strobilus and the macrosporangia are located at the base.



Macro- and microsporophylls of spikemosses bearing sporangia

The microspores develop the male and the megaspores evolve the female gametophytes. The development usually starts before dispersal and sometimes the gametophyte reaches full development and evolves the sex organs inside the sporangium. The division of the uninucleate microspore results in the formation of a prothallial and a larger antheridial cell. The antheridial cell goes under anticlinal divisions and forms a unistratose wall then it produces spermatogenous tissue inside containing 128 or 256 cells. Under adequate circumstances each spermatogenous cell develops into a biflagellate sperm after spore dispersal. As the microspore wall cracks and the antheridium degenerates the sperms become released. The female gametophyte is developed inside the sporangium as well. The free-nuclear division of the megaspore results in enlargement and as the spore becomes cellular it opens its wall by a trifurcate slit. The top of the gametophyte rises up through the slit and forms archegonia. Rhizoids can appear but nutrients are provided from stored materials. The sex organs are submerged, only the necks are visible. The female gametophyte is long-lived and evolves archegonia continuously unless fertilization takes place. The archegonia become fertilized either inside the macrosporangium or after dispersal. The dispersed microspores must approach the macrosporangium thus this process is similar to the pollination.

The zygote develops a suspensor and a proembryo. The suspensor grows longitudinally and pushes the developing embryo into the nutrient-rich gametophytic tissue. The embryo evolves a radicle and a plumule which bears two leaf primordia. As the embryo outgrows the archegonium it emerges above the gametophyte and becomes self-supplying.

6.2.3. Quillworts

They are aquatic or waterside plants. The narrow, long leaves emerge spirally from an undersoil cup-shaped shoot, the axils are overlapping. The leaves are microphylls because their veins are connected to the central vascular tissue by a leaf trace without gap. The cross section of leaves shows four air cavities and the veins run between them in the dense chlorenchyma. The epidermis bears stomata. The shoot has a complex anatomy. The apical part is wide and fleshy but the shoot apex is submerged. The nodes are located very close to each other thus the internodes are extremely short. The shoot apex develops new leaves therefore the longitudinal growth is de-emphasized. The vascular tissue is organized into a central protostele, the inner xylem contains parenchymatic cells and few tracheids, the phloem is surrounded by a meristematic cylinder whose role is not fully understood. It functions as a cambium producing vascular tissue inward but it develops cortex outward. The outer part of the cortex disintegrates in each year and falls down with the abscising leaves. The stem lacks of endodermis and is covered by the remains of the leaves from previous years. The epidermal cells go under secondary thickening. The base of the stem develops two or three elongated lobes which are considered as side branches bearing adventitious roots and they are called rhizophores. The endogenous roots are attached to the central cylinder; they branch dichotomously and are protected

by calyptra. The central cylinder forms eccentric protostele. As the cortex disintegrates continuously a cavity runs along the stele.

Each leaf is able to develop sporangium. The outer leaves usually remain sterile and the inner ones transform into macrosporophylls. The microsporophylls are located at the center thus these are developed the latest. As the growing period draws to an end the leaves evolve sterile sporangia. No morphological difference can be observed between the male and the female sporangia. They appear at the wide leaf bases on the adaxial side. The wall is multistratose and sporogenous tissue fills the sporangium. These eusporangia can reach a length of 7 mm and a special structure called ligule occurs at the top. It is associated with a velum which covers the sporangium partially. The cavity of the sporangium is separated by sterile trabecules and filled with a two layers thick tapetum. The microsporangium is able to produce even a million spores. Most of the macrosporocytes degenerate in the macrosporangium but hundreds of them create spore tetrads. The dehiscence of the spores is irregular and sometimes takes place after leaf abscission. The microspores have spiky surface which helps them to connect to the megaspores.

The spores of quillworts germinate solely inside the sporangia. The male gametophyte is fully closed to the microspore. The antheridium has a unistratose wall and each spermatogenous cell forms a multiflagellate sperm. The development of the female gametophyte starts with free-nuclear cell division and after cellularization the spore wall opens. The top of the gametophyte evolves rhizoids and submerged archegonia appear among them.

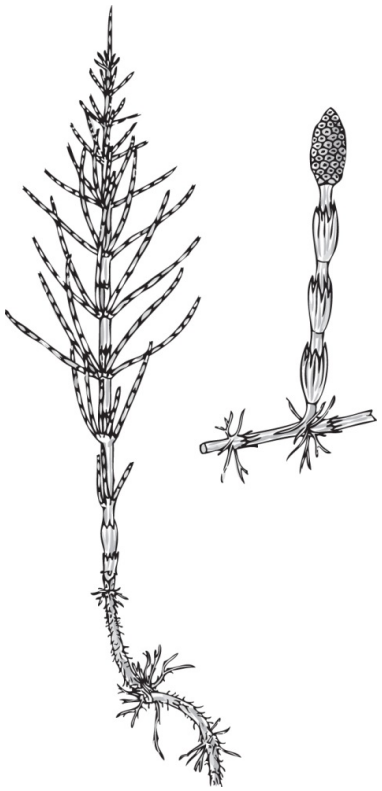
Each female gametophyte creates only one zygote. It forms a spherical mass of cells which later develop the embryonic tissues of the new sporophyte: a large foot, a radicle and a leaf primordium. The shoot is evolved secondarily between the radicle and the leaf. The self-supporting sporophyte stays connected to the female gametophyte for a long time.

6.2.4. Horsetails

The sporophyte is quite large; some tropical species can reach a height of 5 m. The shoot is made up of an undersoil, creeping rhizome and upright, photosynthesizing stems above the surface. The leaves are very small and they transform shortly into scales and take no part in the photosynthesis. Some species develop reserving bulbs on the rhizome. The stems either have a rich branching system or remain unbranched. The nodes and internodes are very well differentiated in the stem and in the rhizome as well. The stem is striated and the ribs alternate at the following internodes. The leaf axils are fused and create a collar. The leaves contain one non-branching vein. The side branches alternate with the leaves and they break through the leaf collar during development. The growth is supported by a pyramid-shaped apical cell. Some cells of the nodes become meristematic and function as an intercalary meristem increasing the length of the internodes. Large amounts of silex encrustate into the epidermal cell walls and create rosettes. The stomata are located on the sides of the ribs and they can be submerged depending on the environment. A central canal runs in the vascular cylinder surrounded by the remains of the pith parenchyma. Opposite the ridges carinal canals are found and associated with the bundles, they take part in water conduction. The central cylinder is surrounded by a layer of pericycle and an endodermis. The cortex contains parenchymatic cells and vallecular canals are positioned between the ribs. The cells become sclerenchymatic under the ridges thus the stem has outstanding strength. Although the bundles run separately in the internodes, they become united reaching the nodes and form sifonostele; the continuity of the central canal is interrupted by a membrane. The bundles alternate with each other at the following internodes. The internodes have eustele because of the vascular canals. The endogenous roots are evolved from nodes and bear protostele. Their surface is covered by root hairs.

Vegetative reproduction is carried out by fragmentation of the rhizome and the upstanding stems. The horsetails are homosporous. The sporophylls are arranged into strobili. Some species have separate fertile and vegetative or sterile shoots (*Equisetum arvense*). The fertile stem appears in early spring and is brown, non-photosynthesizing and bears the strobilus. The green sterile stem is produced after the fertile one wilted. Others develop the stobilus at top of the vegetative shoot (*E. hyemale*). Another group of horsetails evolve a chlorophyll-free shoot with an apical strobilus and after spore dispersal this shoot transforms into a green, branching stem (*E. sylvaticum*). The strobilus is composed of an axis bearing several sporangiophors. The stobilus of some species shows transition between sporophylls and sporangiophors thus it is plausible that the sporangiophor is a structure of sporophyll origin. The sporangiophors explicate force to each other and become hexagonal during development. They bear 8-10 sporangia on the abaxial side whose multistratose wall become one-layered by the degeneration of the inner cells. In contrast with the previously mentioned groups the sporangium of horsetails is developed from one cell. Each one of them is supplied by one vein. The sporogenous tissue and the developing spores are surrounded by a plasmodial tapetum which later produces the outer spore wall. As the spores reach maturity the stalks of the spor-

angiophors elongate and curve up thus they move away from each other and the sporangia dehisce longitudinally. The spore wall has a complex structure; it has secondary thickenings along 4 spirals. The formed strips separate from each other and from the inner wall but remain attached to it at one point as the spores fall out. These appendages are called elaters which are very sensitive to humidity and follow the occurring changes by hygroscopic movement.



The vegetative or sterile and fertile shoots of *Equisetum arvense* (common horsetail)

The green spores germinate very quickly, during one and a half days. The shape of the gametophyte accommodates to the density of surrounding plants. The separated prothalli are disk-like and have a diameter of a few mm. They are stabilized by unicellular rhizoids and develop photosynthesizing lobes on the surface. The gametophytes are either dioecious or monoecious; sometimes the developments of the different sex organs are delayed. The antheridia appear on the surface and the bottle-shaped archegonia are submerged into the prothallus, only the necks emerge above the lobes. The male sex organs are produced continuously for a year period but the archegonia are present only between the days of 30 and 80. In some cases the gametophytes bear only the antheridia and the others are dioecious but the archegonia are developed first then the gametophyte evolves male organs (protogyny). The antheridium originates from 2 cells, one of them creates the jacket of the organ and the other produces sporogenous tissue. Many multiflagellate sperms are formed and released by the burst of the jacket. The process is triggered by water. The archegonium is developed from one cell and the neck contains 4 rows of cells. More egg cells can be fertilized in a gametophyte thus more embryos develop. The embryo divides and forms 4 cells: the leaf primordia and the shoot are evolved by the two smaller cells, the two bigger cells create the foot and the radicle. The embryo of horsetails lacks of suspensor. The radicle grows through the prothallus and as it reaches the soil the sporophyte becomes self-supporting.

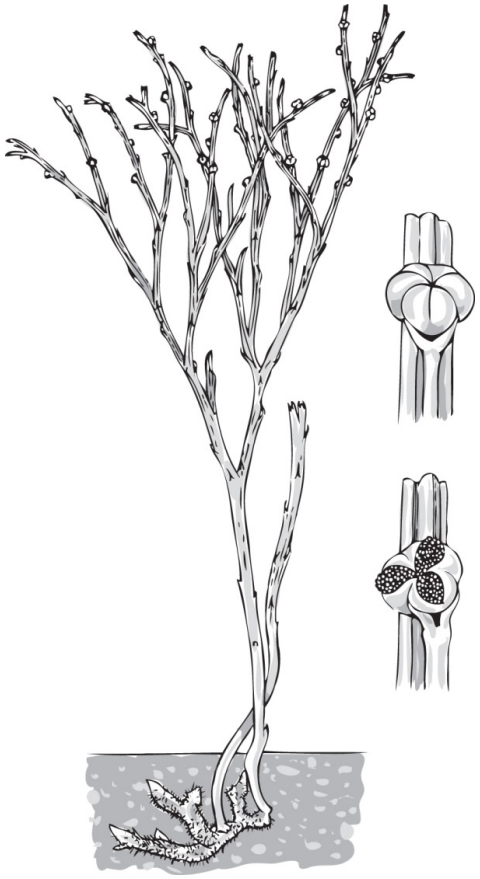
6.2.5. Ferns

Whisk ferns

The *Psilotum* species have a height of 30 cm. The creeping undersoil rhizome develops upstanding, dichotomous stems. The growth is supported by a tetrahedral apical cell and a 3-layered shoot ape4. The outermost layer is the protoderm, the innermost is the procambium and ground meristem is situated between them. The whisk ferns lack of roots, the epidermal cells develop rhizoids instead. The upstanding stems are angular and bear small appendages called enations or prophylls which lack of vascular tissue but a leaf trace can be observed at the base. The central

cylinder is pentarch but it can transform into di- or triarch toward the apex. The plants have actinostele. The nuclei of sieve elements degenerate during maturation and they bear large sieve plates on their cross walls. The stele is surrounded by endodermis and followed by a relatively large cortex. The cortex is made up of 3 layers: reserving parenchyma next to the endodermis, sclerenchyma and chlorenchyma. The latter one is the main photosynthetic tissue since the leaf-like prophylls have small surface. The epidermis is covered by cuticle and the stomata and the connecting air spaces partition the cortex. The undersoil shoots usually contain mycorrhizal fungi in the cortical cells.

The spores are produced in three-lobed, short-stalked synangia. The sporangia are located at top of the short side branches and three of them fuse together creating a synangium. The sporangium has a few layers thick jacket and is filled with sporogenous tissue surrounded by tapetum. During sporogenesis the cell walls disintegrate and the cells transform into a plasmodial tapetum. The sporocytes evolve spore tetrads by meiosis; the separating reniform spores are colorless. During spore maturation the sporangium jacket cells thicken except in three lines where the sporangium will dehisce later on due to water loss. The whisk ferns have eusporangium which is developed from superficial cells by anticlinal divisions. The following divisions result in sterile cells forming the sporangium wall and a sporogenous tissue is evolved inside whose outer layer occasionally forms tapetum.



Sporophyte of *Psilotum* (whisk fern) bearing synangium

The spores germinate very slowly. The gametophytes are rarely bigger than 2-3 mm. They are dichotomous and covered by rhizoids. They lack of chlorophyll; nutrients are supplied by endophytic fungal associations thus the gametophytes are saprotrophic. The strongly reduced stele contains tracheids, some phloem elements and undeveloped endodermis. Many species of the whisk ferns are tetraploid and their monoecious gametophytes are diploids. The sex organs are evolved by superficial cells. The hemispherical antheridia protrude from the surface, their wall is unistratose and few multiflagellate sperms are produced. The submerged archegonia have short neck which is made up of 4 rows of cells.

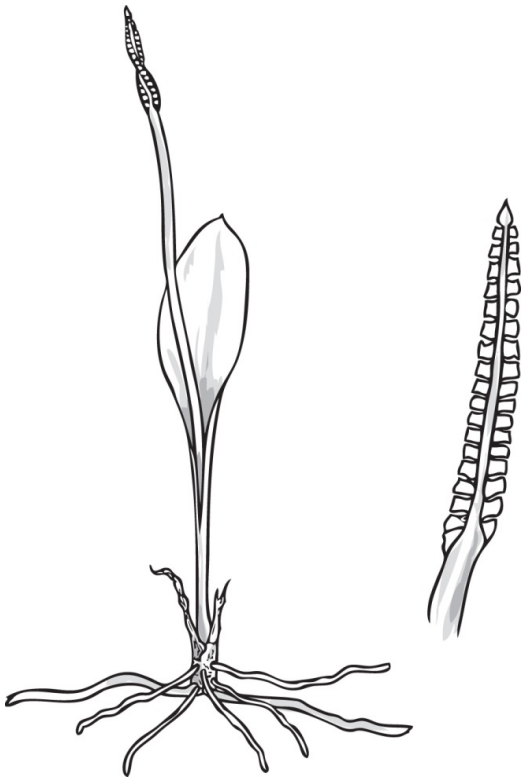
After fertilization the zygote goes under transversal division. The basal cell develops the foot, the apical one forms the plumule. The embryonic shoot evolves a branching rhizome which emerges from the gametophyte and associates

with the symbiotic fungi. Some branches of the rhizome grow toward the surface due to negative geotropism and the plant becomes separated from the gametophyte.

Ophioglossoid ferns

The short, vertical sporophyte has an undersoil stem from where fleshy adventitious roots originate. The species belong to the Ophioglossum genus develop special adventitious buds on the root which could regenerate new ferns. In such way expansive colonies are formed by one plant. Although several leaf primordia appear on the stem arranged into a spiral, only one of them develops a leaf and it degenerates each year. There are some pronounced differences between the leaves of the moonwort and the adder's tongue ferns: the former bears a lobed, dichotomous veined leaf, the latter has an entire, reticulate leaf where the veins are fused near to the margin. The entire leaf is due to a reduction therefore it is a novel feature. The development of the leaves is very slow, it takes years until a primordium rises above the soil surface. The epidermis has stomata at both sides; the mesophyll is homogenous and divided by air spaces. The stem contains protostele which later transforms into an ectophloic sifonostele. The stele becomes split as the leaf primordia appear thus the bundles are separated by parenchymatic gaps. This structure is characteristic for all macrophyllic plants. The vascular tissue contains secondary elements produced by cambium. The cortex is a starch reserving parenchyma. After secondary growth the stem is covered by periderm. The endogenous roots lack of root hairs. The cortex bordered by a developed endodermis functions as food storage. Simple bundles alternate in the vascular cylinder, the stele is diarch or tetrarch. Symbiotic mycorrhiza formation is common between the root and some fungi.

The sporangia are located on a branched or straight stalk. This fertile axis is developed from a pair of leaves and emerges at the meeting point of the petiole and the lamina. The Ophioglossum species have large sporangia arranged into two longitudinal rows and a bundle belongs to each one of them. Between the few layers thick sporangium wall and the sporogenous tissue a bistratose tapetum can be found; its cells fuse into a plasmodium during the ontogeny and the remaining sporocytes produce the spore tetrads. The sporangium dehisces along a line perpendicular to the sporophyll axis. Each sporangium could contain 15 000 spores.



Morphology of ophioglossoid ferns

The gametophyte is a fleshy, chlorophyll-free rhizome-like structure under the soil which always forms mycorrhiza with symbiotic fungi. The length of the cylindrical gametophyte is rarely longer than 5 cm and has a thickness of less than 0.6 cm. It is long-lived and differentiates tracheids later in the ontogeny. The Ophioglossoids are

monoecious ferns, the sex organs appear together on the same plant. The antheridia are large and produce multiflagellate sperms, the archegonia are sunk into the gametophyte, only the neck emerges above the surface.

The fertilization happens during summer. The zygote divides into a spherical group of cells in the ventral side of the archegonium and later develops the foot, the radicle and the leaf primordium; the development of the shoot apex is delayed. The young sporophytes stay connected to the gametophyte for a long time until the first fertile leaf becomes present.

True ferns

The morphology will be presented by the Polypodiaceae family and a heterosporous water fern (*Salvinia natans*).

Polypodiaceae

Both isosporous and homosporous groups belong to the leptosporangiate ferns. The growth of the shoot is controlled by one apical cell. Based on the organization of the vascular tissue species exist with protostele, sifonostele, solenostele and dictiostele. The central cylinder is surrounded by a developed endodermis in some species; otherwise the cortex and the cylinder are unseparated. The bundles have their own endodermis ring in the dictiostele. The tracheids have large diameter and pits provide continuous transport through them. The phloem consists of sieve cells without any companion cells. The roots have stem origin except of the embryonic ones and they are formed between the leaf axils. Protostele is mostly characteristic, diarch stele can be observed in some groups. The central stele is surrounded by a pericycle and a developed endodermis. The cortex contains sclerenchymatic tissue. Lateral roots emerge from the endodermis cells opposite the protoxylem elements. No secondary thickening is present in the root and the shoot of the ferns. Leaves are the most striking organs of the sporophyte. They are compound and connected to the stele with one or more bundles. Simple leaves are due to reduction. The venation is dichotomous or reticulate, the mesophyll is undifferentiated and the abaxial epidermis bears stomata. In some ferns the epidermis cells contain chloroplasts and are able to photosynthesize. The leaves are developed near to the shoot apex and regenerate in each year.

The sporangia form groups called sori (singular: sorus) on the leaves. The sori appear on the abaxial surface or rarely on the margin. Segregation of the vegetative and reproductive role occurs within one leaf and between separated leaves: the sporangia can be formed either on the whole surface of a leaf or just on distal leaflets. In extreme cases chlorophyll-free leaves are specialized on only producing sporangia. The sporangia are developed from the peripheral cells of the receptacle: an upper cell heightens and goes under divisions creating the stalked sporangium. In the distal, enlarged head an archesporial cell develops the inner layer of the sporangium wall with the tapetum and the sporocytes whose number varies between 12 and 16. Meiosis results four equivalent spores which form a tetrad. During spore maturation the cells of the tapetum degenerate and serve as a food supply. The stalk of the sporangium elongates; the radial and tangential walls of certain cells thicken in a ring creating the annulus. The remaining cells with thin walls form a stomium between the annulus and the stalk. The spores have a bistratose wall, the inner intine and the outer exine which is usually ornamented. The sporangia become released when the indusium covering the sori shrink due to turgor loss. The tension generated by the decreasing water content in the annulus opens the sporangium along the stomium and the spores fall out. When the annulus entirely strains back, the sporangium reaches its most open state. Simultaneously, in the annulus cells the tension forces the plasma to move away from the walls and it results in the closing of the sporangium. This returning motion can be repeated several times depending on the water content. During this catapult-like movement the spores become dispersed. The sporangium produces usually 48-56 spores in the leptosporous ferns.

Despite of the great number of spores only a few gametophytes develop in the nature. The germination of the spores is a light-induced process. It results in the formation of a protonema-like filament bearing some rhizoids. Under adequate circumstances the apical cell of this protonema divides horizontally and forms a heart-shaped unistratose gametophyte. The gametophytes are monoecious and protandrous which means that the antheridia mature before the development of the female sex organs. Both gametangia originate from one initial cell. The upraised antheridia are located near to the margin of the thallus, the archegonia are sunk into the gametophytic tissue in the middle and only the necks are visible. The jacket of the antheridium contains 3 cells: the lower ones are ring-like, the uppermost is a lid cell. During water uptake the two lower cells become swollen and they crack the lid thus the multiflagellate sperms are able to leave the male sex organ. The sperms become active by losing the surrounding plasma. The neck of the archegonium contains four rows of cells, these neck canal cells usually stay together after division. The central cell develops the ventral canal cell and the egg cell. As they take up water the swollen canal

cells burst the neck creating a duct toward the egg cell. The sperms reach the archegonium by chemotaxis which also can be triggered by exogenous malic acid.

Although more egg cells could be fertilized on a prothallus only one zygote starts to develop. It forms a quadrant where each cell is determined. It means that they are specifically responsible for the development of certain organs. The radicle appears toward to the archegonial neck, the foot faces to the prothallus, the leaf primordia and the shoot apex grow laterally. The gametophyte functions until the appearance of the new leaves then it turns brown and degenerates. The newly formed leaves have a simpler structure than the mature ones. The embryonic root is always supplemented by adventitious ones which later give the bulk of the root mass.

Salvinia natans

Salvinia is a floating, rootless water fern. The leaves are arranged into three whorls, two of them float on the surface. The third whorl is submerged and the highly fragmented leaves look like roots at first sight. The floating leaves are covered by waxy, papillated trichomes. The stem contains sifonostele. The vegetative reproduction of Salvinia is very effective, the shoot apex has unlimited growth, the stem is branching and exfoliated side branches allow fast expansion.

The heterosporous Salvinia keeps the sporangia in a sporocarp which is basically a sorus covered by a highly modified indusium. The water ferns are monoecious plants; the sporocarps developed at the leaf axils contain either the microsporangia or the macrosporangia. The sporangia originate from one cell: first the macrosporangia are created and their receptacles hold the microsporangia laterally. If the macrosporangia are fully developed, the microsporangia stay immature or vice versa. Eight macrosporocytes go under cell division producing 32 megaspores but only one of them matures. This megaspore become large and fills the whole macrosporangium. Both types of sporangium develop a plasmodial tapetum which later solidifies and forms a lobed body (massulae) above the spore. The massulae partially cover the top of the megaspore creating an additional outer layer called the perispore. During autumn the sporocarps submerge to the benthic zone, the walls of the sporangia disintegrate and the spores are released but they stay connected by the massulae. The spores germinate after they leave the sporangia. The gametophytes of the Salvinia are endosporous. The male gametophyte developed by the microspore bear the antheridia in two groups. The megaspore floats to the surface and germinates; the female gametophyte is photosynthetic and forms several archegonia where the embryos grow.

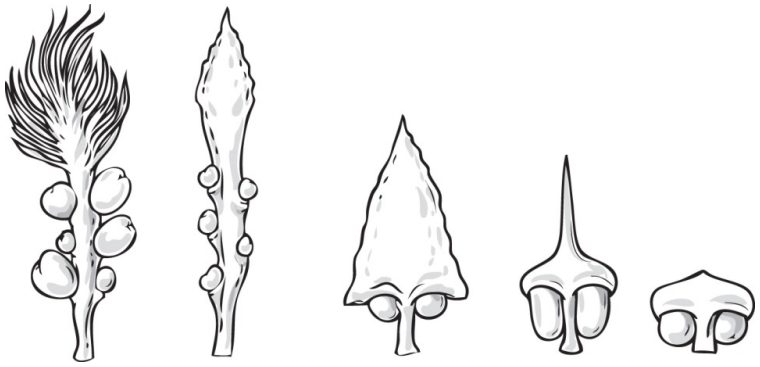
6.3. Gymnosperms

6.3.1. Cycads

The sporophyte has a shorter or longer vertical stem with a conical top and fleshy roots emerge at the bottom. The large, compound leaves are closely packed in a spiral at the top creating a canopy and the axils remain at the stem after abscission. These leathery leaves are very similar to the ones of palm trees and ferns. The annually exchanged leaves stay connected to the plant and they only fall down years after shriveling. The epidermal cells have thick outer walls and the stomata are submerged on the abaxial surface. The adaxial epidermis is followed by a sclerenchymatic hypodermis; the mesophyll is divided into a palisade and a spongy parenchyma. The shoot apex is made up of an arched meristem which becomes fully differentiated during the appearance of the strobilus thus a new apical meristem is formed in a lateral position. The central cylinder gives a thin part of the stem, the thick cortex reserves starch. The surface is covered by a waterproof periderm. Mucilage cavities are common in the cortex, in the cylinder and in the petioles as well. The cambium between the xylem and the phloem is inactive thus the amount of vascular tissue stays constant and no annual rings are formed. Some of the fleshy roots emerge above the soil surface and help to increase the efficiency of gas exchange. They develop root nodules which give place to Anabaena and Nostoc symbionts. Such cyanobacteria live in the intercellular spaces of the dermal tissue and they are protected by the elongated root cap.

The cycads are heterosporous and dioecious plants, pronounced sexual dimorphism is characteristic of the sporangia. The strobilus is formed among the apical leaves of the male plant and it is made up of microsporophylls. These leaves are brown, fleshy and each bears 25-30 microsporangia on the back. The microsporangium has a short and thick stalk and a multistratose wall. Many spores are produced in one microsporangium and supplied by the plasmodial tapetum which also participates in the development of the outer spore wall. The macrostrobilus formed by macrosporophylls is brown; the leaves are big and contain 2 or more oval, short-stalked macrosporangia or ovules

located either on the margin or on the abaxial side. In Zamia species the sporophylls create a cone attached to the stem by a stalk. The Cycas genus has separate sporophylls at the top of the stem without forming a cone.



Developmental series of the macrosporophylls of cycads with decreasing number of ovules: *Cycas*, *Cycas media*, *Dioon*, *Macrozamia*, *Zamia*

The macrosporangia are covered by a few layers thick integument but the enclosing is not perfect: there is a small pore called micropyle at the top of the ovule. The integument contains 6-9 bundles indicating that the ovule is formed by fusion of several structures. The ovule contains a mass of diploid cells called the nucellus and one of its cells, the macrosporocyte, produces 4 megaspores by meiosis. Three of them degenerate toward the micropyle and the remaining one enlarges. The ovule is connected by the funiculus opposite to the micropyle and this area is called chalaza. Therefore the surviving megaspore is positioned closest to the chalaza.

The microspores are uninucleate than after asymmetric division a prothallial and a larger cell is formed. The latter goes under division and produces a generative and a vegetative or tube nucleus. The pollen leaves the microsporangium at this 3-cell stage. Simultaneously, some cells of the integument degenerate near to the top of the ovule creating a pollen chamber and their content transform into a colloidal or pollination drop. The drop collects the pollen grains which get inside the chamber as the droplet becomes evaporated. The Zamia species are pollinated by insects especially by true weevils (Curculionidae family) whose reproduction cycle is strongly related to the life cycle of the plant. The pollen germinates through a pore where the exine is undeveloped and it creates a cylindrical haustorium called the pollen tube. The 3-4 mm long tube degrades the diploid tissue of the ovule taking up nutrients as it makes its way toward the top of the gametophyte. The generative cell divides into a sterile or stalk cell and a spermatogenous or body cell. The megaspore is surrounded by a tapetum-like nourishing layer. After several divisions a multinucleate cytoplasm is created and the whole female gametophyte becomes cellular. At the top of the mature gametophyte usually 4 or fewer cells produce archegonia. Each archegonium contains four neck cells and a central cell. Division of the central cell results in the formation of a ventral canal cell and an egg cell which is visible and has a length of 3 mm. As the archegonia become mature the apical gametophytic cells shrink and move away from the nucellus creating an archegonial or fertilization chamber. By this time the spermatogenous cell forms two multiflagellate sperm cells in the pollen tube. The sperms reach the archegonial chamber and swim toward the archegonia where the canal cells are already degenerated thus the protruded egg cell can be easily fertilized.

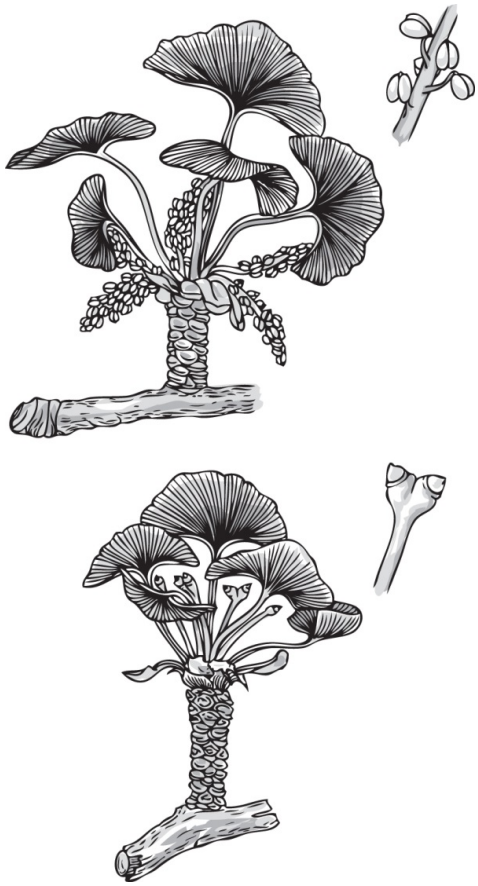
The zygote goes under division and creates a multinucleate embryo which later becomes cellular. As a meristem the developing pro-embryo is continuously pressed into the gametophytic tissue at the chalazal side. The development starts in several archegonia but only one sporophyte is formed from one ovule. The embryo is differentiated into the cotyledons, the plumule and the radicle. The stem between the cotyledons and the radicle is called hypocotyl. The embryonic radicle is protected by the coleorhiza. During development the ovule enlarges, its jacket becomes fleshy and turns to orange color, the middle layer transforms into a drupe-like shell and the inner part remains soft. At the end of this process a seed is formed containing the young sporophyte and it is impregnated into the female gametophytic tissue. The seed is surrounded by the previously mentioned layers of the ovule originated from the integument. The mature seeds fall down or are dispersed and germinate under adequate conditions.

6.3.2. Ginkgophytes

The Ginkgo or maidenhair tree is a deciduous woody plant which can reach the height of 30 meters. During cold periods the dormant shoots are covered by modified leaves called bud scales. This is one of the main features of

woody perennials. The stem is made up of two types of shoots. The main axis is also called the long shoot and the distal nodes of it develop leaves in a spiral. The short shoots appear on the elder branches of the main axis; they are formed by the two years old buds and develop very slowly. In case the long shoot gets damaged, the short shoots transform and take over the role of the main axis. The shoot has eustele and its appearance is related to the presence of macrophylls. The vascular cambium which is another main feature of woody plants makes possible the secondary growth by continuously producing vascular tissues. The cortex is surrounded by the periderm which is a waterproof and air closing layer produced by phellogen on elder branches. Any gas exchange through the periderm is supported by lenticells. The roots are protected by root caps, they have diarch stele which is able to grow secondarily. The leaf is the most characteristic organ of the Ginkgo. The lamina is fan-shaped and divided into two lobes. Two bundles run in the petiole and they branch dichotomously in the lamina. The mesophyll can be separated to a palisade and a spongy parenchyma; the abaxial sides of the leaves bear stomata. Every organ contains mucilage cavities.

The Ginkgo is dioecious, the microsporangia are arranged into a catkin and the macrosporangia sit in a stalk two by two. Both kinds of sporangia are formed at the end of the short shoots. The catkins become fully developed by autumn prior to the flowering and the microsporangia contain microsporocytes at this stage. The meiosis and the microsporogenesis start in the following spring. The microsporophylls emerge along a spiral on the catkin and each has two elongated microsporangia. The microsporangium contains tapetum covered by a 5-6 layers thick jacket. The ovules sit on the petiole-like peduncle two by two. It has two bundles which end at the base of the ovule where the peduncle broadens and creates a collar. The ovule is surrounded by a thick integument but it stays accessible by a small pore, the micropyle. The macrosporocyte goes under meiotic division and creates a linear megaspore tetrad; three of them degenerate near to the micropyle. The distal megaspore is covered by a tapetum-like layer originated from the nucellus but it disappears later. The apical cells of the ovule degenerate creating a pollination droplet and a pollen chamber.



Short shoots of *Ginkgo:* male cones and female ovules grouped in two

The division of the microspore results in the formation of a smaller prothallial and a larger cell. The first prothallial degenerates after a while. The larger cell divides into a second prothallial and an antheridial initial which goes under division producing a vegetative or tube cell and a smaller generative cell. At this stage the pollens are dispersed

by wind, get into the pollination droplets and reach the pollen chamber by its dehydration. The pollination happens in March and April. During germination the pollen tube grows into the ovule tissues. The female gametophyte is fully developed by August. The megaspore goes under free-nuclear divisions for 2 months creating approximately 8000 nuclei and later it becomes cellular. Two archegonia are formed toward the micropyle; the archegonial chamber is located above them. The neck and ventral canal cells degenerate before fertilization. By the time the pollen tube reaches the archegonial chamber, the generative cell divides into a stalk (sterile) and a body (spermatogenous) cell which will form the two motile sperms before fertilization. The mature egg cells protrude through the neck of the archegonium and they sink back to their original positions after fusing with the sperms cells. The fertilization happens between August and October after the ovules fall down.

The free-nuclear division of the zygote results in the formation of a proembryo containing 256 cells. After it becomes cellular its apical segment grows into the gametophytic tissue through the archegonium and takes up the nutrition of it. Two embryos can grow in one ovule but only one of them become fully developed and contained in the seed. The embryo forms a radicle, a hypocotyl, two cotyledons and a shoot apex with 5 leaf primordia. Simultaneously with the embryogenesis, the integument differentiates 3 layers: the outermost fleshy jacket turns to greenish purple color, the middle layer become stone-like and the innermost one forms a thin, papery layer. The fleshy layer gets a characteristic smell during seed maturation. The germination of the seed is hypogeal which means that the cotyledons stay inside the seed coat below ground.

6.3.3. Conifers

The morphology of the Pinus genus will be discussed. The pines are woody, mostly evergreen plants. They grow periodically; the leaf primordia are covered by bud scales during cold periods. They have two types of shoots and leaves: the scale leaves are located at the base of the long and the dwarf shoots and the latter ones bear needle-like leaves at the top which are able to photosynthesize. The number of needles on the dwarf shoots is species-specific, usually varies between one and eight. The dwarf shoots have limited growth and stay on the plant for 2-14 years than they fall down with the needles. The abscission is continuous thus the plant has permanent canopy. Despite of that the needles are macrophylls they have only one non-branching vein. The leaves are adapted to dry climate. The thick-cuticled epidermis is followed by 1-2 layers of hypodermis with thick walls. The stomata sink deep into the mesophyll which has tight cell arrangement and lacks of intercellular spaces. The mesophyll cells are lobed and many chloroplasts are located near to the surface. The needles contain resin ducts. The central vein is surrounded by an endodermis and made up of two open collateral bundles embedded into a transfusion tissue. The tissue contains three kinds of cells: transfer, reserving and tannin-storing cells. The central unit bordered by the endodermis is considered as a secondarily reduced central cylinder.

The shoot apex functions during spring and summer. The procambium forms separated bundles thus the stem has eustele. A parenchymatic pith is framed by the bundles and pericycle surrounds the whole central cylinder. The cortex of the young shoots is green and photosynthesizing, the stem is covered by an epidermis. The vascular cambium produces a simple, homogen wood during secondary thickening. The wood contains only tracheids and their radial walls bear bordered pits. The pith rays have simple structure, they are usually one cell thick. The periodic functioning of the cambium results in the formation of annual rings. The phloem elements are continuously pushed toward the surface, only a few layers function next to the cambium. One cell layer of the outer cortex transforms into phellogen or cork cambium and it develops a secondary dermal tissue called periderm. The periderm of elder shoots penetrates into the phloem at some points creating the bark or tertiary dermal tissue (rhytidome) which is a mixture of periderm and secondary phloem elements. Resin ducts are present in the cortex of stems and roots as well. The roots can be diarch, triarch or tetrarch. The central cylinder is surrounded by a pericycle and a developed endodermis. The cortex is thick and the rhizodermis bears root hairs. The absorption zone is quite short and the young roots usually form mycorrhiza with fungi species. During secondary thickening the roots become woody and develop similar structure as the elder shoots have.

The micro- and macrosporangia of pines are arranged into separate strobili located on the same plant thus they are monoecious. The microstrobili are formed at the base of the shoot apex in a ring and they are protected by bud scales during cold seasons. They have simple structure: the microsporophylls or stamens are closely packed in a spiral on the central axis. The stamens bear two elongated anthers which contain a well-developed tapetum surrounded by a 4 layers thick wall. The mature anther dehisces along a longitudinal line formed by cells with thin walls. As the male flowers become colorful the microsporocytes go under meiotic cell division producing microspores in March and April. During their ontogeny they develop a bistratose wall whose layers move away from each other at the poles creating two air sacks. The microstrobili or cones appear on the young, short side twigs. They

are soft and have a color of reddish purple than after pollination they become woody. The female cones have a more complicated structure. The sporophylls are held by bracts which emerge on the axis of the strobilus. Therefore a cone scale is considered as a female flower, the whole cone is a racemose inflorescence and the microstrobilus is only one flower. The scales bear 2 macrosporangia or ovules. An integument covers the ovule but leaves it accessible through the micropyle. The one differentiated macrosporocyte enlarges and goes under meiotic division creating a linear tetrad. Three of the four megaspores degenerate and the remaining one near to the chalaza uses the others as food storages. The microspores are in a 4-cell stage during dispersal containing 2 prothallials, a generative and a tube cell. The prothallials are shortly degenerated. The pollens are wind-dispersed and take long distance by the air sacks. The cone scales become more open during pollination thus the pollens get onto the top of the integument. The integument produces a pollination drop. If the pollens reach the liquid, they are able to get inside the pollen chamber by the dehydration of the droplet. The interaction between the pollen grains and the apical nucellus cells results in the swell and closing of the micropyle. The pollens germinate haustorium-like pollen tubes. By this time the scales thicken at the top and stay closed until seed maturation. The megaspore surrounded by a spongy, tapetum-like tissue goes under free-nuclear division for 6 months. The female gametophyte becomes cellular in the following May, 13 months after pollination. Archegonial initials are formed near to the micropyle and they develop the archegonia by dividing into a neck initial and a central cell. The neck initial creates the short neck of the archegonium; the central cell produces a ventral canal cell and an egg cell. As the ventral canal cell degenerates the egg cell is ready to fertilization. In the male gametophyte the division of the generative cell results in the formation of a sterile or stalk cell and a spermatogenous or body cell. A year after pollination the branched pollen tube reaches the top of the female gametophyte. The spermatogenous cell produces the two sperm nuclei which stay in the cytoplasm of the stalk cell. As they meet the egg cell one of the sperm nuclei fuses with the egg cell and the other nucleus degenerates in the cytoplasm. The embryogenesis could start in several archegonia but only one embryo is formed in an ovule. The zygote goes under free-nuclear division producing 4 cells which move toward the chalaza and develop 4 cell columns equivalent with 4 proembryos. The process when more embryos are formed in an archegonium is called polyembryony. *In vitro* all embryos reach full development but *in vivo* only one develops a seedling. The embryos are pushed into the chalaza by the suspensors and the surrounding gametophytic tissue turns into liquid and serves as food storage. The fastest growing embryo obtains nourishment thus the others become degenerated. The embryo develops a radicle and a shoot axis with usually 8 needle-like cotyledons than it goes into dormancy. By this time the integument forms the layers of the seed coat. After seed maturation the cone scales open by dehydration or other process (fire) and the winged seeds can be dispersed. The germination of the seeds is epigeal, the cotyledons photosynthesize for a long time.

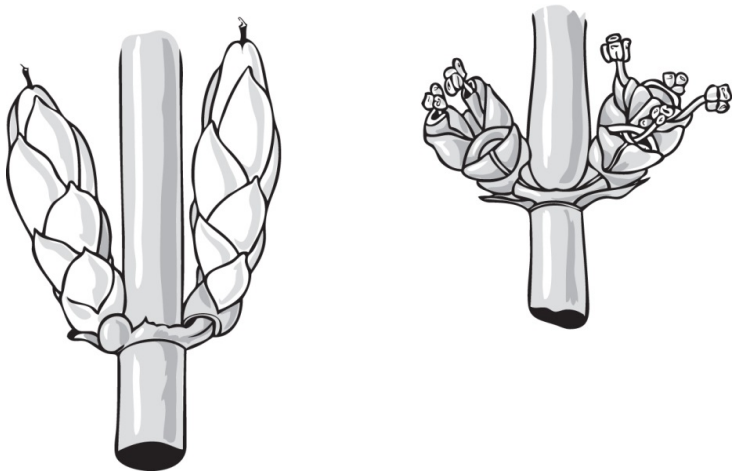
6.3.4. Gnetophytes

Ephedra

Approximately 40 species belong to the Ephedra genus, all of them are xerophyte shrubs or climbing plants except one which is a branching tree with a height of 3 m. The young plants are very similar to the horsetails. The small, scale-like leaves are arranged into whorls by three and have no part in the photosynthesis. Two or three parallel veins run in the leaves without branching. The side branches appear in whorls. Some of the green shoots exfoliate during dry periods. The young shoots are green and photosynthesizing, the elder branches become woody as the slow secondary thickening progresses. The climbing species bear adventitious roots emerging from the nodes of the runners. The stem has quite large parenchymatic pith surrounded by bundles. The cortex contains two kinds of tissues: sclerenchyma and clorenchyma alternate with each other thus the stem is striated. The stomata are located on these ribs. The xylem contains tracheids which become connected by small pores and form long, continuous tubes during secondary thickening. Each wall of the tracheids bears bordered pits. The root has diarch stele.

The genus involves mono- and dioecious plants as well but the strobilus is always unisexual. The male strobilus made up of microsporophylls is short and rounded, the female strobilus is elongated and pointed. The microstobilus has a compound structure: 7 pairs of bracts emerge from a central axis and their arrangement is decussate. The microsporangia are located at the base of the bracts sitting on short stalks. They coalesce and form a sterile stalk and 5 anthers with each one having 2 locules. As the pollens mature the stalk elongates and raises the anthers above the bracts. The anther has a bistratose wall; the locules are covered by the tapetum and filled with a sporogenous tissue. The tapetum cells are binucleate during sporogenesis. By the anthers reach maturity the wall is only formed by a dermal layer and the inner parts become degenerated. The microsporogenesis is a prolonged process and takes place at different times within one strobilus. The female strobilus is composed of 4-7 pairs of decussate bracts and

only the uppermost pair bears one or two short-stalked ovules. The ovule is surrounded by a 2 layers thick jacket; the inner layer is the green, photosynthesizing integument whose apical part forms a tube-like structure.



Female and male strobili of *Ephedra*

Free-nuclear division of the female gametophyte results in the formation of 500-1000 nuclei. Two or three archegonia are formed near to the micropyle. The compact neck contains approximately 40 cells. The nuclei of the ventral canal cell and the egg cell stay together after division. The cells have dense plasma and store starch on the chalazal side while the micropylar pole of the gametophyte is strongly vacuolated. During maturation a deep pollen chamber is formed which reach the top of the archegonia. The micropylar tube secretes a pollination droplet. The microspore goes under division creating a prothallial and a larger cell. The latter one produces a second prothallial and an initial which shortly divides into a generative and a tube cell. The next step is species-specific: the generative cell either forms a stalk and a body cell or directly develops the 2 sperm cells. The plants are wind-pollinated; the pollens gain access into the chamber by dehydration of the pollination droplet. The cytoplasm of the pollens get out of the their wall and shortly the sperms are formed inside the chamber. The pollination is quickly followed by the fertilization, approximately 10 hours elapse. The pollen tube grows through the neck of the archegonium and into the egg cell. The egg cell takes up the nuclei from the tube and it fuses with one of the sperms cells. The other male gametophytic nuclei stay close to the ventral canal cell and the remaining sperm cell can fuse with it. Therefore this process is very similar to the double fertilization of the angiosperms but in fact these are distant concepts.

The development of the zygote starts with a free-nuclear division, the nuclei near to the chalaza form proembryos. They grow at different rates and are pushed to the gametophytic tissue by suspensors. The seed contains only one mature embryo developed from the deeply located proembryo. By the time the mature seed goes into dormancy, it has a firm inner coat covered by a colorful, fleshy shell. The germination is epigeal, two photosynthesizing cotyledons are developed.

Gnetum

Approximately 30 species belong to the Gnetum genus and they are usually used as crop plants. The *Gnetum gnemon* is a tree with a height of 10 m, its leafy shoots are edible and the bark is used as fiber material. The elements of the xylem are well developed, the perforations on the cross walls ensure continuous water conduction. The venation of the leaves is basically dichotomous but each vein branches later on creating a web. The Gnetum species are dioecious. The microsporophylls emerge from a central axis and are arranged into whorls in the axils of bracts. A whorl is made up of 25-30 sporophylls and each one of them bears 2-4 microsporangia. The microspore develops the male gametophyte or pollen grain which contains a prothallial, a generative and a tube cell. The macrosporangium has a 3 layers thick wall, the innermost one is the integument whose apical part creates a micropylar tube. The other two layers are thick and the epidermis bears stomata. 8-10 macrosporocytes are differentiated in an ovule but usually only one gametophyte is formed. The four daughter cells of the macrosporocyte stay together thus the gametophyte is the product of 4 megaspores. During pollination only the chalazal side is cellular, in the apical part of the gametophyte the nuclei form groups of 8 which become cellular and function as undifferentiated archegonia. One or two cells of the groups are the egg cells. As the pollen tubes grow through the nucellus and reaches the archegonia, the generative cell produces 2 sperms and all egg cells can be fertilized in each archegonial cell groups.

The embryogenesis shows great variety but polyembryony and presence of suspensors are common features. The large, fleshy, red seeds contain one embryo and sometimes they fall down before the embryo reaches full maturity.

Male and female stobili of *Gnetum* with ovules arranged into whorls

Welwitschia

The Welwitschia has a unique structure. The stem is fleshy, thick and woody and has a shape of a reversed cone. It extends deep into the soil as a root and can reach a diameter of 1.5 m. Two wide, ribbon-like meristems located at the base provide continuous growth thus the leaves are renewed on the stem and dropped off at the top. The fertile shoots appear at the leaf axils. The plants are dioecious and have compound strobili. According to some authors, the mature female gametophyte is free-nuclear and developed from one megaspore without forming archegonia; others believe that the gametophyte is the joint product of 4 megaspores. By the time of the fertilization the gametophyte becomes cellular. The egg cells create projections toward the micropyle and these will fuse with the arriving pollen tubes. The fertilization takes place at these newly formed ducts.

Chapter 7. SEXUAL REPRODUCTION OF ANGIOSPERMS

(Zoltán Kristóf, Pál Vági)

7.1. The flower

Most sporophytes of angiosperms consist of a root and a leafy shoot; these organs have either embryonic or adventitious origin. The embryo is bipolar having a radicle and a plumule, the cotyledons emerge between them. The roots developed from the shoot are all adventitious. The leaves are macrophylls and show great variety in morphology and size. They are arranged along a spiral but decussate and whorled arrangements are also common. The branching system follows the leaf arrangement as the side branches emerge from the leaf axils. The leaf can be divided into three parts: lamina, petiole and axil. The petiole is developed by an intercalary meristem located at the base of the lamina. Sessile leaves lack of this meristem and have no petiole. The shape of the lamina is diverse and compound leaves also can occur. The axils usually bear stipules. The most common venation types are dichotomous, reticulate and parallel. The leaf anatomy show general features similar to other macrophyll-bearing plant groups: the mesophyll is thick on the adaxial side and spongy on the back, the stomata are arranged accordingly to this structure. The epidermal cells lack of chloroplasts. The veins contain xylem and phloem elements and usually are surrounded by a bundle sheath which is made up of parenchymatic cells. The xylem is located toward the adaxial surface. The leaves fall down from the shoot along a special layer called abscission zone.

The angiosperms are flowery plants. Apparently the organization of the flower shows great variety but all have the same basic structure. The flower is a reproductive shoot with limited growth having a central axis which could bear four kinds of attachments. It can be considered as a stobilus because at least one type of sporophyll appears on the axis. The flowers are either solitary or form groups called inflorescence. The flower is held by a stem-like peduncle whose apical part widens creating a torus or receptacle. The macrosporophylls or carpels are located in the center and they can fuse together forming a pistil thus the ovules are enclosed. This is the main feature of angiosperms. The pistil is surrounded by the microsporophylls or stamens. The stamens consist of filaments and anthers which are located at the top and created by the fusion of 4 microsporangia. The anther has two lobes or thecae (singular: theca) which are united by a sterile tissue, the connective with a bundle. Each theca is made up of two pollen sacs filled with sporogenous tissue. Four layers can be distinguished in the wall of the theca: epidermis, endothecium, transient layer formed by parenchymatic cells and tapetum. Sterile leaves also occur in the flower and they are called perianth. A heterochlamideus flower contains two kinds of leaves, sepals and petals. When the perianth is formed by uniform leaves or tepals the flower is called homoiochlamideus. The petals form the corolla, the sepals give the calyx and all of the tepals are called the perigonium. Some flowers lack of perianth or bear reduced, green leaves. A flower is entire if it contains all of the above mentioned attachments. The sepals are the least modified leaves and they are very similar to foliage leaves considering the anatomy. Each flower component is inserted on the receptacle and they form whorls. When the perianth is located below the pistil, the ovary is superior (hypogynous flower). If the receptacle widens and bends back, the perianth leaves get into line with the ovary; in that case the ovary is half-inferior (perigynous flower). When the perianth is fused to the ovary wall, the ovary is located below the insertion point and called inferior (epigynous flower). The pistil formed by the carpels has three parts: the basal, cavernous ovary is connected to the stigma by the style. The stigma receives the pollens thus modifications increasing the surface are common: it can be lobed or branched. Based on the number of carpels, the gynoecium can be monocarp or polycarp whether it is formed by one or more carpels. When the carpels are fused by their selves creating more pistils, the gynoecium is apocarp. When the carpels create one pistil and the ovary has as many locules as the number of carpels, the gynoecium is syncarp. If the locules are barely separated or the ovary lacks of septums, the pistil is paracarp. The surface of the carpels bearing the macrosporangia is called placenta. The placentation is either parietal when the ovules are located on the pistil wall or axial when they are held by a central axis. If the ovary lacks of septums and axis, the ovules emerge from the base of the ovary and the placentation is central. The macrosporangium of angiosperms is identical with the ovule and it is connected to the placenta by the funiculus. They are covered by a bistratose integument which leaves the ovule open by the micropyle. If the micropyle and the funiculus are aligned, the ovule is positioned straight and called orthotropous. When one side of the funiculus grows faster than the other, it positions the ovule backward and the micropyle faces with the placenta; in that case the ovule is called anatropous. Similar position is created by the bending of the ovule

and it is called amphitropous. The funiculus can be attached to the ovule on its lateral side and if the axes of the two are parallel the position is campylotropous.

7.2. Microsporogenesis, microgametogenesis

Previous to the meiotic division the sporogenous cells are surrounded by a callose wall in the anther. The division results in the formation of microspore tetrads. They either stay together permanently in the callose layer as a tetrad or separate after a while. Their outer wall (exine) is composed of sporopollenin which is a product of the tapetum. As the exine develops the microspores leave the callose wall. The second layer of the wall is the intine which is a microsporous product and its main component is pectocellulose. The exine has species-specific ornamentation which is a result of centripetal thickening. The microspores are uninucleate, their cytoplasm is homogenous with small vacuoles. After significant vacuolization the plasma becomes asymmetric and an unequal division results in the formation of a smaller generative and a larger, vacuolated vegetative or tube cell. The latter one takes up the generative cell by endocytosis. From this point the generative cell is separated from the spore wall but it may have its own wall. After the first division the microspore is called pollen grain. In most species the pollens are dispersed in this 2-cell stage but in others the generative cell is already divided into two sperm cells and the pollens are trinucleate. The sperms stay together and are located near to the vegetative nucleus; the three nuclei form the so called male germ unit. Their sequence has an important role during the double fertilization. If the pollen is binucleate during dispersal, the division of the generative cell happens in the germinating pollen tube. In conclusion, the pollen tubes always contain the sperms when they reach the egg apparatus.

7.3. Megasporogenesis, megagametogenesis

The macrosporocyte (also called megasporocyte or mother cell) is differentiated in the nucellus inside the ovule. It produces a linear megaspore tetrad by division. The megaspores can stay together and some of them may degenerate. Based on how many megaspores form the female gametophyte the development of the embryo sac is monosporic, bisporic or tetrasporic. The mature gametophyte consists of 7 cells. During monosporic development the remaining megaspore near to the chalaza goes under mitotic division three times and produces 8 uniform nuclei. The nuclei move to their places and the gametophyte becomes cellular. At the micropylar end the egg cell and two synergids form the egg apparatus. At the chalazal end three antipodals are located which later help to provide nutrition to the embryo. At the center of the megaspore the remaining two polar nuclei fuse partially to form a large central cell. It develops the secondary endosperm after fertilization. The above described process is also called Polygonum type embryo sac development.

After double fertilization the developing seedling takes up nutrition from the surrounding gametophytic and sporophytic tissues. The seed is the propagating structure containing the mature embryo and it is developed from the ovule. The seed coat layers originate from the integument. The female sporophyte supplies the embryo through the funiculus but after a while it comes off and leaves a scar called hilum. Based on the remaining food storage, the seed can be either endospermic or perispermic (some of the nucellus remains but the endosperm is consumed). If all nutrition from the gametophytic and sporophytic tissues is taken up the seed is supplied by the cotyledons. The seed are enclosed by the ovary. The wall of real fruits develops solely from the ovary, if other tissue (hypanthium or base of the perianth) participates in the formation the fruit is called false. Therefore all fruits originated from an inferior ovary are false. The ovary contains more ovules and each one of them can develop a seed after fertilization but this process requires more pollen grains and germinating pollen tubes.

7.4. Pollination

Matured pollen grains have to reach the appropriate stigma. Pollinators can be animals – mainly insects – wind or even water. It is important to transport the pollen grains onto the stigma of the same species. In low diversity ecosystems, wind-pollination can be effective, but those species that scattered in large area, the animal-pollination is more efficient. In tropical forest we can find beautiful examples of extremely specialised interactions between plants and animal pollinators. As a result of long coevolution the success or even survival of the partners depends on this collaboration. This specialisation ensures that the pollinator delivers the pollen grains to another flower of the same species. In our climate there are both wind-pollinated and animal-pollinated species. However bees as the most important insect pollinators visit many different flowers, at a given time they prefer only one species. This behaviour ensures that they carry pollen to the same species. Flowers are also actively involved in the directing

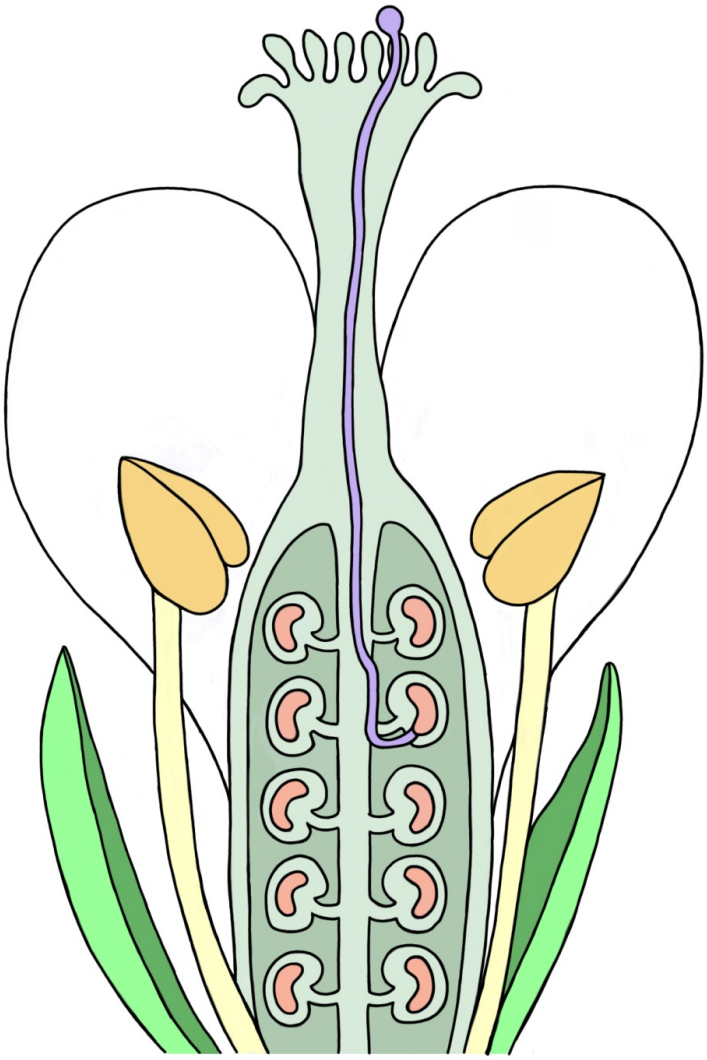
of pollinators, as nectar production is not continuous. Of course, we also have specialised plant-pollinator interactions. For example, the flower of an orchid (*Ophris fuciflora*) mimic female bumble-bee, provides a false promise of sex for male bumble-bees. The structure of flower and the chemical composition of attractants determine the pollinator. The flowers offer pollen, nectar, protection etc. for pollinators, but sometimes cheating. Of course there are insects as well, who steel the nectar without transporting the pollen. Bumble-bees often make holes at the base of narrow, long flowers dedicated for other pollinator to reach the nectar. The form and colour of flowers is the result of adaptation for pollinators.

The target of pollination is generally a flower of another plant, and self-pollination is quite rare. Selfing for a long time is genetically detrimental, and plants developed different ways to avoid it. Time shift in pollen dispersal and stigma receptability is a common solution. We call it proterandria when pollen dispersal is the earlier, and proterogynia, when stigma ripening is the first. Another solution is the pollen incompatibility. Self-incompatibility has two different types. Both incompatibilities are a genetic mechanism that control the genotype similarities and prevent fertilisation. In the case of sporophytic self-incompatibility stigma block the germination of pollen grains that contain similar proteins to the stigma on the surface. As those proteins in the pollen wall are coming from the sporophytic tapetum, it called sporophytic incompatibility. In the case of gametophitic incompatibility, all the pollen grains permitted to germinate and the control of genetic similarities takes place only in the stigma. As pollen tube is a gametophyte structure it called gametophitic incompatibility.

According to the surface of the stigma, we distinguish wet and dry stigma. Wet stigma covered with a sticky exudate containing sugars and different chemicals. This exudate secreted under the cuticle, and it invades the surface of the stigma after rupture of the cuticle. The shape of stigma, the length of papillae, and the area of the receptive surface are developed during the long adaptation to pollination. Wind-pollinated plants generally have feather like, tiny quite large stigma, ensure that airborne pollen grains easily stick on them. For successful pollination one or several pollen grain not enough even for those species that have only one ovule in the ovary. Stigma provides surface for far more pollen grains than strictly enough for fertilisation. There is competition between pollen grains and growing pollen tubes for fertilisation of ovules.

7.5. Pollen tube grows

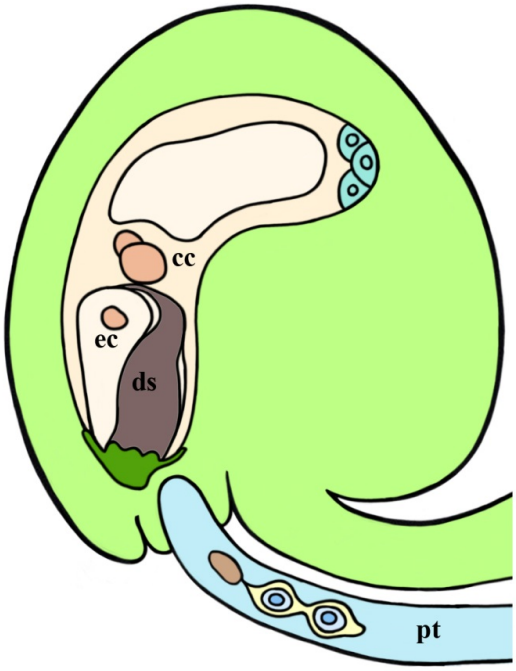
As a result of successful pollen stigma interaction, an intimate connection is established between the stigma papilla and the pollen wall. Pollen grains take up water and other compounds provided by stigma papillae. Due to the swelling of pollen grains, the pores or slits – that the germinating places of the pollen tube – are exposed, and pollen germination can start. The intine layer protrudes and pollen tube grows onto the surface of the stigma. The vegetative cell enters into the tube with the vegetative nucleus first, and generative cell or sperm cells behind it. The pollen tube enters the tissue of stigma and grows downward in the intercellular space or loose walls of the transmission tissue. The style can be solid or hollow type with a preformed channel covered with epithel cells. Pollen tube grows on the tip where intensive vesicle traffic can be seen towards the surface. The material of tube wall is significantly callose, a 1-3 glucose polymer. The surrounding tissues feed the pollen tube, supply energy and material source for growing. The distance between pistil and ovule is sometimes a very long way to go (e.g. 20-30 cm in maize). During pollen tube grows the vegetative cell is always situate at the tip region and left empty space behind. To separate the empty region of the tube from the growing tip the cell periodically creates transversal walls. Reaching the end of the style, pollen tubes enter into the ovary and continue their way on the inner surface of the ovary or on the central axis, if any. The guidance of tube is partially mechanical (elongated cells in the transmission tissue) and partially chemical. The latter is more important near the ovules where pollen tubes are attracted by chemical signals toward the micropyle.



Pollen tube growth

7.6. Fertilisation

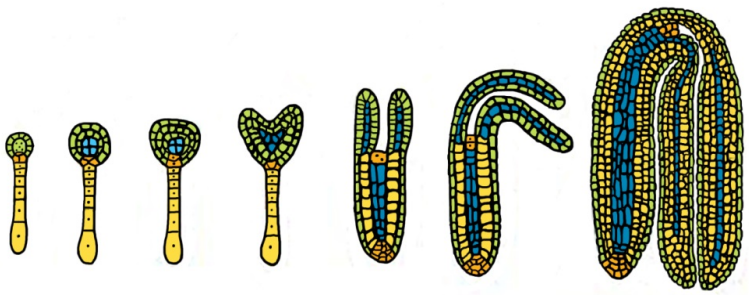
After successful pollination characteristic changes take place in the embryo sac. The joined nuclei of the central cell moves toward the egg apparatus, and in the majority of plants one of the two synergids starts to degenerate. This degenerating synergid is the target that pollen tube grows into. This synergid creates a protrusion between the basal surface of the egg cell and the neighbouring central cell. After entering the synergid cytoplasm, the pollen tube opens and releases the sperm cells into the synergid. The sperms are transported through the protrusion of the synergid to the place of fertilisation, and one of them fuse with the egg cell, the other with the central cell. The fusion is not always complete, and a part of the cytoplasm can be excluded, which is one of the possible mechanisms of maternal inheritance of cytoplasmic genes.



Fertilization ec=egg cell, cc= central cell, ds= degenerating synergid, pt= pollen tube

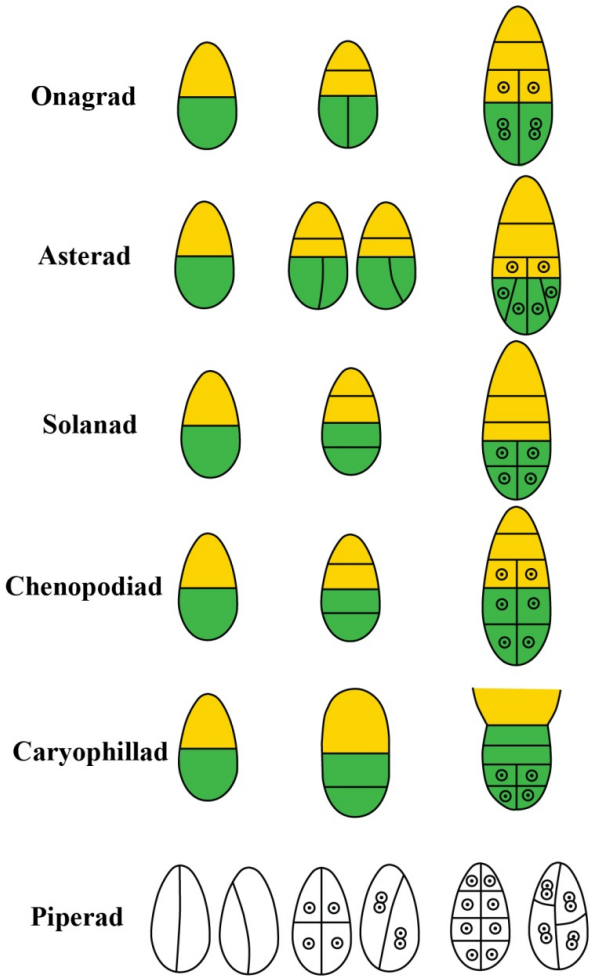
7.7. Embryo development

During the first mitotic division of the zygote the chromosomes of the sperm and egg cells are mixed and divide with common mitotic spindle producing two cells. The wall of this division in the vast majority of species is formed in transversal direction. The cell face the micropyle is the basal cell, while the chalasal one is the apical cell. This division is the first step of proembryo development. There are different ways to develop the embryo from these two cells. Only a part of the developing structure takes place in the mature embryo formation (embryo proper) while the remaining cells forms a short living structure, the suspensor. In the well-known embryo development of Arabidopsis, and Capsella bursa-pastoris, the majority of the embryo proper develops from the apical cell, and basal cell forms the filamentous suspensor. A few cells of suspensor however that neighbouring the cells developed from the apical cells take part in the organisation of root apex. This region is the hypophysis. The apical cell with subsequent oblique divisions forms a 2, 4, and 8 cell structure. The next division is periclinal, and the proembryo become 2 cell layered globular structure. The outer forms the epidermis layer with anticlinal divisions, while the inner one dividing in different directions forms the body of the embryo. The suspensor cells take up nutrients from the surrounding tissues and transport to the developing embryo proper. With the initiation of the cotyledons the globular proembryo becomes heart shaped. In this stage we can distinguish the shoot apical meristem between the cotyledons, and the root meristem in the hypophysis region. The suspensor cells degenerate, and after intensive elongation of the cotyledons, the embryo enter into the torpedo stage. Finally the embryo matures and the division stops.



Embryo development (*Capsella*)

This division pattern (Onagrad or Crucifer type) is only one of the many types of embryo development. The different types cannot be connected to taxonomic groups; lilies have same type as Arabidopsis, while Asteraceae and Gramineae belong to the same Asterad type. Consequently there is no typical monocot and dicot embryo development.



Developmental types of proembryo

7.8. Endosperm development

In angiosperms during double fertilisation the central cell is also fertilised. This cell develops into endosperm, a storage tissue, that can be ephemeral, storing reserves temporarily, until the cotyledon or the embryo body absorbs them, but in many species endosperm remains a living tissue that stores oils, proteins and carbohydrates for the germinating embryo. Endosperm development follows different pathways. In nuclear development the endosperm undergoes free nuclear divisions before the walls are formed. In cellular type cell division is normal, with immediate wall formation. In helobial type the first division is unequal with wall formation but the bigger cell follows the nuclear devepopmental pathway. The smaller cell remains inactive.

Chapter 8. Fungi

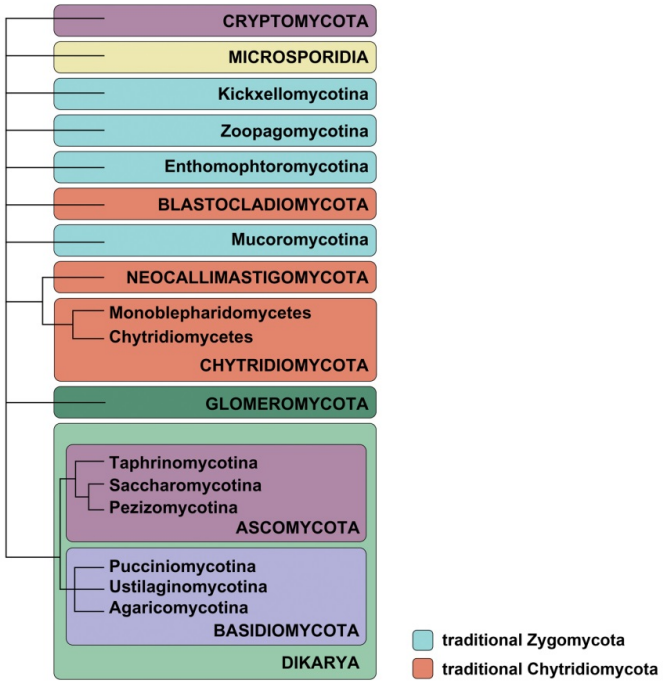
(Gábor M Kovács)

Different lineages of the tree of eukaryotic organisms contain organisms considered as fungi.

The Opisthokonta clade of eukaryots contains the main group, the true fungi (Regnum Fungi). Opisthokonta belongs to Unikonta as does the Amoebozoa lineage, which contains the Eumycetozoa, the so-called slime-molds still considered by some outmoded approaches as fungi. Among the Chromalveolata are the Straminipila with the Oomycota fungal group.

So, “fungi” as a term does not represent a monophyletic group. The main groups differ fundamentally, probably the only common feature being the lack of plastids, indicating that fungi are heterotrophic organisms. This chapter focuses on the true fungi (Regnum Fungi) and Oomycetes but excludes slime molds. When features refer to other groups as well, that will be indicated. The main groups of the true fungi will be discussed according to their “traditional” grouping, so only seven groups will be recognized: the Microsporidia, Cryptomycota (described recently as a basal lineage of true fungi), Chytridiomycota (these fungi will be termed as chytrids), the Zygomycota (these fungi will be termed as zygomycetes), the Glomeromycota, Ascomycota and Basidiomycota. These latter two form the group Dikarya refering to the dikaryotic stage of the life cycle existing in both group. Three main groups, subphyla will be mentioned in dikarya phyla – the Saccharomycotina, Taphrinomycotina and Pezizomycotina of Ascomycota and the Pucciniomycotina, Ustilagomycotina and Agaricomycotina of Basidiomycota.

The main goal of this part is to briefly introduce some terms and features of fungal organization and of plant-fungal interactions. Diverse mycological courses at the university offer more detailed information about different aspects of the amazing word of fungi.

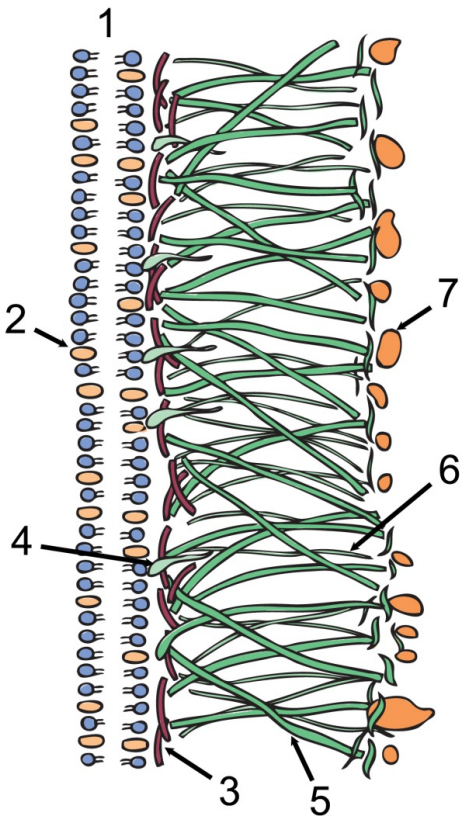


The main groups of the Kingdom Fungi. The traditional Chytridiomycota and Zygomycota are indicated; in this chapter, fungi belonging to these groups are referred as chytrids and zygomycetes, respectively.

8.1. The fungal cell

8.1.1. The fungal cell wall

Both the structure and composition of the fungal cell wall have unique characteristics. The polysaccharide β(1,4) N-acetil-glucose-amin, generally known as chitin, is a unique cell wall component of the fungi, but the amount of chitin of cell walls of different groups may differ strikingly, e.g., baker's yeast has only a small amount (1% of cell wall dry weight) of chitin in its cell wall. In some groups (e.g. in some zygomycetes) the chitin is partially deacetylized by an enzyme (chitin deacetylase) and so the cell wall will contain chitosan (deacetylized chitin). The chitin is synthesized by the membrane attached chitin synthase enzyme. Its zymogene is transported into the cell membrane by the vesicles called chitosomes. The fungal cell walls contain polysaccharides mainly β(1,3) and β(1,6) glucans synthesized by the transmembrane glucan synthase enzymes. Most proteins of the cell wall are present in glycolized form (even 90% of the proteins could be glycolized). A majority of the glycoproteins are mannans or mannoproteins, the proteins being connected by mannose. Some proteins are anchored in the cell membrane and play crucial roles in cell wall integrity.



Schematic structure of the cell membrane and cell wall fungi. 1: cell membrane; 2: ergosterol; 3: chitin; 4: anchore-proteins; 5: β(1,3) glucan; 6: β(1,6) glucan; 7: mannoproteins.

The Oomycetes have also cell walls and some species have a small amount of chitin in their walls, but the vast majority has no chitin at all. On the other hand, their cell walls contain cellulose, a β(1,4) glucan, which is never present in true fungi.

8.1.2. The fungal cell membrane

The organization of the fungal cell membrane is the same as the general eukaryotic cell membrane. Nevertheless, special fungal sterols affect membrane fluidity of the fungi. The most widely known are the ergosterols, but metilen-

and etilene cholesterols, brassicosterols and cholesterols occur in some fungal lineages. The special membrane components have great importance in antifungal therapy; several fungicides target those molecules or their synthesis pathway. For example, the azols target the ergosterols and disintegrate the membrane, whereas poliens target the synthesis pathway of ergosterols.

8.1.3. The flagellum

Among the true fungi only chytrids have flagella. The motile zoospores have one posterior flagellum (opisthokont) with no tinsel (whiplash). The flagellum has 9+2 microtubules arranged in the typical eukaryotic pattern. The chytrid rumen fungi have posteriorly multiflagellate (up to 16 whiplash flagella) zoospores. The organization of the flagellar apparatus at the base of the flagellum is a characteristic feature of different groups of the chytrids.

Zoospores of fungi belonging to the Straminopila lineage have one or two flagella in anterior (akrokont) or lateral (pleurokont) position. At least one of the flagella is tinsel, the special straminipilous flagellum type; on their surfaces, at the position of two definite microtubules, these flagella have two rows of very fine hairs with special branching structures. The tips of the flagella are narrower than the main body of the flagellum as the two central microtubules are longer than the surrounding nine.

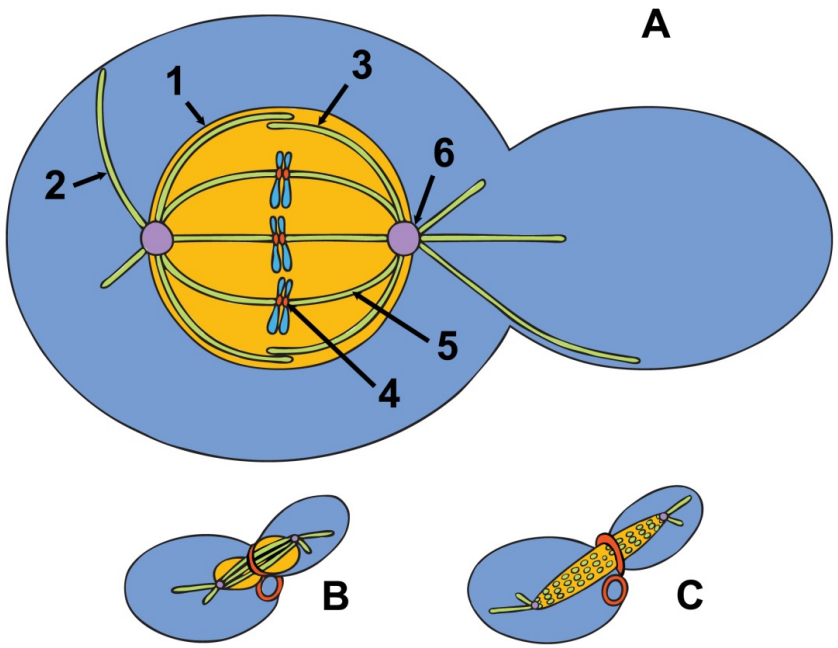
8.1.4. The nucleus

The fungal genomes belong to the small eukaryotic genomes, though some have relatively large or extreme small genomes, too. Considerable differences occur between the genome sizes of oomycetes (e.g. *Albugo laibachii* 37 Mb, *Phytophtora infestans* 240 Mb). The fungal chromosomes and nuclei are relatively small, and the chromosome number generally is also low (4-8), although much higher chromosome numbers may occur as well (e.g. 21 of *Ustilago maydis* (corn smut)).

The number of nuclei in single cells may vary albeit is characteristic of different fungal groups and/or life stages. Coenocytic hyphae and thalli have many nuclei in each cell or thallus. For example, the species of the coenocytic Glomeromycota could have even thousands of nuclei in one asexual chlamydospore. Special stages of the lifecycle of fungi with monokaryotic and dikaryotic hyphae: Ascomycota of the family Morchellaceae belonging to the order Pezizales (cup fungi) have multinuclear ascospores, sometimes even more than eight nuclei in one spore. Dikaryotic hyphae, i.e. with two nuclei in one cell, are unique to the Ascomycota and Basidiomycota. That is why the clade of those two groups is called Dikarya. The dikaryotic hyphal stage is relatively short in the life cycle of Ascomycota, where such hyphae are formed only at the sexual reproductive, ascomata and ascus stages. In contrast, the life cycle of the Basidiomycota is dominated by the dikaryotic phase.

8.1.5. Cell division

Baker's yeast has long served as the model organism of the eukaryotic cell cycle and cell division. Accordingly, our knowledge of fungal cell division is relatively strong though far from complete, especially about the regulatory steps of meiotic cell division. Many fungi perform special, so-called closed cell division (both meiotic and mitotic), during which the nuclear membranes, thus the nuclei, remain intact. These cell divisions are endonuclear, as chromosomes are segregated within the nuclei. The special organelles, the spindle pole bodies (SPB) play a crucial role in the orientation of microtubules (MTs); in some fungi, other MT-organizing-centers (MTOCs) also appear during cell division. The kinetochore MTs connected to the SPBs segregate the chromosomes within the nuclei, while the interpolar MTs, also connected to SPBs, help separate the two poles of the nucleus. The astral MTs are outside the nucleus, and connected to SPBs. The size, form and organization of the SPBs may vary between different fungal groups.



Schematic structures of the mitosis of budding yeast. Cell in the **A**: G2-M phase **B**: anaphase **C**: early thelophase. 1: nuclear membrane; 2: astral microtubules (MT); 3: interpolar MT; 4: kinetochor; 5: kinetochor MT; 6: spindle pole body (SPB).

Closed, endonuclear mitosis has great importance in hyphal growth, which is based not on cell-division but on hyphal tip-growth, hence the divisions of nuclei follow the extending growing hyphae. Unicellular fungi have special cell division types. During the mitosis of budding yeasts no equal offspring cells appear, but during the budding the new cell grows out from the mother cell. After endonuclear mitosis ends the new cell separates from the mother cell. In fission yeasts (*Schizosaccharomyces*) the mitosis shows different mechanisms that are called fission. After endonuclear mitosis of the nucleus and migration of the new nuclei into the poles, an actin ring forms and constricts as the new septum develops and segregats the two cells. Both yeast-types serve as model organisms not only for cell cycle regulation but also for the mechanisms of different hyphal growth and developmental processes. The budding cells of baker's yeasts emerge at a certain point of the cell, and the budding itself is a polarized grow similar to the directional growth of hyphal tips.

8.1.6. Special cell organelles

Several cell organelles as mentioned above are unique to fungi. For example, the chitosomes which transfer the zymogenes of the chitin synthase to the cell membrane, or the spindle pole body (SBP) which plays a crucial role in endonuclear cell divisions as well as many other processes such as synchronized nucleus migration of Dikarya and the migration of the nuclei into the basidiospores.

Nevertheless, several other organelles are characteristic of fungi. The hyphal ascomycetes have a special cell organelle in their hyphae, the Woronin-body. These organelles generally are located around the septal pores. They are peroxisome-related organelles with single-layered membrane covers, and their body is mainly formed by various proteins;the exact chemical composition of Woronin-bodies is not well understood. The number and the shape of Woronin-bodies varies, albeit probably characteristic to a taxon, e.g. different families in the order of cup fungi (Pezizales) have Woronin-bodies with different forms. Plugging of the septal pores when hyphae are damaged could be one of their main functions. However, in *Magnaporthe grisea*, the plant pathogen causing brown rot of rice, Woronin-bodies help the fungus ito resist host plant defenses and survive in tissues poor in nutrients.

8.2. Organization of fungi

8.2.1. Thallus

The coenocytic thallus of chytrids is considered as a distinct organization type. The multinuclear thalli have various forms in Chytridiomycota. The motile zoospores of chytrids develop in zoosporangia, and also the chytrids can form thick-walled resting structures. The entire thallus of some biotrophic chytrids resides within a cell of the host and has no separate vegetative and reproductive parts: the whole thallus will develop into a reproductive structure (zoospores, gametes or resting spore). In this case the thallus is holocarpic. Eucarpic thalli have a reproductive part and a vegetative, so-called rhizoid part serving for nutrient uptake and fixation of the fungi. The eucarpic thallus is monocentric when producing only one sporangium and polycentric when several sporangia develop on one thallus. The same chytrid species can develop both mono- and polycentric thalli. Monocentric thalli can develop completely in a host cell, or only the rhizoids colonize the cells, these are the endobiotic and epibiotic thalli, respectively.

8.2.2. Unicellular organization

Unicellular organization occurs in several fungal groups. The most widely known are the yeasts, a term used for a form-group of unicellular coccal fungi that reproduce by budding. Although the unicellular yeast form is discussed before hyphal organization it should be emphasized that the yeast form evolved from the hyphal form, so we consider hyphal organization to be an ancestral, plesiomorphic character. The best known yeasts belong to the Saccharomycotina subphylum of the Ascomycota, represented by fungi like the baker's yeast (*Saccharomyces cerevisiae*) and the human pathogenic *Candida albicans*. There are basidomycetous yeasts as well, e.g. the important human pathogen *Cryptococcus neoformans*. This species belongs to the Tremellales (Agaricomycotina) together with mushrooms with macroscopic fruitbodies. This also shows that the yeast-form evolved in several fungal lineages. Some fungi spend only a phase of their life cycle as yeasts. The meiospores (basidiospores) of the smut fungi could live and propagate as saprotrophic yeasts. They convert into the plant pathogenic phase when two compatible cells meet, fuse and form a dikariotic hypha that colonizes the host plant. As mentioned previously, because of their special mitosis, the fission yeasts are distinguished from the budding yeasts. Nevertheless, both cellular organizations are coccal, as they cannot move by themselves. This feature fundamentally affects their nutrient uptake and their possibility to exhaust their environment on solid surfaces. They form similar colonies as bacteria, the size of the colony being determined and limited by exhaustion of the substrate.

Unicellular organization can be found in several fungi with motile zoospores in their life cycle. In Kingdom Fungi only the chytrids have both sexual and asexual motile flagellar cells which are generally posterior whiplash opisthokonts. Oomycetes have one or two akrokont or pleurokont flagella, at least one being a tinsel.

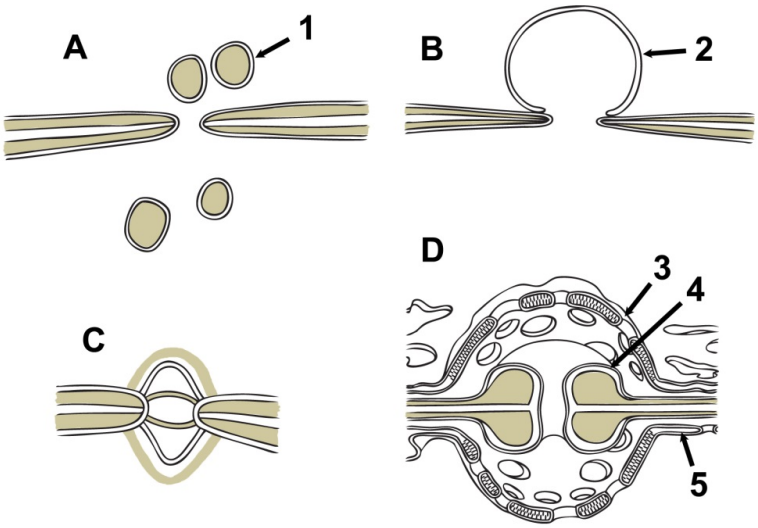
Unicellular forms were detected and visualized when the recently described basal lineage of Regnum Fungi, the Cryptomycota, was discovered. The spore-phase of the obligate endocellular parasite *Microsporidia* might be considered a special unicellular form as well, but it is beyond the scope of this chapter to discuss cellular organization of those highly specialized organisms.

8.2.3. Hyphal organization

The hyphal organization of fungi is unique among the living organisms, there being few examples with similar growth and organization features, such as structures of some bacteria, the pollen tubes of plants, and some neuronal projections. Hyphae have a tubular structure, and those tubes can be divided by cross walls called septa. Septal hyphae are characteristic of the hyphal ascomycetes and basidiomycetes but also can be found in some minor basal groups. Non-septate hyphae are characteristic of most Zygomycota and the arbuscular mycorrhizal fungi (Glomeromycota). Of course, these hyphae also develop cross walls when, for example, reproductive structures (e.g. sporangia) develop or to isolate damaged or senescent hyphal regions. The non-septate hyphae are coenocytic, so one continuous hyphal segment may contain multitudes of nuclei. Then there are monokaryotic hyphae, when one nucleus is in one hyphal segment or the special dikaryotic hyphae when two nuclei are in one segment. Such hyphae occur only in the phyla Ascomycota and Basidiomycota, as mentioned above, the reason why the clade of those two groups is called Dikarya.

The cross walls of the hyphae, the septa, can have different anatomies. Completely continuous septa with no pores do occur, but septa with some kind of pore are more general or even septa with several pores in some groups. The anatomy of the septal pore can be characteristic of different phylogenetic lineages. Although zygomycetes generally have coenocytic, i.e. nonseptate hyphae, some have characteristic septa with pores containing special plugs.

Ascomycetes generally have septa with simple pores, but the anatomy of those pores and the organization of organelles surrounding them may vary and be characteristic of some groups.



Structures of some septal pore types. A: Simple pore of a vegetative hyphae with Woroning bodies; **B**: Simple pore with pre-cap of a generative hypha. A-B: Ascomycota. C: Simple pores with different structures. D: dolipore with parenthesome. C-D: Basidiomycota. 1: Woronin-body; 2: pore-cap; 3: parenthesome; 4: dolipore; 5: wall-ER.

Membranous structures, special striate plugs in the pores or even pore-caps can cover the pore. The Woronin-bodies discussed above generally are detectable near the septal pores, too. The septal pore anatomy of vegetative and generative (ascogenous) hyphae of the same ascomycete species may differ significantly, and the pore organization of vegetative hyphae is generally more complex than that of generative hyphae.

Basidiomycete hyphae have diverse septal pore organization, too. Some smut fungi (in Ustilaginomycotina) have no septal pores. Several groups in Ustilaginomycotina and Pucciniomycotina have simple pores. A special pore anatomy, the dolipore, is exclusive to the phylum Basidiomycota. The border of this pore is swollen like a donut, and different structures (e.g. membrane-like bands) could occur in the tube of the pore. The dolipore can be covered by the parenthesome, a membrane organization continuous with the wall endoplasmatic reticulum (ER). The parenthesome can be sacculate, continuous or porate.

Bear in mind that the pores represent a direct physical connection of neighboring hyphal segments, their cytoplasm is continuous. Cellular organelles can migrate across the pores, even nuclei can sometimes migrate to neighbor segments. This is one reason why hyphal segments cannot be considered as analogous to the autonomous eukaryotic cell.

8.2.4. Mycelium, tissue

Fungal hyphae can group together to form a more or less organized multicellular structure resembling tissues of multicellular eukaryotes. However, these are not real tissues, but as the literature in English uses this term, we also do so, but bear in mind that fungal tissues do not fulfill the definition of real tissues.

We term the organized hyphal mass a mycelium. Although simple hyphae can usually be visible, the mycelial structures are the more obvious fungal parts. The several different types, forms and levels of mycelial organization have different functions. Characteristic structures include rhizomorphs, hyphae grouped together to form cord-like structures. Rhizomorphs help to find and exploit the nutrients of the environments of the fungi, but they can also

serve as resting propagules and, being robust structures, they provide physical integrity for the fungi. They can grow to various distances but some are extremely effective, such as *Serpula lacrymans*, whose rhizomorphs can grow for several meters to find woody substrates, or members of the genus *Armillaria*, which includes the largest living organisms. The robust rhizomoprhs of such species helps to preserve the multi-hectare-sized continuous genet of the *Armillaria solidipes*. Differentiated rhizomorphs have a thick-walled, compact rind covering their surface and the medial part consisting of hyphae with thinner walls and bigger lumina. Some ectomycorrhizal fungi have differentiated rhizomorphs with central hyphae of large diameter and partly or totally dissolved septa, making transport more effective. One concept uses the term rhizomorph only for differentiated structures and hyphal cords when there are no differentiated parts, only the cord-like organization of similar hyphae.

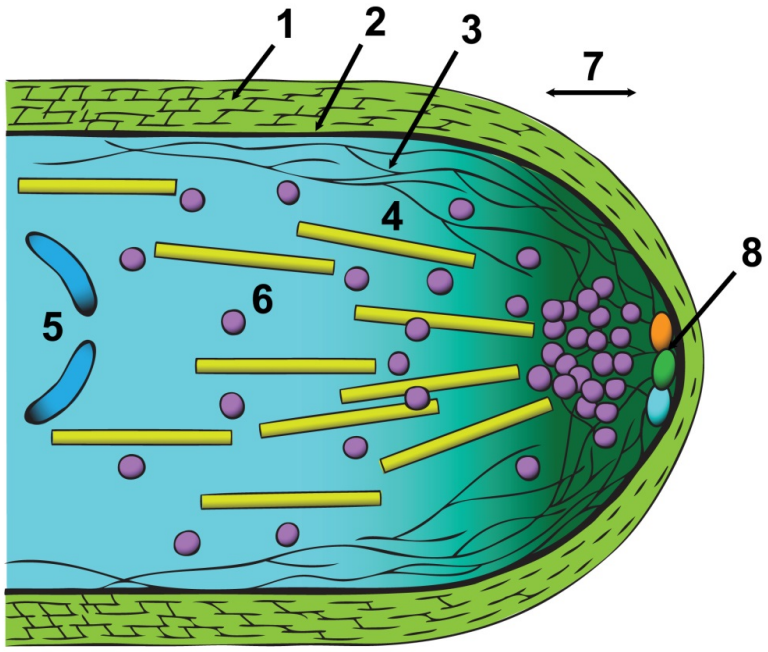
The hyphal mantle of ectomycorrhizae is another characteristic mycelial tissue that can even represent the main biomass of an ectomycorrhizal root tip. The two main anatomical types of those mantles are plectenchymatous, when the hyphae forming the mantle can be easily detected, or pseudoparenchymatous when it to be composed of nontubular cells such as inflated, polygonal or isodiametric in shape. We use the same terminology for other layer-like tissues formed by hyphae, e.g. the peridium (excipulum) enclosing sporocarps. Several subtypes of the two main types have been defined. For example, two main versions of the pseudoparenchymatous type are the angular and the epidermoid, depending if the cell walls are straight or wavy, respectively.

Sclerotia comprise other important mycelial structures, resting bodies which can tide the fungus over suboptimal periods. Their hyphal tissue is kept together by an extracellular glucan matrix as well. Sclerotia with differentiated tissue may have a melanized compact rind and a medular tissue with thinner walled hyaline hyphae. Similarly to rhizomorphs, sclerotia are defined in several different categories. *Botrytis cinerea,* a well known sclerotium-forming fungus, the plant pathogen casual agent of grey-rot, whose sclerotia overwinter on plant stems; the life cycle of the fungus starts from those sclerotia in the next vegetation period. Another widely known sclerotium-forming fungus is the ergot (*Claviceps purpurea*), which infects cereals and forms sclerotia in their spikes. These sclerotia contain the medically important ergot alkaloids in high concentration. The sclerotia overwinter and another mycelial structure, the stroma, develops from them during the spring. This stroma has a stem-like part and a head in which several perithecia develop to produce asci and ascospores.

Mycelial tissues form the fungal fruiting bodies, the sporocarps. The main functions of sporocarps are the support and development of spore producing structures, to hold and protect them and to help the spore dispersal. Sporocarps are sexual or asexual, depending on whether they produce sexual or asexual spores. Sexual sporocarps occur in the Ascomycota and are termed ascocarp or ascoma, and Basidiomycota (basidiocarp or basidioma). Some zygomycetes also form sexual sporocarps. The main characteristics of sporocarps will be discussed at the part dealing with sexual reproduction.

8.3. Characteristics of hyphal growth

As discussed above, hyphal growth has unique mechanisms and organization characteristic of fungi and only few other organisms show similar features. Hyphal growth is apical with continuous increase and extension of the cell membrane and cell wall at the hypal tip. Several driving forces are directed to the hyphal tip, such as like turgor pressure, ion concentration gradients and organization of cytoskeleton. The growth can be trophic, when the main driving force of the growth is nutrient or water uptake as the substrate is depleted. The growth generally has direction and is polarized, but few examples of the mechanisms are well understood.



Organization of a growing hyphal tip. 1: cell wall; 2: cell membrane; 3: actin; 4: microtubules; 5: Golgi, 6: vesicules; 7: Spitzenkörper; 8: polarisome; The color gradient indicates the concentration gradient of Ca^{2+}.

Polarized, directed growth occurs when new hyphae start to develop e.g. when a spore germinates or a hypha branches. In the higher groups of fungi a special organization called “Spitzenkörper” could appear in the tip of the growing hyphae. This electron opaque part contains many vesicles transporting cell wall materials or the zymogene of the chitin synthase, these latter vesicles are the chitosomes. Intensive exocytosis occurs at the tip region and endocytosis at a proximal region of the hypha. A protein complex called polarisome is located at the growing hyphal tip close to the cell membrane, which complex has a crucial role in determining the direction of hyphal growth and in organizing the actin microfilaments in the hyphal tip. We can also find the same polarized growth when the budding progeny cell develops in budding yeasts.

8.4. Reproduction of fungi

The fungal life cycle of the fungi has two main types of reproduction: sexual and asexual. Some fungi show only one known reproduction type. Asexual forms (anamorph) were often described separately and given different names than the sexual form (teleomoph). The complete form having both reproductive forms is called a holomorph. Fungi known only as anamorphs were previously grouped into the form-group Deuteromycetes (Fungi Imperfecti). This group is not used anymore, because with molecular phylogenetic techniques the systematic position of a fungus can be determined even if the sexual structures are not known.

8.4.1. General characteristics of sexual reproduction of fungi

Meiotic development of haploid nuclei, their fusion, and the emerging diploid nuclei or zygote are the key-steps of sexual reproduction. If a diploid nucleus/cell undergoes further mitotic divisions, we consider that as the diploid phase of the life cycle. The haploid nuclei/cells arise from the meiosis of the diploid nuclei, and if the haploid cells go through mitotic cell divisions, that is the haploid phase of the life cycle. A life cycle is considered as haplo-diploid if both phases exist. Generally a phase exists if mitotic cell divisions happen in that nuclear-state. If the first division of the diploid zygote/nucleus is meiotic, the nuclei return to the haploid state immediately and the life cycle is haploid. The life cycle is diploid when only the haploid cells/nuclei represent the haploid state and fuse after they arise from a meiosis. Both Ascomycota and Basidiomycota have a special phase in their life cycle,

the dikaryotic phase, when two haploid nuclei are in one hyphal segment. These dikaryotic hyphae develop when two monokaryotic cells or hyphae fuse (somatogamy or plasmogamy) but their nuclei do not.

When a monokaryotic haploid stage is represented by distinct cells that fuse, we term them gametes and the fusion is called gametogamy. The gametes can develop in special structures termed a gametangium.

The differences necessary for successful sexual reproduction of fungi are represented by mating types. Homothallic fungi can sexually reproduce even if only one strain originating from the same meiospore/hypha is present, whereas heterothallic fungi require two different compatible mating types to complete sexual reproduction. Mating types are determined by mating loci (MAT loci). Homothallism has several modes, the simplest being when one version of the MAT locus and the strains/cells containing it are compatible and can undergo sexual reproduction. The main modes of heterothallism are grouped according to the number of MAT loci. The simplest version has one MAT locus with two types (alleles) and two strains/cells with different MAT loci can successfully complete sexual reproduction. This type is the bipolar heterothallism. In tetrapolar heterothallism two MAT loci with at least two alleles determine the mating type. Two strains/cells can complete sexual reproduction only if both MAT loci are different. Several genes can function as MAT loci; often they code pheromones and their receptors or regulate genes coding such products.

8.4.2. Sexual reproduction and its structures in the main fungal groups

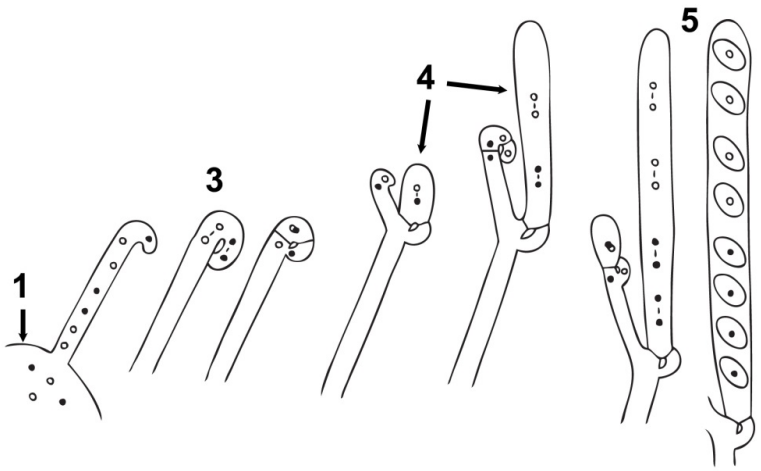
Names of the main groups of fungi were coined according to the structures developed during their sexual reproduction. Sexual reproduction of the main fungal groups differs significantly between each other and even within those groups.

Oomycetes produce gametangia. The oogonium contains haploid oocytes produced by meioses. Beside the oogonium, antheridia develop and produce haploid nuclei via meioses. These nuclei migrate to oogonia across a fertilization tube developed by the oogonium to fertilize an oocyte. Their fusion produces diploid oospores that germinate and produce coenocytic non-septate hyphae with many nuclei. This life cycle is diploid. Differences in lifecycles occur within the group: different numbers of oocytes develop in the oogonia, and the oospores can produce not only coenocytic hyphae but also sporangium-producing zoospores. Both the oogonia and the antheridia can produce hormones that reciprocally stimulate and regulate their development.

Chytrids have several different types of sexual reproduction. Some have gametes which fuse (gametogamy). They can be similar in size (izogamy) or different (anyzogamy). Moreover, a bigger, non-motile oocyte sometimes develops and is fertilized by a motile gamete (oogamy). In some chytrids the gametangia fuse (gametangiogamy) and in others gametes fertilize gametangia. Somatogamy can also happen when thalli of chitrids fuse.

Gametangia develop during the sexual reproduction of zygomycetes. Compatible coenocytic hyphae with haploid nuclei develop gametangia, generally opposite to each other, and these gametangia fuse (real gametangiogamy). Afterwards, the nuclei also fuse (karyogamy) and a thick walled, generally spherical zygospore develops. Homothallic zygomycetes do not need two gametangia for sexual reproduction and consequently could produce azygospores. Zygospores are held by suspensors which develop from the remaining parts of the two opposing hyphal outgrowths. The name of the Zygomycota originated from the Greek name of yoke (“zygos”), as the opposing gametangia and the zygospore held by two suspensors resemble this structure. The zygospore, strictly speaking, is not a spore but a resting zygote. After karyogamy the diploid nucleus undergoes meiosis, in some cases during spore development, in others during germination of the zygospores. This life cycle is haploid. When the zygospore germinates, a sporangium developed from the hypha produces endogenous haploid mitospores.

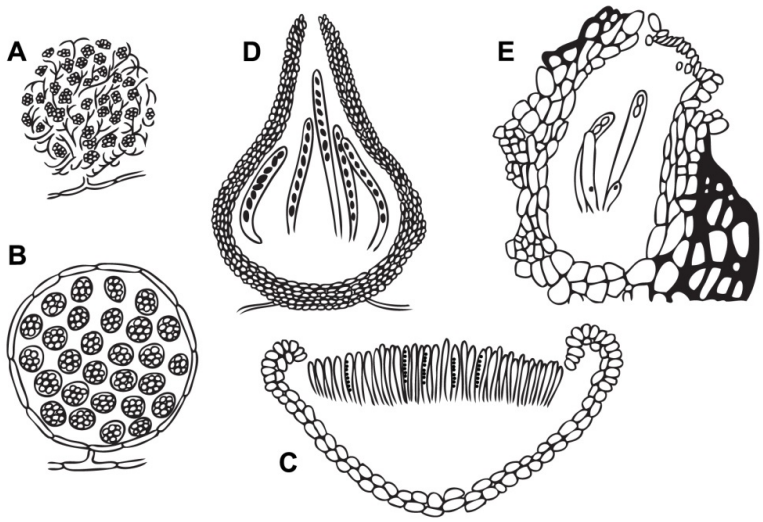
The name of the Ascomycota refers to the sac-like structure (ascus) in which the meiospores (ascospores) develop. The reproductive features discussed below refer to the hyphal taxa of the Pezizomycotina. An ascogonium develops with haploid nuclei and produces a trichogyn, a fertilization tube to the antheridium developed from a compatible monokaryotic hypha nearby. The haploid nucleus migrates from the antheridium to the ascogonium, from which dikaryotic hyphae with two nuclei of different origin will develop in each segment. The dikaryotic hyphae form crosiers which enable proper segregation of the two different nuclei after mitotic cell division.



Development of an ascus. 1: ascogonium, 2: ascogenous hyphae; 3: crozier; 4: ascus initial; 5: ascus with ascospores.

These dikariotic hyphae can participate in ascoma development. During ascus development the two nuclei of the terminal cell of an ascogenous hypha fuse (karyogamy). The diploid nucleus undergoes meiosis, and a post meiotic mitosis of the haploid nuclei will result the general eight nuclei of the eight ascospores. The life cycle of hyphal ascomycetes is dominated by the haploid phase; the dikaryotic phase is relatively short and a diploid nucleus is present only during karyogamy, followed immediately by a meiosis. The characteristics of the asci (shape, number of ascospores, organization of spores, chemical reactions of ascus wall, ascus wall layers etc.) are important features in the taxonomy of these fungi. Ascospores vary in shape and in size from a few microns to a couple of hundred microns. Both unicellular and septate spores can be found with few (e.g. *Lewia*) or many (e.g. *Cordyceps*) segments. The numbers of nuclei in ascospores can differ, e.g. the Morchellaceae (Pezizales) the ascospores have many nuclei. Ornamentation of spores can serve as an important taxonomic character.

The asci of hyphal ascomycetes may develop in different types of ascomata.

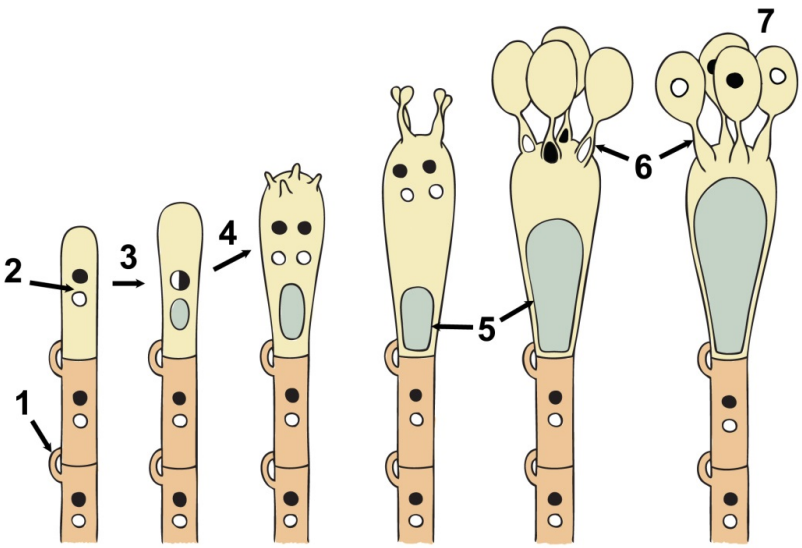


Types of ascomata. A: gymnothecium; B: cleistothecium; C: apothecium; D: perithecium; E: pseudothecium.

The asci are surrounded by a loose hyphal net in gymnothecia. In cleistithecia the asci develop in a closed spherical ascoma with no definite operculum. A chasmothecium is a special type of cleistothecium wherein the asci form in a single basal fascicle; this ascoma is characteristic of the powdery mildews (Erysiphales). The perithecium is a flask-shaped ascoma in which the asci form in a palisade termed a hymenium. The perithecium has an aperture (ostiolum) where the spores can emerge. Perithecia can develop singly (e.g. *Sordaria*) or sometimes are embedded in a compact mycelial structure called a perithecial stroma (e.g. ergot, *Claviceps pupurea*). In a pseudothecium the asci develop in cavities of a compact hyphal aggregate (ascostroma). The apothecium is a cup-like open ascoma

and the asci with sterile cells (parahpyses) among them develop in a layer (hymenium) on the open side. The apothecia could have stipes as do the mushroom-form morels or can form closed hypogeous ascomata characteristic of the truffles.

In the general life cycle of hyphal basidiomycetes the monokaryotic phase is relatively short, the hyphae developing from haploid basidiospores fuse (somatogamy) and produce dikarytic hyphae. This dikaryotic phase dominates the life cycle of the basidiomycetes. During the sexual reproductive phase the final cells of generative hyphae develop into a basidium. The nuclei fuse (karyogamy), and the diploid nucleus undergoes meiotic division. The four haploid nuclei migrate into the developing basidiospores across the spore-holding sterigma.



Development of a holobasidium and basidiospores. 1: clamp; 2: nuclei; 3 karyogamy; 4: meiosis; 5: vacuole; 6: sterigma; 7: basidiospore.

In chiastobasidia the second division of the meiosis is parallel with the axis of the basidium, in stichobasidia this division is perpendicular with the axis. A probasidium is where karyogamy happens, and a metabasidium is the place of the meiosis. In some species where a postmeiotic mitosis happens, the faith of the four additional nuclei is characteristic of the species.

Basidia may be grouped by several features. Holobasidia are not divided by walls, whereas fragmobasidia are segmented. When a fungus has heterobasidia, its basidiospores can produce secondary spores, while the basidiospores of fungi with homobasidia germinate with hyphae.

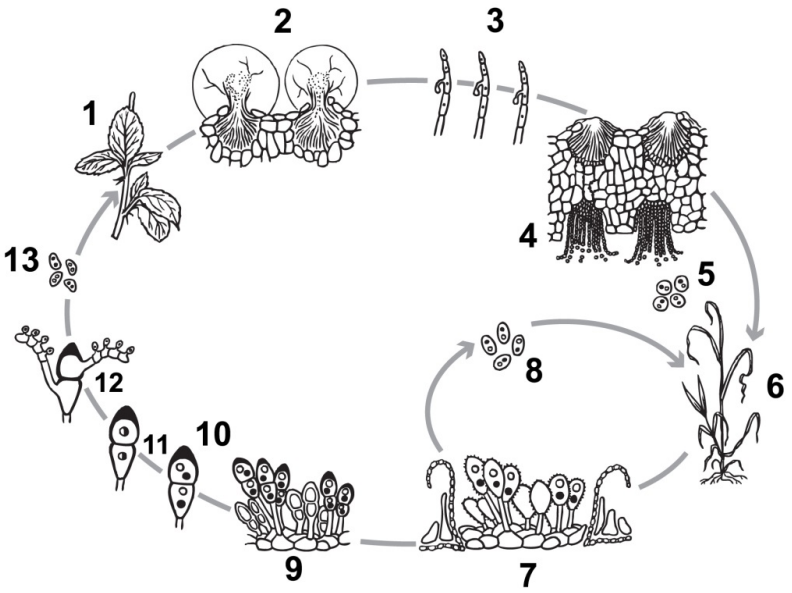
Basidia generally produce four exogenous basidiospores, but some species with less (e.g. two: *Agaricus bisporus*) or more (e.g. up to nine: *Phallus*) spores per basidium. The size, shape, and ornamentation of the basidiospores can be characteristic of the taxa, as are the number of nuclei in the spores or the dispersal type (active vs. passive) of the basidiospores.

The dikaryotic hyphae of hyphal Agaricomycotina produce sporocarps (basidiocarps or basidiomata) where basidia and basidiospores develop. To expand the surface for spore production the trama employ variable anatomies (gills, pores, etc.). Basidiomata have two main types according to the spore producing tissue. In the hymenial type the basidia develop in a layer (hymenium). Mushrooms with cap (pileus) and stem (stipe) generally produce the basidia in a hymenium. The basidioma can develop with its hymenium exposed throughout its development (gymnocarpic). In hemiangiocarpic basidiomycetes the young basidioma is completely covered by a sheath (universal veil) which breaks during development of the basidioma, and its remnants form a cup (volva) at the base of the stem and often leave fragments on the cap surface. Another veil covers the hymenium (partial veil) which also breaks, the remaining parts form web-like structures or flaps at the margin of the cap and a ring (annulus) on the stem. In other taxa basidia can form not only in a hymenium but in a tissue mass called the gleba, that is enclosed by an outer skin or

peridium. Many gastroid fungi (e.g. puffballs) have such basidiomata which can open with pores (angiocarp basidioma) or the peridium breaks (cleistocarpic basidioma).

8.4.3. A complex life cycle

Rust fungi belonging to the subphylum Puccioniomycotina (Basidiomycota) illustrate well the potential complexity of a fungal life cycle. The rusts include several important plant pathogens, such as the stem rust (*Puccinia graminis*), the crown rust (*Puccinia coronata*) or the coffee rust (*Hemileia vastatrix*). Rusts are obligate intracellular biotrophic pathogens that develop haustoria in the host cells. Rust life cycles vary in complexity, stem rust being the most complex type.

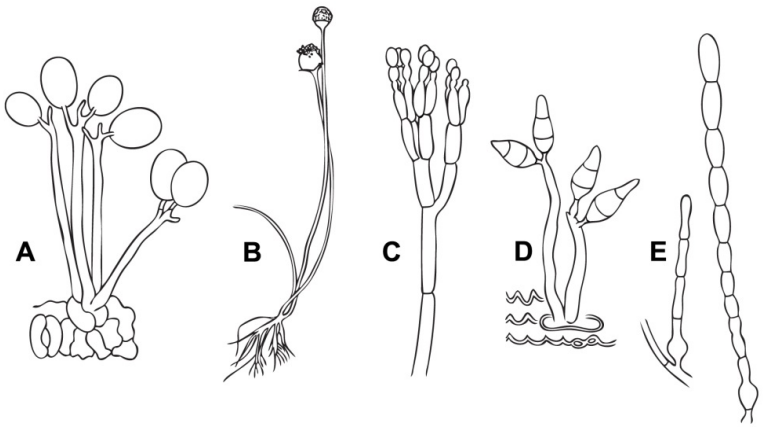


Life cycle of the stem rust (Puccinia graminis). 1: *Berberis*; 2: spermogonium (pycnium), with nectar, monokaryotic hyphae and spermatia (pycniospores); 3: plasmogamy, fusion of spermatia and flexuous hyphae; 4: aecium; 5: aeciospores; 6: gramineous host; 7: uredinium; 8: urediniospores; 9: telium; 10: teliospores; 11: karyogamy; 12: meiosis, basidium and basidiospore formation; 13: basidiospores.

It has two hosts to complete its life cycle: such rusts are called heteroecious (autoecious rusts complete their life cycle on one host). The stem rust is macrocyclic, as its life cycle contains all the five possible spore forms. Rusts form haustoria in both monokariotic and dikaryotic phase (M- and D-haustorium, respectively) during their life cycle.

8.4.4. Asexual reproduction of fungi

A great diversity of structures and forms aid asexual reproduction of fungi. The most important probably are the asexual mitospores that can develop in closed sporangia, or the internal or terminal parts of hyphae that develop into resting spores (chlamydospores). Conidia are asexual non-motile spores produced exogenously. Conidia play fundamental roles in dispersal of many fungi and can even be the exclusive dispersal structures of anamorphic fungi.



Asexual reproductive structures of some fungi. A: Sporangiophores with zoosporangia of *Plasmopara* (Oomycota). B: Sporangiophores with a opened and closed sporagia of *Rhizopus* (Zygomycota). C: Conidiophore and conidia of *Penicillium* (Ascomycota). D: Conidiophore and multicellular conidia of *Magnaporthe* (Ascomycota). E: Juvenile and mature conidiophore of *Blumeria* (Ascomycota).

The development of conidia (conidiogenesis) has two main types. During blastic conidiogenesis the conidium initial enlarges, and emerges from a hyphal tip. In thallic conidiogenesis a septum delimits the conidium initial from the end segment of the hypha. Several sub-types of both versions occur according to e.g. the manner of delimitation and mode of septum/cell wall development.

8.4.5. Asexual reproduction in the main fungal groups

The asexual dispersing structures of the oomycetes are either flagellate motile zoospores (e.g. in water molds) or sporangia in which those zoospores develop. The dispersing zoosporangia can either release the zoospores or germinate and develop coenocytic hyphae upon arrival on an appropriate surface. Some species undergo both processes depending, for example, on the temperature of the environment.

In chtyrids the mitotic zoospores represent the asexual reproductive phase. The arbuscular mycorrhizal fungi (Glomeromycota) have no sexual life cycle, they produce asexual chlamydospores generally in the soil but in some species chlamydospores can develop in colonized roots as well. Hyphal fragments and colonized root segments can also serve as propagules of Glomeromycota.

The zygomycetes develop sporangia in which mitospores are produced endogenously. There is an interesting tendency within the group: the number of the meiospores within a sporangium decreases and the number of sporangia on one sporangiophore increases. In some species the sporangia can disperse as well, these structures resembling conidiophores and conidia.

Asexual reproduction of ascomycetes is very diverse from both structural and functional points of view. The most important and general is production of conidia, but chlamydospores are also frequently produced. The diverse conidia and conidiophores sometimes develop in asexual sporocarps with different characteristics (e.g. aecervulus, pycnidium, sporodochium).

Asexual reproduction, especially asexual spore production is less important in Basidiomycota than in Ascomycota. However, the various spore types excluding basidiospores of rust and smut fungi could be considered as asexual spores which have great importance in the effective spread of those pathogens.

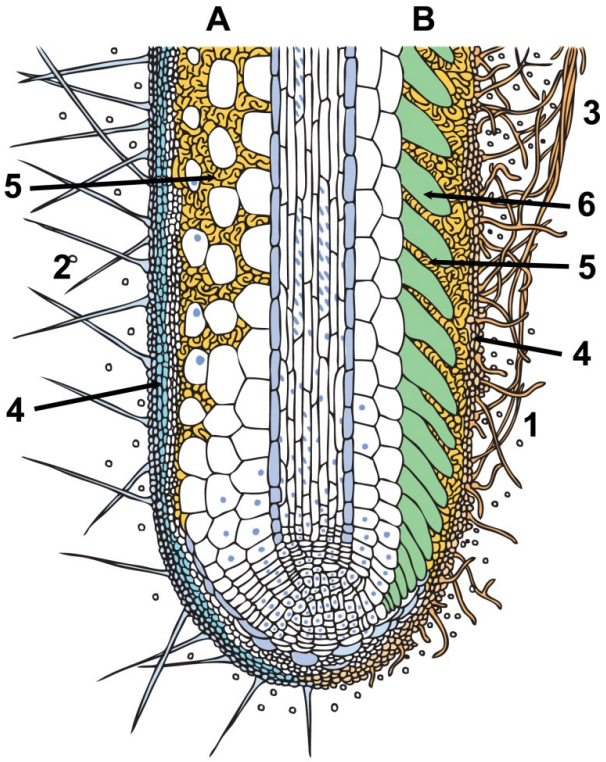
8.5. Plant-fungal interactions

8.5.1. Mycorrhizae

Most land plants live in mutualistic symbiosis with fungi in their roots: this structural, functional unit is called mycorrhiza. Mycorrhizae are “dual organs of absorption formed when symbiotic fungi inhabit healthy absorbing

organs (roots, rhizomes or thalli) of most terrestrial plants and many aquatics and epiphytes." (Trappe). Different types of mycorrhizae can be distinguished according to the plant and fungal partners and structural characteristics. Important distinctions are whether the hyphae colonizing the plant grow intracellularly (endomycorrhizae) or only intercellularly in the plant tissue (ectomycorrhizae) or both (ectendomycorrhizae). The most common types are arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM).

ECM are formed with fungi belonging to Asco- and Basidiomycota or a few zygomycetes, many of which produce macroscopic sporocarps. ECM plants are mostly woody plants, trees and shrubs. ECM have three main functional-anatomical parts: (i) special intraradical hyphal structures termed the Hartig-net formed in the intercellular spaces, (ii) the fungal mantle covering the root surface and (iii) the hyphal structures emanating from the mantle surface (e.g. cystidia, hyphae, rhizomorphs).



Main anatomical features of ectomycorrhizae (ECM). A: Cortical and **B**: Epidermal Hartig-net. 1: extraradical hyphae; 2: cystidia; 3: rhizomoph; 4: hyphal-mantle; 5: Hartig-net; 6: root epidermal cells; 7: cortical cells.

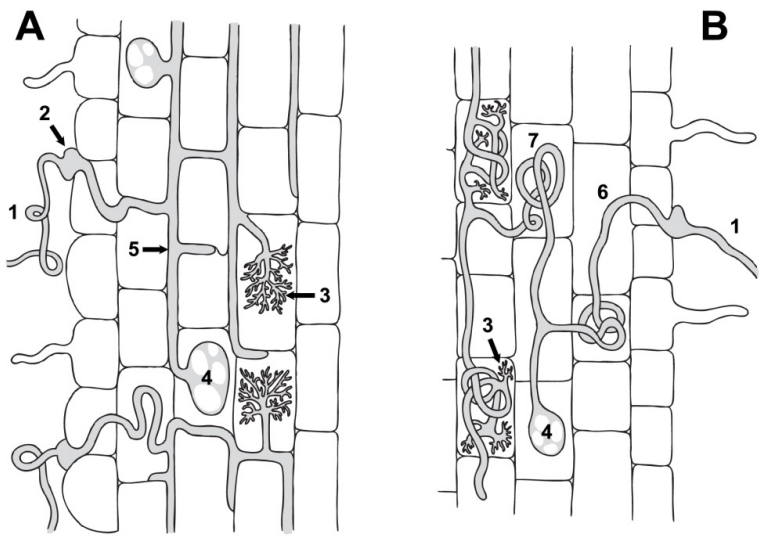
Two types of Hartig-net are distinguished. The cortical Hartig-net surrounds some layers of cortical cells and occurs in most gymnosperm and many angiosperm ECM plants. The epidermal Hartig-net surrounds radially elongated epidermal cells and occurs in most angiosperm ECM plant. As discussed above, two main types are distinguished based on the anatomy of the hyphal mantle. The hyphal organization can be detected in plectenchymatic mantles, whereas the cellular organization is characteristic of pseudoparenchymatic mantles. The main function of emanating hyphae is nutrient uptake from the soil. The hyphae can form rhizomophs, some can have differentiated anatomy, i.e. they have central hyphae with a big lumen and partially or completely disappeared septa which features make the nutrient transport more effective.

The most prevalent mycorrhiza type is the arbuscular mycorrhiza (AM). There are AM forming plants in all main terrestrial plant groups, on the other hand, all AM fungi exclusively belong to the phylum Glomeromycota. These fungi are obligate biotrophic endocellular symbionts. Their name refers to the special, multi-branched intracellular structure, the arbusculum resembling a small tree. Because of the high density of fine branches on the arbuscules, the surface of the plant cell membrane is multiplied, owing to a special membrane (periarbuscular membrane,

PAM) that surrouns the arbuscules and contains special transporters and aquaporins etc. Arbuscules are ephemeral structures, they function for a couple of days,collapse and new arbuscules arise.

Prior to the colonization of the roots, the plant and fungal partners stimulate each other and their mutual recognition plays a crucial role in the success of the establishment of the interaction. The roots excrete strigolactons which stimulate the growth and branching of AMF hyphae and also the germination of AMF chlamydospores. The fungi produce “myc-factors” (lipochitooligosaccharides) which initiate processes necessary for the successful colonization in the plants. The hyphae run on the surface of the roots and develop a swollen structure (appressorium or hypho-podium) from which a hypha grows into the root. The plant cells undergo a complete reorganization when the AMF hypha enters and grows through the cell, this special organization is called the pre-penetration apparatus (PPA). The endoplasmic reticulum (ER) forms a tube like structure which assigns the direction of the hyphal growth. The plant cell nucleus also moves to the penetration site and migrates in front of the growing hyphae through the cell. The intracellular growth of the hyphae needs continuous membrane development, so there is an intensive production of vesicules fusing into the plant cell membrane surrounding the hyphae. This process is controlled by the exocytosis regulation.

The arbuscules, albeit different, show several similarities with the intracellular haustoria of endocellular biotrophic pathogens. The AMF could also develop structures named vesicles in the roots, mainly in the intercellular spaces. The main function of these vesicles is storage. Their appearance could be seasonal and some AMF species do not form vesicles at all. Two main types of AM anatomy can be distinguished, of course, with several intermediate forms as well.



Two main types of root colonization in arbuscular mycorrhizae (AM). A: Arum-type **B**: Paris-type. 1: extraradical hyphae; 2: appressorium/hyphopodium; 3: arbusculum; 4: vesiculum; 5: intercellular hyphae; 6: intracellular hyphae; 7: hyphal coils.

In the Arum-type the fungal hyphae grow intercellularly and well-developed arbuscules are formed on branches entering the neighboring cells. In the Paris-type the hyphae grow intracellularly, develop hyphal coils in some cortical cells and smaller arbuscules develop on these coils. Both the fungal and the plant partner influence the type developed.

8.5.2. Endophytic fungi

Endophytic fungi spend at least one phase of their life cycle colonizing plant tissues inter- or intracellularly causing no symptoms of tissue damage. This definition is not a phylogenetic term, endophytic fungi can thus be found in several fungal groups. The best known endophytes (C-endophytes) belong to the family Clavicipitaceae (ergot family, Pezizomycotina, Ascomycota) and colonize aboveground tissues of grasses. The rare intercalar growing of hyphae was found in these endophytes. Fungal endophytes can be grouped according to several aspects, e.g.

plant tissues colonized, systemic, non-systemic spread in plant. A form-group of root-colonizing endophytic fungi is the so called dark septate endophytes (DSE) that belong to a few orders of the phylum Ascomycota. DSE fungi are septate and generally have melanized hyphae that colonize the cortical cells and intercellular regions of roots and form a densely septated intracellular structure called microsclerotia. Although C-endophytes have been intensively studied, our general knowledge on the function and diversity of endophytes is limited especially if compared to some types of mycorrhizae.

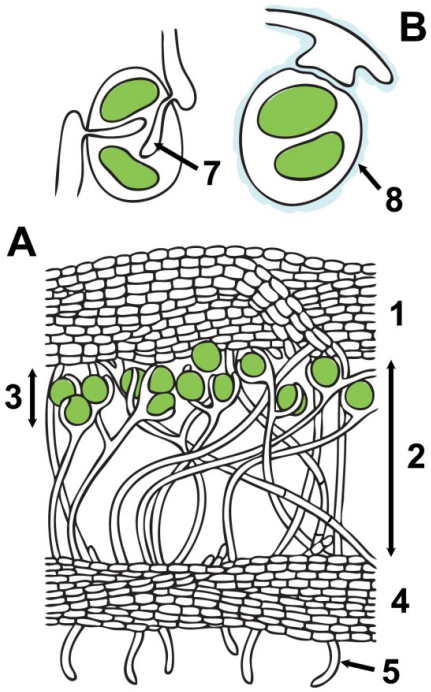
8.5.2. Plant pathogenic fungi

Plant pathogenic fungi are spread through all fungal groups and their interaction with plants is diverse, with few common structural characteristics. Biotrophic pathogens need living host cells/tissues to exhaust while nectrotrophic pathogens first kill the host tissues to be able to take the nutrients from the host. Accordingly, there are fundamental differences between the molecular mechanisms, possible defense reactions of those two types. E.g. programmed cell death (PCD), which helps necrotrophic fungi, could protect the spread of biotrophic pathogens.

The fungal binding on the host surface is a fundamental step of the successful infection. The chemical and physical characteristics of this surface have fundamental effects on the adhesion and germination of fungal propagules on the plant, e.g. hydrophobic surfaces, like the outermost cuticle layer of the plants, could induce spore germination. Similarly to AMF, several plant pathogenic fungi develop appressoria at the entry points. Plant pathogenic fungi can have different mechanisms to enter the plant. Pressure is the main driving force of the entry of the rice pathogen *Magnaporthe grisea*. The changes of the wall and chemical content of the appressorium of the fungus induce osmotic water influx which produces enormous pressure pushing the hypha across the plant cell wall. Other pathogens use enzymes or enzymes and pressure together to enter the host plants. In stem rust, the hyphae grow on the leaf surface till they reach a guard cell of a stoma and the growing on the guard cell induces the turning downwards of the hyphae which therefore grows through the stoma and colonize the plant. Biotrophic endocellular parasites can develop special intracellular structures called haustoria through which they take the nutrients up from host cells.

8.6. Lichens

The lichen is special association of a mycobiont (fungus) and a photobiont (alga or cyanobacterium) forming a stable self-sustaining thallus. It should be emphasized that lichens are rarely formed by a single mycobiont and a single photobiont species. The biomass of lichens is dominated by the mycobiont and lichens are identified and named according to the fungal partner. The photobiont is almost a slave of the mycobiont, it cannot reproduce sexually or spread on its own and even its cell cycle is completely controlled by the mycobiont. The photobiont can be isolated and maintained alone while the mycobiont generally cannot be kept in pure isolate. There are approximately 100 photobiont species, the majority is green algae (85%) the others are cyanobacteria (15%). On the other hand there are 14 000 – 15 000 lichen forming fungal species, almost all belonging to Ascomycota (Pezizomycotina), while there are approximately 20 lichen forming basidiomycetes. The mycobionts can reproduce sexually and spread on their own but when such reproduction happens, only the fungal partners disperse.



Schematic structure of a lichen thallus. A: Cross section of the thallus. **B**: Main types of the algal-fungal interaction. 1: upper cortex; 2: medulla; 3: layer of algae; 4: lower cortex; 5: rhizina; 6: algal cell; 7: haustorium; 8: hydrophobic sheath.

Three main types of lichen thalli can be distinguished: the foliose, the fructicose and the crustose lichen. The lichen thallus can have several layers. An upper and a lower cortex of compact tissue are formed by the mycobiont. The medulla layer with a loose hyphal layer and an algal (gonidial) layer is between the two cortices. The interface between the algal and fungal partner can be either an intracellular haustorium formed by the fungus in the algal cells, or an apoplastic surface where the hypha tightly lays on the algal cell wall, and this junction (intraparietal haustorium) is covered/isolated by a hydrophobic layer.

The growth of the lichen thallus is extremely slow. As the lichen itself can reproduce and disperse only if both partners are involved, only asexual, vegetative reproduction could propagate a lichen. Asexual vegetative reproductive structure containing both myco- and photobionts are the isidium (protuberance of the cortex with different shape) and soredium (small powdery granules with no cortex).

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