tissues located outside, like aliens in the famous movie. Root phloem is arranged in several strands whereas xylem typically has a radial, sometimes star-shaped structure with few rays (Fig. 5.34). In the last case, phloem strands are located between rays of xylem.

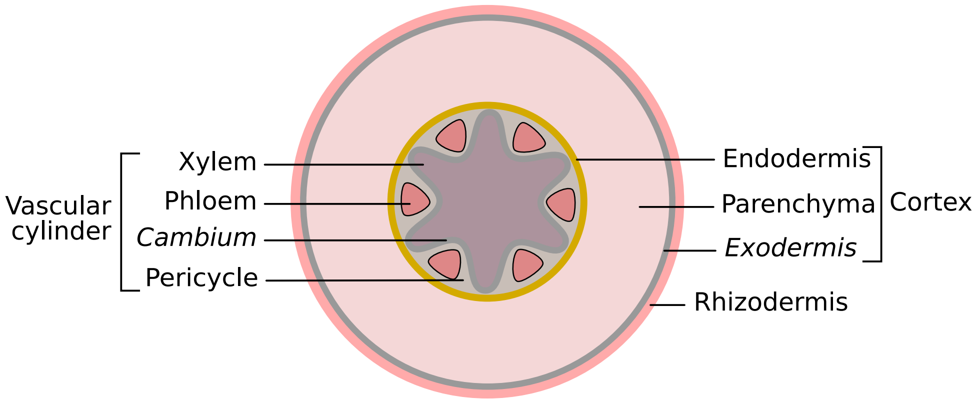


Figure 5.34. Anatomy of root: cross-section through the maturation zone.

Root tissues develop in the way similar to stem, RAM gave rise to ground meristem, procambium, and the protoderm, which in turn make all primary tissues mentioned above. Later, pericycle develops into lateral roots or the vascular cambium which in turn produces into the secondary xylem and phloem. The secondary root is similar to secondary stem (see below).

5.5.3 Water and Sugar Transportation in Plants

Plants need water to supply photosynthesis (the oxygen is from water!), to cool down via transpiration, and to utilize diluted microelements. Dead velamen (paper-like), rhizoids (hair-like), and living rhizodermis (rhizoderm) are responsible for water uptake.

In rhizodermis, root hairs increase the surface area where the plant has to absorb the nutrients and water. To take water, hair cells increase concentration of organic chemicals (the process which needs ATP) and then use osmosis. There are two ways that water transport may go: apoplastic or symplastic. *Apoplastic* transport moves water through the cell walls of cortex: from the rhizodermis to the endodermis. Endodermis cell walls bear **Casparian strips** (rich of hydrophobic suberin and lignin) which prevent the water from passing through the cell wall and force *symplastic* transport (Fig 5.35) through cytoplasms and plasmodesmata. Symplastic transport there is directed to the center of root only and requires ATP to be spend.

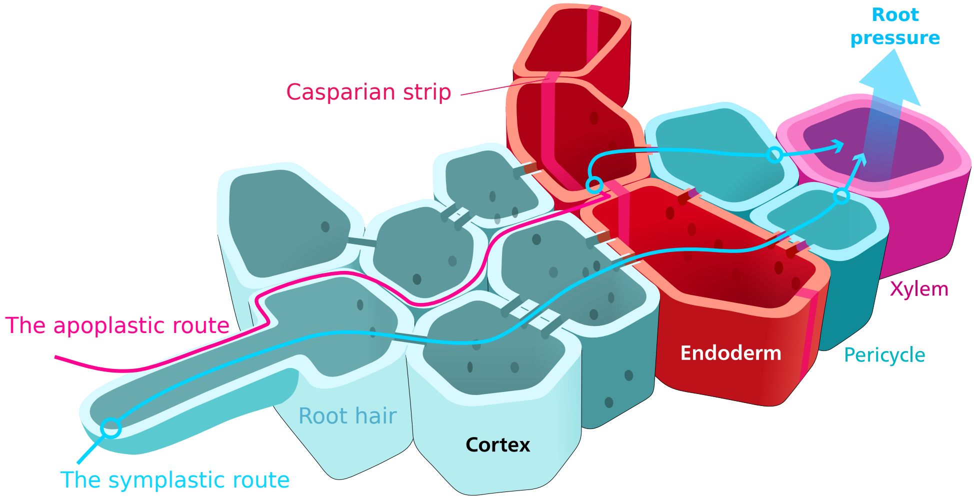


Figure 5.35. Symplastic and apoplastic transport in root.

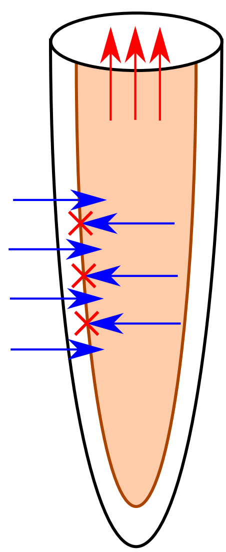


Figure 5.36. The origin of root pressure: water comes into vascular cylinder but cannot go back because of endoderm (brown line). The only possible way is to go up.

By pumping water inside vascular cylinder and not letting it back, endodermis cells create the **root pressure** (Fig. 5.36). It is easy to observe on tall herbaceous plants cut near the ground: drops of water will immediately appear on the cutting. Inside tracheary elements of xylem, water moves with the root pressure, capillary force and the sucking pressure of transpiration. The latter means that water column does not want to break and if water disappears from the top (stomata on leaves), it will move water inside plant. The main direction of water movement is from roots to leaves, i.e. upwards.

Products of photosynthesis (sugars) are moving inside living cells of phloem; these cells (sieve tubes) use only symplastic transport to distribute glucose and other organic compounds among all organs of plants. In fact, phloem transports these components in all directions: to the flowers (usually upwards), and at the same time to the roots (usually downwards).

Chapter 6

Growing Diversity of Plants

When plants developed basic tissues and organs and thus became mature enough to survive on land, they started to increase in their diversity. All plants studied in this and following chapters belong to plants$_2$, or kingdom Vegetabilia which is split into three phyla (Fig. 6.1): Bryophyta (mosses and relatives), Pteridophyta (ferns and allies), and Spermatophyta (seed plants). The most striking differences between these phyla lay in the organization of their life cycles.

Land plants have a sporic life-cycle (Fig. 4.13) that begins with a diplont (sporophyte); the mother cell of spores goes through the meiosis and produces haploid spores. These spores develop into haplont which produces female and male gametangia (gamete "homes"). Female is called *archegonium*, the male—*antheridium*; the archegonium produces oocyte which is fertilized by the antheridium's spermatozoon in the process of oogamy. When this fertilization happens, it forms a diploid zygote which then matures into a *young sporophyte growing on a gametophyte*. This kind of same species parasitism is almost unique in the living world. Only viviparous animals (like mammals with their pregnancy) could be compared with land plants.

6.1 Bryophyta: the mosses

Bryophyta has gametophyte predominance while Pteridophyta and Spermatophyta both have sporophyte predominance (and the main difference between Pteridophyta and Spermatophyta is that Spermatophyta has seeds). Bryophyta has approximately 20,000 species. They do not have roots, but have long dead cells capable of water absorbency via apoplastic transport, these cells are called **rhizoid cells**. Their sporophyte is reduced to **sporogon**, which is simply a sporangium with **seta** (stalk), and is usually parasitic. Gametophyte of bryophytes starts its development from a **pro-**

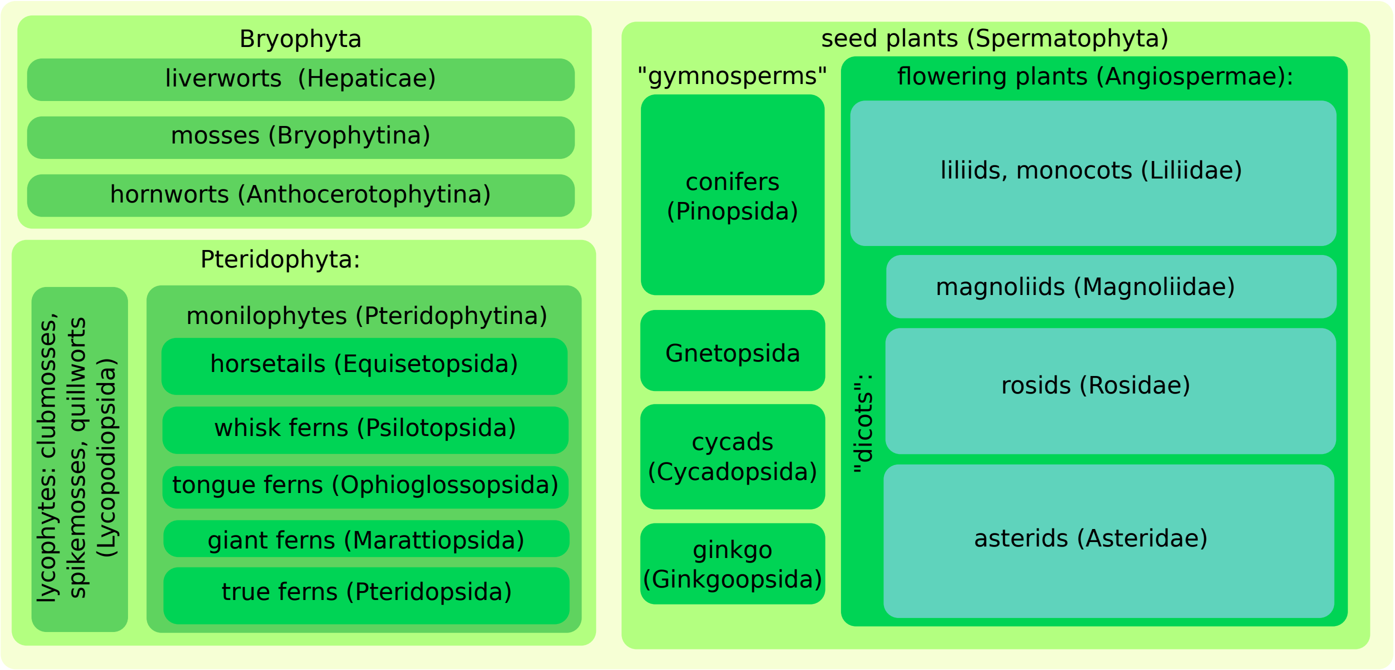


Figure 6.1. Plants$_2$ classification: detailed scheme.

tonema, thread of cells. Bryophyta are poikilohydric; they go through dehydration or extremely low water concentration without any serious physiological damage to the plant.

Life cycle of mosses is similar to the general life cycle of land plants described above. They begin with a gametophyte with an archegonia and antheridia. The antheridium produces biflagellate spermatozoa which fertilizes the egg and produces diploid zygote; zygote grows into a sporogon and its cells (mother cells of spores) go through meiosis which produces haploid spores. Spores will be distributed with the wind, land on the substrate and germinate into protonema stage which then develops into a green, well-developed gametophyte. Most of moss gametophytes have a shoot body that consists of a stem and leaves (but no roots) while others have a thallus body, which is a flat, leaf-like, and undifferentiated structure.

* * *

There are three main groups, also known as subphyla, of Bryophyta: Hepaticae (liverworts), Bryophytina (true mosses), and Anthocerotophytina (hornworts).

Hepaticae are phylogenetically closest to green algae. Their thallus typically has dorsal and ventral parts, and the sporogon is bag-like. Inside the sporangium, there is no central column (columella) but elaters are present, which are cells that loosen spores. One of the most widespread liverwort is *Marchantia*, it is commonly found in wet shady places. It became a frequent weed in greenhouses.

Bryophytina consists of multiple classes (Fig. 6.2), the most important are **Sphagnopsida**—peat mosses, **Polytrichopsida**—hair cap mosses, and **Bryopsida**—green mosses. Bryophytina have a radially structured shoot-like body with a stem and thin leaves. Their sporogon is long and has columella, but does not have elaters. Sporogons of true mosses are usually supplied with **peristome**, structure which helps in spore distribution. Some advanced true mosses (hair cap moss, *Polytrichum*) have tall gametophyte with proto-vascular tissues, while others (stinkmoss, *Splachnum*) employ insects for the distribution of spores. Peat moss (*Sphagnum*) is probably the most economically important genus of Bryophyta.

Anthocerotophytina (Fig. 6.3) evolutionary are closests to the next phylum, Pteridophyta (ferns and allies). Hornworts have a flattened thallus body, their long photosynthetic sporogon has columella and elaters. The presence of stomata on sporogons and the ability of some hornwort sporogons to branch and sometimes even live independently from the gametophyte provide a support for the advanced position of this group. Hornworts are rare and quite small (first millimeters in size), and like liverworts, they prefer shady and wet places.

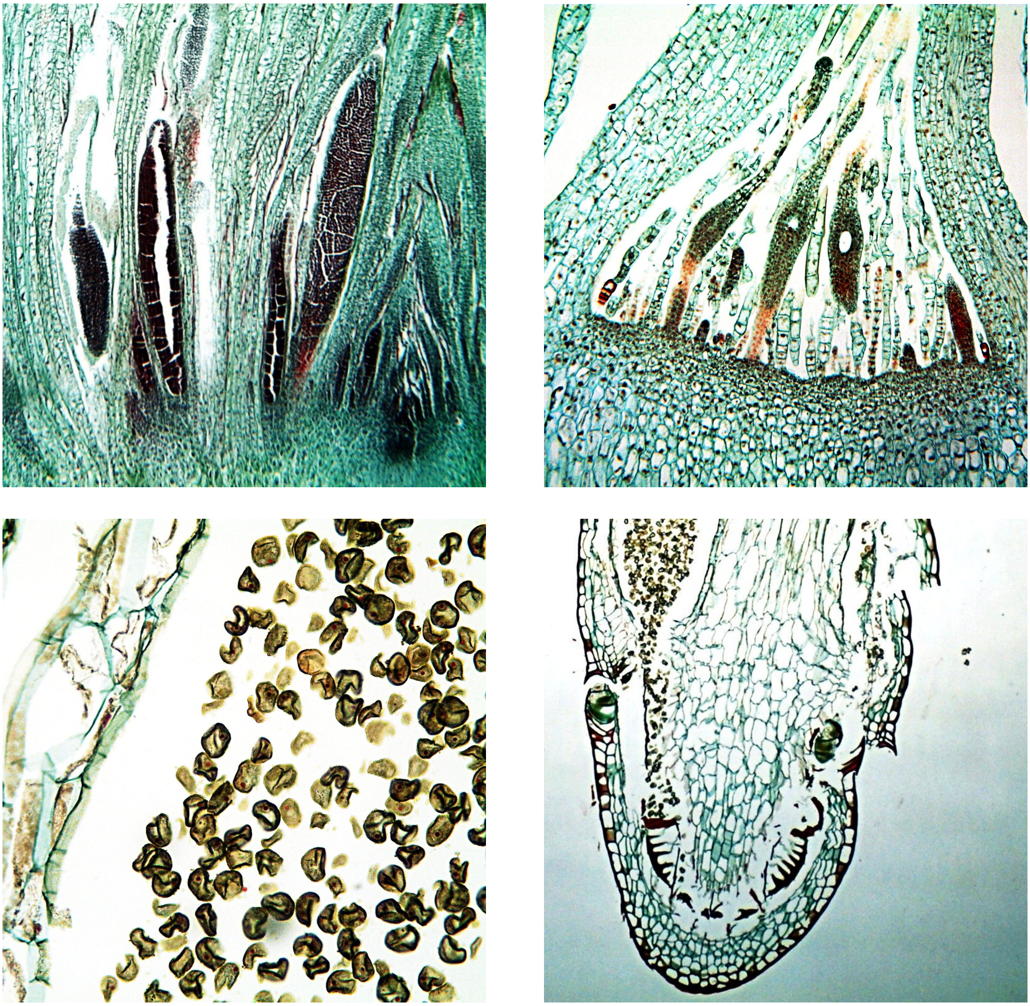


Figure 6.2. Left to right, top to bottom: *Mnium* (Bryopsida) antheridia, archegonia, spores and the base of sporogon. Magnifications $\times 100$ (first and second) and $\times 400$ (third) and $\times 50$ (fourth).

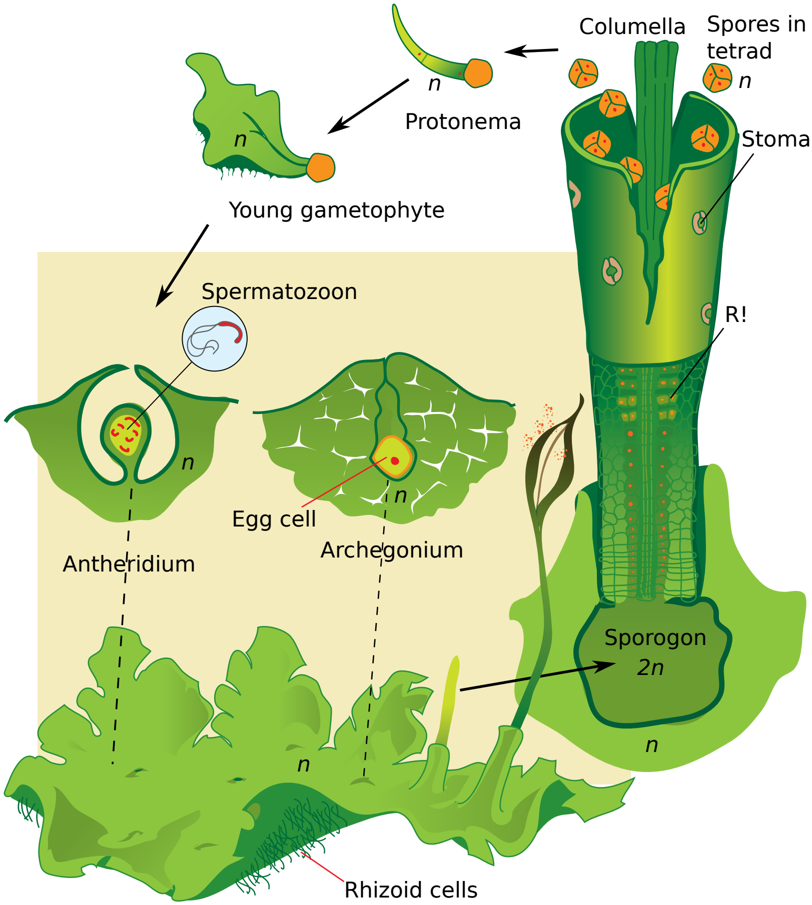


Figure 6.3. Life cycle of *Phaeoceros* (Anthocerotophytina).

Mosses have become known as the "evolutionary dead end" because their poikilohydric gametophyte requires water for fertilization and does not have a root system; this restricts the size and requires dense growing. However, if the sexual organs are near the soil surface, then the parasitic sporogon would not grow tall enough, and consequently would not be able to effectively distribute spores with the wind.

Three natural forces "tear" the body of moss: wind and light require plant to be taller whereas water requires it to be smaller (Fig. 6.4). Mosses did not resolve this conflict.

The only way to fix the situation properly would be to make the sporophyte taller, independently growing and therefore and reduce dominance of the gametophyte. This is what ferns (Fig. 6.5) did.

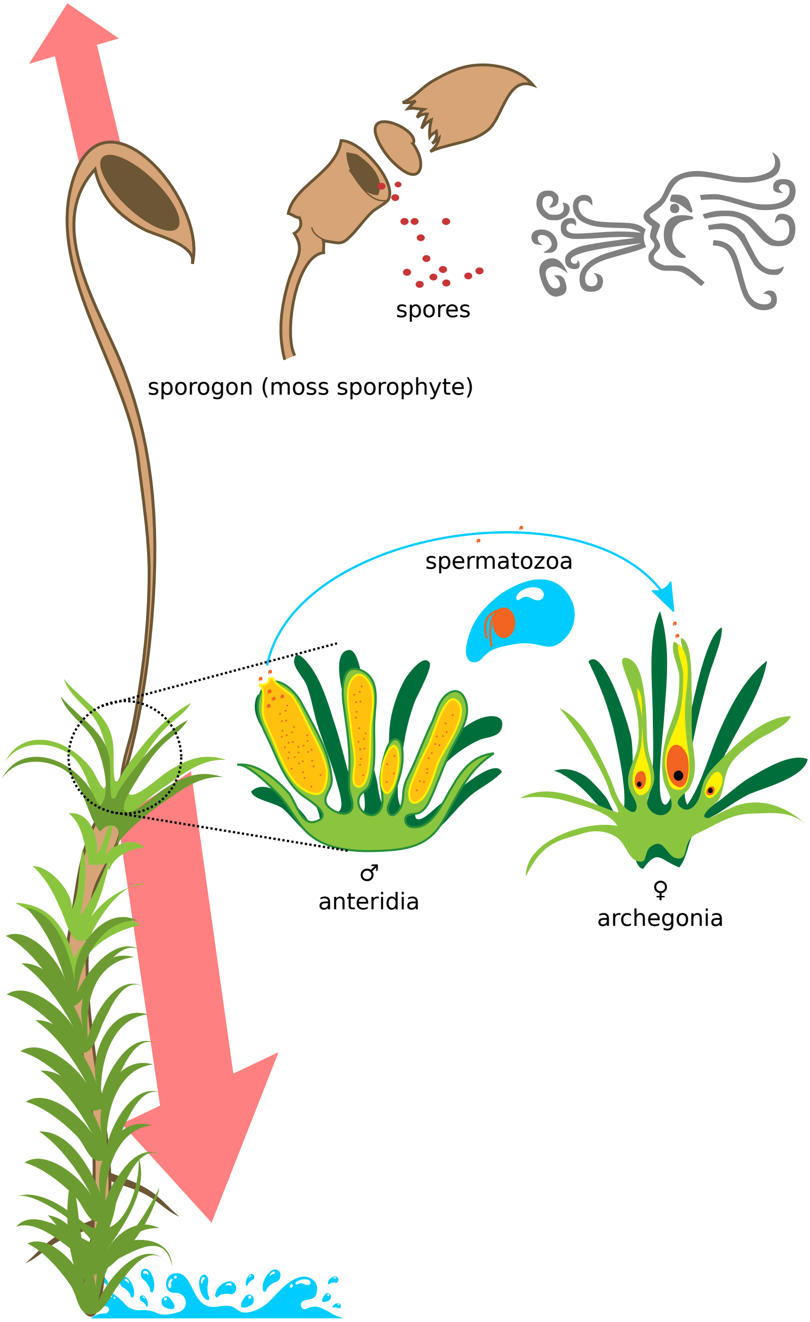


Figure 6.4. Two forces which disrupt moss evolution.

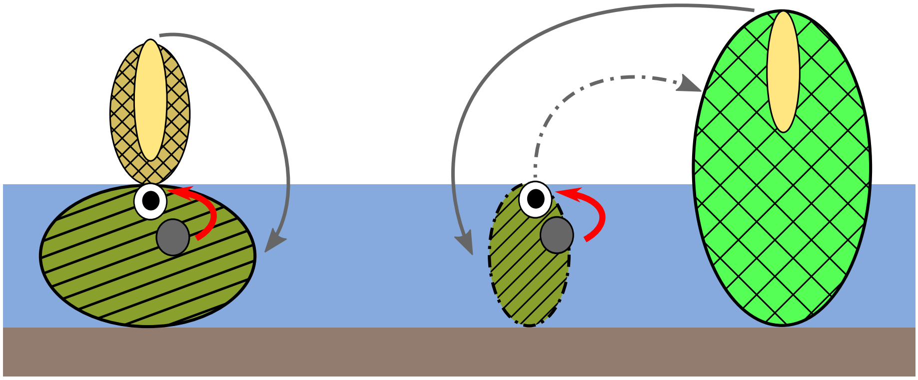


Figure 6.5. Mosses (left) *vs.* ferns (right). Water level is blue, sporangia are yellow, gametangia gray. Red arrows show fertilization (in water), grey arrows designate life cycles. Dotted lines is *independence* of fern sporophytes from their ephemeral gametophytes.

6.2 Pteridophyta: the ferns

Pteridophyta, ferns and allies, have approximately 12,000 species and six classes (Fig.6.6). They have a sporic life cycle with sporophyte predominance whereas their gametophytes are often reduced to prothallium, small hornwort-like plant. Another frequent variant is the underground, mycoparasitic gametophyte. Pteridophyta (with one exception) have true roots. Most of them have vascular tissues and are homoiohydric. This is why seed plants together with ferns have a name **vascular plants**. Pteridophyta sporophytes always start their life from an embryo located on the gametophyte. While Pteridophyta have true xylem and phloem, they do not have developed secondary thickening.

Most ancient pteridophytes appeared in Silurian period, they were rhyniophytes. Rhyniophyles had well-developed aboveground gametophytes and relatively short, dichotomously branched leafless sporophytes. The next important steps were formation of leaves and further reduction of gametophytes.

6.2.1 Diversity of pteridophytes

Lycopodiopsida, or lycophytes have at least four genera and more than 1,200 species. Lycophytes belong to **microphyllous** lineage of pteridohytes. This means that their leaves originated from the emergences of the stem surface, and therefore are more similar to moss leaves than any other leaves of pteridophytes and seed plants. Lycophyte sporangia are associated with leaves and often form **strobilus** which is a condensation of sporangia-bearing leaves (**sporophylls** when they are leaf-like or **sporangiophores** when they are divergent). Their spermatozoon usually has 2 flag-

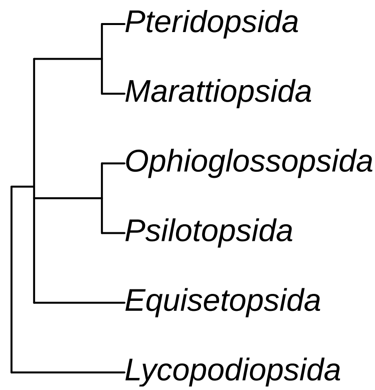


Figure 6.6. Phylogeny of the six classes of Preridophyta.

ella (like mosses) but are sometimes also multiflagellate (like spermatozoa of other ferns). Lycophytes used to be the dominant plants of Carboniferous tropical swamp forests and their remains became coal. Contemporary lycophytes are much smaller but still thrive in wet and warm places. More basal lycophytes (clubmosses *Huperzia* and *Lycopodium*) have equal spores and underground gametophytes, whereas more advanced *Selaginella* (spikemoss) and *Isoëtes* (quillwort) are both heterosporous (see below) with reduced aboveground gametophytes. Quillwort is a direct descendant of giant Carboniferous lycophyte trees, and despite being an underwater hydrophyte, it still retains the unusual secondary thickening of stem. Many spike mosses are poikilohydric (another similarity with mosses).

Equisetopsida (horsetails) is a small group with one genus, *Equisetum*, and has about 30 different herbaceous species that typically live in moist habitats. The leaves of these plants are reduced into scales, and the stems are segmented and also photosynthetic; there is also an underground rhizome. The stem epidermis contains silica which makes it have an abrasive surface, and because of this, American pioneers would use this plant to scour pots and pans. This is how it received the nickname "scouring rush." The stem has multiple canals, this is somehow similar to stems of grasses. The sporangia are associated with hexangular stalked sporangiophores; there are also elaters which are not separate cells but parts of the spore wall. Gametophytes are typically minute and dioecious, but the plants themselves are homosporous: smaller suppressed gametophytes develop only antheridia while larger gametophytes develop only archegonia.

Psilotopsida (whisk ferns) is a small tropical group which consists of only two genera, *Psilotum* and *Tmesipteris*, with only seven different species. They are herbaceous plants that grow as epiphytes. Whisk ferns are homosporous, and their sporangia are fused into **synangia**. Psilotopsida have protostele like the some lycophytes, and long-lived underground gametophytes; they also have multiflagellate spermatozoa similar to all other ferns. Both *Psilotum* and *Tmesipteris* lack roots; in addition, *Psilotum* also lacks leaves.

Ophioglossopsida (tongue ferns) is a small group that consists of approximately 75 species, and are closest relatives to whisk ferns. Ophioglossopsida have an underground rhizome (sometimes with traces of secondary thickening) with aboveground bisected leaves: one half of each leaf is the leaf blade while the other half becomes the *sporophyll*. The gametophytes also grow underground. *Ophioglossum vulgatum*, known also as the adder's tongue fern, has chromosome number $2n$ =1,360 which is the largest chromosome number ever!

Marattiopsida (giant ferns) are tropical plants, with several genera and about 100 species. These are similar to true ferns and have compound leaves that are coiled when young. They are also the biggest ferns, as one leaf can be six meters in length. They have short stems, and leaves with stipules. Their sporangia have multi-layer walls and are fused into synangia (not like true ferns). At the same time, they are located on the bottom surface of leaves (like in true ferns). Gametophytes are relatively large (1–2 cm), photosynthetic, and typically live for a long time. These ferns were important in the Carboniferous swamp forests.

Pteridopsida (true ferns) have more than 10,000 species and make up the majority of living **monilophytes** (all classes of Pteridophyta except lycophytes). Their leaves are called **fronds** because of apical growth; young leaves are coiled into **fiddleheads** (Fig. 6.7). True ferns are **megaphyllous**: their leaves originated from flattened branches. True ferns have unique sporangia: **leptosporangia**. Leptosporangia originate from a single cell in a leaf, they have long, thin stalks, and the wall of one cell layer; they also open actively: when sporangium ripens (dries), the row of cells with thickened walls (**annulus**) will shrink slower than surrounding cells and finally would break and release all spores at once. Leptosporangia are also grouped in clusters called **sori** which are often covered with umbrella- or pocket-like **indusia**. Gametophytes of Pteridopsida are minute and grow aboveground. Some genera of true ferns (like mosquito fern *Azolla*, water shamrock *Marsilea* and several others) are heterosporous.

True ferns are highly competitive even to angiosperms. In spite of their "primitive" life cycle, they have multiple advantages: abilities to photosynthesize in deep shade (they are not obliged to grow fast), to survive high humidity, and to make billions of reproductive units (spores). Ferns do not need to spend their resources on flowers and fruits, and are also less vulnerable to vertebrate herbivores and insect pests, probably because they do not employ them as pollinators and, therefore, can poison tissues against all animals.

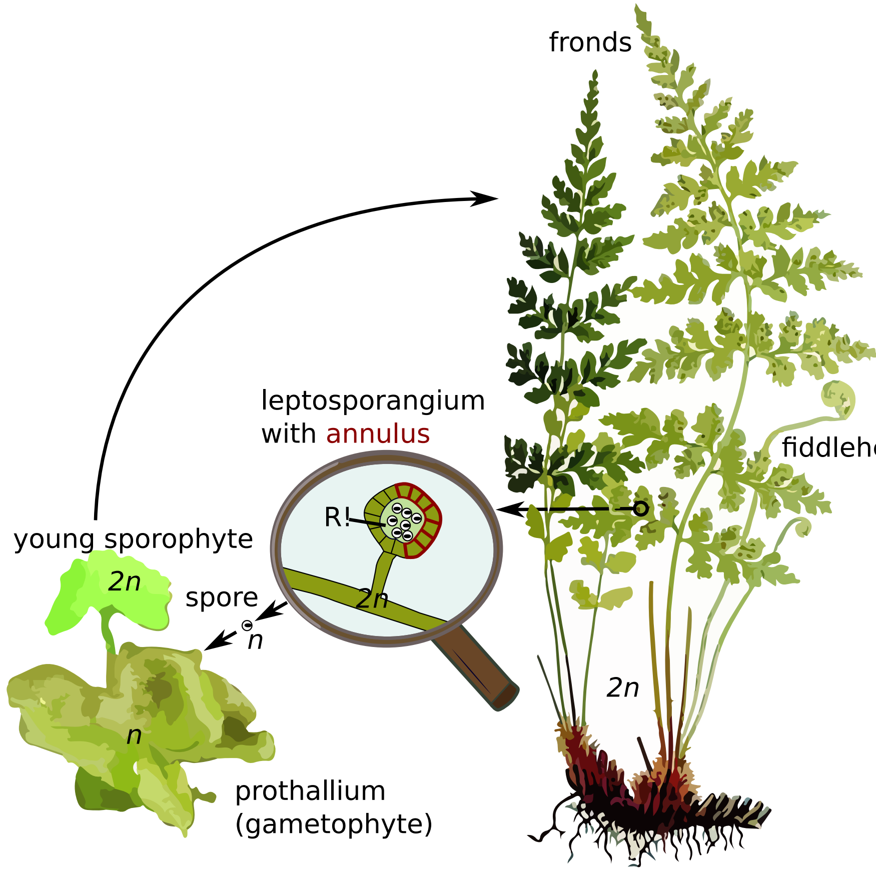


Figure 6.7. Selected stages of *Cystopteris* life cycle, representative of Pteridopsida.

6.2.2 Heterospory: Next step on land

Vertebrate animals became fully terrestrial (amphibians became first reptiles) only when their fertilization became completely independent from water. Plants started to perform the similar "evolutionary efforts" even earlier, but while reptiles actively approach the sexual partner, plants cannot do the same because their tissues and organs evolved for completely different purposes. Instead of the active sex, plants use "carpet bombing" with spores; this was invented to increase the chance that two spores land nearby and the distance between sperm and egg cell will be minimal.

However, since simple increase in the number of spores is a great waste of resources, plants minimized spore size; this will also allow for the longer distance of dispersal. On the other hand, some spores must remain large because embryo (if fertilization occurs) will need the support from the feeding gametophyte. Consequently, plants ended up with division of labor: numerous, minuscule male spores which grow into male gametophytes with antheridia only, and few large female spores which make female gametophytes producing only archegonia(Fig. 6.8).

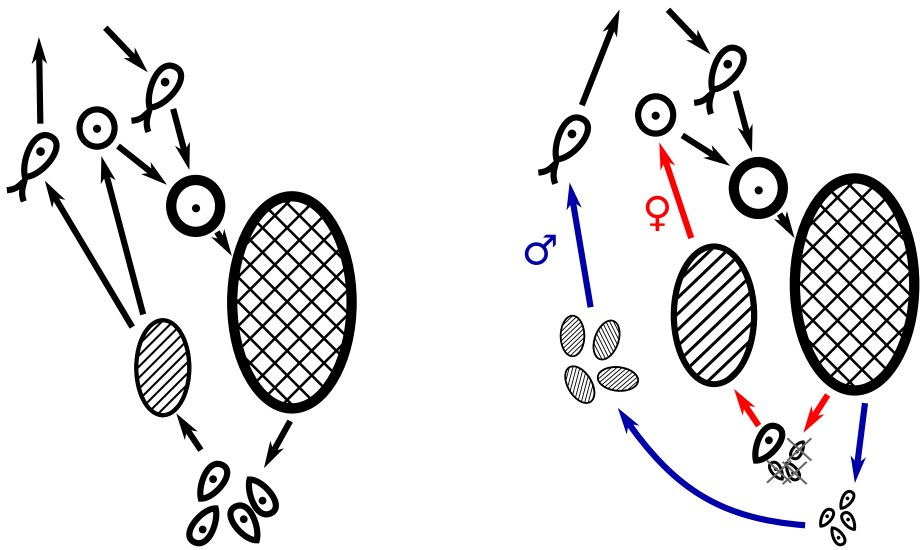


Figure 6.8. From homosporous to heterosporous life cycle.

This **heterosporic** cycle makes fertilization less dependent on water and more dependent on spore distribution and gametophyte features (Fig. 6.9). It also allows for numerous improvements in future.

Division of labor allows resources to be used more efficiently and also restricts self-fertilization. In the plant evolution, there was a high need for heterospory because it independently arose in several groups of pteridophytes and even among mosses. In the extreme cases of heterospory (Fig. 6.10), a female spore does not leave the mother plant and germinate there, "waiting" for the fertilization from the male gametophyte developed nearby; in fact, this is incipient pollination, the step towards the *seed*.

Heterosporous plants produce one female spore, **megaspore**, which is rich in nutrients; megaspores are not widely dispersed, but the female gametophyte that comes of it provides nutrition and protection for the zygote, embryo, and young sporophyte. Heterosporic life cycle (Fig. 6.11) starts with a male gametophyte and a female gametophyte, both of which produce gametes. Once fertilization occurs, a zygote develops into sporophyte. The sporophyte will then produce two different sporangia types: female **megasporangia** and male **microsporgangia**. Meiosis in megasporangium will frequently result in *one* female spore, megaspore (similar to the meiosis in the ovaries of vertebrate animals), whereas in the microsporangium, meiosis

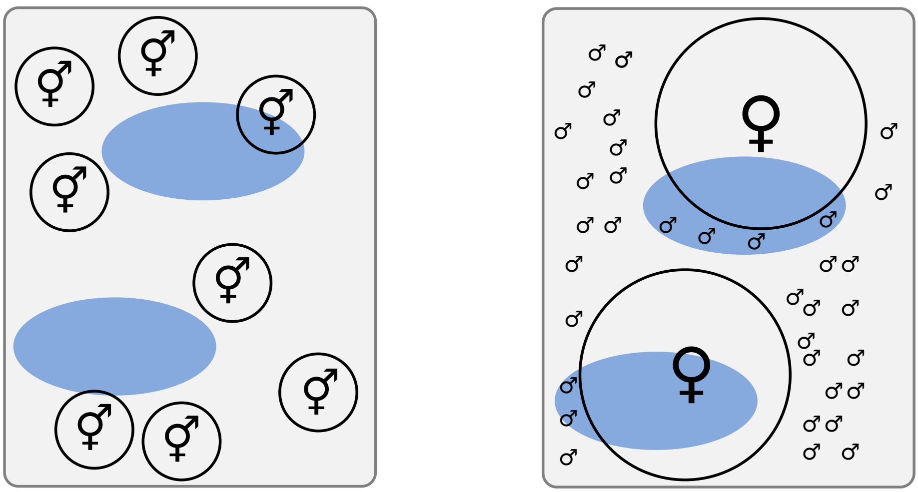


Figure 6.9. Simple scheme which illustrates the heterosporic way of fertilization. Two drops of water (blue) do not provide the connection between two gametophytes of homosporous plant (left) but are enough for gametophytes of heterosporous plant (right) using the same amount of resources.

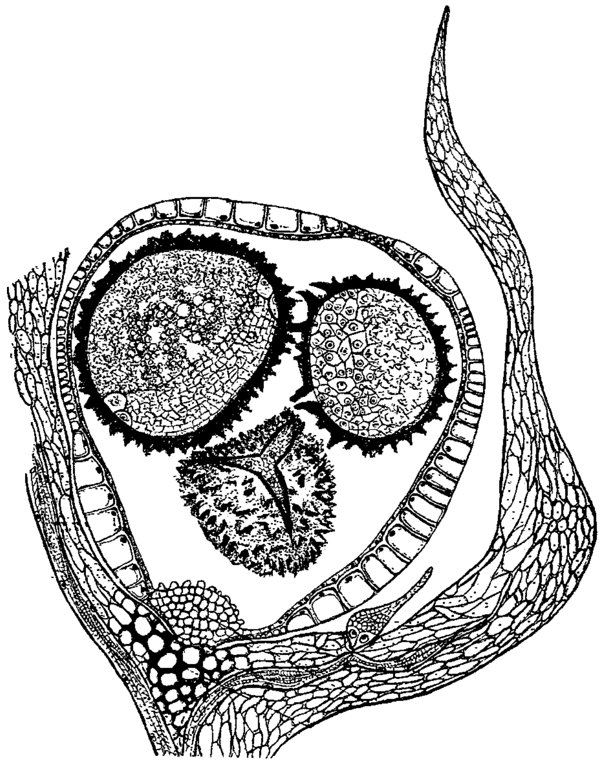


Figure 6.10. Megasporangium of the meadow spike-moss, *Selaginella apoda* (*from Lyon, 1901*). All three megaspores germinate into female gametophytes without leaving sporangium.

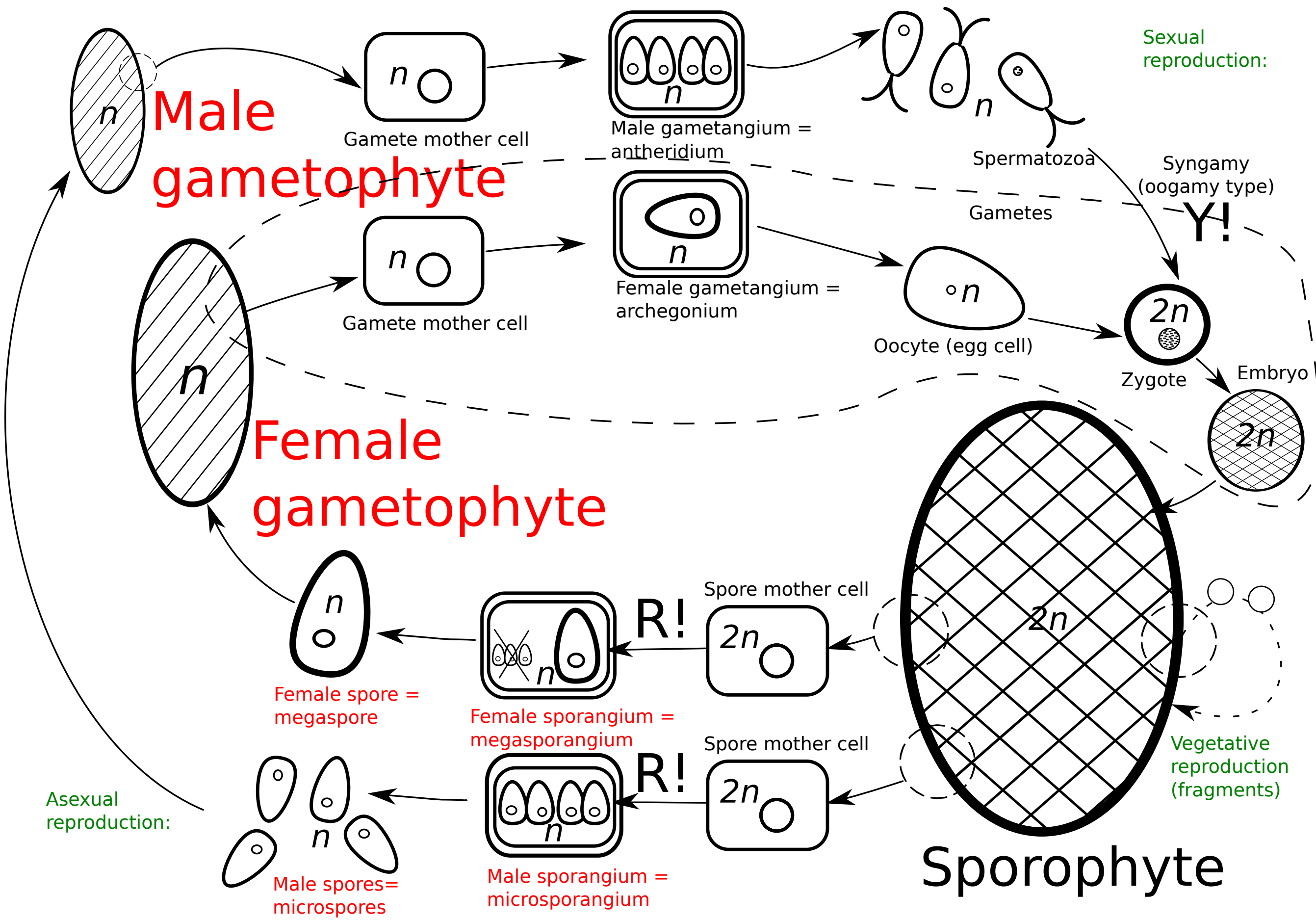


Figure 6.11. Life cycle of heterosporic plant. Innovations (comparing with the life cycle of land plants) are in red.

and subsequent mitoses will make numerous **microspores**; both the megaspore and microspores will develop into gametophytes and the cycle will repeat.

In all, heterospory allows for separation between male and female haploid lineages. Male gametophytes become so small that they could easily be transported as a whole. Whole male gametophytes start to be a moving stage—this is origin of *pollination*.

Chapter 7

The Origin of Trees and Seeds

Competition over resources (primarily water and sun light) always drove plant evolution. The most logical way to escape competition was to enlarge the body. But if only primary tissues are available, this growth is strictly limited.

Without secondary thickening, the trunk will easily break under the weight of growing crown, and the plant will die. This is easy to see in plants which still dare to develop the tree-like habit without secondary growth: tree ferns and palms. In addition, tree ferns have no bark which limits their distribution to the really wet places.

On the other hand, thickening of stem will allow for branching, and branching allow for even bigger aboveground body. But then, new problems associated with both size and life cycle will pose another great challenge.

7.1 Secondary Stem

In many seed plants, secondary growth begins in their first year within the stem and continues on for many more years. These plants are classified as *woody*. They develop *secondary tissues* like periderm and wood, and even *tertiary* structures like bark.

The first step in producing secondary phloem and xylem (other names are metaphloem and metaxylem) is to form the vascular cambium, which involves cell division inside the vascular bundles and the parenchyma that are between the bundles (Fig. 7.1). The vascular cambium divides in two directions. The cells that are formed to the outside become the *secondary phloem*, and those formed to the inside are the *secondary xylem* (Fig. 7.3). After several years, central pith disappears under the pressure of growing wood, and only traces of primary xylem (protoxymem) can be seen *under* the thick

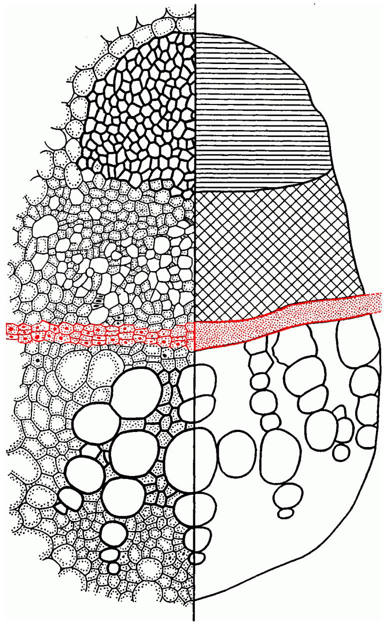


Figure 7.1. Vascular bundle on the stage of cambium (red) formation. Xylem is located downward, phloem upward. Note that cambium forms also *between* vascular bundles.

secondary xylem. Altogether, these tissues (pith + primary xylem + secondary xylem) are **wood** (Fig. 7.2).

The secondary phloem forms outside of the vascular cambium, and traces of primary phloem (protophloem) are visible above it. It is rich in fibers, and unlike the wood, it does not form annual rings.

Most of cambium cells are **fusiform initials** forming axial vessel elements, while some cambium cells are **ray initials** and they form **rays**: combinations of parenchyma cells and tracheids transporting water, minerals and sugars (because it is dark inside the stem and only respiration is possible) *horizontally*. Rays are visible best on the **tangential** section of the stem (when section plane is tangent to the stem surface); two other possible sections (**radial** and **transverse**) show axial components of the stem better. In the secondary phloem, rays are sometimes *dilated* (wedge-shaped).

The cambium usually does not work evenly all year round. In temperate climates, a *ring* forms for each growing season and makes it possible to determine the age by counting the growth rings. This is because at the end of season cambium makes much smaller ("darker") tracheary elements. Trees growing in climates without well-expressed seasons will not make annual rings. To tell the age of a tree, researchers

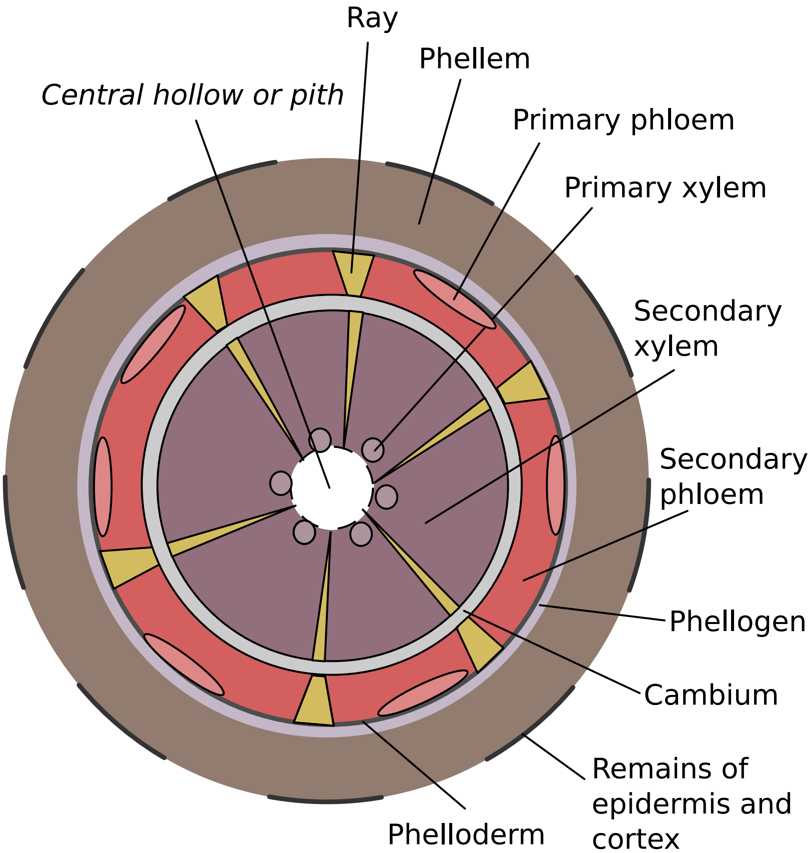


Figure 7.2. Anatomy of the secondary stem. Radial view.

observe the number and thickness of annual rings that are formed. This is called *dendrochronology*.

Some trees (like oaks, *Quercus*) have large vessel elements are found primarily in the wood formed early in the season (early wood); this pattern is known as **ring porous.** Large vessel elements of other trees (like elm, *Ulmus*) occur more evenly in both early and late wood. This pattern is known as **diffuse porous**wood: with large vessel elements in both early and late wood.

Vesselless wood of conifers is of a simpler structure with relatively few cell types. There are simple rays and frequently *resin ducts*; resin is secreted by specialized cells.

In the tree trunk, the lighter wood near the periphery is called **sapwood** and has functioning xylem where most of the water and minerals are transported. Darker wood closer to the center is called **heartwood** and is a non-functional, darkly colored

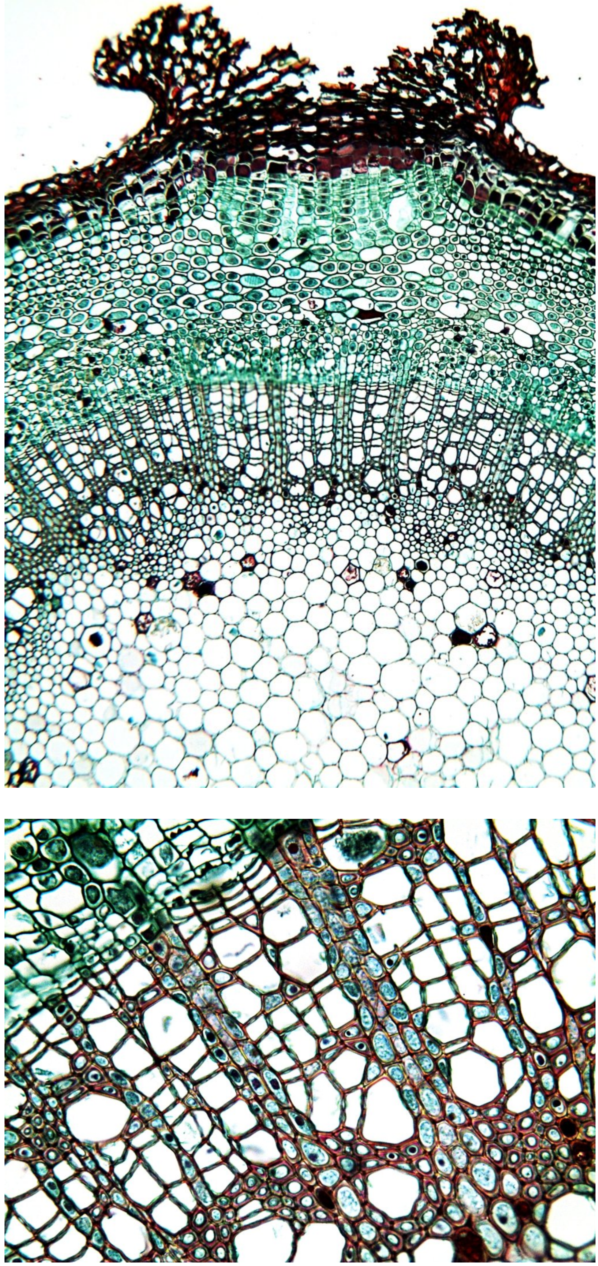


Figure 7.3. Top to bottom: *Sambucus* secondary stem in the beginning of growing, lenticel is on the top, *Sambucus* cambium (top left) and secondary vascular tissues. Magnifications $\times 100$ (first) and $\times 400$ (second).

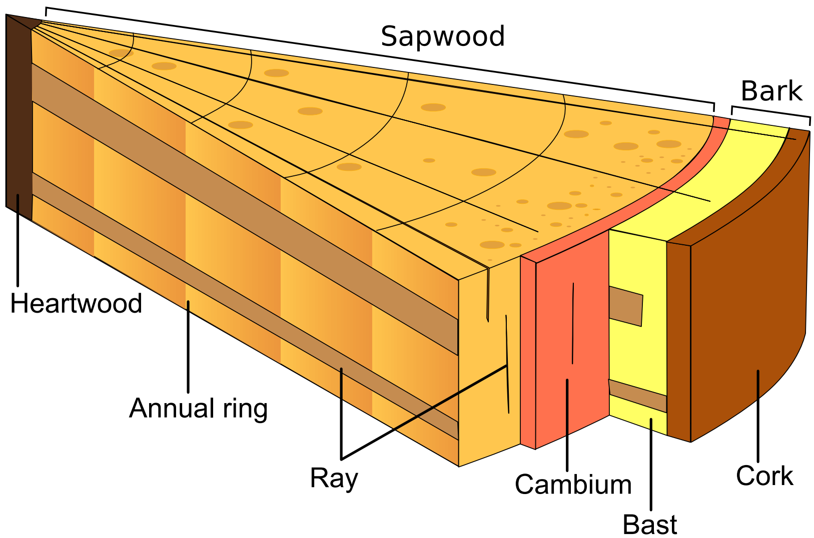


Figure 7.4. Piece of trunk. Radial and transverse views.

xylem (Fig. 7.4). Tracheary elements are dead cells and to block them, plants uses **tyloses** which also help control winter functioning of vessels. A tylose forms when a cell wall of parenchyma grows through a pit or opening into the tracheary element; they look like bubbles.

Most liliids (for example, palms) do not have lateral meristems and true wood. Some thickening does occur in a palm but this happens at the base of the tree, as a result of adventitious roots growing. Palms may also have diffuse secondary growth which is division and enlargement of some parenchyma cells. These processes do not compensate the overall growth of plant, and palms frequently are thicker on the top than on the bottom. Few other liliids (like dragon blood tree, *Dracaena*) have **anomalous secondary growth** which employs cambium but this cambium does not form the stable ring.

Constantly thickening stem requires constantly growing "new clothes", secondary dermal tissue, periderm. Periderm is a part of bark. *Bark is everything outside vascular cambium*. It is unique structure which is sometimes called "tertiary tissue" because it consists of primary and secondary tissues together:

- trunk = wood + vascular cambium ("cambium") + bark
- wood = secondary xylem + primary xylem + [pith][1]
- bark = bast (primary + secondary phloem) + periderm + [cortex] + [epidermis]

[1] "Optional" tissues are given in brackets, synonyms in parentheses.

- periderm = [phelloderm] + cork cambium (phellogen) + cork (phellem)

Each year, a new layer of phellogen (cork cambium) appears from the parenchyma cells of the secondary phloem which makes bark multi-layered and uneven. On the surface of a young stem, one may see **lenticels**, openings in phellem layer which supply the internals of the stem with oxygen; together with rays, lenticels work as ventilation shafts. To produce lenticels, some phellogen cells divide and grow much faster which will finally break the periderm open.

Apart from the lenticels, older or winter stems have **leaf scars** with **leaf traces** on their surface. The first are places where leaf petiole was attached, and the second are places where vascular bundles entered the leaf.

The secondary structure of root reminds the secondary structure of stem, and with time, these two organs become anatomically similar.

7.2 Branching Shoot

Secondary stem allows for extensive branching. In seed plants, branching is based on the axial buds. These buds are located in axils of leaves and develop into secondary shoots. There are two main types of branching: monopodial and sympodial (Fig. 7.5).

Monopodial branching is when the buds do not degrade and all the shoots continue to grow.

Sympodial branching is when the terminal buds do degrade (make FU and/or die out) and the lateral shoot closest to the terminal bud now becomes the terminal shoot and continues the vertical growth. This happens because the terminal SAM suppresses the downstream meristems by producing the auxin hormone (apical dominance). Apical dominance is a basis of multiple gardening trimming techniques.

Monopodial branching creates the conical (spruce-like) crown whereas sympodial branching will create crowns of many different shapes. Monopodial growth is considered to be more primitive. Some monopodial trees may even die if the terminal bud is damaged.

Even more ancestral mode of branching is **dichotomous**, when every branch splits into two; this is frequent in lycopods and some other Pteridophyta.

7.3 Life Forms

Thickening and branching change the appearance of plant. The most ancient classification employ both branching and thickening and divide plants into trees, shrubs

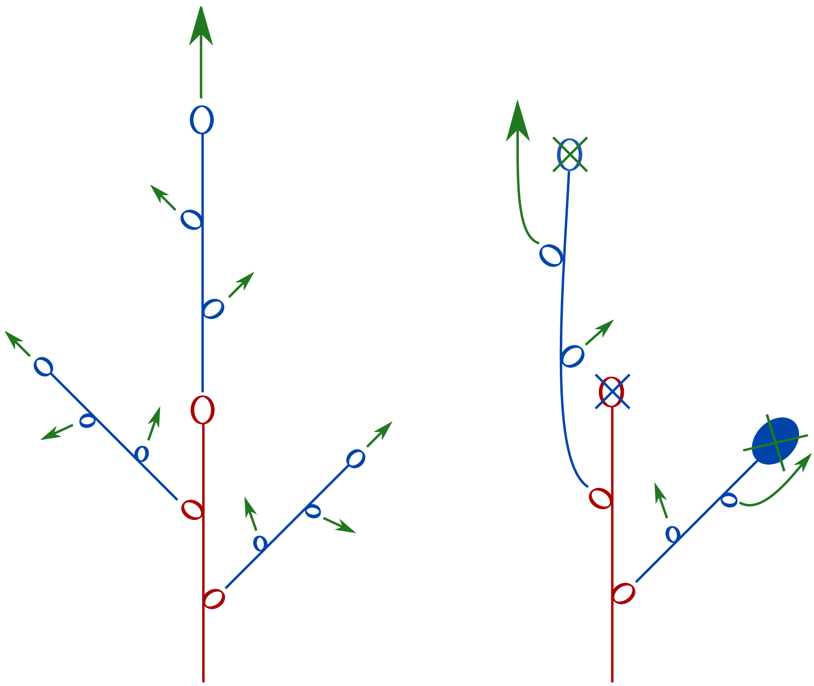


Figure 7.5. Monopodial (left) and sympodial branching. First, second and third years of growth are red, blue and green, respectively. Note that rightmost branch developed the FU (blue oval).

and herbs. This approach was the first classification of *life forms*. Life forms tell not about evolution, but about how plant lives. We still use this classification. With some modifications, it plays a significant role in gardening:

Vines Climbing woody and herbaceous plants

Trees Woody plants with one long-lived trunk

Shrubs Woody plants with multiple trunks

Herbs Herbaceous plants, with no or little secondary xylem (wood). Sometimes, divided further into annuals (live one season), biennials (two seasons) and perennials.

This classification system has many downfalls. What is, for example, the raspberry? It has woody stems but each of them lives only two years, similar to biennial herbs. Or what is duckweed? These small, water-floating plants with ovate non-differentiated bodies are hard to call “herbs”. As one can see, the actual diversity of plant lifestyles is much wider than the classification above.

7.3.1 Architectural Models Approach

During the winter, it is easy to see that some tree crowns have similar principles of organization. In the winter-less climates, the diversity of these structures is even higher. On the base of branching (monopodial or sympodial), location of FU, and direction of growth (**plagiotropic**, horizontal or **orthotropic**, vertical), multiple *architectural models* were described for trees. Each model was named after a famous botanist such as Thomlinson, Corner, Attims, and others. In temperate regions, one of the most widespread models is Attims (irregular sympodial growth): birches (*Betula*) and alders (*Alnus*) grow in accordance with that model (Fig. 7.6). In tropical regions, many plants (like palms and cycads) have single thick trunks crowned with large leaves, this is Corner model (Fig. 7.7).

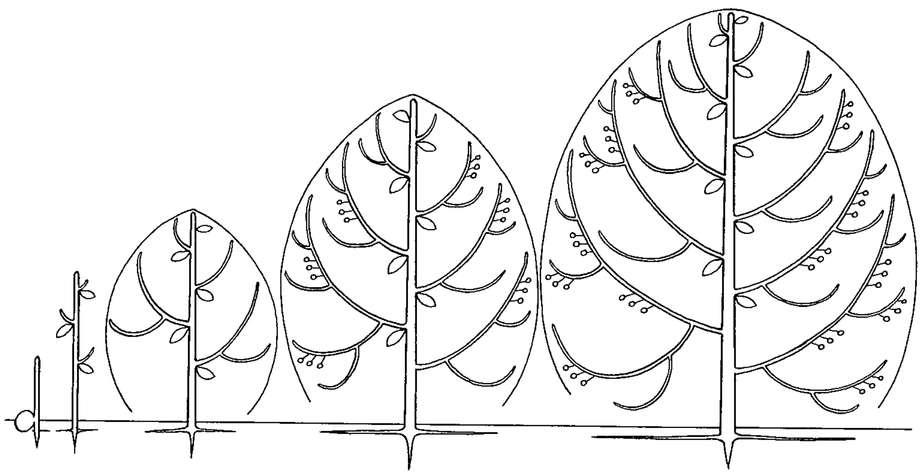


Figure 7.6. Attims architecture model of tree growth. (*From Halle et al. (1978)*).

7.4 Modified Shoot

Like leaves and roots, shoots and stems also have modifications. Some examples are rhizomes, stolons, tubers, bulbs, corms, thorns, spines, cladophylls, and stem traps. **Rhizomes** (example: ginger, *Zingiber*) are underground stems that burrow into the ground just below the soil surface, and usually tend to have small, scale-like leaves that are not photosynthetic. Buds from the axils of the leaves make new branches that will grow to become aboveground shoots. **Stolons** (runners) are aboveground horizontal shoots, which sprout and produce a new plants (example: strawberry, *Fragaria*). **Tubers** (example: potatoes, *Solanum*) are enlarged portions of rhizomes. The "eyes" of potato are actually lateral buds and the tuber body is comprised of many parenchyma cells that contain amyloplasts with starch. Corms and bulbs are shoot

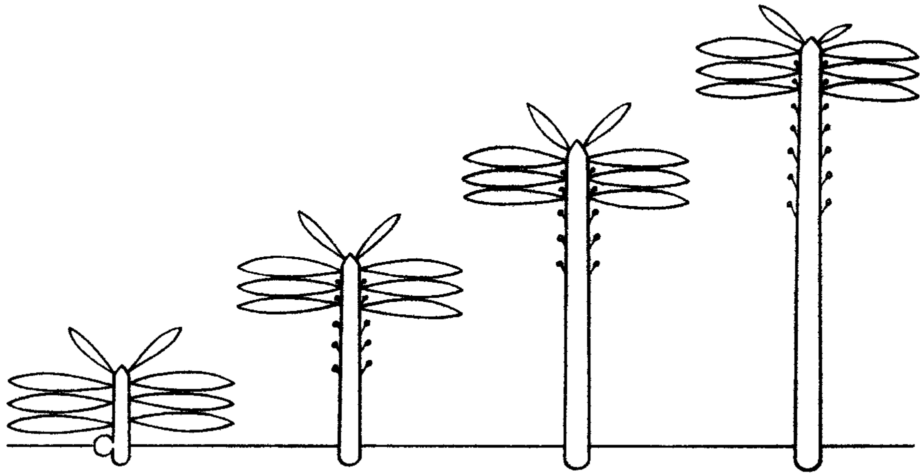


Figure 7.7. Corner architecture model of tree growth. (*From Halle et al. (1978)*).

structures that are used for storage. A **corm** (example: crocus, *Crocus*) is a short, thick underground storage stem with thin scaly leaves. A **bulb** (example: onion, *Allium*) differs from a corm in the fact that it stores its nutrients in its fleshy leaves (Fig. 7.8).

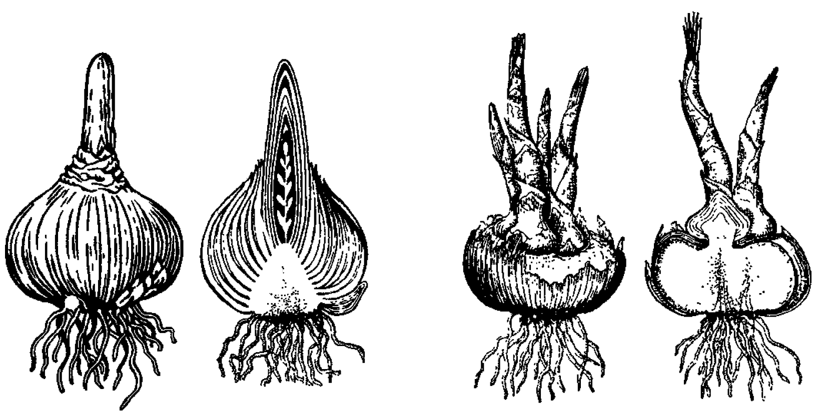


Figure 7.8. Bulbs (left) and corms. (*Modified from various sources*).

Thorns (example: hawthorn, *Crataegus*) are defensive shoots that help to protect the plant from predators. **Spines** are not modified stems, but rather modified, reduced leaves or stipules, or bud scales (example: almost all cacti, Cactaceae family). **Prickles** (example: rose, *Rosa*) are modified surface tissues of stem.

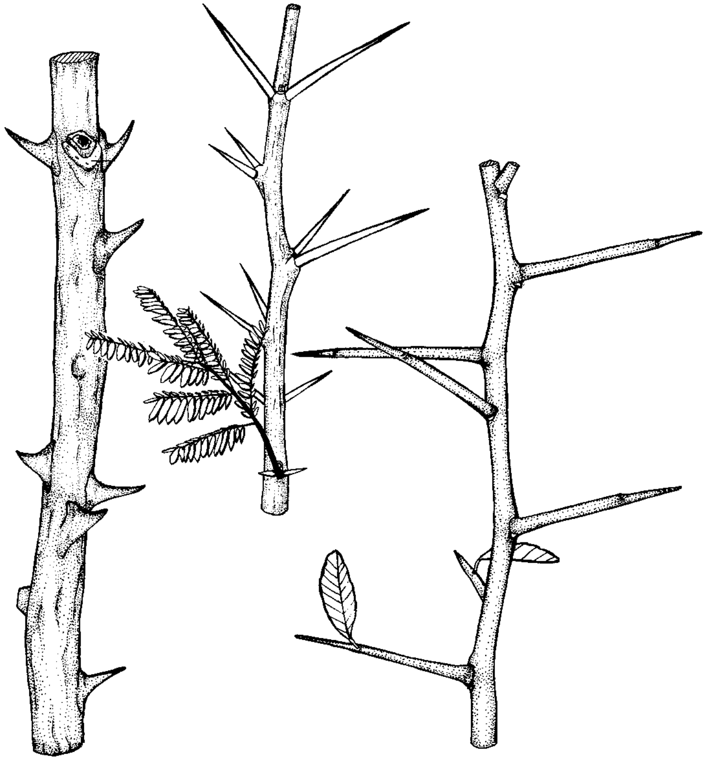


Figure 7.9. Prickles, spines (from stipules) and thorns (from Charles-Dominique et al., 2016).

Cladophylls (examples: Christmas cactus, *Schlumbergera*; ribbon plant, *Homalocladium*) are leaf-like, flattened shoots. **Phyllodes** are actually leaf modifications (example: Australian acacias, *Acacia*) they visually similar to cladophylls but originated from flattened leaf petioles. Shoot **insect traps** are used by some carnivorous plants, such as bladderwort (*Utricularia*). The following table emphasizes the diversity of organ modifications:

Function \ Organ	Leaf	Stem/shoot	Root
Absorption	Absorption leaves (bromeliads)	Rhizoids	*Default*
Defense	Spines, scales	Thorns, prickles	Spines
Expansion	Plantlets	Rhizomes, stolons, runners	Adventive buds
Interactions	Traps, sticky epidermis, urns, colored leaves	Traps, insect nests	Haustoria, mycorrhizae, root nodules, nematode traps, insect nests
Photosynthesis	*Default*, phyllodes	Cladophylls	Green roots (orchids)
Storage	Succulent leaves, pitchers	Bulbs, corms, tubers	Storage roots
Support	Tendrils, false stems, floats, suckers	*Default*, tendrils	Buttress, aerial and contractile roots, suckers

Please note that superficially similar structures (e.g., shoot and leaf tendrils) might have different origin.

7.4.1 Raunkiaer's Approach

Christen Raunkiaer used a different approach to classify life forms which is useful to characterize the whole *floras* (all plant species growing on some territory), especially temperate floras. He broke plants down into six categories: epiphytes, phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes.

Epiphytes do not touch soil (they are aerial plants), *phanerophytes* have their winter buds exposed, *chamaephytes* "put" their winter buds under the snow, winter buds of *hemicryptophytes* on the soil surface, *cryptophytes* in the soil and/or under water, and *therophytes* do not have winter buds, they go through winter as seeds or vegetative fragments (Fig. 7.10)[2]. Typically, northern floras have more plants of last categories

[2] They also distinguish aerophytes, "aerial plants".

whereas first categories will dominate southern floras. Note that Raunkiaer "bud exposure" is not far from the hardiness in the dynamic approach explained below.

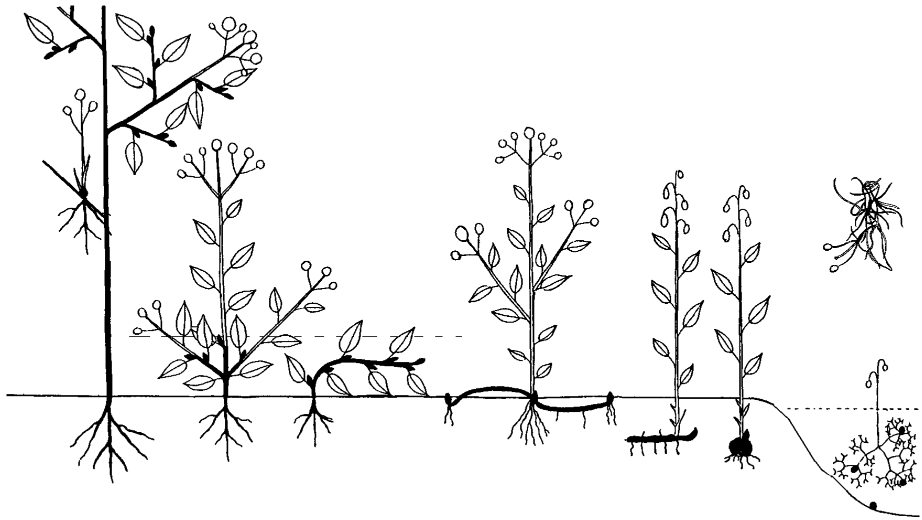


Figure 7.10. Raunkiaer life forms. From left to right: epiphyte (on branch), phanerophyte, chamaephyte, hemicryptophyte, two cryptophytes (with rhizome and with bulb), therophyte (in water) and aerophyte (in air). Dashed line on the left is the projected snow level. (*From Raunkiaer (1907), extended*).

7.4.2 Dynamic Approach

There are many life forms classifications. This is because life forms represent numerous *secondary patterns* in plan diversity, along with the main pattern which taxonomy wants to describe.

Dynamic life forms classification uses the fact that in nature, there are no strict borders between different life forms. If we supply the pole to some shrubs, they may start to climb and therefore become vines. In colder regions, trees frequently lose their trunks due to low temperatures and form multiple short-living trunks: they become shrubs. Conversely, in tropics, many plants which are herbs in temperate regions, will have time to develop secondary tissues and may even become tree-like.

Dynamic approach uses three categories: hardiness, woodiness, and slenderness (Fig. 7.11). *Hardiness* is a sensitivity of their exposed parts to all negative influences (cold, heat, pests etc.) This is reflected in the level of plant exposure, plants which are hardy will expose themselves much better. *Woodiness* is the ability to make dead tissues, both primary and secondary (reflected in the percentage of cells with secondary walls). High woodiness means that plants will be able to support themselves without problems. *Slenderness* is an ability to grow in length (reflected in the proportion of linear, longer than wide, stems). Low slenderness results in rosette-like plants. Combining these three categories in different proportions, one may receive all possible life forms of plants.

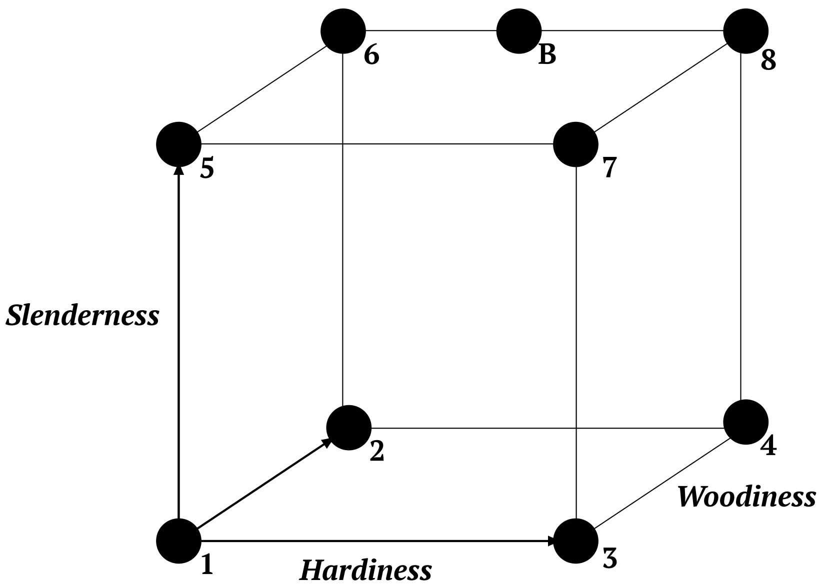


Figure 7.11. Dynamic life forms: 3D morphospace.

These three categories could be used as variables of the 3D morphospace. Every numbered corner in the morphospace diagram (Fig. 7.11) represents one extreme life form:

1. Reduced floating annuals like duckweed (*Lemna*). Please note that zero hardiness is impossible; duckweed hardiness is just low.
2. Short annual herbs like marigold (*Tagetes*); they accumulate wood if warm season is long enough.
3. Bulb perennials like autumn crocus (*Colchicum*).
4. Australian "grass trees" (*Xanthorrhea*) with almost no stem but long life.
5. Herbaceous vines like hops (*Humulus*).
6. Monocarpic tree-like plants like mezcal agave (*Agave*).
7. Perennial ground-cover herbaceous plants like wild ginger (*Asarum*).
8. Trees like redwood (*Sequoia*).

What is even more important, all possible positions on the "surface" and inside this cube also represent life forms. For example, the dot marked with "B" are slender, woody but only partly hardy plants. The partial hardiness means that vertical axes will frequently die, and then new slender woody axes develop from scratch. Woody wines and creeping bushes will correspond well with this description. As you see, this morphospace not only classifies existing plants but also could predict possible life forms.

7.5 Origin of the Seed

When plants developed the secondary growth, the almost unlimited perspectives opened for enlarging their body. However, these giants faced a new problem.

Big animals like elephants, lions, and whales tend to produce minimal number of offspring but increase the child care to ensure survival. This is called ***K*-strategy**, this is opposite to ***r*-strategy** of usually smaller creatures which employs big numbers of offspring, and most of them will not survive (Fig. 7.12).

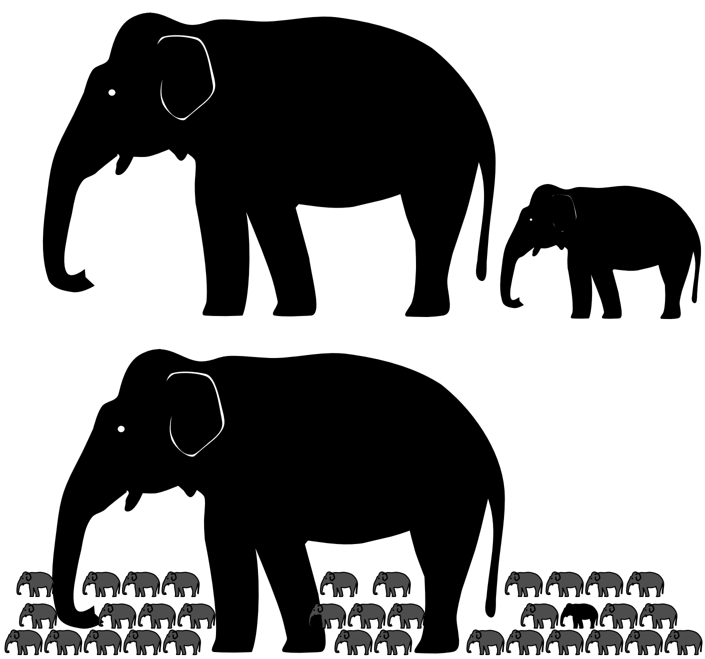


Figure 7.12. *K*-strategic elephant and *r*-strategic (like codfish) elephant. The second does not exist. Why?

Analogously, bigger plants would need to do the same as K-strategic animals: make few daughter plants but defend and supply them with all needs until they mature. However, big secondary thickening spore plants were not capable of family planning; they still made billions of spores and then left them to fend for themselves. Naturally, only few from these billions would survive to become fertilized.

Spore reproduction is cheap and efficient but as birth control is not available, results are unpredictable. Even worse, these spore tree forests were not at all stable: in accidentally good conditions, many spores would survive and make sporophytes which start to grow simultaneously and then suppress each other and even die from over-population. But if the environmental conditions are bad, then none of the gametophytes will survive so there would be no new saplings to replace the old trees.

It is similar to the so-called "dinosaur problem". This situation arose when giant Mesozoic reptiles also lost the control for their offspring: their egg size was limited due to physical restrictions, therefore, young dinosaurs were so much smaller than adults; then the only possible strategy was to leave them alone (Fig. 7.13). As a result, at the end of Mesozoic dinosaurs either decreased in size (became birds), or went extinct.

Plants, however, kept their size and survived. This is because they developed the seed (Fig. 7.14).

A *seed is the result of enforced control of the sporophyte over the gametophyte*. The idea of a seed is to hide most of the heterosporous life cycle *inside mother plant* (Fig. 7.15). In seed plants, everything happens directly on the mother sporophyte: growing of gametophytes, syngamy, and growing of daughter sporophyte. Consequently, the female spore (megaspore) never leaves the sporangium. It germinates inside, waits for fertilization and then the zygote grows into and embryo, still inside the same sporangium.

What will finally leave the mother plant is the *whole female sporangium with gametophyte and embryo on it*. This is the **seed**. It can be defined as *chimeric structure with three genotypes*: seed coat (mother plant megasporangium, $2n$), endosperm (female gametophyte, n), and daughter sporophyte (embryo, $2n$).

It should be noted here that flowering plants have endosperm of different origin; it is called *endosperm*$_2$ and usually is triploid ($3n$) whereas female gametophyte endosperm is haploid (n) **endosperm**$_1$. The other note is that apart from seed coat (which originates from **integument**(s), megasporangium extra cover(s)), mother sporophyte also gives **nucellus** (wall of megasporangium) which sometimes is used as a feeding tissue for the embryo. This last tissue is called **perisperm**.

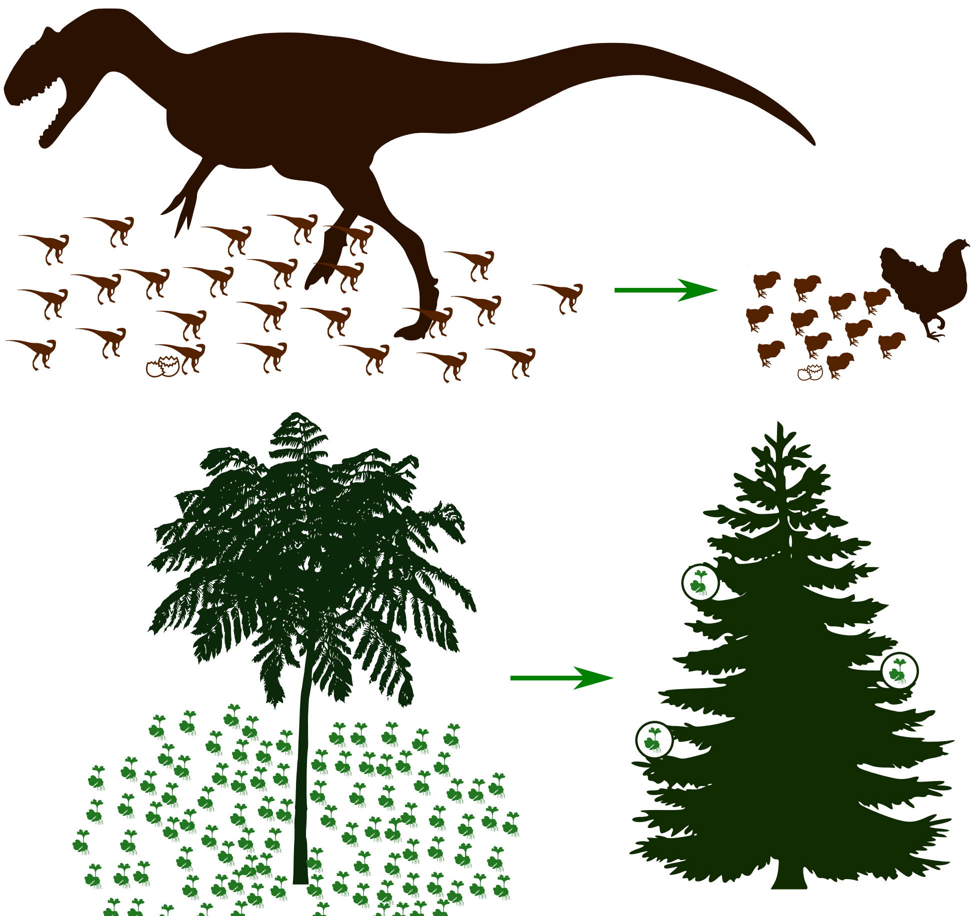


Figure 7.13. How dinosaurs and ferns solved the problem of conflicting strategies.

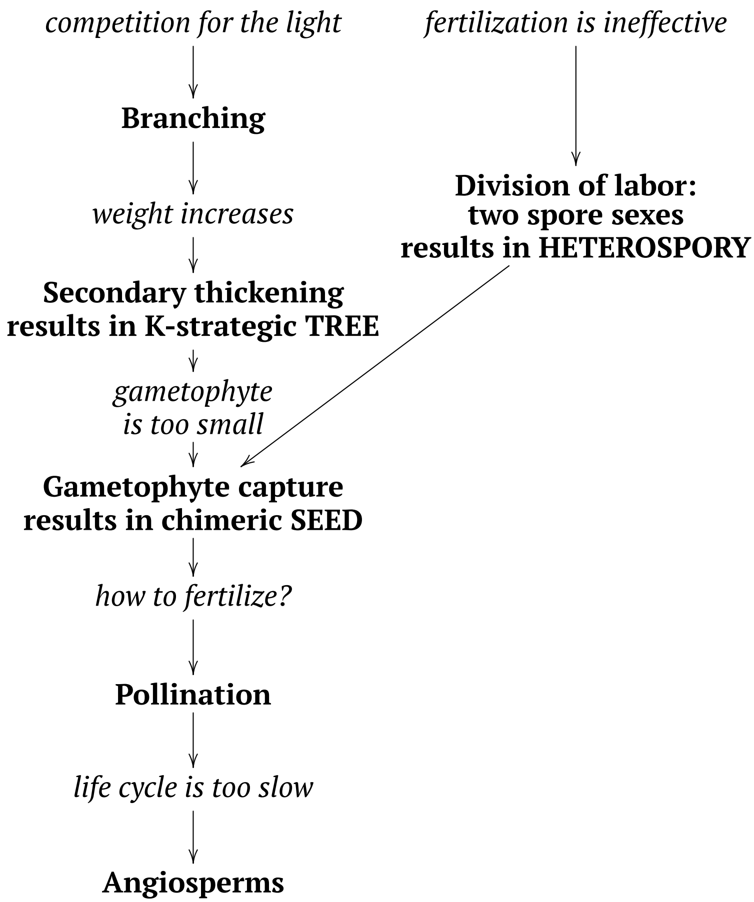


Figure 7.14. How secondary thickening, heterospory and seed are connected: *challenges* to land plants and their **responses**. This is part 2, part 1 is on Fig. 5.3.

One problem is still left. How will sperms reach female gametophyte and egg cell? The target is now high above the ground, on a branch of the giant tree. The only possible solution is pollination.

Pollination is the distribution of the *whole male gametophytes* which are called **pollen grains**. Plants have no legs so they always need a third party in their sex, this is mostly wind or insects.

A pollen grain is *not a spore*, mother sporophyte cares about male lineage too, and male spore grows into very small male gametophyte. It contains multiple haploid cells; some of which are sperms.

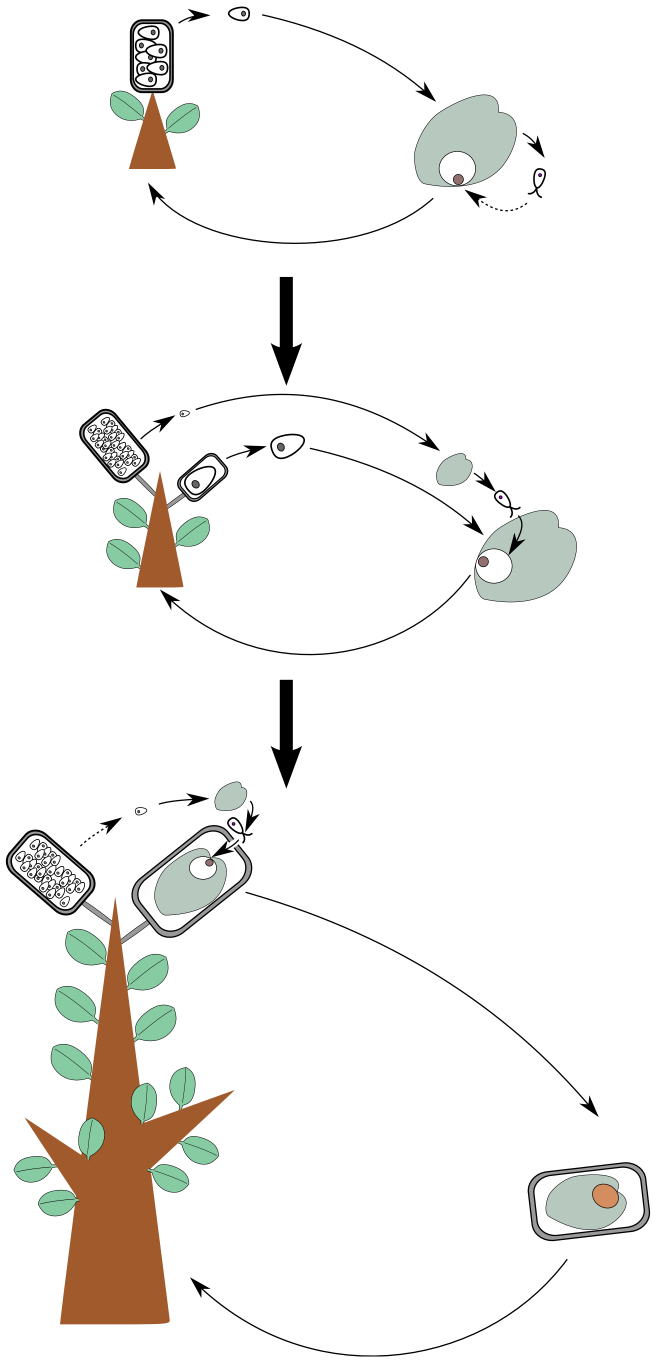


Figure 7.15. The origin of seed (see explanation in the text). Sporophyte is on the left, gametophytes and seed—on the right or/and on the top. First stage—isosporic life cycle, second stage—heterosporic life cycle, third stage—seed plant life cycle.

The lesser problem is: How would these sperms will swim to the egg cell? Some seed plants will excrete the drop of liquid from the top of the **ovule** (integument(s) + megasporangium), whereas the other, more advanced way is to grow a sperm delivery tool, the **pollen tube** (Fig. 7.16) made from one of the pollen grain cells. Fertilization with pollen tube is often called **siphonogamy**.

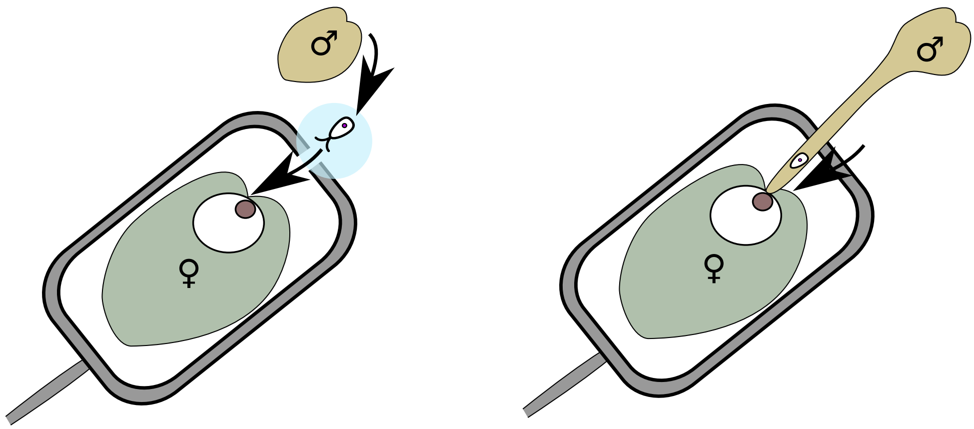


Figure 7.16. Open fertilization in seed plants (left) with the help of liquid extracted by mother plant; and fertilization with pollen tube (right), or *siphonogamy*, with the help of pollen tube growing from male gametophyte. Among extant seed plants, only cycads and ginkgo have the open fertilization.

Consequently, seed plants with the pollen tube do not have flagella even on male gametes; these cells are **spermatia**: aflagellate, non-motile male gametes. (Below, we will continue to call all male gametes "sperms"). Pollen tube also allows only two male gametes per gametophyte: in living world, male gametes are usually competing for fertilization—this selects the best genotypes; whereas in higher seed plants, competition is between pollen tubes. Haploid pollen tube grows inside alien tissue of diploid sporophyte, so this growth is extremely slow in many seed plants. However, angiosperms made their pollen tubes grow fast.

With all these revolutionary adaptations, seed plants were first to colonize really dry places, and, in turn, allowed all other life to survive in arid climates.

The cycle of a seed plant (Fig. 7.17) begins with a sporophyte ($2n$) and has both the female and male organs where some cells undergo meiosis. Inside the ovule (which is the megasporangium with extra covers), female gametophyte (n, future endosperm$_1$) produces the egg cells. Male gametophytes (pollen grains) ripen in the **pollen sac** which is the microsporangium. The pollen sac sends out the pollen grains which meet up with the ovule. The pollen grain then releases the sperms which fertilize the egg cell, and a zygote is formed. The zygote grows into embryo (which uses endosperm as a feeding tissue) and then into the sporophyte.

Several plant lineages met this “seed challenge”, there were seed lycophytes and also seed “horsetails”. However, seed ferns made it first and became ancestors of *seed plants*.

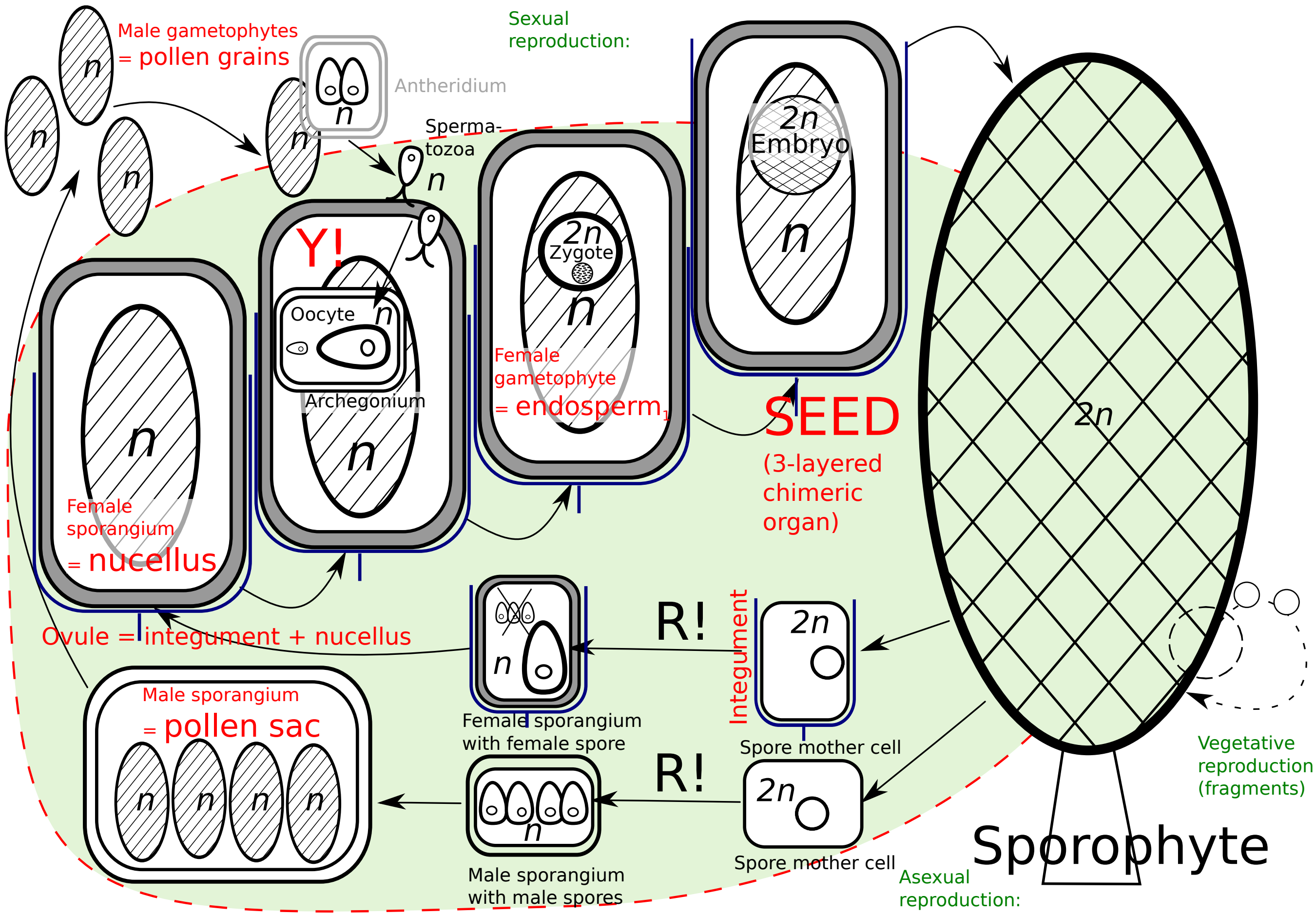


Figure 7.17. Life cycle of seed plants. Innovations (comparing with the heterosporic life cycle) are in red.

7.5.1 Seed Structure and Germination

Seeds are diverse. For example, in an onion (*Allium*), a seed (Fig. 7.18) has endosperm, one **cotyledon** (embryonic leaf), *radicle* (embryonic root), and the lateral embryonic bud (*plumula*).

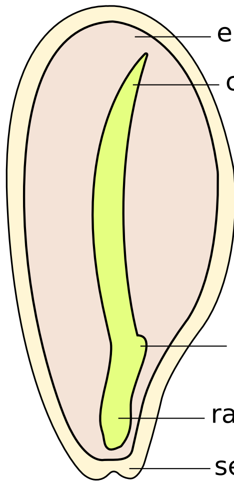


Figure 7.18. Monocot seed.

Beans (*Phaseolus*) and other Leguminosae are examples of seeds without endosperm—actually, it was there, but growing embryo usually eats it out completely. These seeds have two large cotyledons. Grass (Gramineae) seeds contain several specific organs, namely coleoptile, coleorhiza, and scutellum. The *scutellum* is an enlarged cotyledon, *coleoptile* is the bud cover, and *coleorhiza* covers the embryonic root, radicle (Fig. 7.19). Onion and grasses are monocots with lateral embryonic bud. Other seed plants have a terminal embryonic bud and two or multiple cotyledons. Pine (*Pinus*) is an example of a plant that has multiple (five or more) cotyledons. Some plants like orchids (Orchidaceae) do not have developed embryo and even endosperm in seeds, their germination depends on a presence of symbiotic (mycorrhizal) fungus.

The first step in germination and starts with the uptake of water, also known as *imbition*. After imbition, enzymes are activated that start to break down starch into sugars consumed by embryo. The first indication that germination has begun is a swelling in the radicle. In onion and pea (*Pisum*), a structure that looks like a hook goes up through the soil and expose cotyledons and both hypocotyl and epicotyl (first internode). In beans, grasses, and palms, only epicotyl is exposed aboveground whereas cotyledons and hypocotyl remain underground.

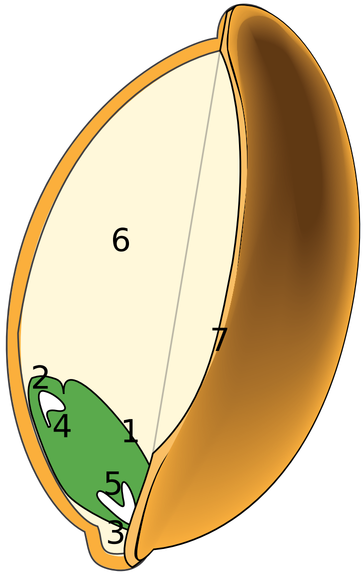


Figure 7.19. Grass seed. 1 scutellum (= cotyledon), 2 coleoptile (bud cover), 3 coleorhiza (radicle cover), 4 embryo bud (= plumula), 5 radicle (= embryo root), 6 endosperm, 7 seed coat.

7.6 Spermatophyta: seed plants

Seed plants consist of approximately 1,000 species of non-angiosperms (gymnosperms) and about 250,000 species of angiosperms. They have a sporic life-cycle with sporophyte predominance, and seeds. The gametophyte is reduced to cells inside the ovule or pollen grain. Males have a minimum number of cells being three and females being four. The antheridia are absent and in flowering plants (Angiospermae) and Gnetopsida the archegonia are also reduced. The sporophyte will always start as an embryo located inside the nutrition tissue, endosperm_1 which is the female gametophyte or in endosperm_2 (see the next chapter). Spermatophyta have axillary buds (buds in leaf axils). Like ferns, they are megaphyllous and homoiohydric, and have a secondary thickening. Higher groups of seed plants lost flagellate spermatozoa and developed pollen tubes. The classes of Spermatophyta are Ginkgoopsida, Cycadopsida, Pinopsida, Gnetopsida, and Angiospermae.

Ginkgoopsida is just one species; ginkgo or maidenhair tree (*Ginkgo biloba*). This plant is long extinct in the wild but is grown on Chinese temple grounds as a decorative tree. Ginkgo is a large tree bearing distinctive triangle-shaped leaf with dichotomous venation. This plant is also dioecious (as an exception among plants, *Ginkgo* has sexual chromosomes like birds and mammals) and the pollen is transported by wind to female (ovulate) trees. The pollen grains of the ginkgo plants produce two multi-flagellate spermatozoa; the edible seed is fruit-like and becomes ripe after lying on the ground for a long time. Maidenhair tree has symbiotic cyanobacteria in cells. As ginkgo probably went through the population bottleneck, there are very few, almost no, phytophagous insects that can damage ginkgo leaves. The only fungus which is capable to eat them, *Bartheletia*, is also a living fossil.

Cycadopsida—cycads is a class with few genera and about 300 species that grow mostly in tropics. Only one species grows naturally in the United States, *Zamia pumil*a, and can be found in Florida and Georgia. Cycads are palm-like plants with large, pinnate leaves. Their wood is rich of parenchyma since stem has anomalous secondary thickening. They are all dioecious and its cone is large and protected by prickles and woody plates. The ovules of these plants are attached to modified leaves (**megasporophylls**) that are gathered in upright cones. Like ginkgo, they have multi-flagellate spermatozoa, archegonia and large oocyte. Cycad seeds are distributed by animals. Life cycle is extremely slow.

Pinopsida—conifers are the most widely known and economically important among gymnosperms. Conifers consist of approximately 630 species. Most of them are temperate evergreen trees, but some are deciduous, such as larch (*Larix*). The stem has a large amount of xylem, a small cork, and minute pith. The ovules are attached to specialized leaves, **seed scales**, and are compacted in cones with **bract scales** (Fig. 7.20). Some conifers, like junipers (*Juniperus*) and yews (*Taxus*), lack woody cones; these plants have fleshy scales. Seeds are distributed by wind and animals.

In all, conifer life cycle takes up to two years. Conifers do not have flagellate spermatozoa; their non-motile male gametes (spermatia) move inside long, fast-growing pollen tube. Among families of conifers, Pinaceae (pine family) have resin and needle-like leaves; *Pinus* have them in shortened shoots, **brachyblasts**, and their large cones have woody scales. Cupressaceae (cypress family) do not have resin, produce small cones that have a fused bract and seed scales, have dimorphic leaves, and some of their genera (like "living fossil" *Metasequoia* from China) are deciduous in an unusual way: they drop whole branches, not individual leaves.

Gnetopsida—gnetophytes are sometimes called chlamydosperms. They are a small class with only three genera that are not at all similar: *Ephedra*, *Welwitschia*, and *Gnetum*. While these plants morphologically remind of angiosperms, they are molecularly related more to other gymnosperms. *Ephedra* are horsetail-like desert leafless shrubs, *Gnetum* are tropical trees, and *Welwitschia* are plants which have a life form that is really hard to tell (Fig. 7.21).

Ephedra has archegonia, but in *Gnetum* and *Welwitschia* they are reduced. On the other hand, *Ephedra* and *Gnetum* have **double fertilization**: both male nuclei fuse with cells of the one female gametophyte (endosperm$_1$): with egg cell and another

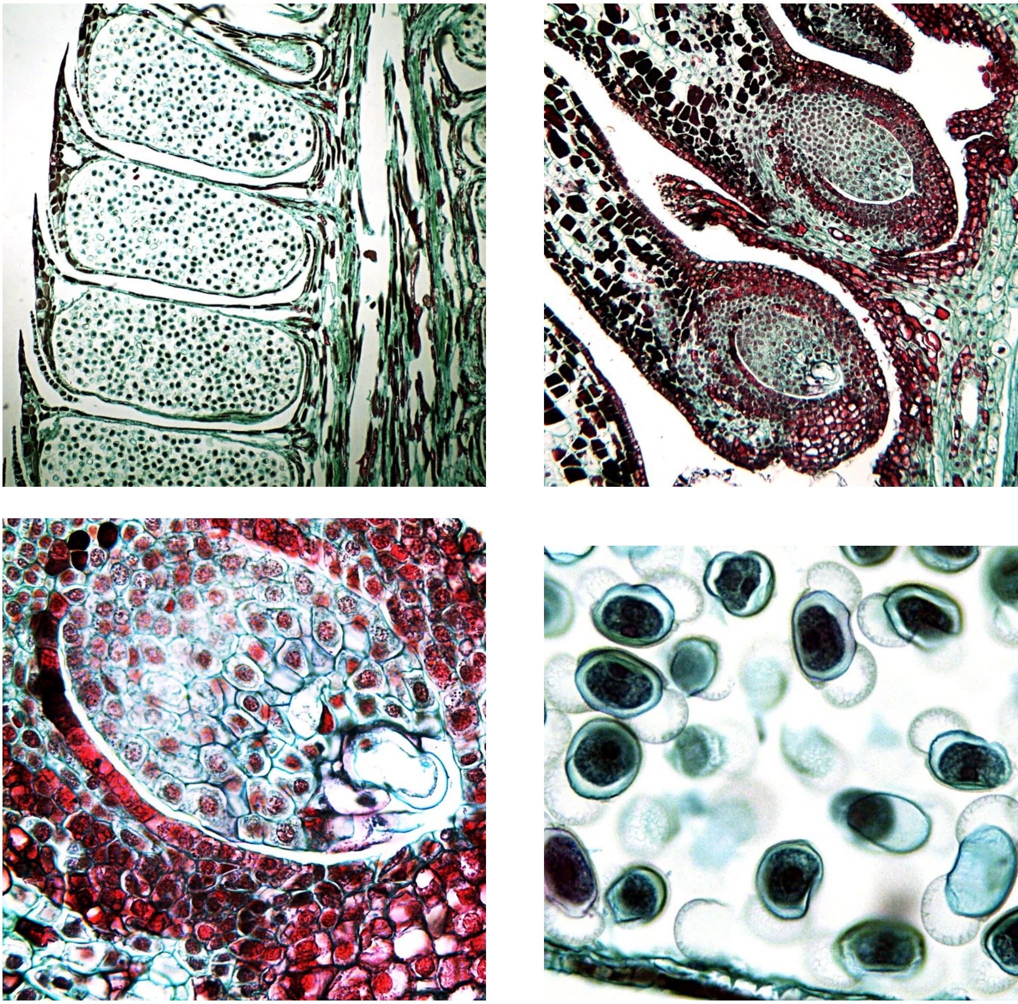


Figure 7.20. Left to right, top to bottom: *Pinus* (Pinopsida) microsporangia (pollen sacs), ovules sitting on seed scales, female gametophyte (endosperm$_1$) and multicellular male gametophyte (pollen). Magnifications $\times 100$ (first and second) and $\times 400$ (third and fourth).

haploid cell, sister to the egg. Double fertilization in gnetophytes results in two competing embryos, and only one of them will survive in future seed.

Both *Gnetum* and *Welwitschia* have vessels (like angiosperms). *Gnetum* also has angiosperm-like opposite leaves with pterodromous venation, like, for example, coffee tree (however, this probably is a result of modification of dichotomous venation). Ovules of chlamydosperms are solitary and covered with an additional outer integument; the male gametes are spermatia moving inside pollen tube.

Figure 7.21. Gnetopsida "even man out" game: *Gnetum*, *Welwitschia*, *Ephedra*, and … *Coffee*. Which is where?

Welwitschia is probably most outstanding among gnetophytes. There is only one species that occurs in the Namibian desert. The best way to describe this plant is an "overgrown seedling." It has a small trunk with two wide leaves that have parallelodromous venation. The secondary thickening is anomalous, wood has vessels. Plant is insect-pollinated, and its winged seeds are dispersed by the wind. Fertilization is not double, but, along with pollen tubes, involves the most crazy structures: *prothallial tubes* which grow from female gametophyte and meet with pollen tubes to make zygote.

* * *

Life cycles determine the basic diversity of plants, they designate plant phyla. Let us compare three types of life cycles again (Fig. 7.22) and again (Fig. 7.23). What is visible on all these schemes, as well as on all similar schemes from above, is growing complexity of cycle, growing reduction of haploid stage, and growing self-similarity within the cycle.

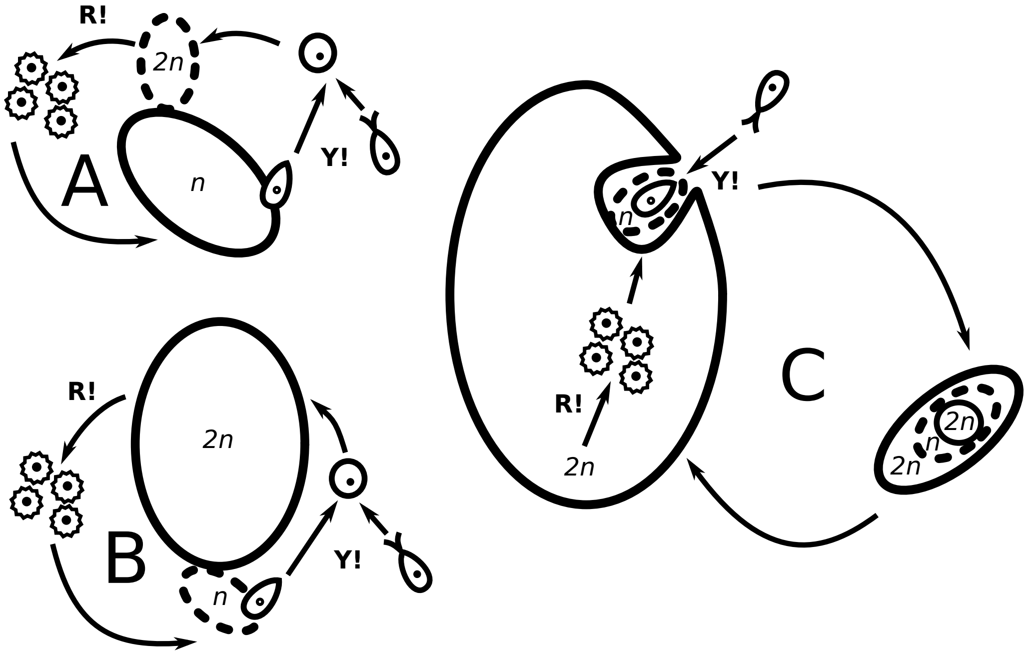


Figure 7.22. Life cycles of mosses (A), ferns (B) and seed plants (C): black and white scheme.

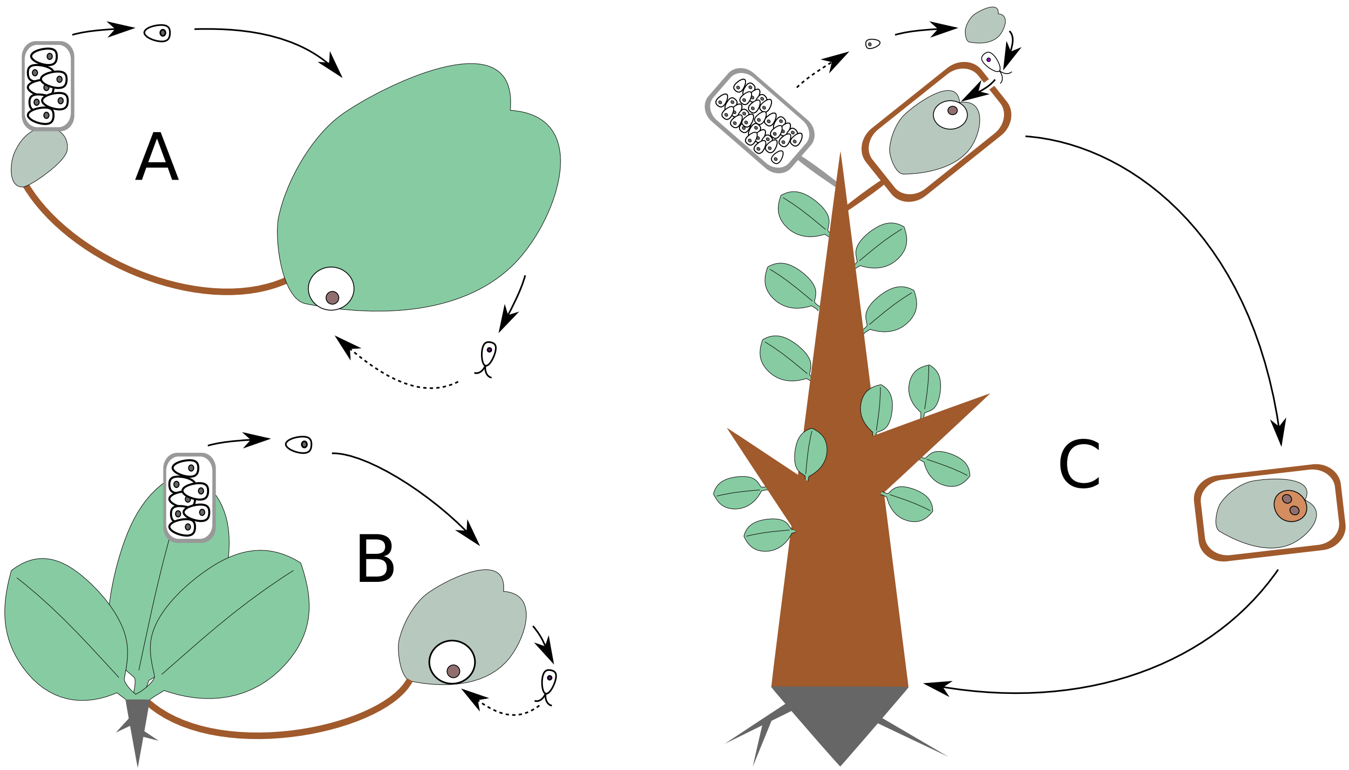


Figure 7.23. Life cycles of mosses (A), ferns (B) and seed plants (C): color scheme.

Chapter 8

The Origin of Flowering

8.1 Spermatophyta 2.0

Flowering plants (angiosperms, Angiospermae) are sometimes referred to as "Spermatophyta 2.0.", or "upgraded gymnosperms". In fact, there is no single character which unequivocally differs flowering plants from other seed plants. Only several characteristics combined together will distinguish angiosperms. Flowering plants have their ovules inside an additional cover: **pistil** which corresponds with megasporophyll (sporangium-bearing leaf); later, the pistil develops into the *fruit*. These plants have an almost complete reduction of gametophytes: three or even two cell of the pollen (male gametophyte) and seven (sometimes even four) cells in **embryo sac** (female gametophyte), there are no archegonia or antheridia. Like gnetophytes, they have double fertilization. The sperms (spermatia) come through the pollen tube (like in conifers and gnetophytes). One sperm fertilizes the egg cell, and the other sperm fertilizes the biggest cell of embryo sac (Fig. 8.1).

While the first fertilization results in a "normal" diploid zygote which grows into embryo, the second fertilization ignites the process of feeding tissue development. This feeding tissue is **endosperm**$_2$, frequently triploid ($3n$) since it *originates from the sperm and cell with two nuclei* and sperm, or diploid ($2n$), if the biggest cell of embryo sac (**central cell**) had one nucleus only.

Double fertilization may be explained in several ways:

1. the second fertilization results in second, "altruistic" embryo which sacrifices itself to feed the sibling;

2. second fertilization is only a signal which initiates the development of endosperm and it does not really matter which genotype it has;

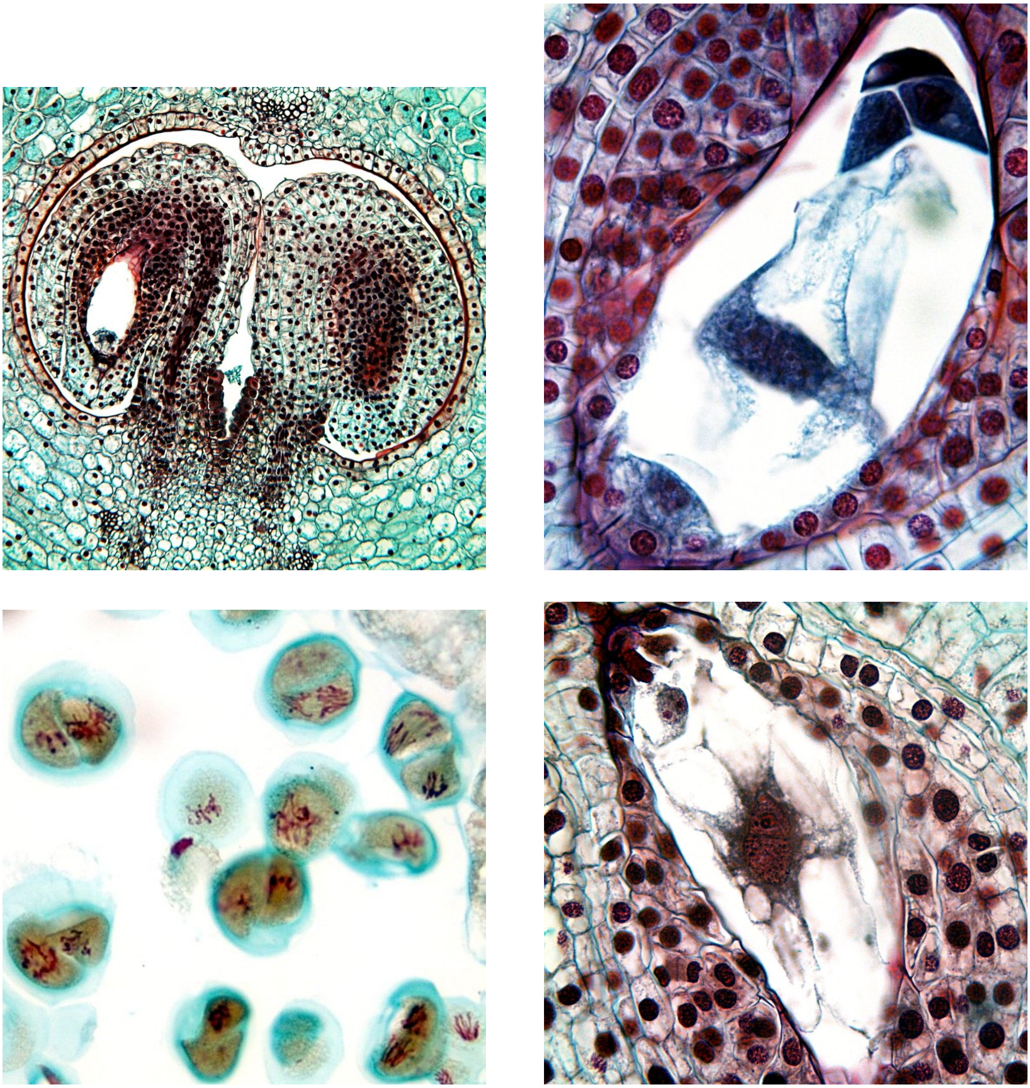


Figure 8.1. Left to right, top to bottom: *Lilium* (Liliidae) ovules, female gametophyte (embryo sac), meiosis II in pollen sacs and double fertilization (egg cell on top is fusing with first sperm, second sperm nucleus in the center is fusing with the nucleus of the central cell). Magnifications $\times 100$ (first) and $\times 400$ (others).

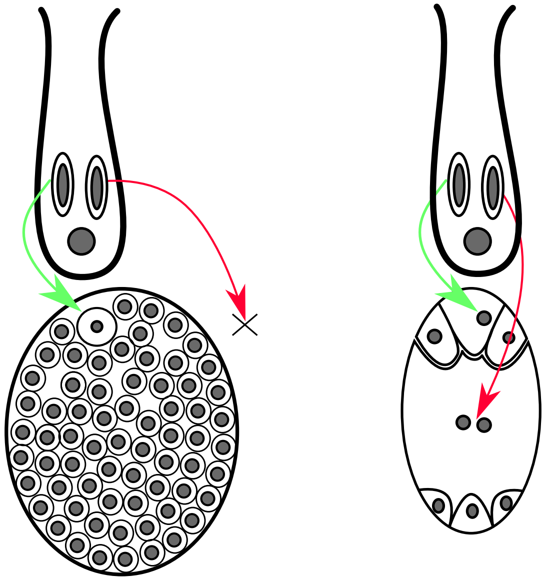


Figure 8.2. Single fertilization (left) and double fertilization (right). Egg fertilization is in green color. Note that in double fertilization second sperm fertilizes (red arrow) cell *sister to egg* (central cell in angiosperms), originated from the *same megaspore*.

3. to make a functional nutrition tissue, angiosperms need a polyploid genome whereas its origin is not so important.

Second hypothesis explains well how angiosperms saved time and resources. Third hypothesis is indirectly supported by the fact that in animals, namely two families of scale insects, there is a similar process (zygote descendant joins sister cell of the egg) which resulted in special polyploid bacteriome, tissue rich of symbiotic bacteria.

One way or another, flowering plants abandoned pre-fertilization development of the nutrition tissue, and changed $endosperm_1$ to $endosperm_2$ (Fig. 8.2).

* * *

In the Mesozoic era, gymnosperms were the dominating plants of the tree story. However, in the uderstorey, herbaceous spore plants did not surrender to seed plants and were still dominating. Amazingly, there were almost no herbaceous gymnosperms! The explanation is that gymnosperms, being quite advanced in general, had a slow and ineffective life cycle.

While ferns and mosses have one "gunshot" in their life cycles (this is fertilization, because dissemination of spores is mainly random), seed plants have *two*: first, they

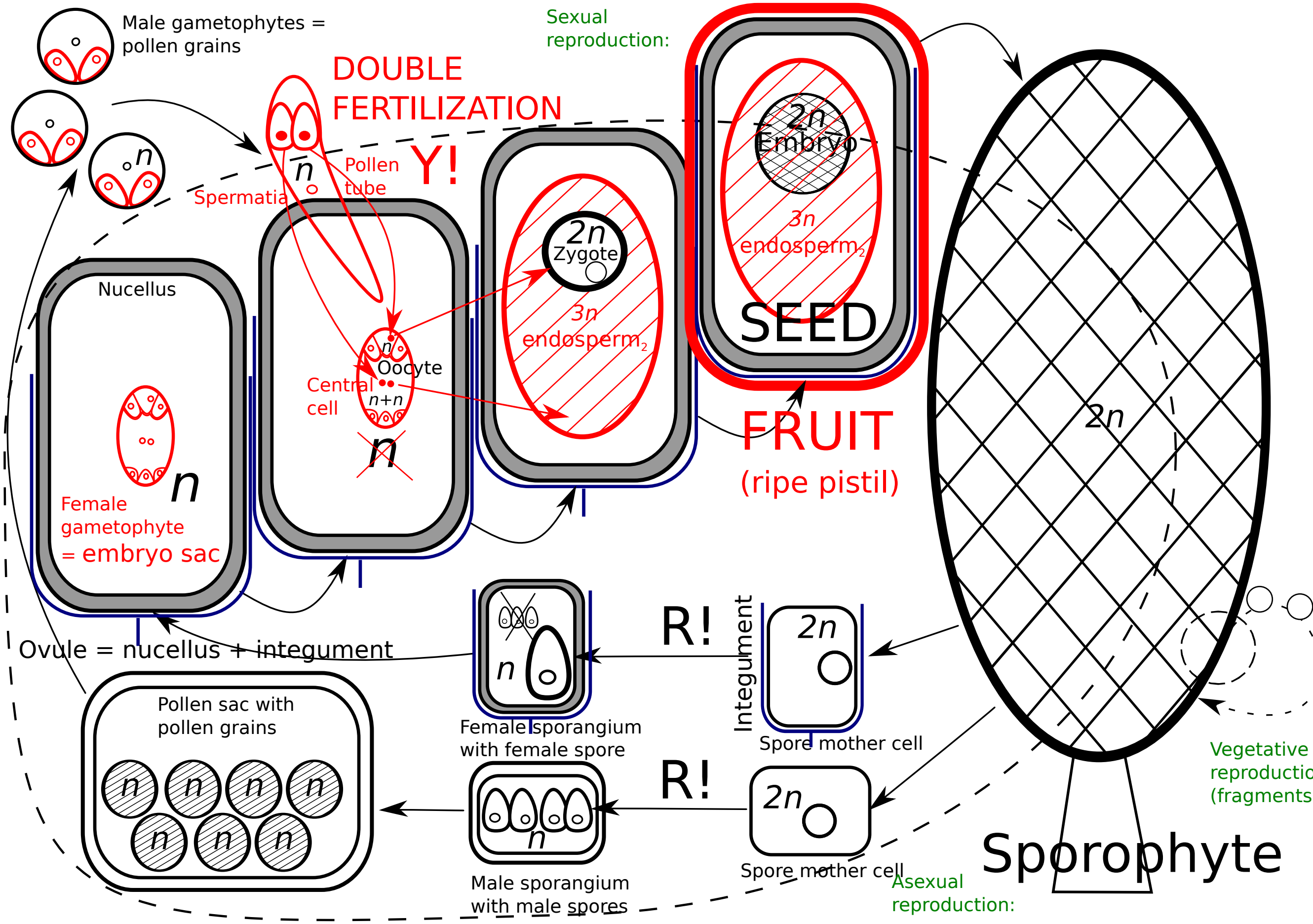


Figure 8.3. Life cycle of angiosperms. Innovations (comparing with the the ancestral seed plant life cycle) are in red.

want to *pollinate* the target plant, and second, they still need to *fertilize* egg cell. Naturally, keeping these two "gunshots" is more complicated then keeping one.

Second shot ancestrally uses water, but higher seed plants managed to get rid of it with pollen tube. First shot used wind which is a natural pollination agent. However, more sophisticated pollination (like insect pollination) was hard to achieve, partly because it requires edible parts like nectar or excess pollen.

If gymnosperms were to increase the speed of life cycle, make more sexual structures, grow rapidly, improve vegetative reproduction, make better pollination and seed dispersal, they could win the competition with ferns in the understory. This is exactly what happened with flowering plant ancestors. Flowering plants grow fast and restore missing (eaten) parts with high speed, they **parcellate** (clone from body parts) easily, they have small and numerous floral units (flowers) which are frequently bisexual but protected from self-pollination and adapted to insect pollination, they guard ovules with pistil wall, their pollen tube grows in hours (not days and weeks), they use fruits to distribute seeds.

Since gymnosperm fertilization occurs *after* gametophyte development, there is frequently a waste of resources: if fertilization does not occur, then all nutrition tissue (endosperm_1) will be lost; such empty seeds are unfortunately not rare among gymnosperms. Fertilization of angiosperms involves the *signaling event*: when second sperm fertilizes central cell, it "rings a bell" saying that the first fertilization is now completed. Endosperm (endosperm_2 in that case) will start to develop only after the fertilization, and resources will not be wasted. This agile life cycle is the main achievement of angiosperms.

There is a growing evidence that these ancestors were *paleoherbs*, herbaceous plants (and maybe, even water plants like one of the most primitive angiosperms, fossil *Archaefructus*, or basal extant *Ceratophyllum*). Right after they won a competition with herbaceous spore plants, they started to conquer the tree storey again, and now, angiosperms dominate the Earth. There are more than 250,000 species of them which is more than any other group of living beings except insects. There are about 300 families and around 40 different orders. The only places that angiosperms do not grow are the open ocean and the central Antarctic.

* * *

The life cycle of angiosperm (Fig. 8.3) begins much like that of other seed plants; however, when it reaches the point of fertilization, it changes. The male gametophytes, pollen grains, produce pollen tubes which rapidly grow to the ovule and deeper, to the embryo sac. The embryo sac typically has seven cells and eight nuclei (two nuclei in the central cell). The first sperm fertilizes the egg and produces the zygote whereas the second sperm fertilizes the central cell and produces the mother cell of the endosperm$_2$:

1. 1st sperm cell (1st spermatium, n) + egg cell (n) $\rightarrow$ zygote ($2n$)
2. 2nd sperm cell (2nd spermatium, n) + central cell ($2n$ or sometimes n) $\rightarrow$ mother cell of endosperm$_2$ ($3n$ or sometimes $2n$)

(At the time of fertilization, central cell could be haploid, with one nucleus, or diploid, with two nuclei; this is because it runs mitosis without cytokinesis at the end. Consequently, nucleus of the second sperm fuses with either one or two nuclei and endosperm$_2$ is either diploid or (more often) haploid.)

At the end of life cycle, the flowering plant develops the fruit (Fig 8.4). Each part of the fruit is of different origin: fruit skin and wall are from mother plant pistil, seed coat is from mother plan ovule, endosperm$_2$ is a result of second fertilization, and embryo is a daughter plant resulting from the first fertilization.

What is interesting, the embryo of angiosperms is still parasitic: it lives on endosperm which originates from (fertilized, ignited) cell of female gametophyte—in essence, still similar to mosses.

8.2 The Flower and the Fruit

8.2.1 The Flower

A **flower** (Fig. 8.6) is a compact generative shoot that is comprised of three zones: sterile (*perianth*), male (*androecium*), and female (*gynoecium*) (Fig. 8.5). Perianth is typically split into green part (*calyx*, consists of *sepals*) and color part (*corolla*, consists of *petals*). Sometimes perianth consists of similar parts which are neither sepals nor petals: *tepals*. This might be seen in the tulip (*Tulipa*) flower where tepals change their color from green (like in calyx) to red, white or yellow (like in corolla).

The general characters that a flower has are sex, merosity, symmetry, and the position of the gynoecium. **Merosity** is simply the number of parts in each whorl of a plant structure, whether it is the number of sepals, petals in a corolla, or the number of stamens. The position of the gynoecium refers to whether the ovary is superior or inferior (Fig. 8.9). *Inferior ovary* (cucumber, *Cucumis*, apple *Malus* or banana *Musa*) will develop into a fruit where stalk and remnants of perianth are on the opposite ends, whereas *superior ovary* will make fruit where stalk is placed together with perianth (like in tomatoes, *Solanum*). More terms are described in the following separate small glossary:

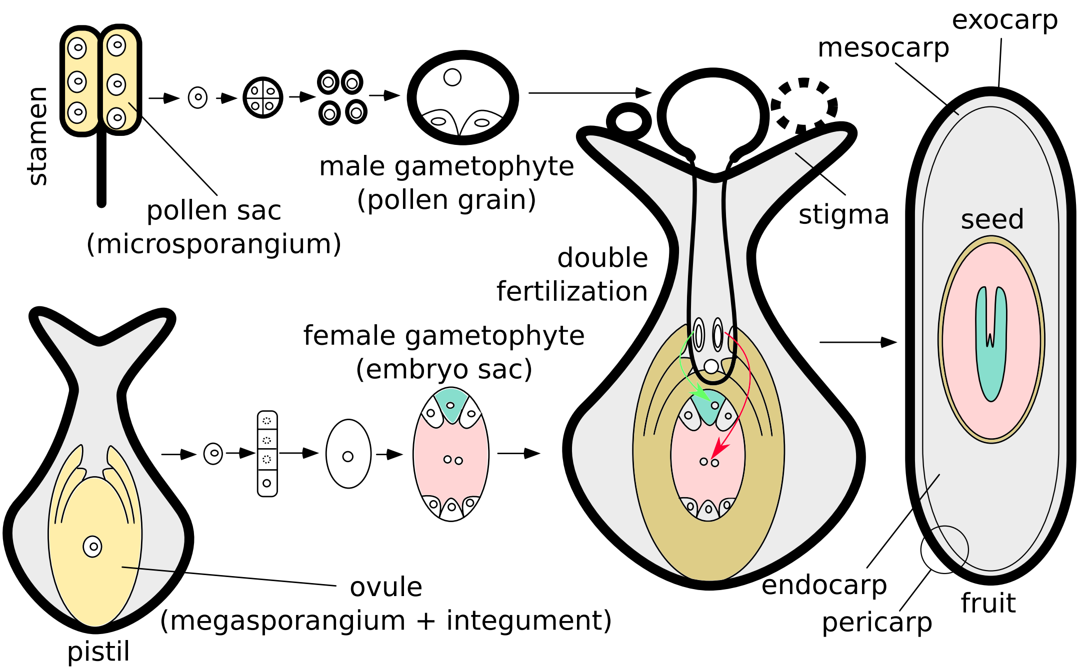


Figure 8.4. The origin of fruit. Note correspondences between different parts (shown with color).

FLOWER PARTS occur in whorls in the following order—sepals, petals, stamens, pistils.

(The only exceptions are flowers of *Eupomatia* with stamens then perianth, *Lacandonia* with pistils then stamens, and some monocots like *Triglochin*, where stamens in several whorls connect with tepals.)

PEDICEL flower stem

RECEPTACLE base of flower where other parts attach

HYPANTHIUM cup-shaped receptacle (Fig. 8.7)

PERIANTH = CALYX + COROLLA

SEPALS small and green, collectively called the CALYX, **formula**: K

PETALS often large and showy, collectively called the COROLLA, **formula**: C

TEPALS used when sepals and petals are not distinguishable, they form SIMPLE PERIANTH, **formula**: P

Figure 8.5. Zones in hellebore (*Helleborus*) flower: sterile perianth, male androecium and in the center, female gynoecium (inside, three ovules are well visible).

ANDROECIUM collective term for stamens: **formula**: A

STAMEN = FILAMENT + ANTHER

ANTHER structure containing pollen grains

FILAMENT structure connecting anther to receptacle

GYNOECIUM collective term for pistils/carpels, **formula**: G. Gynoecium can be composed of:

1. A single CARPEL = simple PISTIL, this is MONOMERY
2. Two or more fused CARPELS = compound PISTIL, this is SYNCARPY
3. Two or more unfused CARPELS = two or more simple PISTILS, this is APOCARPY

(Note that variant #4, several compound pistils, does not exist in nature.)

To determine the number of CARPELS in a compound PISTIL, count LOCULES, points of placentation, number of STYLES, STIGMA and OVARY lobes.

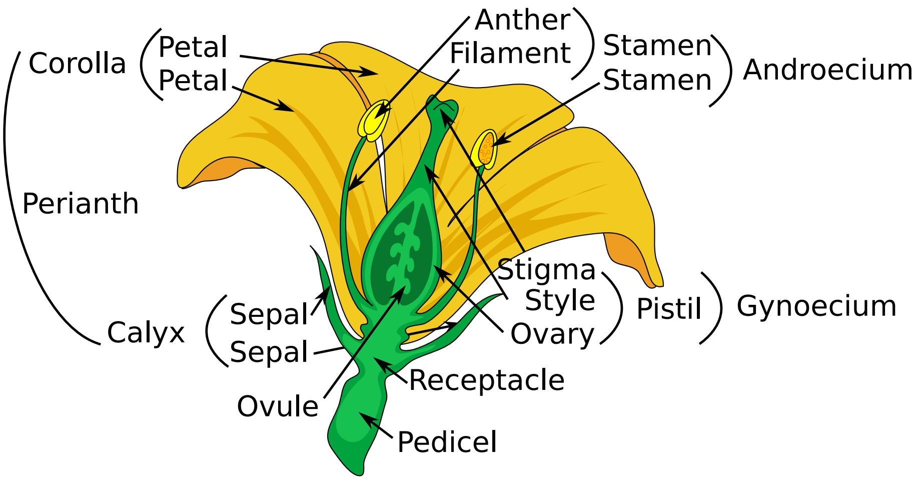


Figure 8.6. Most important parts of the flower.

PISTIL Collective term for carpel(s). The terms CARPEL and PISTIL are equivalent when there is no fusion, if fusion occurs then you have 2 or more CARPELS united into one PISTIL.

CARPEL structure enclosing ovules, may correspond with locules or placentas

OVARY basal position of pistil where OVULES are located. The ovary develops into the fruit; OVULES develop into seeds after fertilization.

LOCULE chamber containg OVULES

PLACENTA place of attachment of OVULE(S) within ovary

STIGMA receptive surface for pollen

STYLE structure connecting ovary and stigma

FLOWER Floral unit with sterile, male and female zones

ACTINOMORPHIC FLOWER A flower having multiple planes of symmetry, **formula**: $\ast$

ZYGOMORPHIC FLOWER A flower having only one plane of symmetry, **formula**: $\uparrow$

PERFECT FLOWER A flower having both sexes

MALE / FEMALE FLOWER A flower having one sex, **formula**: ♂ / ♀ (Fig. 8.8)

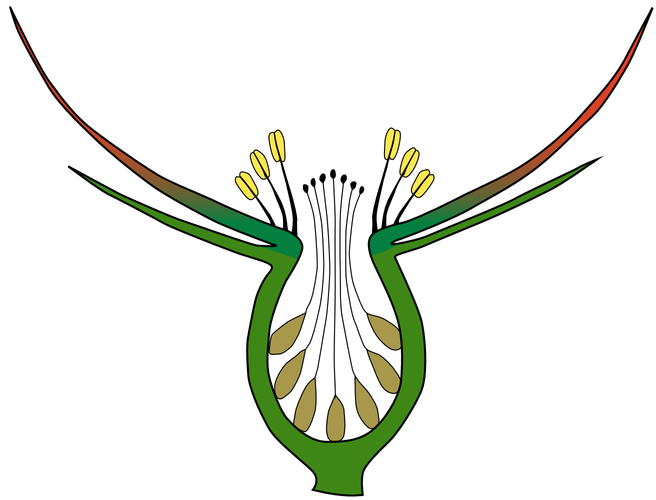


Figure 8.7. Flower with hypanthium (cup-shaped receptacle).

MONOECIOUS PLANTS A plant with unisexual flowers with both sexes on the same plant

DIOECIOUS PLANTS A plant with unisexual flowers with one sex on each plant, in effect, male and female plants

SUPERIOR OVARY most of the flower is attached below the ovary, **formula**: $G_{\underline{\ldots}}$

INFERIOR OVARY most of the flower is attached on the top of ovary, **formula**: $G_{\overline{\ldots}}$

(Inferior ovary only corresponds with monomeric or syncarpous flowers.)

WHORL flower parts attached to one node

Flower formula and diagram

Since there are so many terms about flowers, and at the same time, flower structure and diversity always were of immense importance in botany, two specific ways were developed to make flower description more compact. First is a flower formula. This is an approach where every part of flower is designated with a specific letter, numbers of parts with digits, and some other features (whorls, fusion, position) with other signs:

$\ast K_4 C_4 A_{2+4} G_{\underline{(2)}}$: flower actinomorphic, with four sepals, four petals and six stamens in two whorls, ovary superior, with two fused carpels

Figure 8.8. Diagram of male (left) and diagram and scheme of female (central and right) flowers of sedges (*Carex*). Note the perigynium (external cover of pistil).

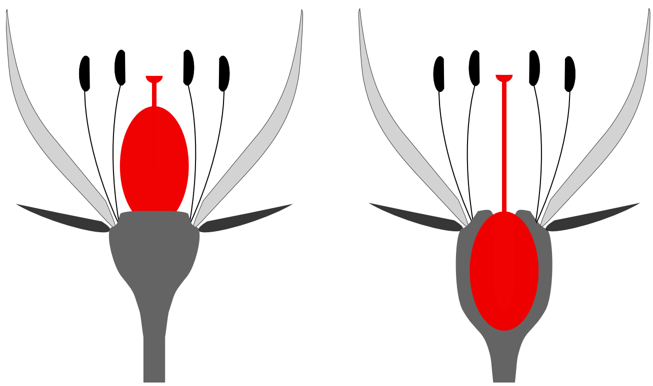


Figure 8.9. Position of ovary: superior (left, *hypogynous flower*) and inferior (right, *epigynous flower*).

> $\uparrow K_{(5)}[C_{(1,2,2)}A_{2,2}]G_{\underline{(2\times 2)}}$: flower zygomorphic, with five fused sepals, five unequal fused petals, two-paired stamens attached to petals, superior ovary with two subdivided carpels
>
> $\ast K_{(5)}C_{(5)}[A_5 G_{\overline{(3)}}]$: actinomorphic flower with five fused sepals and five fused petals, five stamens attached to pistil, ovary inferior, with three fused carpels

The following signs are used to enrich formulas:

PLUS "+" is used to show different whorls; *minus* "–" shows variation; "∨" = "*or*"

BRACKETS "[]" and "()" show fusion

COMMA "," shows inequality of flower parts in one whorl

MULTIPLICATION "×" shows splitting

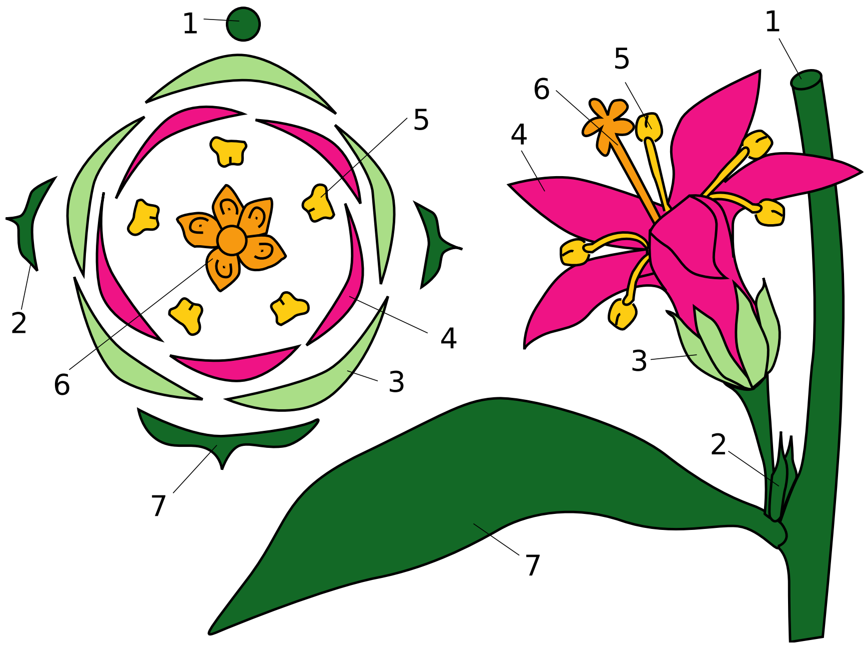


Figure 8.10. How to draw a diagram (graphical explanation): compare numbers on plant and on diagram.

INFINITY "∞" shows indefinite number of more than 12 parts

Flower diagram is a graphical way of flower description. This diagram is a kind of cross-section of the flower. Frequently, the structure of pistil is not shown on the diagram. Also, diagrams sometimes contain signs for the description of main stem (axis) and flower-related leaf (bract). The best way to show how to draw diagram is also graphical (Fig. 8.10); formula of the flower shown there is $\ast K_5 C_5 A_5 G_{\underline{(5)}}$.

ABC model

All parts of flower have a specific genetic developmental origin explained in the *ABC model* (Fig. 8.11). There are three classes of genes with expression which overlaps as concentric rings, and these genes determine which cells develop into particular organ of the flower. If there are A and C genes expressed, cells will make sepals and pistils. In areas where A and B are active, petals will form; areas where B and C are active are the sites where stamens will appear. A will make a sepal, C will "create" a carpel:

- A alone $\rightarrow$ calyx

- A + B → corolla
- C + B → androecium
- C alone → gynoecium

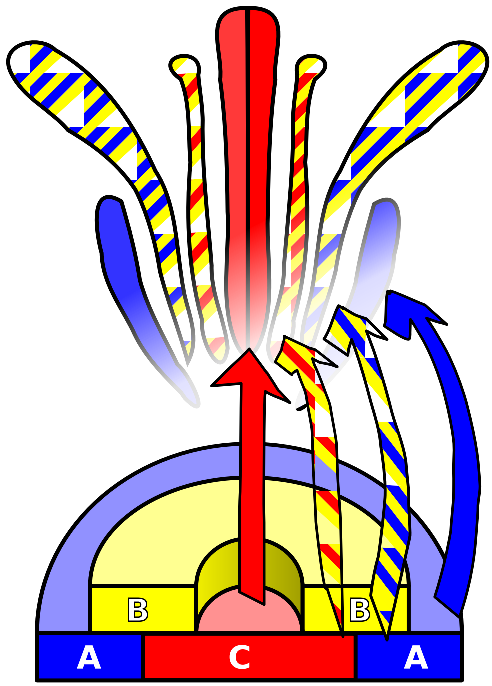


Figure 8.11. ABC model of flower development.

Origin of flower

An example of a primitive magnoliid flower would be *Archaefructus* which is a fossil water plant from the lower Cretaceous time period in China. Its fructifications (flower units, FU) were very primitive and did not yet form a compacted flower, instead, there were multiple free carpels, and paired stamens (Fig. 8.12).

Another ancestral flowering plant is *Amborella*,a small forest shrub of New Caledonia (Fig. 8.13), which is an island in the Pacific Ocean.

Amborella has irregular flowers, a stylar canal, unusual 5-celled embryo sacs that have one central cell, and only four other cells (egg cell and its "sisters"). A stylar canal is a canal that leads to the ovary that the pollen tubes pass through so these plants are not completely "angiospermic", this represents one of the stages of the origin of pistil (Fig. 8.14).

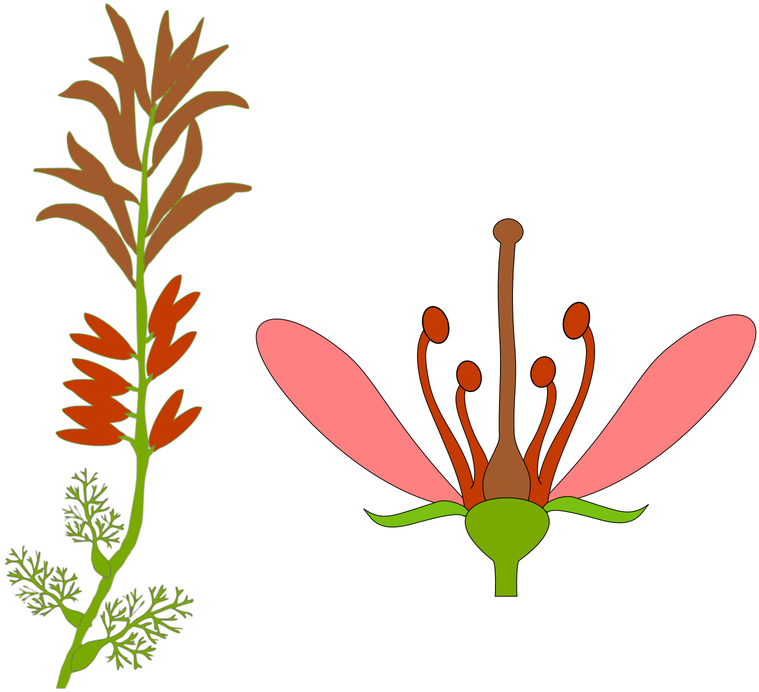


Figure 8.12. Comparison of *Archaefructus* flower (left) and typical flower (note colors). (*Modified from various sources*.)

8.2.2 The Inflorescence

Inflorescence is an isolated generative shoot (shoot bearing FU). Together, inflorescences make **generative shoot system**. Its diverse structure is of not lesser importance than the structure of vegetative shoot system.

The vast diversity of inflorescences can be split into four groups, or "models" (Fig. 8.15). Sole flower is sometimes considered as a "Model 0".

Two models are most widespread. Model I inflorescences are based on the **raceme** (*monopodially branched* generative shoot). They are simple or double and mostly monopodial (Fig. 8.17).

Model II inflorescences (Fig. 8.16) bear or consist of closed (*sympodially branched*) units. The most complete but more rare variant is **thyrsus**, whereas reduced variants (*monochasia* and *dichasia*) are more frequent.

Figure 8.13. *Amborella trichopoda*, sister group to all other flowering plants. White ruler equal to 1 mm.

Figure 8.14. *Amborella* pistil, longitudinal section: stylar canal is green, embryo sac red.

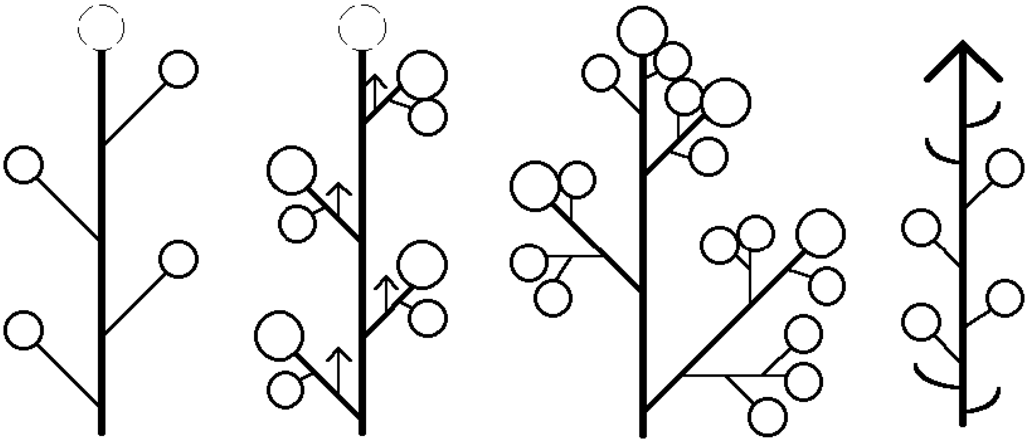


Figure 8.15. Four kinds of inflorescences (left to right): Model I (raceme-based), Model II (thyrsoid) , Model III (panicle) and Model IV (intercalate).

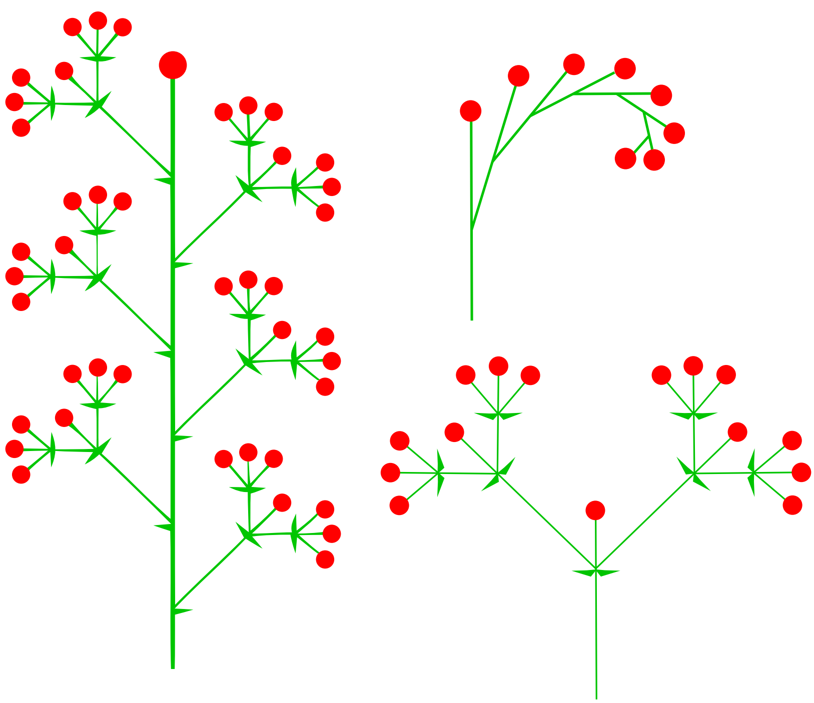


Figure 8.16. Model II inflorescences (from top to bottom): thyrsus, dichasium and monochasium (cincinnus).

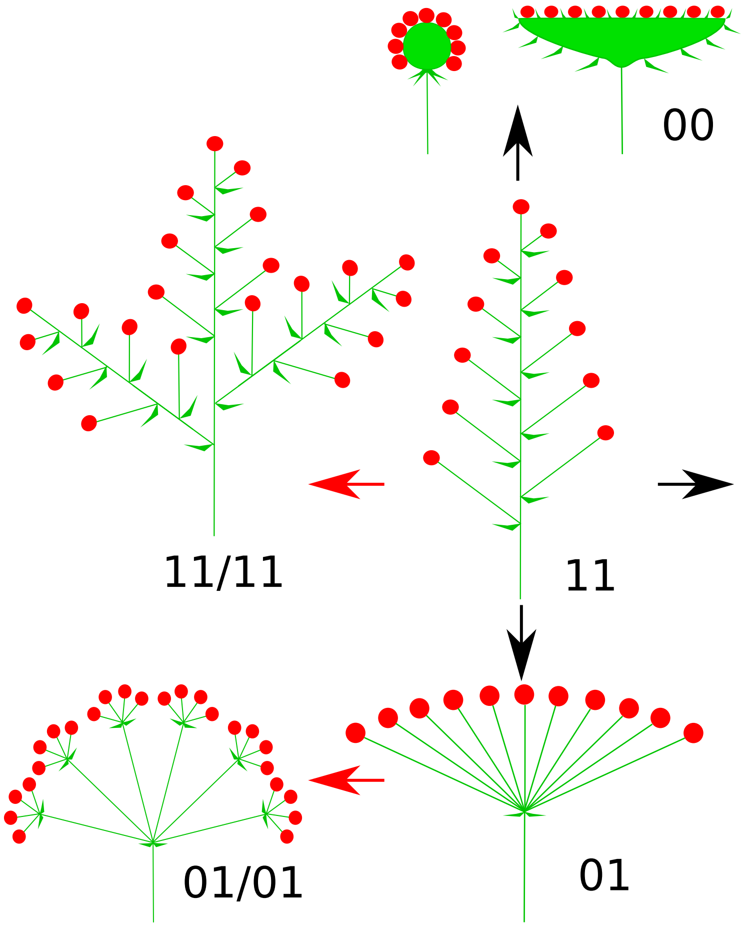


Figure 8.17. Different Model I inflorescences and their evolutionary connections. Digits represent the simple encoding system: first position is main axis, second position are secondary axes (flower pedicels), 1 means developed, 0 reduced. Double inflorescences have four digit positions, for the first and second orders of branching. Some names: 11 raceme, 11/11 double raceme, 10 spike and spadix, 01 umbel, 01/01 compound umbel, 00 head.

8.2.3 Pollination

Pollination could be of two types: self- and cross-pollination. **Cross-pollination** can happen in both abiotic and biotic ways. Abiotic would be represented by gravity, wind, or water; biotic would be performed by agents like insects, birds, bats, or in some cases tree mammals like possums. Wind-pollination is seen as being wasteful and unintelligent due to the fact that the plant needs to produce so much more pollen without any precise targeting.

Adaptation to the particular pollination agent results in different pollination syndromes. For example, cup-shaped flowers are usually pollinated with massive animals like beetles and even bats. Funnel-shaped flowers as well as labiate flowers (with lips), are adapted to flies and bees. Flowers with long spurs attract butterflies and birds (like hummingbirds or sugarbirds).

Self-pollination often exists like a "plan B", in case cross-pollination is, for some reason, impossible. Sometimes, self-pollinated flowers even do not open; these flowers are called **cleistogamous**.

If pollination needs to be avoided, apomixis will prevent it. **Apomixis** requires reproductive organs, but there is no fertilization. One type of apomixis is **apospory** when an embryo develops from the maternal diploid tissue, but does not go through the meiosis stage. In this process, asexual reproduction will have become vegetative. Another type of apomixis would be **apogamy** (parthenogenesis) when embryo develops from an unfertilized gamete after diploidization has occurred. Here, vegetative reproduction evolved from sexual reproduction.

8.2.4 The Fruit

A *fruit* is defined as *ripened ovary, flower, or whole inflorescence*. The origins of the fruit coat and the **pericarp** (Fig. 8.18) which is comprised of the *exocarp*, *mesocarp*, and *endocarp*, are mostly from the wall of the pistil.

Fruits can be simple, multiple, or compound. **Simple fruits** come from a single pistil (like cherry, *Prunus*). **Multiple fruits** are formed from many pistils of the same flower (strawberry, *Fragaria*). A **compound fruit** (infructescense) would be a pineapple (*Ananas*) or fig (*Ficus*) which comes from multiple flowers (inflorescence).

Fruits can be dry or fleshy. An example of *dry fruit* is a nut like peanut (*Arachis*) or walnut (*Juglans*). Examples of *fleshy fruits* include apples (*Malus*) or oranges (*Citrus*).

Fruits also delegate dispersal function to their different parts. **Dehiscent fruits** (like canola, *Brassica*) open and delegate dispersal to individual seeds.

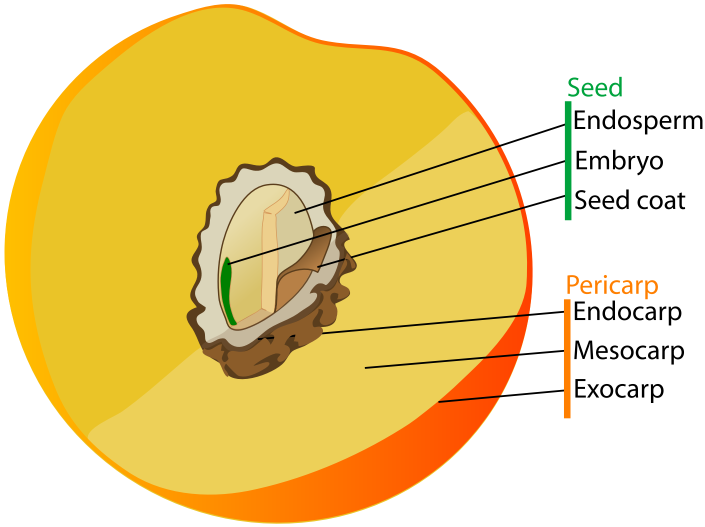


Figure 8.18. Scheme of drupe (e.g., peach) with three levels of pericarp. Note that pit is essentially endocarp + seed.

Indehiscent fruits (like papaya, *Carica*) will not open and will be dispersal units (**diaspores**) themselves.

Schizocarp fruits (like in spurge, *Euphorbia* or maple, *Acer*) are in between: they do not open but break into several parts, and each of them contains one seed inside. For example, maple fruit consists of two "wings", each of them contains the part of fruit and one seed.

In addition, simple fruits could be monomerous (1-seeded) like nut or achene (sunflower, *Helianthus*), or bear multiple seeds (like follicle in tulip, *Tulipa*).

All these different variants have their own names partly described in the following table:

Type	Consistency	Opening	Example(s)
Simple	Fleshy	Indehiscent	Drupe, Berry, Hesperidium, Pome
Simple	Dry	Dehiscent	Capsule, Legume (pod), Silique (Fig. 8.21)
Simple	Dry	Schizocarpic	Regma, Samara, Shizocarp
Simple	Dry	Indehiscent	Caryopsis (grain), Nut (incl. acorn), Achene
Multiple	Fleshy	Indehiscent	Multiple drupe
Multiple	Dry	Dehiscent	Follicle
Multiple	Dry	Indehiscent	Multiple nut
Compound	Fleshy	Indehiscent	Compound berry
Compound	Dry	Indehiscent	Compound nut

8.3 Three plant families you wanted to know but were too afraid to ask

Angiosperms is a giant (quarter of million species) class with four subclasses (Fig. 8.19):

Magnoliidae being the most primitive with flowers of numerous free parts (like water lily, *Nymphaea*, fossil *Archaefructus* and *Amborella*);

Liliidae or **monocots** are grasses, palms, true lilies and many others with trimerous flowers;

Rosidae with pentamerous or tetramerous flowers and free petals;

Asteridae most advanced, bear flowers with fused petals and reduced number of carpels.

Rosids and asterids each comprise about ⅓ of angiosperm diversity.

* * *

Among the numerous taxonomic groups described by scientists in the last 300 years, families of flowering plants hold the distinct place. They were established in col-

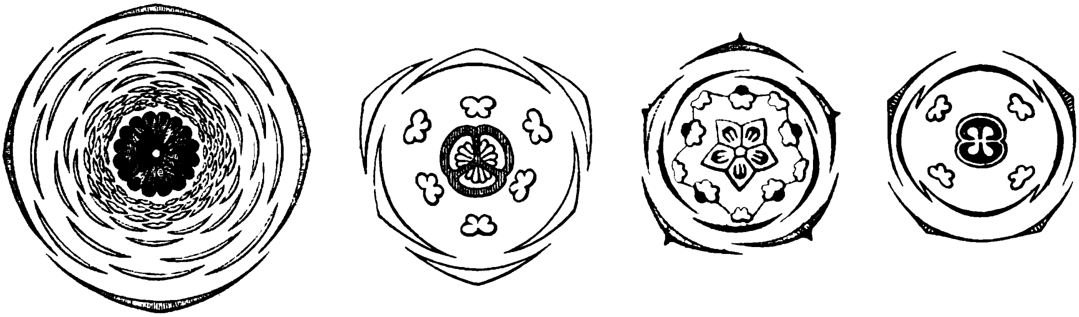


Figure 8.19. Flower diagram "portraits" of flowering plants subclasses (left to right): Magnoliidae, Liliidae, Rosidae, Asteridae. (*Modified from Eichler, 1875*). See also Fig. 8.10 for graphical explanation of the flower diagram.

laborative efforts of French botanists, namely Michel Adanson and Antoine Jussieu. Adanson based his research on methods which are now frequently called "bioinformatics" and therefore was long ahead of his time. Jussieu proved Adanson's ideas by establishing the living garden where plants were arranged by these families. At first, families were not accepted by "fathers of botany" like Carolus Linnaeus. But with time, more and more facts were accumulated which support the ideas enclosed in the families differentiation. The most amazing was almost absolute support of plant families concepts with new molecular methods. Many groups which looked stable (like orders of birds and mammals) appeared less robust than plant families. This is why plant families are so important.

Practically, families provide a great help in knowing plants. For example, the flora of whole North America has 20,000 species of plants. It is almost impossible to remember them all. However, there are only 200 plant families in North America. Therefore, knowing the family saves lots of time and efforts in plant determination.

Several plant families are especially important since they play a big role in economics, form widespread types of vegetation, or are simply extremely rich in species. Three of these families will be characterized below. Characterization of family should follows the plan below:

1. Meta-information: name, position in classification, number of species, distribution
2. Ecological preferences
3. Morphology and anatomy of stem, leaf and root
4. Generative organs from inflorescence to fruit, including flower diagrams and formulas. Seed.

5. Representatives and their importance

8.3.1 Leguminosae, or Fabaceae—legume family

Belong to rosids (Rosidae). Up to 17,000 species, third largest angiosperm family after Compositae (aster family) and Orchidaceae (orchids). Widely distributed throughout the world, but preferably in tropics. Have root nodules with *nitrogen-fixing bacteria*. Leaves alternate, pinnately compound (once or twice), with stipules.

Three subfamilies (Caesalpinioideae, Mimosoideae, Papilionoideae) often treated as separate families. Sepals 5, united. Petals 5, in Papilionoideae they are free, unequal and have special names: *banner*, *keel* and *wing* (Fig. 8.20), in Mimosoideae they fuse and form tube. Stamens often 10 with 9 fused and one free stamen; in Mimosoideae, stamens are numerous. Singe pistil with single carpel. Flower formula of Mimosoideae is

$$\ast K_{(5)} C_{(5)} A_{5-\infty} G_{\underline{1}}$$

Papilionoid legumes have formula like

$$\uparrow K_{(5)} C_{1,2,2} A_{1,[4+5]} G_{\underline{1}}$$

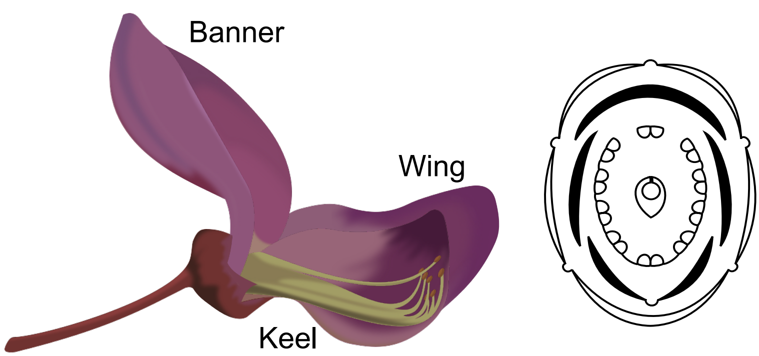


Figure 8.20. Leguminosae. Flowers of Papilionoideae subfamily.

Fruit is a legume (pod): dehiscent with one camera; this is different from silique of cabbage family (Cruciferae) which has two cameras (Fig. 8.21). Mature seeds without endosperm.

* * *

Representatives of Leguminosae:

- Mimosoideae: stamens numerous, petals connected

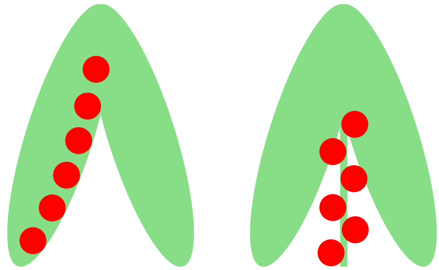


Figure 8.21. Opened pod (Leguminosae) *versus* silique (Cruciferae), seeds are red.

  - *Acacia*—dominant tree of African and Australian savannas, often with phyllodes
  - *Mimosa*—sensitive plant
- Papilionoideae: stamens 9+1, petals free; this subfamily contains many extremely important food plants with high protein value
  - *Glycine*—soybean
  - *Arachis*—peanut with self-buried fruits
  - *Phaseolus*—bean
  - *Pisum*—pea

8.3.2 Compositae, or Asteraceae—aster family

Belong to asterids (Asteridae). More than 20,000 species—second place in flowering plants. Cosmopolitan, but better represented in temperate and subtropical regions. Prefer open spaces. Herbs, rarely woody plants; store carbohydrates as inulin (not starch), sometimes have resin or laticifers (subfamily Cichorioideae). Leaves are alternate or opposite, without stipules, with pterodromous venation.

Flowers in involucrate heads which mimic one flower (Fig. 8.22). Calyx reduced to hairs or bristles (pappus), petals fused in tube or ligula (with 5 or 3 teeth). Stamens 5, fused by anthers, pollen lifted up and distributed by outer sides of stigmas, this is *secondary pollen presentation* (Fig. 8.23). Pistil has 2 carpels, ovary inferior. Fruit is achene, mature seed has almost no endosperm. Flower formula of the tubular (disk) flower is

$$\ast\, K_{\infty} C_{(5)} A_{(5)} G_{\overline{(2)}}$$

Ligulate (ray) flower typically has formula like

$$\uparrow K_{\infty} C_{(3 \vee 5)} A_{(5)} G_{\overline{(2)}}$$

Figure 8.22. Compositae: head and one ligulate (ray) flower.

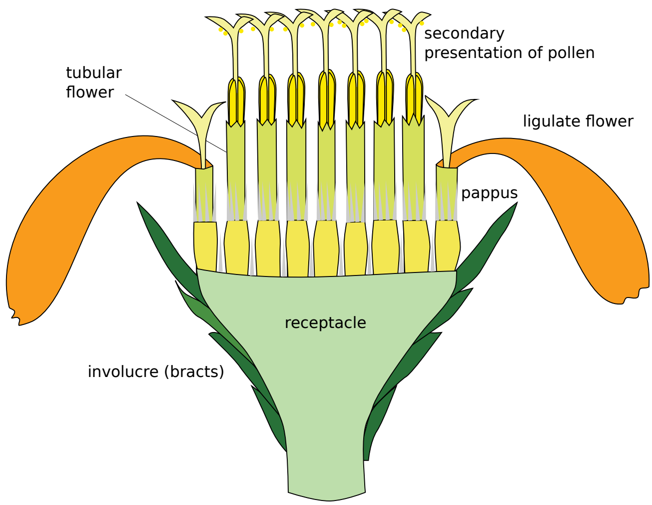


Figure 8.23. Features of Compositae: two types of flowers, secondary pollen presentation, pappus.

Fruit of aster family is one-seeded **achene** (it is a frequent mistake to call it "seed"). In achene, walls of inferior ovary are tightly fused with seed coat. Achenes frequently bear diverse dispersal structures: trichomes, teeth, hooks and others.

* * *

Oil plants, vegetables, ornamentals and medicinal plants distributed in multiple subfamilies, most important are three:

- Carduoideae: mostly tubular flowers
  - *Centaurea*—knapweed
  - *Cynara*—artichoke
  - *Carthamus*–safflower
- Cichorioideae: mostly 5-toothed ligulate (pseudo-ligulate) flowers + lacticifers with latex
  - *Taraxacum*—dandelion
  - *Lactuca*—lettuce
- Asteroideae: tubular + 3-toothed ligulate flowers
  - *Helianthus*—sunflower (BTW, "canola", or Brassica napus from Cruciferae is the second main source of vegetable oil)
  - *Artemisia*—sagebrush
  - *Tagetes*—marigold and lots of other ornamentals

8.3.3 Gramineae, or Poaceae—grass family

Belong to liliids (Liliidae, monocots). Approximately 8,000 species distributed throughout the world, but most genera concentrate in tropics. Prefer dry, sunny places. Often form turf (tussocks)—compact structures where old grass stems, rhizomes, roots, and soil parts are intermixed. Grasses form grasslands—specific ecological communities widely represented on Earth (for example, North American prairies are grasslands). Stems of grasses are usually hollow and round. Leaves with sheaths.

Flowers reduced, wind-pollinated, usually bisexual, form complicated spikelets. Each spikelet bears two *glumes*; each flower has *lemma* and *palea* scales (Fig. 8.24). Perianth is reduced to lodicules. Stamens from 6 to 1 (most often 3), with large anthers. Flower formula is

$$\uparrow P_{0-3}A_{0-3+2-3}G_{\underline{(2)}}$$

Fruit is a *caryopsis*; it includes flower scales. Seed contains embryo with *coleoptile*, *coleorhiza* and *scutellum* (Fig. 7.19).

* * *

Most primitive grasses are bamboos (Bambusoideae subfamily). There are many other subfamilies. Two are especially economically important:

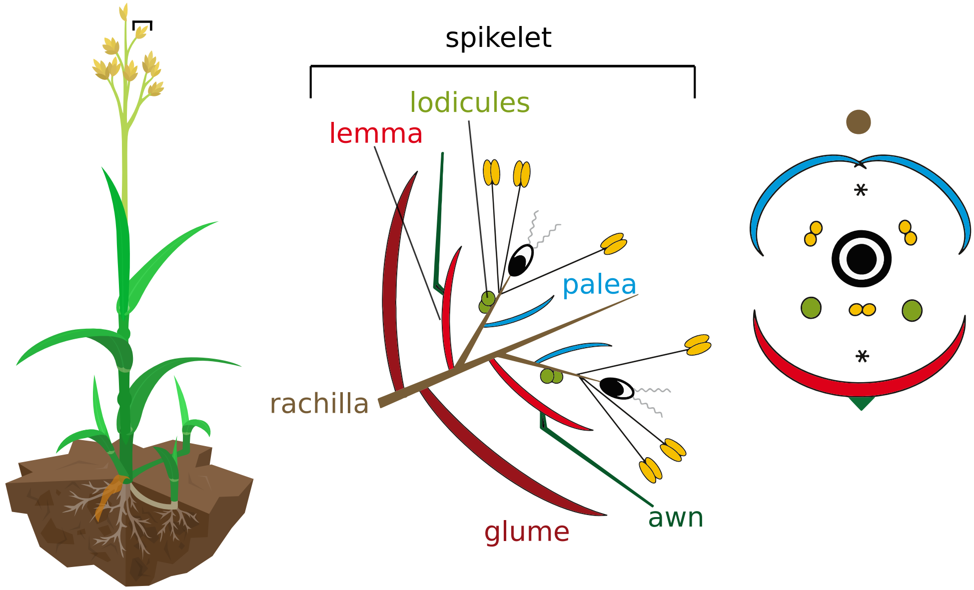


Figure 8.24. Gramineae: one plant, scheme of spikelet and flower diagram.

- Pooid (Pooideae) grasses usually are C_3 plants, wheat (*Triticum*), rice (*Oryza*), barley (*Hordeum*) and rye (*Secale*) belong to this group.
- Panicoid (Panicoideae) grasses are mostly C_4 plants like corn (*Zea*), sorghum (*Sorghum*) and sugarcane (*Saccharum*).

Chapter 9

Plants and Earth

9.1 Geography of Vegetation

Plants are main components of terrestrial ecosystems, they are primary producers, and almost all terrestrial life if based on plants. Consequently, plants will determine how a particular territory might look, which could be, for example, grassland, tundra, or forest. These *types of vegetation* (i.e., visually different plant communities) will have different occurrence on Earth. Below is the list of the most important types (they also called *biomes*):

Tundra Small-sized plants adapted to the short season, wet soils and sometimes also permafrost

Taiga Conifer forests

Deciduous forest Broadleaved temperate forests. The other type of deciduous forests are dry forests of tropical climates.

Grassland Prairie (North America), steppe (Eurasia), savanna (Africa and Australia), llanos (north South America), pampas (south South America)

Shrubland Chaparral (North America), maquis (Mediterranean), fynbos (South Africa), bush (Australia)

Desert Different from shrubland by plants staying apart and soil surface visible

Tropical forest Selva, tropical rain forest: humid and warm environment, the peak of Earth biodiversity

Naturally, these biomes are directly related with the climate, mostly with the coldest temperatures and amount of precipitation. If the Earth would be one continent, then these vegetation types will be arranged from a pole to equator exactly in the order from the list above. However, the real picture is more complicated (Fig. 9.1.)

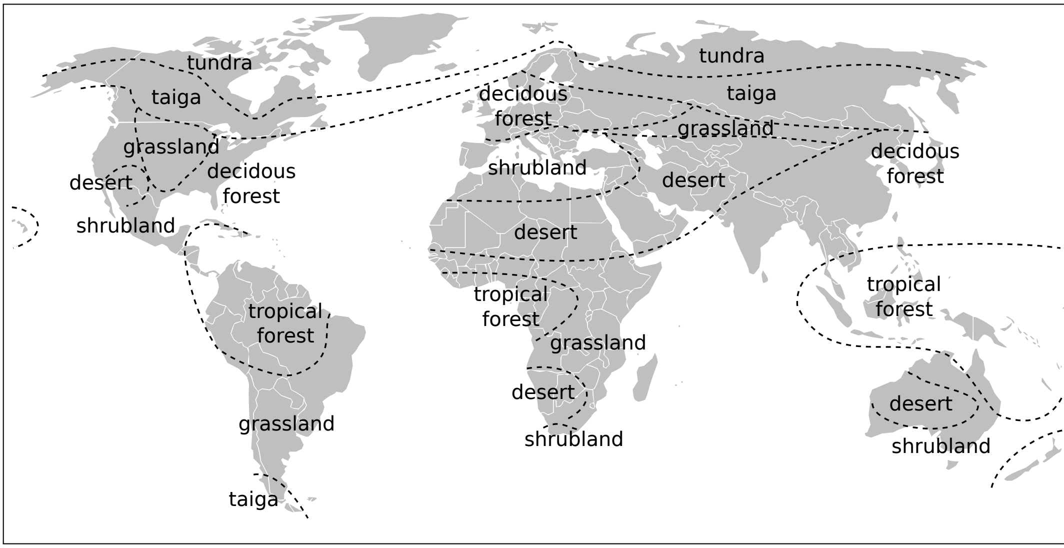


Figure 9.1. Biomes (types of vegetation) of Earth. Please note that this map is largely simplified.

Some smaller biomes, especially different kinds of wetlands (like sphagnum bogs or mangroves) are significantly dispersed, sometimes even *intra-zonal* (occur in different climatic zones).

9.2 Geography of Vegetabilia

While taiga forest looks similar in Alaska (North America) and Patagonia (South America), a closer look will immediately reflect that species, genera and even families of plants are quite different. As an example, both Alaska and Patagonia forests include large conifers, but while in Alaska we frequently see members of Pinaceae family like spruces (*Picea*) or firs (*Abies*), in Patagonia these trees are absent and "replaced" with superficially similar trees of Araucariaceae and Podocarpaceae conifers.

Analogously, Arizona desert is similar to African Kalahari but while American deserts are rich with cacti, similarly looking African plants belong to completely different group, succulent spurges (*Euphorbia*). The effect of these differences on the botanically educated traveler is a bit similar to the nightmare when you first see a familiar thing but approach it—and realize that this is something completely alien and strange.

These *floristic* differences are due to the various geological and biological histories of these places. *Plant biogeography* studies them, explains them and creates the *floristic kingdoms* classification (Fig. 9.2) which takes into account not ecological but taxonomical (phylogenetic) similarities and differences.

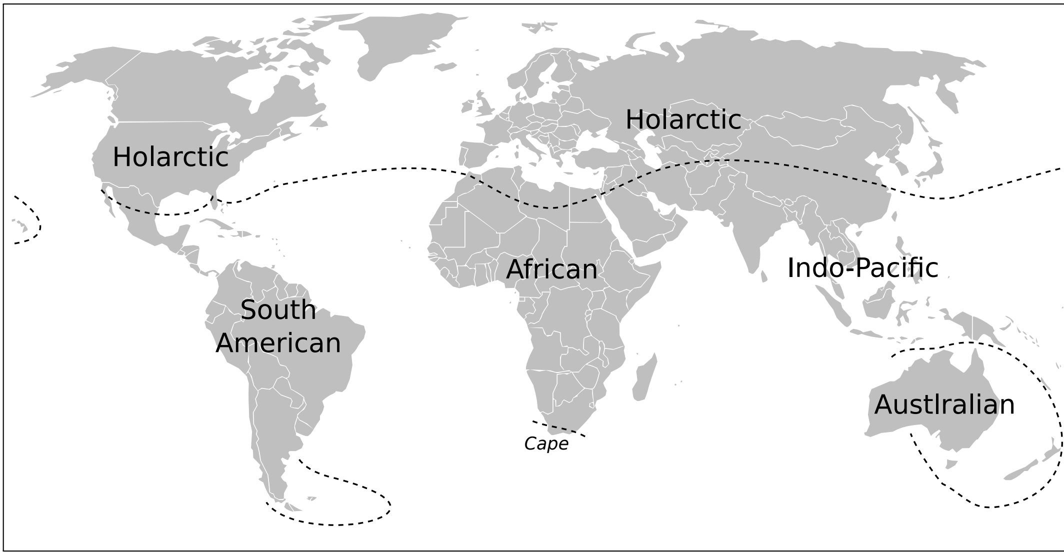


Figure 9.2. Floristic kingdoms of Earth.

There are only five floristic kingdoms:

Holarctic Most of North America and temperate Eurasia. Holarctic kingdom is largest, it covers two continents and most of Northern hemisphere. Typical representatives are pines (*Pinus*) and oaks (*Quercus*).

South American From South Florida to Patagonia and Antarctic islands. Aroids (Araceae family) and bromeliads (Bromeliaceae) are very common South American groups.

African Excluding Mediterranean Africa (very north of the continent). African acacias (*Senegalia*) are common to the most of savannas there.

Sometimes, botanists separate the southern tip of Africa into smallest **Cape floristic kingdom** which has multiple endemic plant genera (like *Berzelia*, kolkol) and even whole families.

Indo-Pacific From India to pacific islands including Hawaii. This kingdom is especially rich of orchids (Orchidaceae); tropical pitcher plants (*Nepenthes*) grow only there.

Australian Australia, Tasmania and New Zealand. Numerous specific plant groups, including *Eucalyptus*, *Banksia* and many others.

Every plant group has a specific *range*—the area of distribution. There are multiple common ranges, e.g., circumpolar (groups distributed across North Pole, both in North America and Eurasia, like spruces, *Picea*) or Gondwanian (groups distributed in the South Africa, Australia and South America, like protea family, Proteaceae). Sometimes, there are *disjunctions* (breaks in range); a typical explanation for the disjunction is long-distance dispersal (like for ispaghula, *Plantago ovata* in California and West Asia) or extinction in the connecting places (like for tulip tree, *Liriodendron* in China and Atlantic states).

Recently, many plants became *invasive* after being introduced willingly (e.g., as forage plants) or accidentally (e.g., with seeds of other plants). These plants (like Eurasian spotted knapweed, *Centaurea stoebe* in North America, or North American box elder, *Acer negundo* in Eurasia) are often *noxious* since they tend to destroy the native vegetation.

It is frequently said that humans stated the new epoch of Earth life, *homocene*—era of *Homo sapiens* dominance, homogenization and great extinction of the flora and fauna. We need to stop that!

Appendix A

Methods of Taxonomy and Diagnostics

The goal of taxonomy is to describe diversity, provide an insight to the evolutionary history (phylogeny), help to determine organisms (diagnostics) and allow for **taxonomic estimations**. The latter means that if we know features of one plant, the taxonomically close one should have similar features. For example, plants from cabbage family (Cruciferae) contain mustard oil (which is responsible for the horseradish taste of many of them). DNA analysis shows that papaya (*Carica* from Moringaceae family) is taxonomically close to Cruciferae. We may guess that papaya also have mustard oil, and this is true! Papaya seeds have the prominent horseradish taste.

* * *

One of the oldest methods of taxonomy is expert-based. Experts produce classifications based of their exclusive knowledge about groups. First taxonomic expert was Carolus Linnaeus (XVIII century). Experts use a variety of methods, including phenetics, cladistics (see below), general evolutionary approach, their ability to reshape available information and their intuition. Their goal is to create the "mind model" of diversity and then convert it to classification, using neighbor groups as a reference (for example, to assign ranks).

A.1 Cladistics

The more contemporary, much more formalized than expert-based is **cladistics**. Below, cladistic procedure is explained using artificial example of three organisms. The goal of the analysis is the creation of a **phylogeny tree** (**cladogram**) which becomes the basis of classification. Below is a short instruction which explains the basics of the cladistic analysis on the artificial example of several "families" of plants.

1. Start with determining the "players"—all subtaxa from bigger group. In our case, it will be these three "families":

   Alphaceae
   Betaceae
   Gammaceae

2. Describe these three groups:

   Alphaceae: Flowers red, petioles short, leaves whole, spines absent
   Betaceae: Flowers red, petioles long, leaves whole, spines absent
   Gammaceae: Flowers green, petioles short, leaves dissected, spines present

3. Determine individual characters (we will need at least $2N + 1$ characters where N is number of studied taxa):

   (1) Flower color
   (2) Petiole size
   (3) Dissection of leaves
   (4) Presence of spines

4. **Polarize the characters**: every character should have at least two **character states** where "0" is ancestral, **plesiomorphic** state, and "1" is derived, **apomorphic** state. To decide which state is plesiomorphic and which is apomorphic, use these kinds of arguments:

   (a) Historical evidence (e.g., from fossils)
   (b) Developmental evidence
   (c) Comparative evidence

5. If this information is absent, find the **outgroup** which is the most ancestral, most early divergent taxon related to our groups. In our case, we will employ outgroup:

   Omegaceae: Flowers green, petioles short, leaves whole, spines absent.

6. Label characters with "1" (apomorphic) or "0" (plesiomorphic):

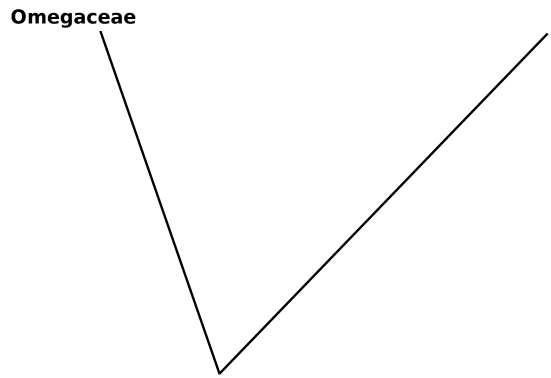
   (1) Flower color green—0; red—1
   (2) Petiole size small—0; big—1
   (3) Dissection of leaves absent—0; present—1
   (4) Absence of spines—0; spines present—1

7. Make character table containing both subtaxa and labeled characters:

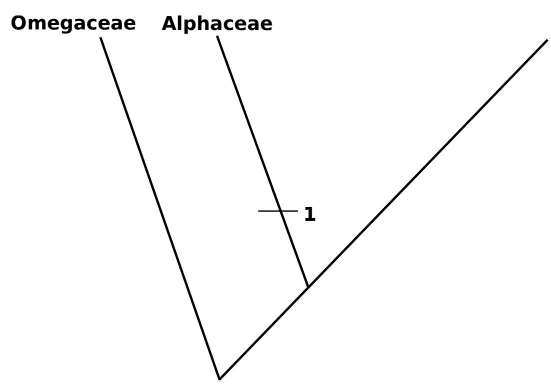
	(1)	(2)	(3)	(4)
Alphaceae	1	0	0	0
Betaceae	1	1	0	0
Gammaceae	0	0	1	1

(Outgroup, Omegaceae evidently has all zeroes.)

8. Start the tree from outgroup (this step is not absolutely necessary but will make phylogeny more clear):

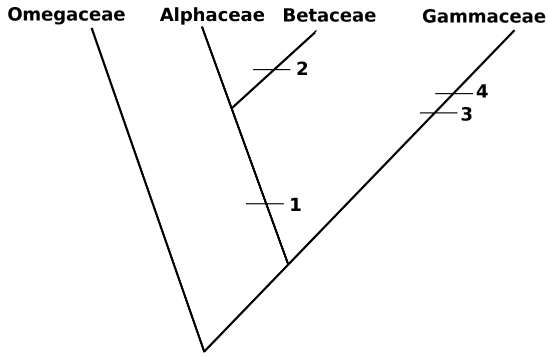


9. Most ancient ingroup (Alphaceae) is a first branch, label it with bar which shows acquisition of the advanced state of first character (red flower color):



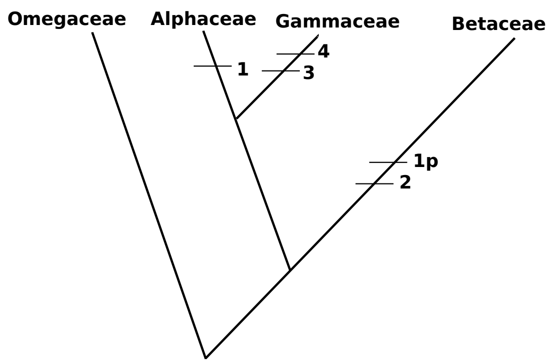
10. Attach more and more sub-taxa. It is possible to do this randomly (like most of phylogeny software), or attach groups to make shortest tree. For example, Betaceae and Gammaceae have equal number of synapomorphies but Betaceae

have only one character different from Alphaceae it is sensible to attach it first, and then attach Gammaceae:



This tree has 4 evolutionary events (length = 4)

11. If Gammaceae was attached first, then resulted tree will be be one step longer:



There are five evolutionary events; in other words, length of tree = 5. ("p" are *parallel* characters (homoplasies); there might be also reversals ("r"), when apomorphic character disappears).

There could be also tree with length = 6, or even more if tree includes character reversals, but all of them will be longer than the first one.

12. Choose the shortest, most **parsimonous** tree. Second tree has 5 events, first tree has 4 events, others could be only longer. Consequently, we choose the first tree. By the way, many computer programs do not follow the procedure above strictly and simply produce all possible trees, and finally choose the shortest.

13. Use the chosen tree as a source of classification:

Order Alphales

1. Family Alphaceae
2. Family Betaceae

Order Gammales

1. Family Gammaceae

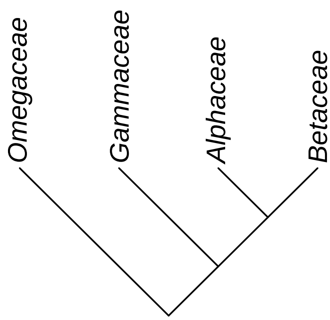
This step is needed only if you wish to convert cladogram into traditional, classification. In fact, cladograms are rank-free and might be used as is.

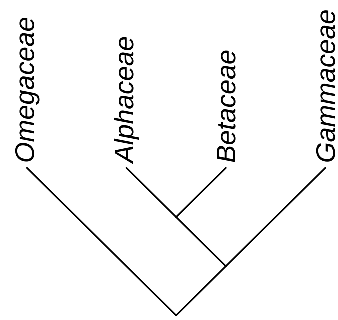
Cladograms often used as source of *time trees* which are made with genetic information and information from fossils. If we know the age of taxonomic group, we can use it as more objective replacement of rank.

* * *

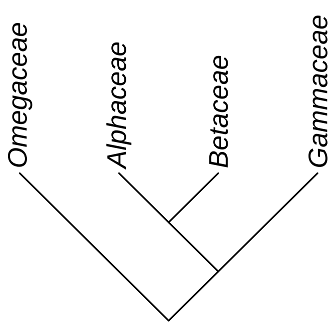
Ability to review and compare phylogenetic trees requires understanding of several basic rules, for example:

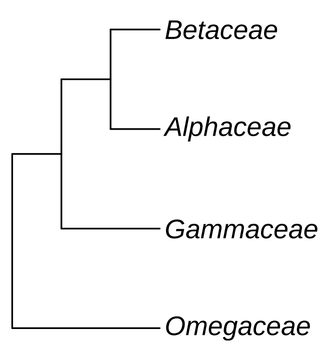
1. Tree edges may be freely rotated in any direction. For example, these trees are same:





2. Direction of branches also does not matter. These trees are same:





* * *

It is not always simple to make classification from a tree. On the previous example, we simply designate the whole branch as a taxon (order which contains our three families). There are situations when only middle part of the branch seems to be acceptable as a taxon. In these cases, remaining part is called **paraphyletic** taxon.

Paraphyletic groups include all immediate ancestors of its members but not all descendants of these ancestors. Good example of paraphyletic taxon are reptiles: when we take mammals and birds from amniote branch, reptiles will be what is left. Gymnosperms (all seed plants without angiosperms) is another example, but in this case *some* molecular trees show that gymnosperms is also a natural branch (i.e., **monophyletic** group). Monophyletic groups include all immediate ancestors and all their descendants.

When the group contains taxa from different branches, it is **polyphyletic**. Polyphyletic groups are not allowed.

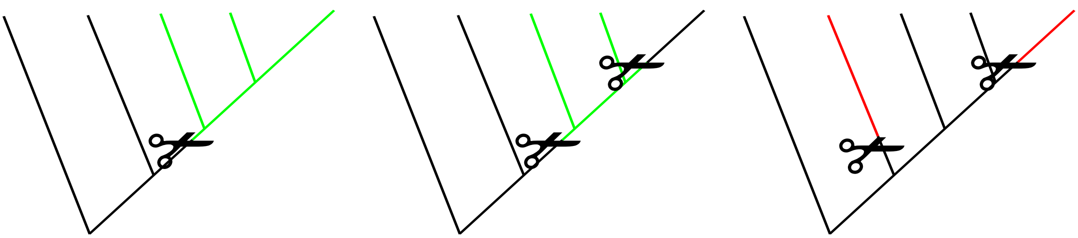


Figure A.1. Monophyletic, paraphyletic and polyphyletic groups, respectively.

Another important distinction between groups of the phylogeny tree is stem and crown groups. All extant members together with their immediate ancestors form a **crown** of taxon (Fig. A.2). If one member of crown went extinct, we can estimate that it was somehow similar to other crown members. In other words, if we find a way ho to re-create mammoth, we probably understand how to feed it because it belongs to the Elephantidae family crown. However, if the fossil, extinct members of taxon branch outside of crown (**stem** groups), there are much less taxonomic estimations. It is hard to guess, for example, how to care for *Archaeopteryx* "dinosaur bird" because such organisms are not exist now and have no living similarities.

Figure A.2. Crown (green skull) and stem (red skull) extinct groups among extant groups.

A.2 Phenetics

The other way of making classification is even more mathematical. This is **phenetics** based on multivariate methods of data analysis. One of its methods is **cluster analysis** which is described below.

1. Contrary to cladistics, phenetics considers characters as **all equal** and **does not employ any evolutionary assumptions**.
2. We need to decide which taxa we will need, assess their descriptions, extract characters—all these is similar to cladistics (see above).
3. Character polarization is not needed, character codes may be specified more or less arbitrarily, and there is no need for outgroup.
4. Character table could be the same as in previous example (again, see above).
5. Then, we will need to create the square matrix (or table) of similarity:

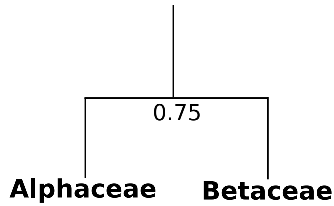
	Alphaceae	Betaceae	Gammaceae
Alphaceae	1		
Betaceae	0.75	1	
Gammaceae	0.25	0	1

Every cell of this matrix contains a value of similarity K:

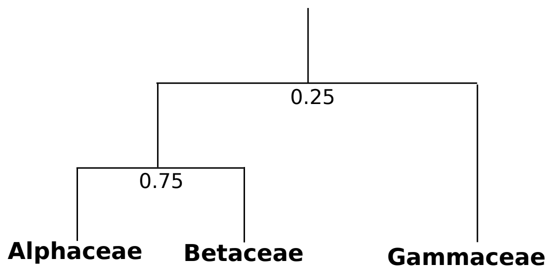
$$K = \frac{\text{number of matching characters}}{\text{number of all characters}}$$

Please note that there are many more relevant coefficients of similarity but they are out of our scope.

6. Then we need to make the dendrogram which is a tree-like structure. Traditionally, dendrogram is built from bottom to top, from more similar to less similar groups. For example, we may start from connecting the closest taxa, Alphaceae and Betaceae:



7. Then we need to attach other taxa which are closest to previous group:



Sometimes, when we have multiple taxa, we end up with several independent groups (clusters). In that case, different clusters could be connected on the base of *average similarity*.

8. Betaceae and Alphaceae are closer, so we can unite them in one order:

Order Alphales

1. Family Alphaceae
2. Family Betaceae

Order Gammales

1. Family Gammaceae

A.3 Dichotomous keys

Diagnostics is a practical science which helps to determine living organisms. One of the best way of determining was invented in the end of 18 century by famous French naturalist, Jean-Baptiste Lamarck. He created the **dichotomous key** (sometimes called descriptive key, or descriptive table). The legend says that when Lamarck demonstrated this key for the first time, he gave it to the random stranger (who had no idea about plants and their names), and plant were determined without problems! How to make such a key? The example is below:

1. We need to start with "players". In this example, it will be same three plant families:

   Alphaceae
   Betaceae
   Gammaceae

2. Assess descriptions of these three groups (we copy this from the above):

   Alphaceae: Flowers red, petioles short, leaves whole, spines absent
   Betaceae: Flowers red, petioles long, leaves whole, spines absent
   Gammaceae: Flowers green, petioles short, leaves dissected, spines present

3. Start with a character which let to split the list into two nearly equal groups. Then add other character(s). It is always good to use more characters!

   1. Petioles long . . . . **Betaceae**.
   – Petioles short . . . . 2.

   2. Flowers red, leaves whole, spines absent . . . . **Alphaceae**.
   – Flowers green, leaves dissected, spines present . . . . **Gammaceae**.

As you see here, key consists of steps. Every step has a number and typically two choices. Number is attached to the first choice whereas the second choice is marked with minus "–". The choice will lead either to the name, or to another step. The choice sentence might contain several phrases, the first is the most important and the last is the least important.

Appendix B

Problems

Below is the set of botanical problems, questions which require careful thinking and analysis of multiple hypotheses. Please remember that it is rare in biology to have just one answer, so most of questions below have many answers.

1. Some asters and other flowering plants grow in the tidal zone of the sea: during the high tide, they are fully covered with seawater; and during the low tide, they are fully emerged. Please guess morphological and physiological features which allow them to grow in these conditions.

2. Most of the flowers do not have odor or have odor pleasant to us. At the same time, insects like smells of corpses, feces, etc. However, only a few flowers use these last odors. Why the majority of flowers do not use odors unpleasant to us?

3. In 1894, Herbert Walles published the short story entitled "Flowering of the Strange Orchid". In this story, the gardener started to cultivate the mysterious orchid, which was brought from some tropical jungles. One day, he did not return from his greenhouse, and his housekeeper went to find him:

   > "He was lying, face upward, at the foot of the strange orchid. The tentacle-like aerial rootlets no longer swayed freely in the air, but were crowded together, a tangle of grey ropes, and stretched tight, with their ends closely applied to his chin and neck and hands.
   >
   > She did not understand. Then she saw from one of the exultant tentacles upon his cheek there trickled a little thread of blood.
   >
   > With an inarticulate cry she ran towards him, and tried to pull him away from the leech-like suckers. She snapped two of these tentacles, and their sap dripped red.

> Then the overpowering scent of the blossom began to make her head reel. How they clung to him! She tore at the tough ropes, and he and the white inflorescence swam about her. She felt she was fainting, knew she must not."

Which else adaptations (except already described above) will be necessary for orchids to start feeding on the blood of mammals? Maybe, some of the above features should be changed?

4. Wind is hazardous for epiphytic plants that grow high on the trees. The fallen plant might survive below but surely will not be able to flower. How do epiphytic plants withstand the wind?

5. Sometimes, scientists find fossil flowers. How to know how these flowers were pollinated?

6. In lower stories of the tropical forest, there are many plants with striped or spotted leaves—with white, red, yellow spots, or stripes. Especially frequently, these leaves belong to one of the plant families, Marantaceae (by the way, they are frequently cultivated indoors). What (do you think) is the reason for the plant to have such leaves?

7. There are no seasons in humid tropical forests, but trees drop their leaves even there. Some trees drop leaves of the last year(s) together whereas other trees drop leaves one by one, every day or week. What are the benefits of each of these strategies?

8. Water plant quillwort is the direct descendant of giant Paleozoic tree-like lycopods. Like its ancestors, it has an ability to secondary thicken its stem. It is easy to understand why secondary thickening is good for trees. However, is it beneficial for the small water plant, or is this just a "vestigial" feature? Please justify your answer.

9. On the Figure B.1, there are two real plants and three "chimeras" made out of fragments of other plants. Which plants are real? Why? Please explain.

10. In many popular books, it is said that reproduction with seeds is in all aspects better than reproduction with spores. However, in the World flora, the number of species of the spore plants is only 5–7 times less than the number of species for seed plants. Which adaptations of spore plants allow them to keep the significant positions in the World flora?

11. Floras of Eurasia and North America often unite in one Holarctic floristic kingdom, because they have many common genera and even species of plants. Interestingly, some genera (e.g., horsetails, blueberries, nettles, anemones, bluegrasses, clovers, wintergreens, bellflowers) have many common species

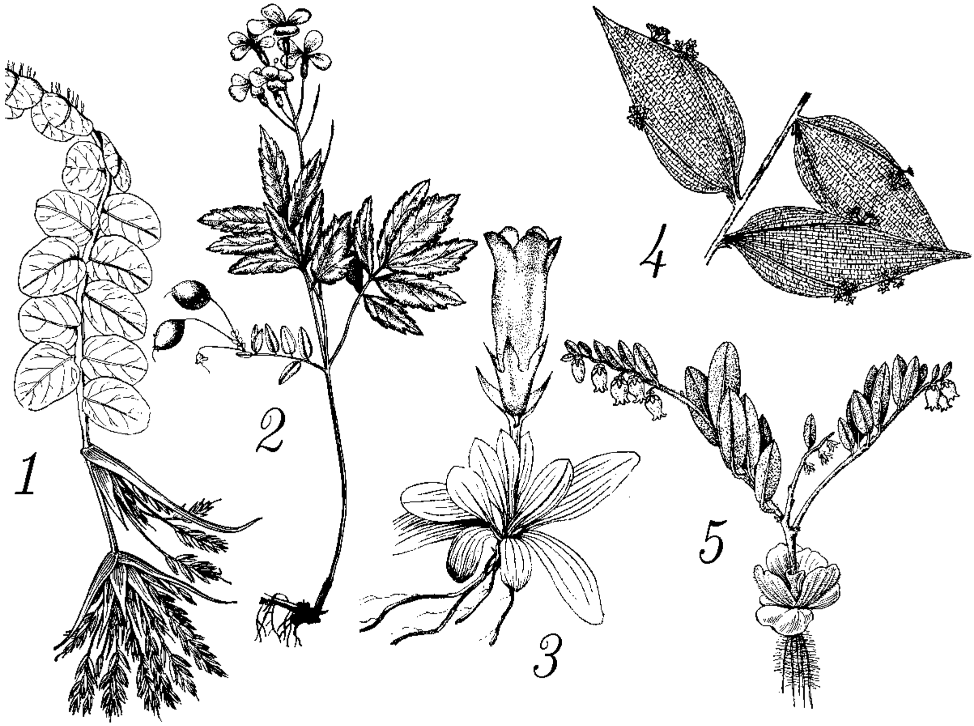


Figure B.1. Real plants and plant chimaeras

on both continents. In contrast, species from other genera (asters, needle grasses, wormwoods, sedges, roses, willows) are different on each continent. Furthermore, there are genera that grow only in either North America or Eurasia (beard-tongues, opuntias, knapweeds). What do you think, what are the reasons of each type of distribution?

12. Some representatives of two families of insect coccids have embryos developed from two different kinds of cells. First kind is just a normal zygote, but the second is the result of the fusion between polar body (meiosis "remain") and one of the daughter nuclei of a zygote. As a result, the second cell is polyploid, frequently with five or even seven sets of chromosomes (this is because the second cell might additionally duplicate its genome). Most organs of the adult insect formed by the first cell, the second cell, gives "bacteriome", the kind of fat tissue which cells bear symbiotic bacteria. What do you think, why coccids have such a complicated process? What are benefits from the presence of two different genotypes in one body?

13. On some islands, there are woody plants that belong to groups that are generally herbaceous (e.g., woody plantains on Hawaii, woody bellflowers on St. Helena). What do you think are reasons for this phenomenon?

14. Within populations of North American painted wintergreen (*Pyrola picta*), there are plants with normal green shoots and also plants with shoots without chlorophyll. These last shoots feed on soil fungi ("mycoheterotrophy"). What are the benefits of this populations structure for the species? Why, in each generation, there are two types of shoots?

15. Some flowers in nature are "double", with increased (comparing with norm) number of petals. How are double flowers beneficial to plants? Which problems might be related to having double flowers?

16. Everybody knows the sensitive plant (*Mimosa pudica*); this is the tropical weed, which after touching its leaves, folds segments and then also moves whole leaves down. Mimosas, however, is a big genus, and some Mimosa species do not react to the touching, some only fold segments (and did not lower leaves), and some do exactly as *M. pudica*, sometimes slower, sometimes faster. What do you think are the advantages and disadvantages of three different sensitivity types above? And what particulars of the plant life promote the sensitivity? Please develop several versions.

17. Some plants are evergreen, and some are deciduous. There are several different strategies of being deciduous: some lose all their leaves literally for one night, some keep falling leaves for few months, and some do not drop leaves in a fall but keep them all winter and drop leaves in spring. What are the advantages of each strategy? Please justify your answer.

18. Every fall, we see fallen leaves. Which other parts plants can drop before the disadvantageous season? Please give some examples.

19. Everybody knows that sunlight is useful for plants. However, gardeners also know that light could be harmful. How exactly could the light of Sun be harmful for plants?

20. Under cover of tropical forest, flowers are not frequent, and frequently plants of the same species flower at different times of the year. Therefore, the distance between simultaneously flowering plants of the same species could be really big. What are the advantages and disadvantages of this flowering rhythm? Please justify your answer.

21. On the Figure B.2, there are different types of plant trichomes (please note that "E" is the top view). What role play each of these trichomes in plant life? Why? Please explain.

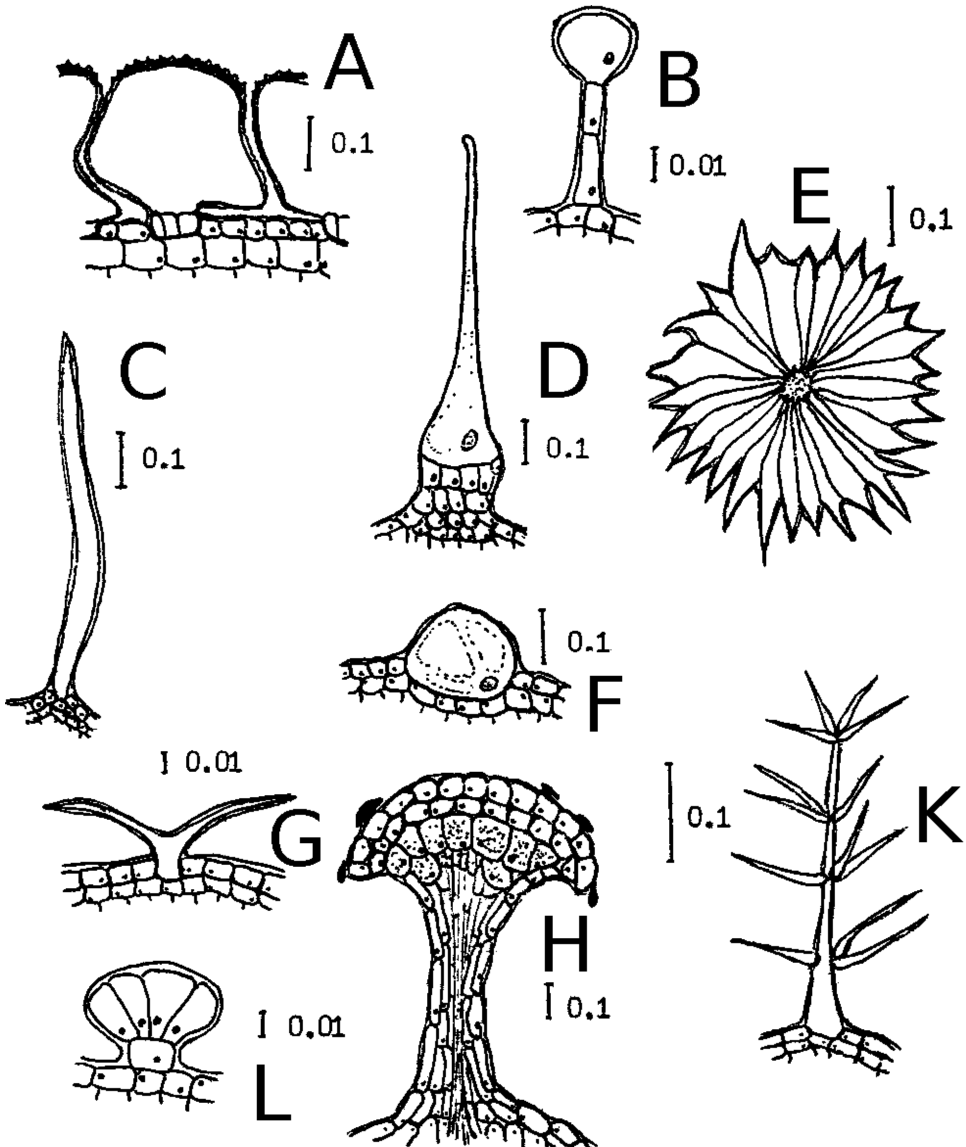


Figure B.2. Plant trichomes

Appendix C

Some useful literature

There are botanical publications which I especially like, and also think that they might be useful to the readers of this book. There are so many of them! But I tried to shorten this list as much as possible. This list is below.

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