Introduction to Botany

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Foreword

While teaching botany for about twenty years, I came to the idea of re-structuring the "classical" course into a more logical sequence of themes which you will find in this textbook.

There were two main ideas that I attempted to embed here: one was to put as much plant-related information as possible into an evolutionary context, and the other was to explain complicated problems with simple words and metaphors. There are very few botany books which are trying to do the same.

One extremely important concept to understand: **plants are not animals!** Obviously, this phrase has many important meanings. First of all, since we humans are animals, it is much easier for us to understand animal life than plant life. Many terms that are associated with animal life (like "stomach" or "blood pressure") are generally well known, even intuitively. Learning botany as a beginner requires to speak about plants, and to speak, you have to learn botanical language. This is why you need to know a vast amount of terms, so be prepared to work hard.

This textbook started from students' lecture notes but now it contains much more information. All figures are either original or modified from those sources where a license allows it (e.g., Wikimedia).

If you like this book, and want to know more about plants (and also want to see more illustrations), please watch my YouTube channel, "Tales from Greenhouse", https://www.youtube.com/channel/UCxPchT-Zp8ADvsVR9lHCRmA

Glossary

***K*-strategy**   population growth when there is small number of offspring with high probability to survive

***r*-strategy**   population growth when there is huge number of offspring with low probability to survive

absorption zone   root: zone of root hairs

achene   one-seeded indehiscent dry fruit of Compositae, cypsella

adventitious roots   originate from stem

anatomy   invisible, internal structure which needs tools like a scalpel and/or microscope to study

anomalous secondary growth   when there are multiple, short lived layers of cambium

apical meristems   RAM (see) and SAM (see)

apogamy   apomixis (see) when an embryo develops from unfertilized gamete, parthenogenesis

apomixis   making seeds without fertilization

apospory   apomixis (see) when an embryo develops from the maternal diploid tissue

ataktostele   vascular bundles dispersed

bipolar plant body   both root and shoot systems present

botany   the scientific study of plants and plant-like organisms

brachyblasts   shortened shoots of pines, larches and some other Pinaceae conifers

bract scales   sterile bracts under seed scales in conifers

buds   embryonic shoots

bulb   short, thick underground storage shoot with prevalence of leaf tissues

calciphytes   plants adapted to over-presence of $CaCO_3$

Casparian strips   part of endodermis cell walls which prevents apoplastic transport

central cell   biggest cell of embryo sac, with two (or sometimes one) haploid nuclei

cladophylls   leaf-like, flattened shoots

cleistogamous   self-pollinated flowers which do not open

collenchyma   living supportive tissue

companion cells   nucleate "helpers" to anucleate sieve tube cells

complex tissues   tissues with more than one type of cells

compound fruit   fruit originated from the whole inflorescence: infrutescence

compound leaves   leaves with two or more level of hierarchy

contractile roots   roots which pull plant deeper in substrate

corm   short, thick underground storage shoot with prevalence of stem tissues

cortex   external layer of primary stem or root

cotyledon   embryonic leaf

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cross-pollination   pollination between genetically different plants

cuticle   plastic-like isolation layer

dehiscent   fruits which open

dichotomous   branching: when terminal bud always divides in two

double fertilization   the process when two brother male gametes fertilize two sister female cells

elongation zone   root: zone of expanding cells

embryo sac   female gametophyte of flowering plants

endodermis   the innermost layer of cortex

endophytic fungi   fungi which grow inside plant body

endosperm$_1$ haploid nutrition tissue originated from female gametophyte

endosperm$_2$ triploid (sometimes diploid) nutrition tissue originated from second fertilization

epicotyl   first internode of the stem

epidermis   complex surface tissue

eustele   vascular bundles in a ring

exodermis   the outermost layer of cortex

fibers   long and narrow sclerenchyma cells

fibrous root system   no primary root visible

fiddleheads   spiral tops of young fern leaves

floral units (FU)   elements of generative system, fructifications

flower   compact generative shoot with sterile, male and female zones, specifically in that order, **other flower terms see in the separate glossary in the text**

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fronds   leaves of ferns

fruit   ripe floral unit (FU)

fusiform initials   cambium cells which make vessel elements

general characters   in leaf description, characters which are applicable only to the leaf as a whole

generative shoot system   all generative shoots together

ground meristem   primary meristem which makes cortex and pith

ground tissue   same as parenchyma (see) but only applied for tissue

halophytes   plants adapted to over-presence of NaCl

haustoria   sucker roots of parasitic plants

heartwood   non-functional part of wood

heliophytes   plants adapted to full sun

hemiparasites   photosynthetic plants, feeding partly on other plants

heterophylly   situation when one plant has more than one leaf type

heterosporic   with male and female spores

homoiohydric   plants that save water

hydrophytes   plants growing in water and frequently using water for the support

hygrophytes   terrestrial or partly submerged plants adapted to the excess water

hypocotyl   root/stem transitional place

idioblasts   solitary cells dissimilar from surrounding cells

indehiscent   fruits which do not open

indusia   covers of groups of sporangia (sori)

inflorescence   isolated generative shoot

integument   extra cover of megasporangium

intercalary   meristems which grow in two directions

internodes   spaces between nodes

lateral meristem   cambium, meristem appearing sideways

lateral veins   smaller veins, typically branching out of the main vein (see)

leaf   lateral photosynthetic organ of shoot with restricted growth

leaf primordia   embryonic leaves

leaf scars   marks of leaf petioles

leaf traces   marks of leaf vascular bundles

lenticels   "openings" in bark allowing for gas exchange

leptosporangia   sporangia with 1-celled wall

main vein   central, most visible vascular bundle of leaf (midrib)

marginal   meristems which are located on margins

maturation zone   root: oldest part of root

megaphyllous   with leaves originated from joint branches

megasporangia   female sporangia

megaspore   female spore

megasporophylls   modified leaves with attached megasporangia

meristems   sites of cell division

merosity   multiple of flower parts numbers

mesophyll   photosynthetic parenchyma of leaf

mesophytes   plants adapted to the average water

microspores   male spores

microsporgangia   male sporangia

monilophytes   all Pteridophyta except lycophytes

monopodial   branching: when terminal bud continues to grow every year

morphology   visible, external structure

multiple fruit   fruit originated from many pistils

mycoparasites   plants feeding on soil fungi

mycorrhiza   roots symbiotic with fungi

nodes   place where leaves are attached

nucellus   wall of megasporangium

ocrea   part of the leaf which goes upwards along the stem

opposite   leaf arrangement: two leaves per node

organ   union of different tissues which have common function(s) and origin

orthotropic   growth: vertical

ovule   seed plants: megasporangium with integument

oxylophytes   plants adapted to acidic substrates

palisade mesophyll   mesophyll of elongated, tightly packed cells

parcellate   reproduce vegetatively with easily rooted body parts

parenchyma   tissue or cell type of spherical, roughly connected living cells

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perforations   openings

pericarp   most of fruit tissue

pericycle   parenchyma layer just outside of vascular tissues

periderm   secondary dermal tissue

perisperm   nutrition tissue originated from nucellus (see)

peristome   mosses: attachment to moss sporangium, helps to distribute spores

petrophytes   plants adapted to grow on rocky substrates

phellem   external layer of periderm, cork

phelloderm   internal layer of periderm

phellogen   cork cambium, lateral meristem making periderm

phloem   vascular tissue transporting sugars

phyllode   leaf-like petioles

phyllotaxis   leaf arrangement

pistil   cupule, additional cover of ovules

pit   structure connecting tracheids

pith   central layer of primary stem or root

plagiotropic   growth: horizontal

plants   are not animals!

plants$_1$ all photosynthetic organisms

plants$_2$ kingdom Vegetabilia

pneumatophores   air-catching heliotropic roots

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poikilohydric   plants that do not save water

pollen sac   seed plants: microsporangium

pollen tube   fungus-like cell which brings spermatia (see) to egg

pollination   transfer of male gametophytes (pollen grains) from microsporangia (pollen sacs) to megasporangia (ovules) or cupules (pistils)

prickles   modified, prickly stem surface growths

primary meristems   intermediate tissues which start out of apical meristems and make primary tissues

primary root   originates from embryo root

primary stem   stem with primary tissues only

primary tissues   tissues originated from RAM or SAM (optionally through intermediate meristems)

procambium   intermediate meristem developing into cortex, pith and procambium,   primary meristem which makes vascular tissues

protoderm   primary meristem which produce epidermis or rhizodermis

protonema   mosses: embryonic thread of cells

protostele   central xylem surrounded with phloem

psammophytes   plants adapted to grow on sandy substrates

quiescent center   core part of root apical meristem

raceme   basic monopodially branched inflorescence (Model I)

radial   section: cross-section

RAM   root apical meristem

ray initials   cambium cells which make rays

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rays   stem: parenchyma cells arranged for horizontal transport

repetitive characters   in leaf description, characters which are applicable to the leaf parts on each level of hierarchy

rheophytes   water plants adapted to fast moving water

rhizodermis   root epidermis, root hairs

rhizoid cells   dead cells accumulating water apoplastically

rhizome   underground horizontal shoot

ring porous   wood: with large vessel elements mostly in early wood

root   an axial organ of plant with geotropic growth

root cap   protects root meristem

root nodules   bulb-like structures which contain nitrogen-fixing bacteria

root pressure   pressure force made solely by roots

SAM   stem apical meristem

sapwood   functional part of wood

schizocarp   fruits which segregate into smaller indehiscent units

sciophytes   plants adapted to shade

sclerenchyma   dead supportive tissue

sclerophytes   plants preventing water loss, they frequently employ sclerenchyma

secondary (lateral) roots   originate from primary root (see)

secondary vascular tissues   secondary phloem and secondary xylem

seed   chimeric structure with mother (seed coat), daughter (embryo) and endosperm genotypes

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seed scales   megasporophylls (see) of conifers

seta   mosses: stalk of the sporogon (see)

sheath   part of leaf which surrounds the stem

shoot plant body   unipolar body: no root system, shoots only

sieve tube cells   living cells which transport sugar

simple fruit   fruit originated mostly from one pistil

simple leaf   leaf with one level of hierarchy

simple tissues   tissues with uniform cells

siphonogamy   fertilization with the help of pollen tube

solenostele   vascular bundles in "hollow" cylinder

sori   clusters of sporangia

spermatium   aflagellate, non-motile sperm cell (plural: spermatia)

spines   reduced, prickly leaves

spiral   leaf arrangement, or alternate leaf arrangement: one leaf per node

spongy mesophyll   mesophyll of round, roughly packed cells

sporogon   moss sporophyte

stele   configuration of vascular tissues in stem or root

stem   axial organ of shoot

stipules   small attachments to the leaf; typically, located near the base of petiole

stolon   aboveground horizontal shoot

stomata   (stoma) pores which opened and closed by guard cells

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succulents   plants accumulate water

surface / volume law   when body size grows, body surface grows slower then body volume (and weight)

sympodial   branching: when terminal bud degrades every year

synangia   adnate sporangia

tangential   section when plane is tangent to surface

tap root system   primary root well developed

tendrils   organ modifications using for climbing

terminal characters   in leaf description, characters which are applicable only to the leaf terminals (leaflets)

thallus   flat, non-differentiated body

thorns   prickly shoots

thyrsus   basic sympodially branched inflorescence (Model II)

tissue   is a union of cells which have common origin, function and similar morphology

tracheary elements   water-transporting dead cells

tracheids   tracheary elements without perforations (openings)

transverse   section: longitudinal

tuber   enlarged portion of rhizome

tyloses   "stoppers" for tracheary elements made by parenchyma cells,   vessel element "stoppers"

vascular bundles   "chords" made of xylem (inner) and phloem (outer) layers

vascular cylinder   "hollow" cylinder made of xylem (inner) and phloem (outer) layers

vascular plants　　Pteridophyta + Spermatophyta

vascular tissues　　tissues which transport Shoot systemliquids

velamen　　absorption tissue made of dead cells

vessel members　　tracheary elements with preforations (openings)

wood　　secondary xylem,　　stem: everything deeper than vascular cambium

xerophytes　　plants adapted to the scarce water

xylem　　vascular tissue transporting water

Chapter 1

Introduction to the Introduction

1.1 Plants, Botany, and Kingdoms

Botany is the scientific study of plants and plant-like organisms. It helps us understand why plants are so vitally important to the world. Plants start the majority of food and energy chains, they provide us with oxygen, food and medicine.

Plants can be divided into two groups: **plants**$_1$ and **plants**$_2$. Plants$_1$ contain **all photosynthetic organisms** which use light, H_2O, and CO_2 to make organic compounds and O_2. Plants$_1$ are defined *ecologically* (based on their role in nature).

Some plants$_1$ can be bacteria or even animals! One example of this a green slug, *Elysia chlorotica* (see Fig. 1.1). Green slugs collect chloroplasts from algae and use them for their entire life as food producers. Therefore, green slugs are both animals and plants$_1$.

Plants$_2$ are **all organisms from Vegetabilia kingdom**. Normally, plants$_2$ are green organisms with a stem and leaves. We can define them also as **multi-tissued, primarily terrestrial and photosynthetic eukaryotes**. This definition is *taxonomical* (based on evolution).

It is possible for the organism to be plant$_2$ but not plant$_1$ (see Fig. 1.2). Those who fall into that category, are fully parasitic plants (mycoparasites like *Pterospora*, root parasites like *Hydnora*, stem parasites like *Cuscuta*, and internal parasites like Pilostyles) which do not practice photosynthesis but have tissues, terrestrial lifestyle and originated from photosynthetic ancestors.

Figure 1.1. Green slug *Elysia chlorotica* caprures chloroplasts from the alga *Vaucheria litorea*.

Plants may be understood on several levels of organization: (from top to bottom) (a) ecosystems or taxa, (b) populations, (c) organisms, (d) organs, (e) tissues, (f) cells, (g) organelles, and (h) molecules (Fig. 1.3).

Botany is considered to be a "slice science" because it covers multiple levels of organization.

1.1.1 Taxonomy

Taxonomy, **systematics** and **classification** are terms with similar meanings; they are all about the overwhelming diversity of living organisms, for there are more than 2,000,000 species (and 300,000 of them belong to plants$_2$). **Phylogenetics** is a more fashionable term; it emphasizes the evolutionary history (**phylogeny**) of taxonomic groups (**taxa**).

This taxonomic organization is hierarchical. Most scientists accept seven main levels of taxonomy (**ranks**): the highest is **kingdom**, followed by **phylum**, **class**, **order**, **family**, **genus**, and lastly, **species**.

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The highest rank, kingdoms are easy to understand as the *pyramid of life* (Fig. 1.4) which is divided into four levels—kingdoms. At the bottom is **Monera**, which con-
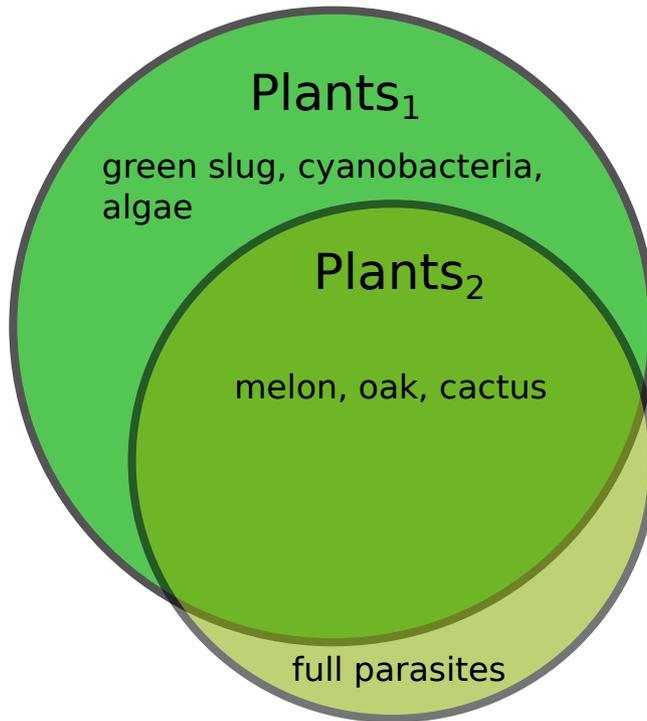
Figure 1.2. Plants$_1$ and plants$_2$.

sists of prokaryotes (Bacteria and Archaea). This is the first level of life: Monera have simplest cells without nucleus. The next level is **Protista**. These are eukaryotes (nuclear cells) without tissues; some examples are algae and fungi. The final level consists of two groups: **Vegetabilia** and **Animalia**. They both have tissues but have obtained them for completely different purposes. Animals have tissues *to hunt and digest*, while plants have tissues mainly *to survive on land*. Viri which are mentioned sideways, are not living things but merely pieces of DNA or RNA which "went astray" out of cells of living organisms of all four kingdoms. Despite of being non-living, viruses are capable of evolution.

Plants$_2$ (kingdom Vegetabilia) contain more than 300,000 species and divided in multiple subgroups (Fig. 5.1).

* * *

Ranks are used to compare taxonomic groups (**taxa**) from different major groups. No precise definitions are available for particular ranks, but it is believed that they
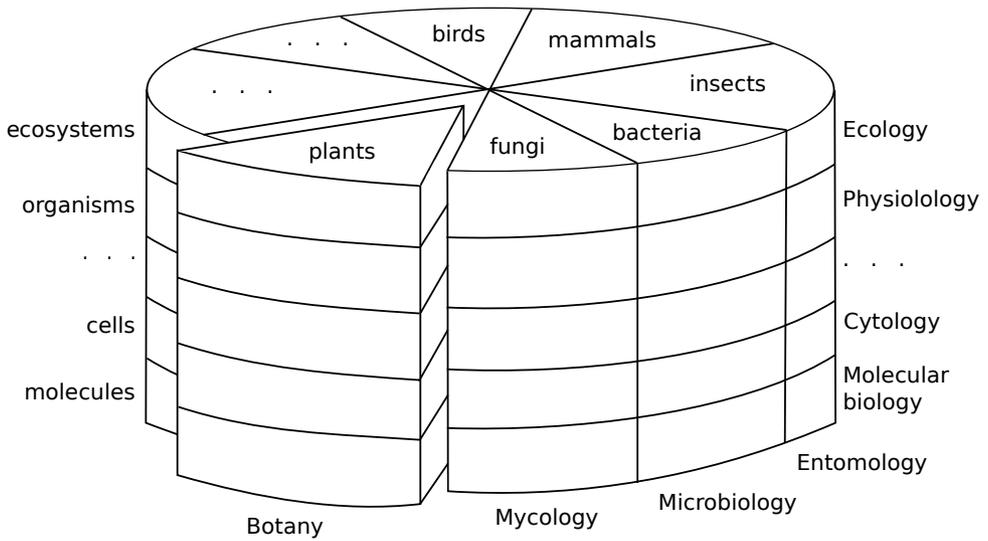
Figure 1.3. Layered pie of biology: levels of organization (left), taxonomic groups (top), "slice" sciences (bottom) and "layer" sciences (right).

are associated with the time of divergence (separation) between taxa. In addition to seven ranks mentioned above plant taxonomy uses intermediate ranks like **subfamily**, **subclass** or **superorder**—when taxonomic structure is too complicated.

Below is and example of names used for different ranks. Please note that names used for some ranks have standardized endings (underlined):

English	Latin	Example 1	Example 2
Kingdom	Regnum	Vegetabilia	Animalia
Phylum	Phylum	Spermato<u>phyta</u>	Chordata
Class	Classis	Angiosperm<u>ae</u> (Magnoli<u>opsida</u>)	Mammalia
Order	Ordo	Lili<u>ales</u>	Primates
Family	Familia	Asparag<u>aceae</u>	Homin<u>idae</u>
Genus	Genus	*Chlorophytum*	*Homo*
Species	Species	*Chlorophytum comosum* (Thunb.) Jacq.	*Homo sapiens* L.

It is frequent when one species has several geographical races without clear borders between them. The example might be the stinging nettle, *Urtica dioica*. In North America, many nettles have narrower leaves and are less stinging than in Eurasia. However, there are many intermediate forms between these races. To reflect this,
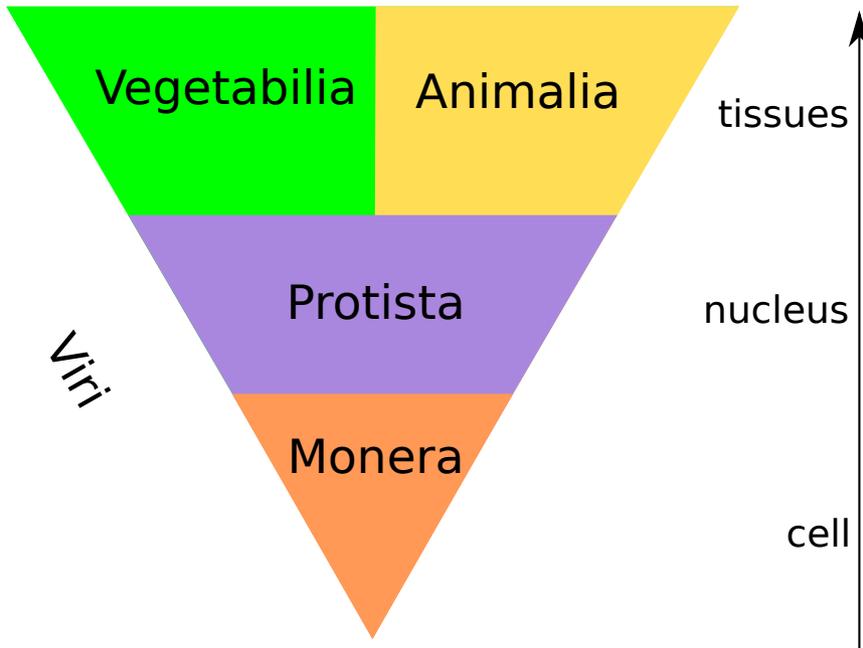
Figure 1.4. Pyramid of Life.

taxonomists introduced two **subspecies**: in this case, *Urtica diuica* subsp. *dioica* ("Eurasian") and *U. dioica* subsp. *gracilis* ("North American"). Another frequently used under-species category which is **cultivar**. Cultivars are frequently used in gardening. For example, many roses in cultivation belong to different cultivars of *Rosa banksiae*, and yellow roses are often *Rosa banksiae* cv. 'Lutea' where the last part of name is for the cultivar.

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Names of species are **binomials** which consist of the name of genus and **species epithet**:
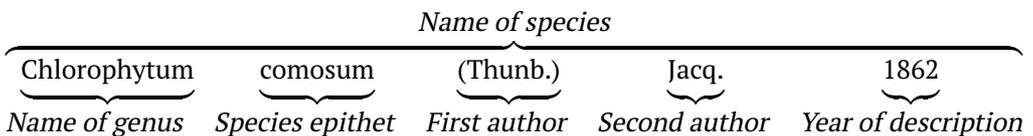
If one does not know the exact species, "sp." shortcut is used instead of epithet, and "spp." is used as a shortcut for multiple unknown species. It is required to use

slanted font when one prints a name of species or genus. All scientific names are capitalized, but the second word in a species name (species epithet) always starts from lower case letter. It is a well-known fact that some species have a hybrid origin, and in these cases, botanists use a multiplication sign ($\times$). For example, common plum (*Prunus* $\times$*domestica*) is a hybrid between blackthorn and cherry plum: *Prunus spinosa* $\times$ *Prunus cerasifera*.

The group of plants or animals must have one and only one name. Ideally, the name should be a stable ID for all occasions. But since biology is a "science of exceptions", some plant families are allowed to bear two names. As an example, legumes (**Leguminosae**) are frequently named "Fabaceae", and grasses (**Gramineae**) have the second name "Poaceae".

Throughout the long history of taxonomy, too many names were given to the same taxa. At the moment, we have almost 20,000,000 names to describe 2,000,000 species. These 18,000,000 "excess names" are **synonyms** which should not be used in science. To regulate the use of names, **nomenclature codes** were created. These codes specify, for example, the **rule of priority**: *when two names are given for the same group, only earlier name is valid*. Consequently, it is recommended to list the author and the year of description along with a name: "*Homo sapiens* L. 1758", which means that founder of taxonomy, Carolus Linnaeus ("L." shortcut) described this species in 1758.

Another important concept of nomenclature is the **nomenclature type**. Practically, this means that every species name must be associated with the physical museum specimen. In botany, these museums are collections of dried and pressed plants, called **herbaria**. Type specimens are of immense importance because there are no labels in nature, and only these specimens will "tell" about real plants or animals associated with particular names.

Names of taxa higher than species also have nomenclature types, but in these cases they are other names, not specimens. This example may clarify the use on nomenclature types. Initially, oleaster family (Elaeagnaceae) contained two genera, *Elaeagnus* (oleaster) and *Hippophaë* (sea-buckthorn). The second genus included *Hippophaë rhamnoides* (Siberian sea-buckthorn, **type species**) and *Hippophaë canadensis* (North American plant). Thomas Nuttall decided to split sea-buckthorns in two genera. Since one of them contains *Hippophaë rhamnoides*, the **type species**, it should keep the name *Hippophaë*. The second genus can be named arbitrarily. Nuttall gave it name "*Shepherdia*". As a result, the species which had name *Hippohaë canadensis* L., became *Shepherdia canadensis* (L.) Nutt.

Plant taxonomy is a science. That means that our understanding of plant groups will always change. It also means that there always are different competing opinions, the *taxonomic hypotheses* which describe plant diversity in different ways. As a

result, some groups of plants could be accepted in a broad sense, including as many subgroups as possible. For example, there might be an opinion of *Homo sapiens* s.l. (*sensu lato* = wide sense) including not only contemporary humans but also Neanderthal men. As a contrast, other opinions may accept groups in a strict sense, and *Homo sapiens* s.str. (*sensu stricto* = strict sense) includes only contemporary humans.

1.2   Styles of Life and Basic Chemistry

Life obtains energy in a few different ways: (1) from sunlight (**phototrophy**); (2) from chemical reactions with inorganic matter (**lithotrophy**); (3) from breaking organic molecules into inorganic molecules, typically carbon dioxide and water (**organotrophy**). To make its body, living beings obtain building blocks either by (a) from the assimilation of carbon dioxide (**autotrophy**), or from other living beings (**heterotrophy**).

These ways combine in six lifestyles. For example, plants$_1$ are by definition **photoautotrophs**. Most plants$_2$ are also photoautotrophs, but there are exceptions: full parasites (see above). Carnivorous plants (like sundew, *Drosera* or the Venus flycatcher, *Dionaea*) are all photoautotrophs. They "eat" animals in order to obtain nitrogen and phosphorus, so the dead bodies serve not as food but as a fertilizer. Note that plants are also **organoheterotrophs** like animals because in addition to photosynthesis, all plant cells can respire.

* * *

To understand life of plants, a basic knowledge of chemistry is needed. This includes knowledge of atoms (and its components like protons, neutrons and electrons), atomic weight, isotopes, elements, the periodic table, chemical bonds (ionic, covalent, and hydrogen), valence, molecules, and molecular weight. For example, it is essential to know that protons have a charge of +1, neutrons have no charge, and electrons have a charge of –1. The atomic weight is equal to the weight of protons and neutrons. Isotopes have the same number of protons but different number of neutrons; some isotopes are unstable (radioactive).

One of the most outstanding molecules is water. Theoretically, water should boil at much lower temperature, but it boils at $100°C$ just because of the hydrogen bonds sealing water molecules. These bonds arise because a water molecule is *polar*: hydrogens are slightly positively charged, and oxygen is slightly negatively charged (Fig. 1.5).

Another important concept related to water is **acidity**. If in a solution of water, the molecule takes out proton (H^+), it is an **acid**. One example of this would be hy-
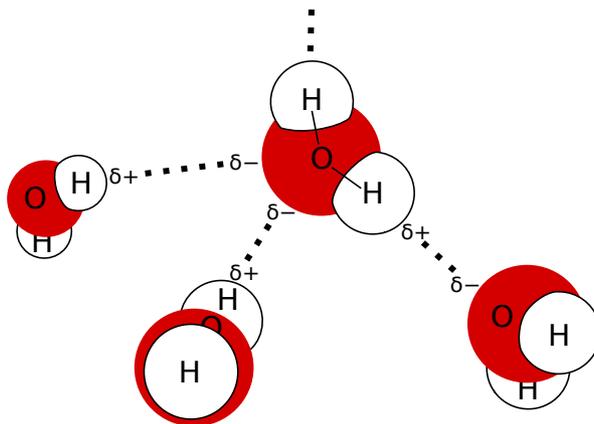
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Figure 1.5. Hydrogen bonds between water molecules, δ shows the partial charge.

drochloric acid (HCl) which dissociates into H^+ and Cl^-. If the molecule takes out OH^- (hydroxide ion), this is a **base**. An example of this would be sodium hydroxide (NaOH) which dissociates into Na^+ and hydroxide ion.

To plan chemical reactions properly, we need to know about **molar mass** and **molar concentration**. Molar mass is a gram equivalent of molecular weight. This means that (for example) the molecular weight of salt (NaCl) could be estimated as $23 + 35$, which equals 58 units. Consequently, one mole of salt is approximately 58 **grams**. One mole of any matter (of molecular structure) always contains $6.02214078 \times 10^{23}$ molecules (**Avogadro's number**).

The density of a dissolved substance is the **concentration**. If in 1 liter of distilled water, 58 grams of salt are diluted, we have 1M (one molar) concentration of salt. Concentration will not change if we take any amount of this liquid (spoon, drop, or half liter).

Depending on the concentration of protons in a substance, a solution can be very acidic. The acidity of a solution can be determined via pH. For example, if the concentration of protons is $0.1\,M$ (1×10^{-1}, which 0.1 grams of protons in 1 liter of water), this is an extremely acidic solution. The pH of it is just 1 (the negative logarithm, or negative degree of ten of protons concentration). Another example is distilled water. The concentration of protons there equals $1 \times 10^{-7}\,M$, and therefore pH of distilled water is 7. Distilled water is much less acidic because water molecules dissociate rarely.

When two or more carbon atoms are connected, they form a **carbon skeleton**. All **organic molecules** are made of some organic skeleton. Apart from C, elements participate in organic molecules (biogenic elements) are H, O, N, P, and S. These six ele-

ments make four types of biomolecules: (1) lipids—hydrophobic organic molecules which do not easily dissolve in water; (2) carbohydrates or sugars, such as glucose (raisins contain lots of glucose) and fructose (honey); by definition, carbohydrates have multiple −OH group, there are also polymeric carbohydrates (polysaccharides) like cellulose and starch; (3) amino acids (components of proteins) which always contain N, C, O and H; and (4) nucleotides combined from carbon cycle with nitrogen (heterocycle), sugar, and phosphoric acid; polymeric nucleotides are nucleic acids such as DNA and RNA.

Chapter 2

Photosynthesis

2.1   Discovery of Photosynthesis

The history of the studies done on photosynthesis dates back into the 17th century with Jan Baptist van Helmont. He rejected the ancient idea that plants take most of their biomass from the soil. For the proof, he performed willow tree experiment. He started with a willow tree of 2.27 kg. Over 5 years, it grew to 67.7 kg. However, the weight of the soil only decreased by 57 grams. Van Helmont came to the conclusion that plants must take most of their weight from water. He did not know about gases.

Joseph Priestley ran a series of experiments in 1772 (Fig. 2.1). He tested a mouse, a candle, and a sprig of mint under hermetically sealed (no air can go in or out) jar. He first observed that a mouse and a candle behave very similarly when covered, in that they both "spend" the air. However, when a plant is placed with either the candle or mouse, the plant "revives" the air for both.

Further ideas were brought about in the late 1700's. Jan Ingenhousz and Jean Senebier found that the air is only reviving in the day time and that CO_2 is assembled by plants. Antoin-Laurent Lavoiser found that "revived air" is a separate gas, oxygen.

But what is the oxygen "maker"? There are many pigments in plants, and all accept and reflect some parts of rainbow. To identify the culprit, Thomas Engelmann ran an experiment (Fig. 2.2) using a crystal prism. He found that *Spirogyra* algae produce oxygen mostly in the blue and red parts of the spectrum. This was a huge find. It tells that the key photosynthetic pigment should accept blue and red rays, and thus reflect green rays. Blue-green **chlorophyll** best fits this description.

Another important fact was discovered by Frederick Blackman in 1905. He found that if light intensity is low, the increase of temperature actually has very little effect on
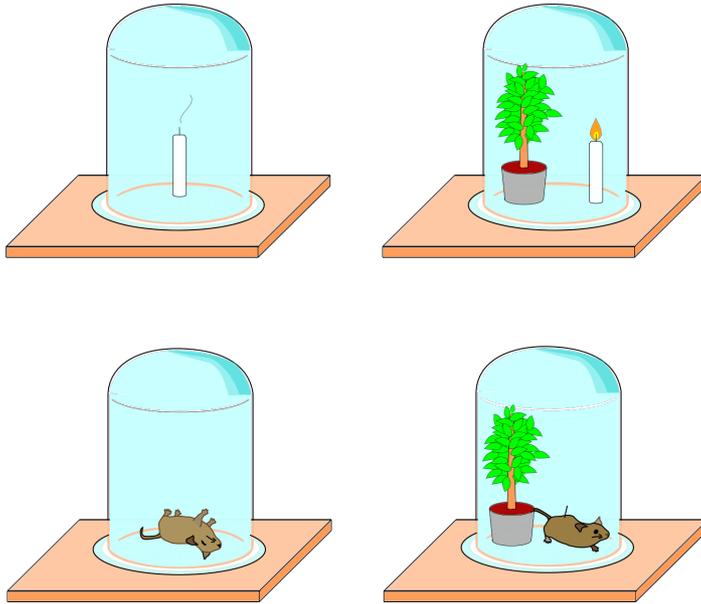
Figure 2.1. Experiments of J. Priestley (1772).

the rate of photosynthesis (Fig. 2.3). However, the reverse is not exactly true, and light is able to intensify photosynthesis even when it is cold.

This could not happen if light and temperature are absolutely independent factors. If temperature and light are components of the chain, light was first ("ignition") and temperature was second. This ultimately shows that photosynthesis has **two stages**. The first is a **light stage**. This stage relates to the intensity of the light. The second stage is the **enzymatic** (light-independent) stage which relates more with the temperature. Light reactions depend on the amount of light and water; they produce oxygen and energy in the form of ATP. Enzymatic reactions depend on carbon dioxide and water; they take energy from the light reactions and produce carbohydrates. Sometimes, enzymatic stage is called "dark" but it is not correct because in darkness, plant will run out of light-stage ATP almost immediately. Only some C_4-related processes (see below) could run at night.

<div align="center">* * *</div>

Since water molecules are spent on light stage to make oxygen and at the same time are accumulating (see below), one of the best "equations" describing photosynthesis as a whole is
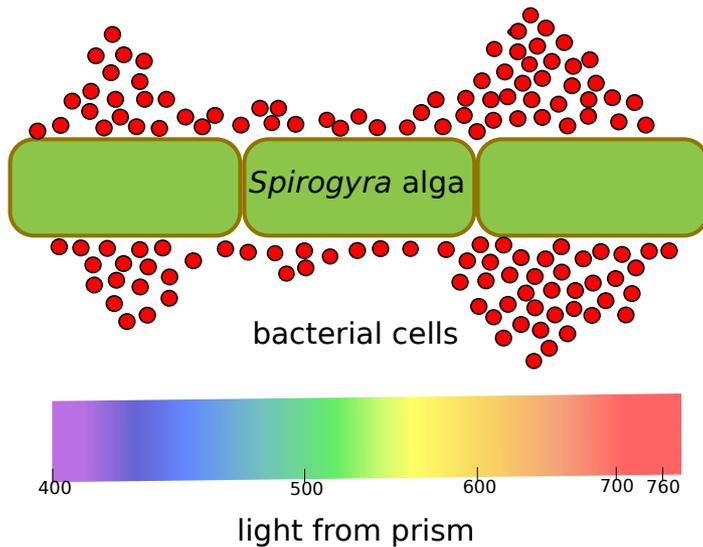
$$CO_2 + H_2O + light \rightarrow carbohydrates + H_2O + O_2$$

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Figure 2.2. Experiment of Th. Engelmann (1881).

2.2 Light Stage

The light stage participants include photosystems ("chlorophyll"), light, water, AT-Pase, protons, and a hydrogen carrier (NADP⁺).

The basic idea of light stage is that *the cell needs ATP* to assemble (later) carbon dioxide into sugar (Fig. 2.4). To make ATP, the cell needs electrical current: **proton pump**. To make this current, the cell needs the difference of electric charge (difference of potentials) between **thylakoid** (vesicle or membrane pocket) and **matrix** (stroma) compartments of the chloroplast (Fig. 2.5). To make this difference, the cell needs to segregate ions: positively charged go from outside and stay inside, negatively charged go from inside to outside. To segregate, the cell needs the energy booster—sun rays caught by the **chlorophyll** molecules embedded in the thylakoid membrane. The chlorophyll molecule is non-polar (similarly to membrane lipids) and contains magnesium (Mg). It is easy to excite the chlorophyll molecule with light; excited chlorophyll may release the electron if the energy of light is high enough.

To make carbo*hydrates* from carbon dioxide (CO_2 apparently has no hydrogen), the cell needs hydrogen atoms (H) from hydrogen carrier, NADP+ which at the end of light stage, becomes NADPH.

The main event of the light stage is that chlorophyll reacts with light, yielding electron (e^-) and becoming oxygenated, positively charged molecule. Then electron, pro-
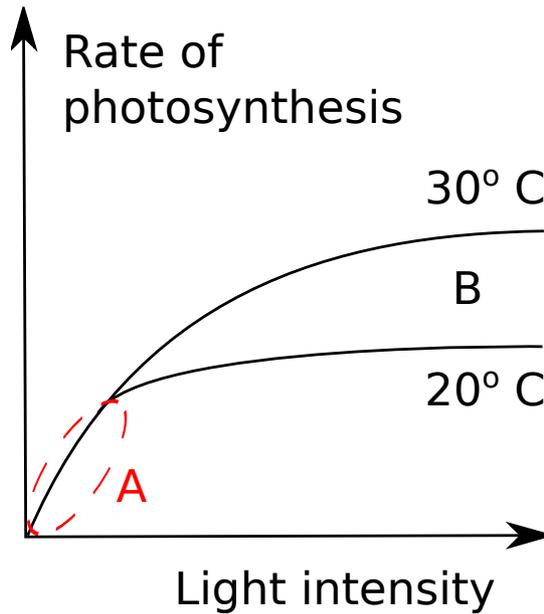
Figure 2.3. Explanation of experiment of F. Blackman (1905). A—low light, little temperature effect; B—high light, significant temperature effect.

ton and NADP$^+$ react to yield NADPH which will participate in enzymatic reactions later on. The positively charged chlorophyll is extremely active chemically, therefore it splits water molecules ("photolysis of water") into protons (which accumulate inside thylakoid), oxygen (O_2) and electron. The electron returns to chlorophyll. When increasing gradient reaches the threshold, the **proton pump** starts to work as protons (H^+) pass along the gradient. The energy of passing protons allows for the ATP synthesis from ADP and P$_i$ (inorganic phosphate). On the other side of membrane, these protons make water with hydroxide ions.

In the previous paragraph, "chlorophyll" is actually two photosystems: photosystem II (P680) and photosystem I (P700). Photosystem II (contains chlorophyll and carotenes) is more important. It splits water, makes proton the gradient and then ATP, and forwards electrons to photosystem I. Photosystem I contains only chlorophylls and makes NADPH.

Ultimately, the light stage starts from light, water, NADP$^+$, ADP and results in an accumulation of energy (ATP) and hydrogen (NADPH) with a release of oxygen which is a kind of exhaust gas (Fig. 2.6).
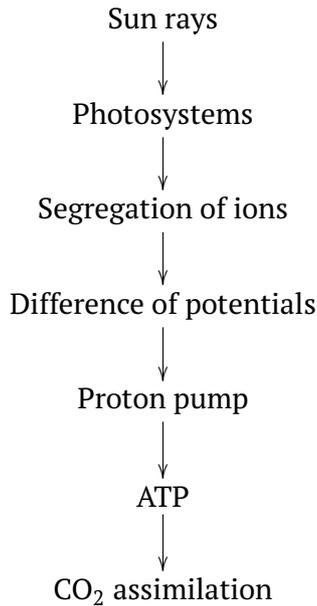
Sun rays
↓
Photosystems
↓
Segregation of ions
↓
Difference of potentials
↓
Proton pump
↓
ATP
↓
CO_2 assimilation

Figure 2.4. The logical chain of light stage reactions (hydrogen carrier not shown).

2.3 Enzymatic Stage

The enzymatic stage has many participants. These include carbon dioxide, hydrogen carrier with hydrogen (NADPH), ATP, ribulose biphosphate (RuBP, or C_5), and Rubisco along with some other enzymes. Everything occurs in the matrix (stroma) of the chloroplast.

The main event of the enzymatic stage is CO_2 assimilation with C_5 into short-living C_6 molecules. Assimilation requires Rubisco as an enzyme. Next, this temporary C_6 breaks into two C_3 molecules (PGA). Then, PGA will participate in the complex set of reactions which spend NADPH and ATP as sources of hydrogen and energy, respectively; and yields (through the intermediate stage of PGAL) one molecule of glucose ($C_6H_{12}O_6$) for every six assimilated molecules of CO_2. $NADP^+$, ADP and P_i will go back to the light stage. This set of chemical reactions returns RuBP which will start the new cycle of assimilation. Consequently, all reactions described in this paragraph are part of the cycle which has the name "Calvin cycle" or "C_3 cycle" (because the C_3 PGA molecules here are most important).

In all, enzymatic stage starts with CO_2, NADPH, ATP and C_5 (RuBP). It ends with glucose ($C_6H_{12}O_6$), NADP+, ADP, P_i and the same C_5. With an addition of nitrogen and phosphorous, glucose will give all other organic molecules (Fig. 2.7).
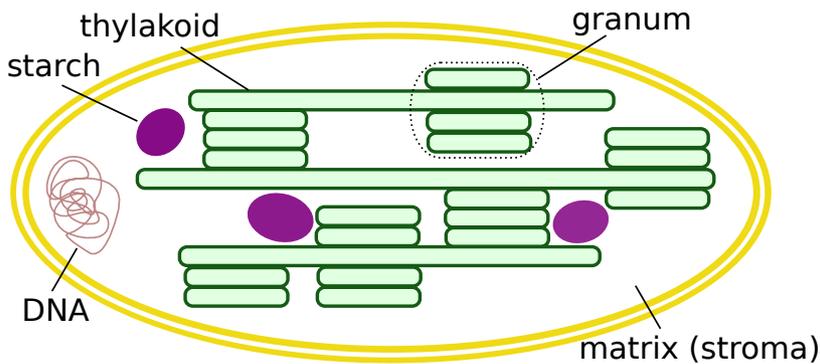
Figure 2.5. Chloroplast.

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To summarize, the logic of photosynthesis (Fig. 2.8) is based on a simple idea: *make sugar from carbon dioxide*. Imagine if we have letters "s", "g", "u", and "a" and need to build the word "sugar". Obviously, we will need two things: the letter "r" and the energy to put these letters in the right order. The same story occurs in photosynthesis: it will need hydrogen (H) which is the "absent letter" from CO_2 because sugars must contain H, O and C. $NADP^+$/NADPH is used as hydrogen supplier, and energy is ATP which is created via proton pump, and the proton pump starts because light helps to concentrate protons in the reservoir.
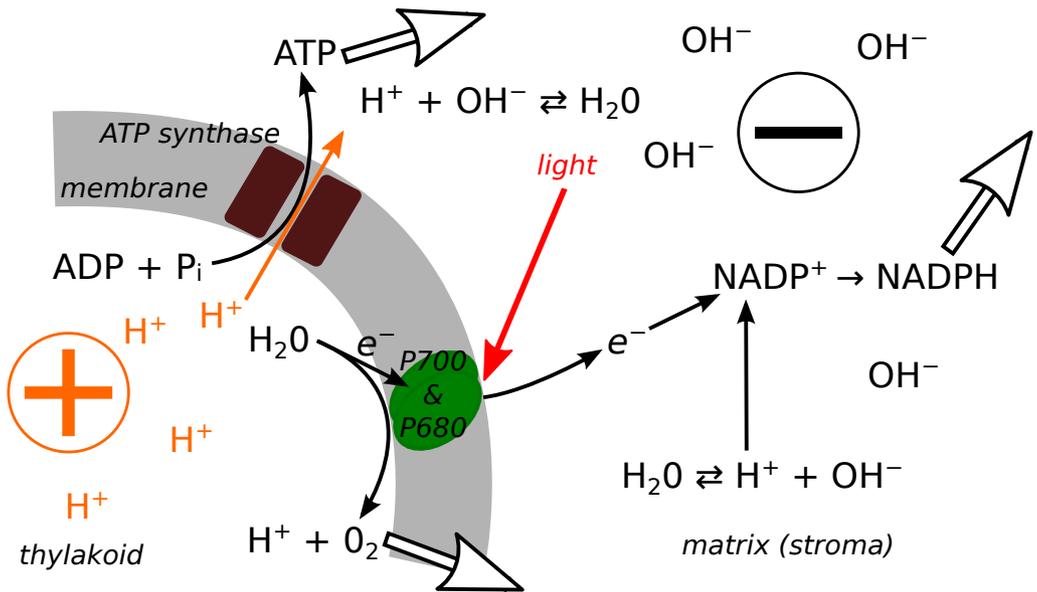
Figure 2.6. Scheme of the light stage of photosynthesis.
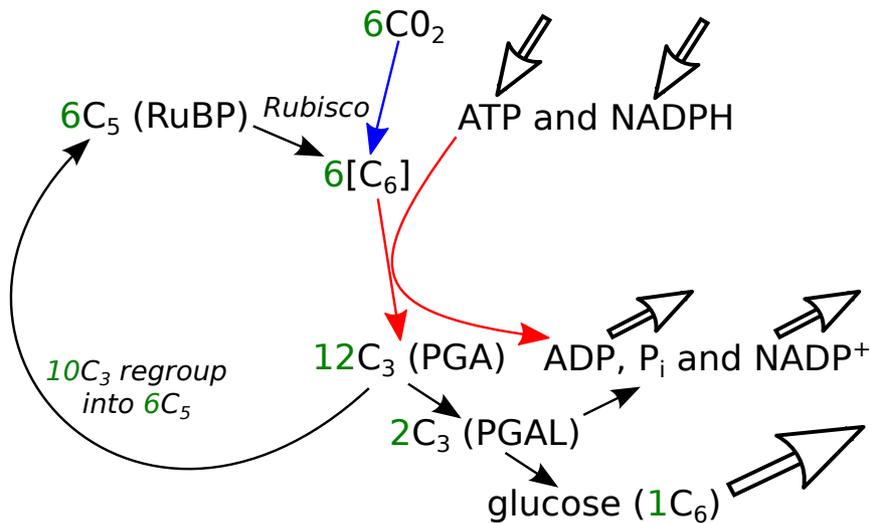
Figure 2.7. Scheme of the enzymatic stage of photosynthesis. Numbers in green show how carbon is assimilated without changing the amount of RuBP.
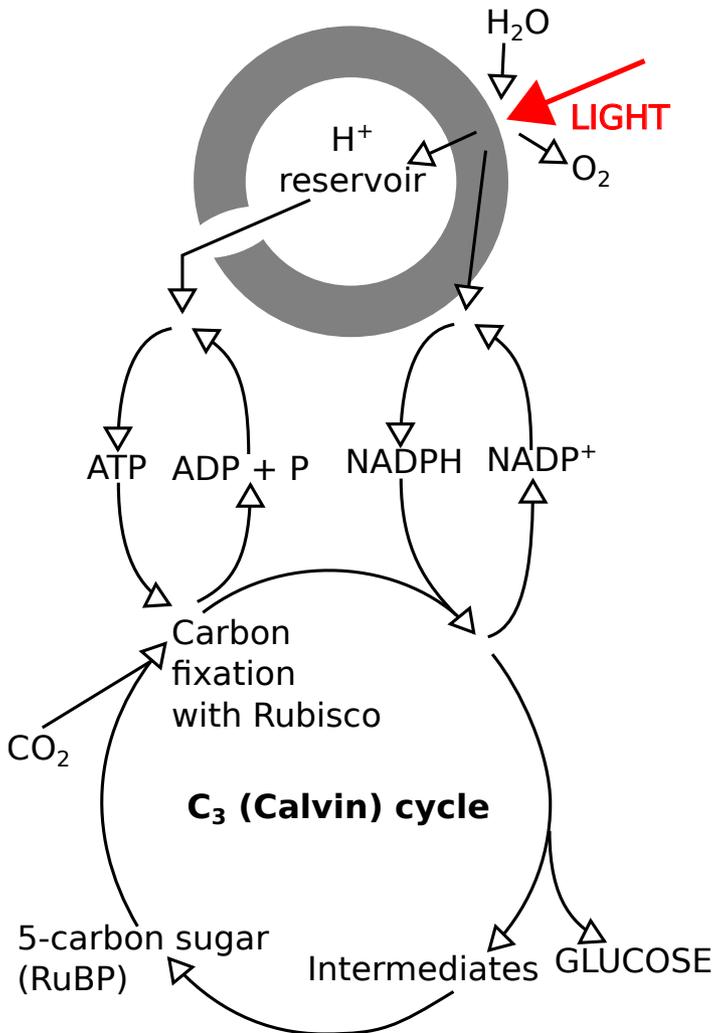
Figure 2.8. Summary of the photosynthesis. (*Based on the idea from Arms & Camp, 1986*).

2.4 C$_4$ Pathway

Rubisco is the enzyme of extreme importance since it starts the assimilation of carbon dioxide. Unfortunately, Rubisco is "two-faced" since it also catalyzes photorespiration (Fig. 2.9). **Photorespiration** means that plants take oxygen instead of carbon dioxide. Rubisco catalyzes photorespiration if there is a high concentration of oxygen (which usually is a result of intense light stage). Rubisco oxygenates C$_5$ (RuBP) which turns into PGA and PGAL, becoming glycolate. This glycolate is returned to the Calvin cycle when the cell uses peroxisomes and mitochondria, and spends ATP. The process of photorespiration wastes C$_5$ and ATP which could be more useful to the plant in other ways.
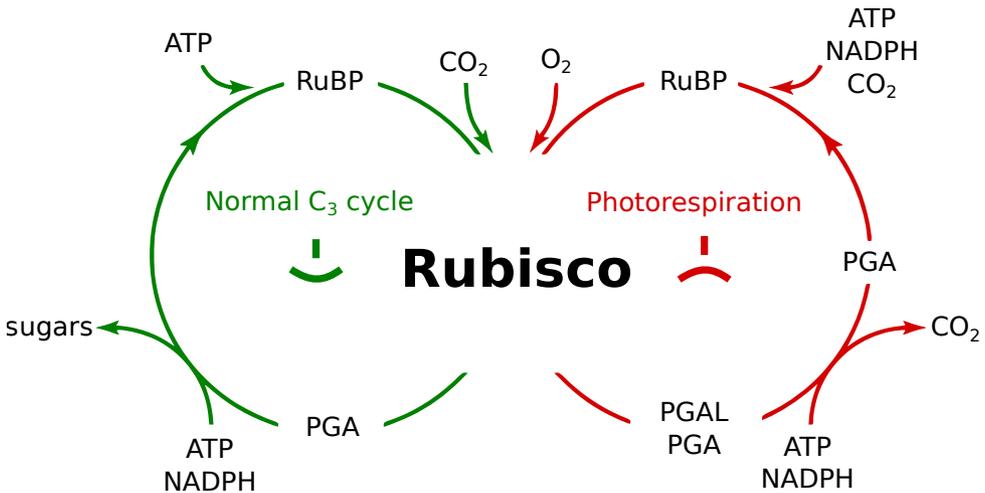
Figure 2.9. Rubisco is two-faced enzyme.

If concentration of CO$_2$ is high enough, assimilation will overcome photorespiration. Consequently, to minimize the amount of photorespiration and save their C$_5$ and ATP, plants employ **Le Chatelier's principle** ("**Equilibrium Law**") and increase concentration of carbon dioxide. They do this by temporarily bonding carbon dioxide with PEP (C$_3$) using carboxylase enzyme; this results in C$_4$ molecules, different organic acids (like malate, malic acid) with four carbons in the skeleton. When plant needs it, that C$_4$ splits into pyruvate (C$_3$) plus carbon dioxide, and the release of that carbon dioxide will increase its concentration. On the final step, pyruvate plus ATP react to restore PEP; recovery of PEP does cost ATP. This entire process is called the "**C$_4$ pathway**" (Fig. 2.10).

Plants that use the C$_4$ pathway waste ATP in their effort to recover PEP, but they still outperform photorespiring C$_3$-plants when there is an *intensive light and/or high*
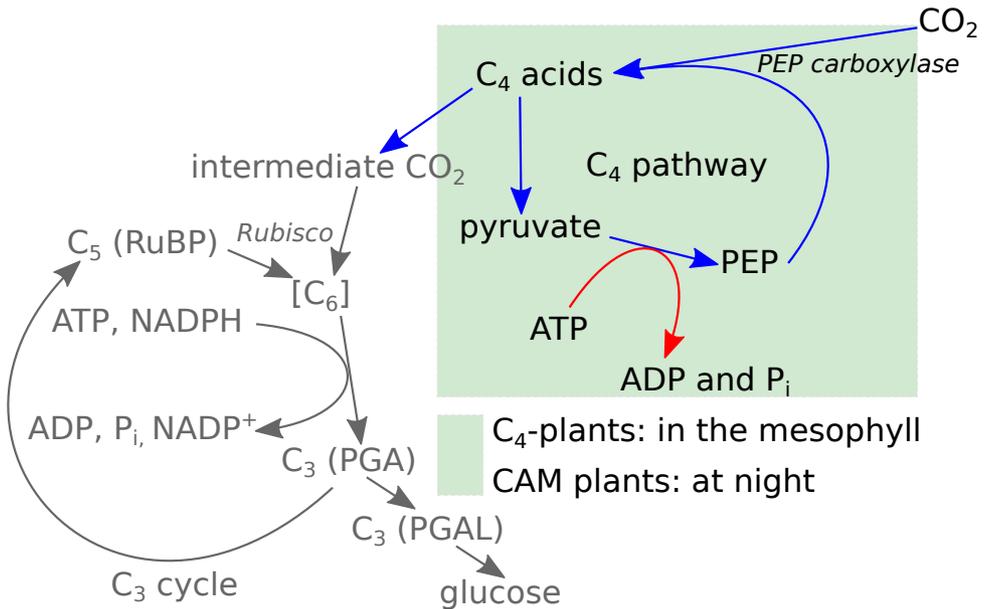
Figure 2.10. C_4 pathway (in blue).

temperature and consequently, high concentration of oxygen. This is why in the tropical climate, C_4-crops are preferable.

Two groups of plants use the C_4 pathway. Many desert or dryland plants are CAM-plants which drive the C_4 pathway at night. They make a *temporal separation* between the accumulation of carbon dioxide and photosynthesis. CAM-plants make up seven percent of plant diversity, and have 17,000 different species (for example, pineapple (*Ananas*), cacti, Cactaceae; jade plant, *Crassula* and their relatives).

"Classic" C_4 plants drive C_4 pathway in leaf mesophyll cells whereas their C_3 is located in so-called **bundle sheath cells**. This is a *spatial*, rather than temporal separation. These C_4-plants make up three percent of plant biodiversity and have more than 7,000 different species (for example, corn, *Zea*; sorghum, *Sorghum* and their relatives).

In all, both variants of C_4 pathway relate with concentration of carbon dioxide, spatial or temporal (Fig. 2.11). Both are called "carbon-concentrated mechanisms", or CCM.

There are plants which able to drive both C_3 and C_4 pathways (like authograph tree, *Clusia*), and plants having both "classic" C_4 and CAM variants (like *Portulacaria*).
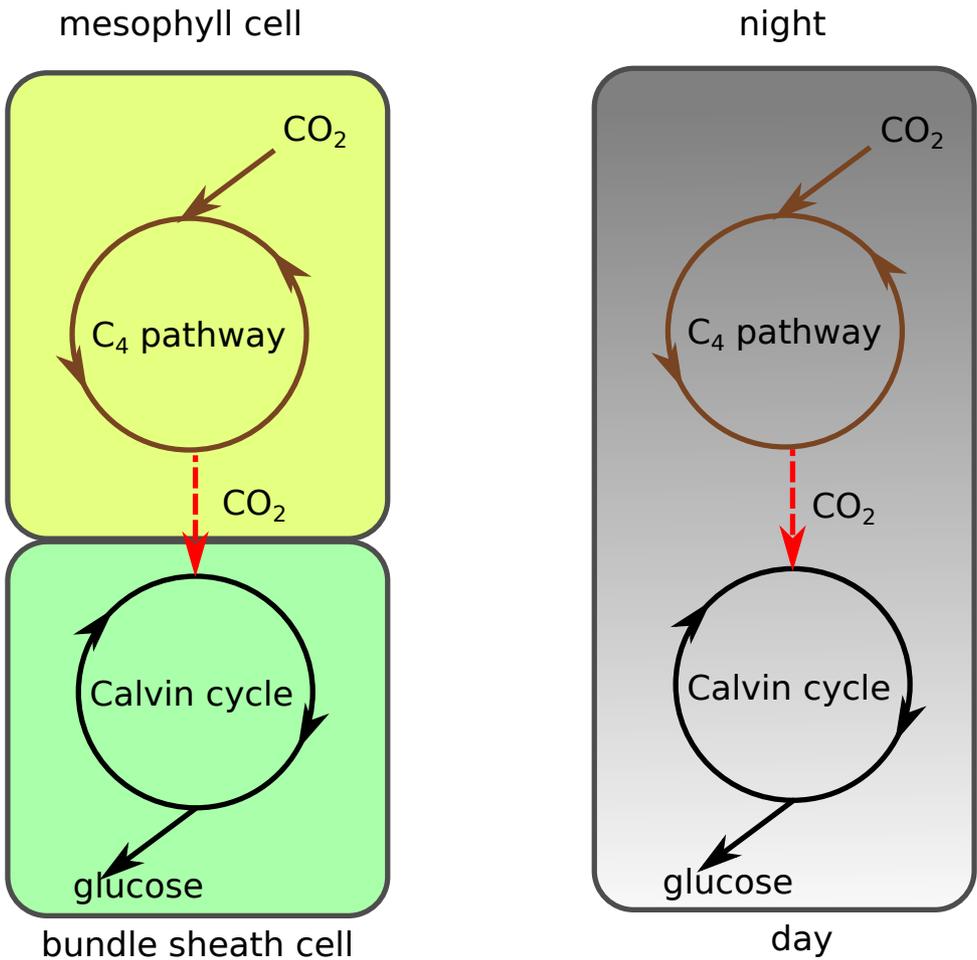
Figure 2.11. C_4 plants (left) and CAM plants (right).

2.5   True respiration

The common misconception about plants is that their only energy-related metabolic process is photosynthesis:

$$CO_2 + H_2O + \text{energy} \longrightarrow \text{carbohydrates} + O_2$$

However, as most eukaryotes, plants have mitochondria in cells and use *aerobic* (oxygen-related) respiration to obtain energy:

$$\textbf{carbohydrates} + \textbf{O}_2 \longrightarrow \textbf{CO}_2 + \textbf{H}_2\textbf{O} + \textbf{energy}$$
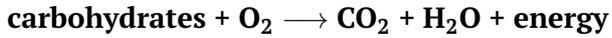
Typically, plants spend much less oxygen in respiration than they make in photosynthesis. However, at nights plants do exactly the same as animals, and make only carbon dioxide!

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Chapter 3

Symbiogenesis and the Plant Cell

3.1 Introduction to Cells

In 1665, Robert Hooke looked at cork under a microscope and saw multiple chambers which he called "cells". In 1838, Schleidern and Schwann stated that (1) *all plants and animals are composed of cells* and that (2) *cell is the most basic unit ("atom") of life*. In 1858, Virchow stated that (3) *all cells arise by reproduction from previous cells ("Omnis cellula e cellula"* in Latin). These three statements became the base of the **cell theory**.

Discovery of cells is tightly connected with the development of microscopy. Nowadays, there are basically three kinds of microscopy: light microscopy, transmission electron microscopy (TEM), and scanning electron microscopy (SEM). Light microscopes use normal light, it can magnify transparent things 1,000 times. Transmission electron microscopes give a more detailed view of the internal organization of cells and organelles. They use an electronic beam, which kills objects as it passes through. In addition, for examination under a TEM, objects are often stained with heavy metals like osmium, and for SEM with gold which is highly reflective for electronic rays. A TEM can magnify things 10,000,000 times. Scanning electron microscopes show an image of the surface of cells and organisms using reflected electronic beam. It can magnify things 1,000,000 times. It is possible to see atoms on these photographs!

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The minimal cell should have three things: protein-synthesizing apparatus (from DNA to RNA and proteins), space designated for all other chemical reactions (jelly-like cytoplasm) and the oily film separating cell from its environment (membrane).

This is like fruit jelly covered with thin layer of butter; "fruit pieces" are protein-synthesizing parts.
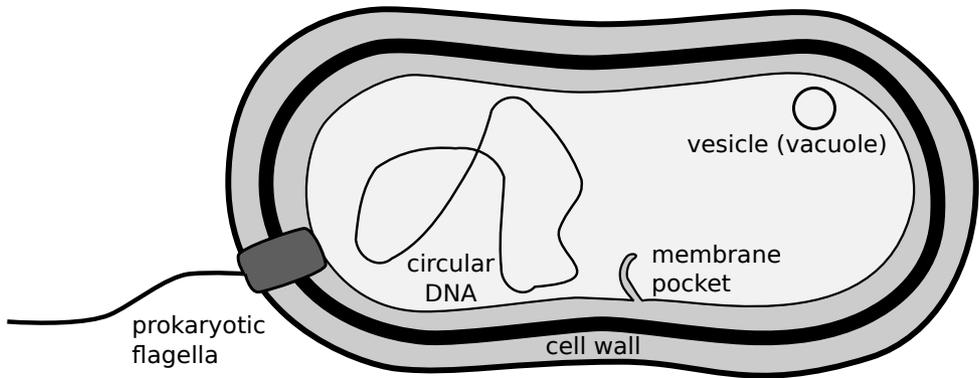

Figure 3.1. Prokaryotic cell.

The cell membrane of all cells has two layers. One end of each layer is polar and hydrophilic, while the other end is hydrophobic. These layers are made with **phospholipids** which are similar to typical lipids but have polar head with phosphoric acid, and two hydrophobic, non-polar tails (Fig. 3.2). Apart from phospholipinds, membrane contains embedded other lipids like cholesterol (in animal cells only) and chlorophyll (in some plant membranes), proteins and carbohydrates. Proteins are extremely important because without them, membrane does not allow large hydrophylic molecules and ions to came trough.
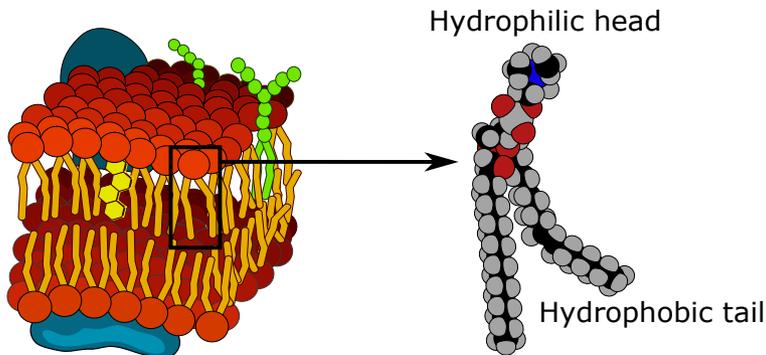
Figure 3.2. Membrane and phospholipids.

Cells which have DNA in a membrane-bound nucleus are known as **eukaryotic**, while those which do not are known as **prokaryotic**. Prokaryotic cells have their DNA surrounded by the cytoplasm. Some have also prokaryotic flagella (rotating protein

structure), a cell wall, vesicles and membrane folds/pockets (Fig. 3.1). Eukaryotic cells have their DNA in a nucleus which separates it from the cytoplasm.

There are many other parts of the eukaryotic cell (Fig. 3.5). The nucleus of the cell contains DNA and proteins. Nucleoli are in the nucleoplasm, this is the place where ribosomal RNAs are assembling. Ribosomes, found in the cytoplasm, help to synthesize proteins. The **endoplasmic reticulum** (ER), usually found near edge of the cell, is where proteins are synthesized, packaged and transported. In many cells, ER is connected with nucleus membrane. The **Golgi apparatus** directs proteins and other substances to the part of the cell where they need to go. Eukaryotic cells must have **mitochondria** and might have **chloroplasts**, both originated via symbiogenesis (see below). Mitochondria are covered with two membranes, the inner membrane has intrusions called **cristae**. Mitochondria break down organic molecules into carbon dioxide and water in a process known as oxidative **respiration**.
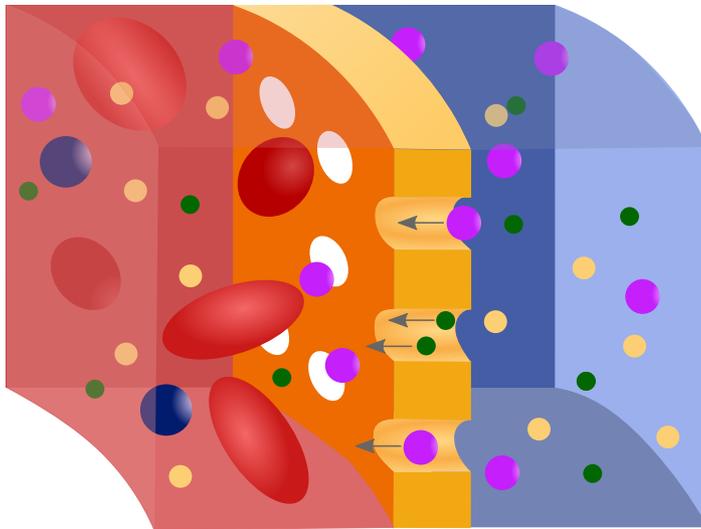

Figure 3.3. Semi-permeable membrane: how it works. Big "red" molecules are larger then pores so they are not allowed to go. Other molecules are smaller then pores and they are allowed to equalize their concentrations which are always *lower* in places where "red" molecules present. This is why they go from right to left and not otherwise.

Cell membranes are semi-permeable (Fig. 3.3), they allow some molecules (typically small and/or non-polar) to go through but others (big and/or polar) will stay outside or inside forever, or until specific pore opens. Water always "wants" to equalize concentrations on both sides of membrane and water molecules typically flow through the membrane to where concentration of other molecules (salts, acids) is *higher* (and, naturally, concentration of water is *lower*). This is **osmosis**.
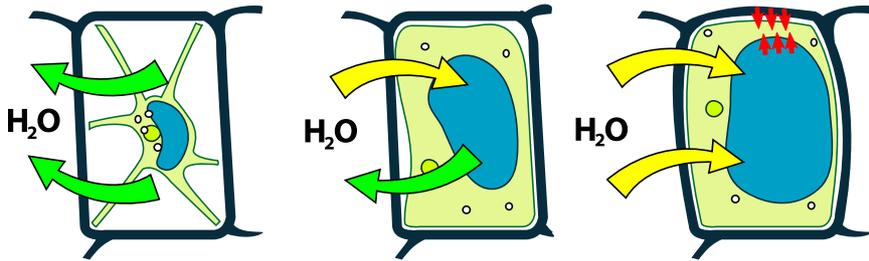
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Figure 3.4. Osmosis in (from left to right) hypertonic (high salt), isotonic and hypotonic (low salt) environments. Blue color is for the vacuole. Red arrows on the right image show turgor—combined pressure of the vacuole and the cell wall.

Cell wall (common in plants and fungi) surrounds the cell and limits how far the cell can expand due to osmosis (Fig. 3.4). Since osmosis may result in uncontrollable expansion of cell, cells without cell walls must find a way to pump out the excess water. **Vacuole**(s) is the large vesicle(s) which can do a variety of things for the cell, for instance store nutrients, accumulate ions, or become a place to store wastes. It plays an important role in the *turgor* (Fig. 3.4).

3.2   Mitochondria and Chloroplasts

To escape from competition, cells which were prokaryotic became larger. To facilitate communication between all parts of this larger cell, they developed cytoplasm mobility using *actin* protein. In turn, this mobility resulted in acquiring **phagocytosis**, which is when a large cell changes shape and can engulf ("eat") other cells. This way, cells that used to be prey became predators. These predators captured prey by phagocytosis and digested bacteria in *lysosomes*, which use enzymes that destroy the cytoplasmic components of the bacterial cells.

The threat of predators result in cells became even larger, and these cells will need a better supply of ATP. Some prey which were not digested, and turned out to be useful in providing ATP. Of course, predator cells should also invent a proper transport through the resulted double membrane! Due to natural selection, those prey, which were purple bacteria, became the cell's mitochondria. This is **symbiogenesis**, or the formation of two separate organisms into a single organism (Fig. 3.6).

Another result of a larger cell (eukatyotic cells are typically 10–100 fold larger than prokaryotic) is that the size of DNA will increase, and to hold it, the cell will form a nucleus. The new predator cells also needed to prevent alien organisms from transferring their genes which will delay the evolution.
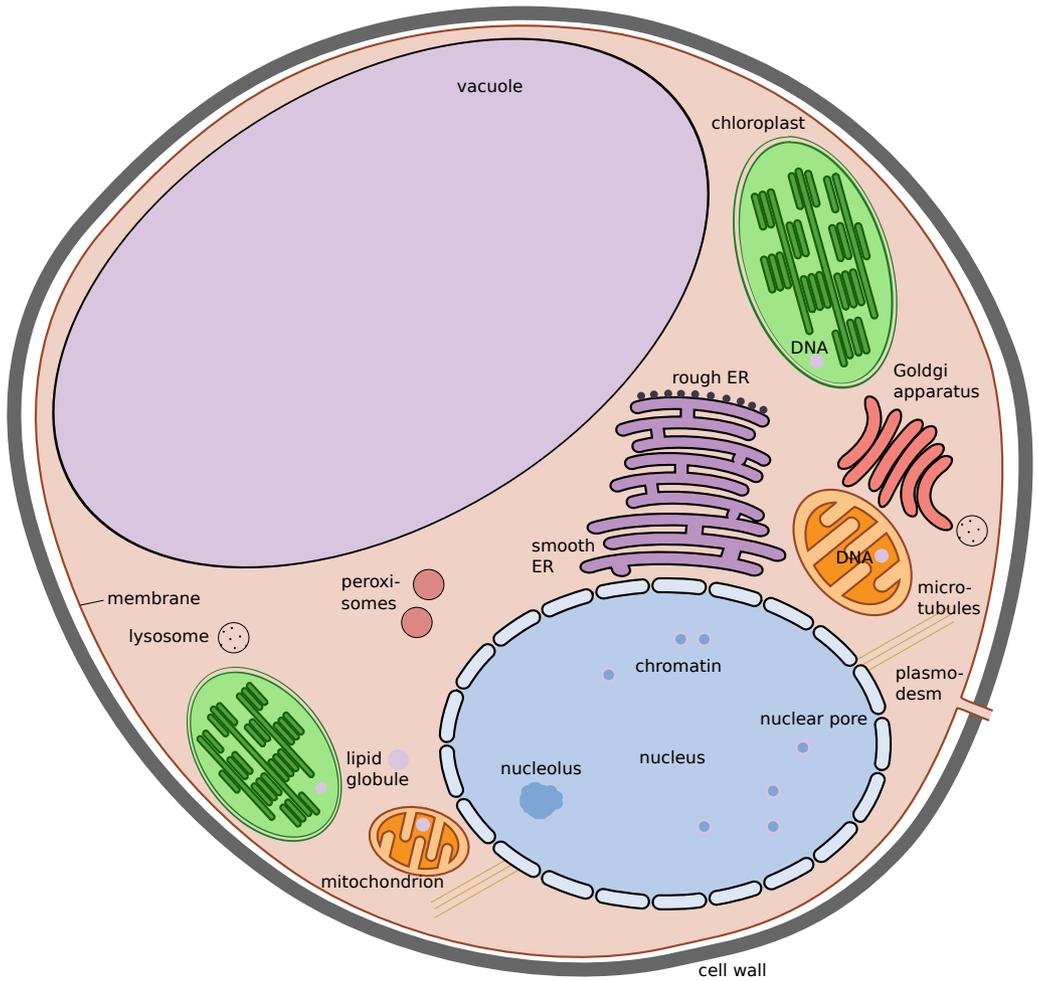
Figure 3.5. Schematic overview of the eukaryotic (plant$_1$) cell.
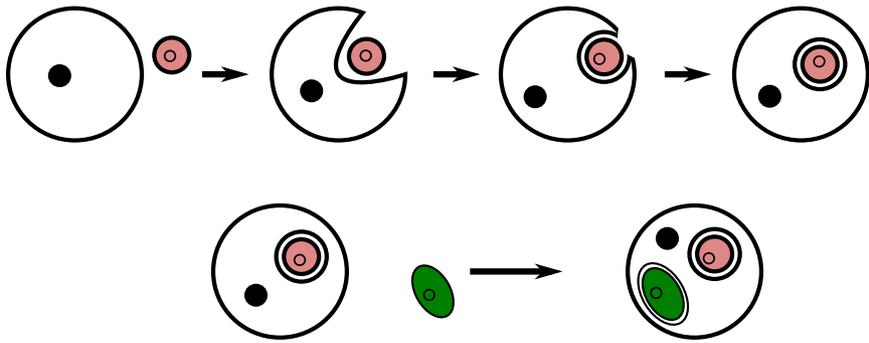
Figure 3.6. Symbiogenetic origin of eukaryotic cell (top row) and algal cell (bottom row).

The other reason is that the nucleus protects the DNA by enclosing it; in case if DNA virus comes into the cell and tries to mock up cell DNA, eukaryotic cell immediately destroys any DNA found in the cytoplasm. One more reason to make nucleus is pressure of antibiotics: nucleus improves isolation from these harmful chemicals. Nucleus formation and symbiogenesis leaded cells to become eukaryotic.

To be called an eukaryote, it is more important to have phagocytosis and mitochondria then nucleus because (1) nucleus is not always exists, it could disappear during the division of cell and (2) some prokaryotes (planctobacteria) also have membrane compartments containing DNA.

On next step, some eukaryotes also captured cyanobacteria (or another photosynthetic eukaryote), which became chloroplasts. These photosynthetic protists are called **algae**.

In all, eukaryotic cells are "second-level cells" because they are cells made up of multiple cells. Cells of all eukaryotes have two genomes, nuclear usually has biparental origin whereas mitochondial genome normally originates only from mother. Plant cells, in turn, have *three genomes*, and chloroplast genome is usually also inherited maternally.

Chloroplasts synthesize organic compounds whereas mitochondria produce most of the cytoplasmic ATP. Both organells are covered with two membranes and contain circular DNA and ribosomes similar to bacterial. Chloroplasts have thylakoids, or inner membrane pockets and vesicles. Chloroplast thylakoids could be long (**lamellae**) or short and stacked (**granes**). In turn, mitochondria could be branched and interconnecting.

Chloroplasts are normally green because of chlorophyll which converts light energy into chemical energy. Some chloroplasts lose chlorophyll and become transparent, "white", they are called **leucoplasts**. Other chloroplasts could be red and/or orange

(**chromoplasts**), because they are rich of carotenes and xanthophyls. These pigments facilitate photosynthesis and are directly responsible for the fall colors of leaves. Since starch is a more compact way of storing energy than glucose, chloroplasts store carbohydrates as starch grains. Transparent **amyloplasts** contain large granules of starch. Storage tissues of potato tubers, carrot roots, sweet potato roots, and grass seeds are examples of tissues rich in amyloplasts.

Having chloroplasts and cell walls are not directly connected, but almost all organisms with chloroplasts have also cell walls. Probably, this is because cell walls do not facilitate cell motility, and for those protists which already have cell walls, obtaining chloroplast will be the nice way for coming out of competition with organotrophic beings.

3.3   Cell wall, Vacuoles, and Plasmodesmata

Among eukaryotic cells, plant cells are largest. Some of them (for example, cells from green pepper and grapefruit) are well visible with the naked eye. Plant cells do not have well-developed internal cytoskeleton, but **cell wall** provides an external one. There are two kinds (or, better, two stages of development) of cell walls, the **primary** and the **secondary**. The primary cell wall is typically flexible, frequently thin and is made of cellulose, different carbohydrates and proteins. The secondary cell wall contains also **lignin** and highly hydrophobic **suberin**. These chemicals completely block the exchange between the cell and the environment which means that the cell with secondary wall will soon die. Dead cells can still be useful to plants in many ways, for example as a defense against herbivores, support and water transport. In fact, more than 90% of wood is dead.

Since every plant cell is surrounded with a cell wall, they need a specific way of communication. This is done through **plasmodestata**—thin cytoplasmic bridges between neighbor cells. A **symplast** is the name of continuous cytoplasm inside of cells. An **apoplast** is cell walls and space outside the cell where communication and considerable metabolic activity take place. Both the symplast and apoplast are important to the transportation of nutrients needed by the cell (Fig. 3.7).

If cells are surrounded by a smaller concentration of salts than in the cytoplasm, the water will flow into the cell. This process is called **osmosis**. In plant cells, most of the water with diluted chemicals is concentrated in vacuole(s). **Turgor** pressure is the combined pressure of the cell and vacuoles wall that supports the shape of cell (Fig. 3.4).

You may think of plant tissue as about staked cardboard boxes where every box is made from wet cardboard paper (cell wall) but has the inflated balloon (vacuole)
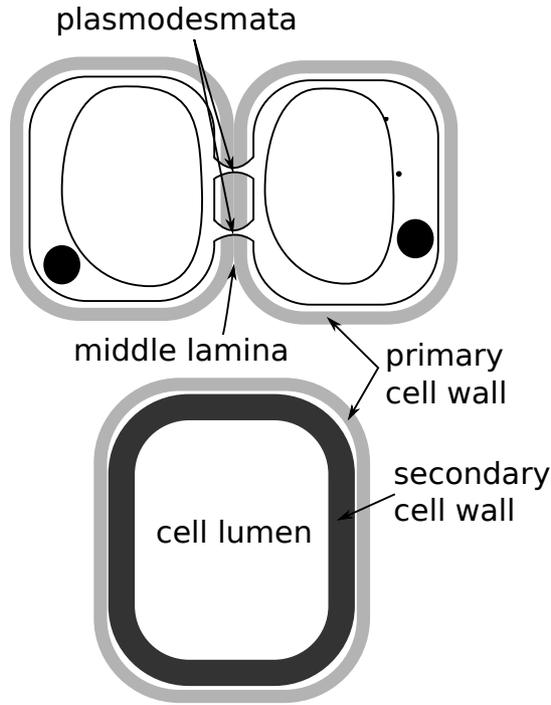
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Figure 3.7. Living cells with primary cell walls (top) and dead cell with primary and secondary cell walls (bottom). Apoplast colored with shades of gray, symplast with dots.

inside, and when the pressure of vacuole decreases (water deficit), plant organs droop. Please see the video http://ashipunov.info/shipunov/school/biol_154/mov/balloon.mp4 to understand this better.

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Comparing with animal cells, plant cells have chloroplasts, vacuoles, cell walls, and plasmodesmata but they hardly have any phagocytosis and true cytoskeleton (Fig 3.8). They are easy to explain: animals do not photosynthesize (no chloroplasts), instead, they need to move quickly (no cell walls and plasmodesmata); animals will support the shape of cell from cytoskeleton (no need for vacuole turgor system) and use molecular pumps to counterpart the osmosis.
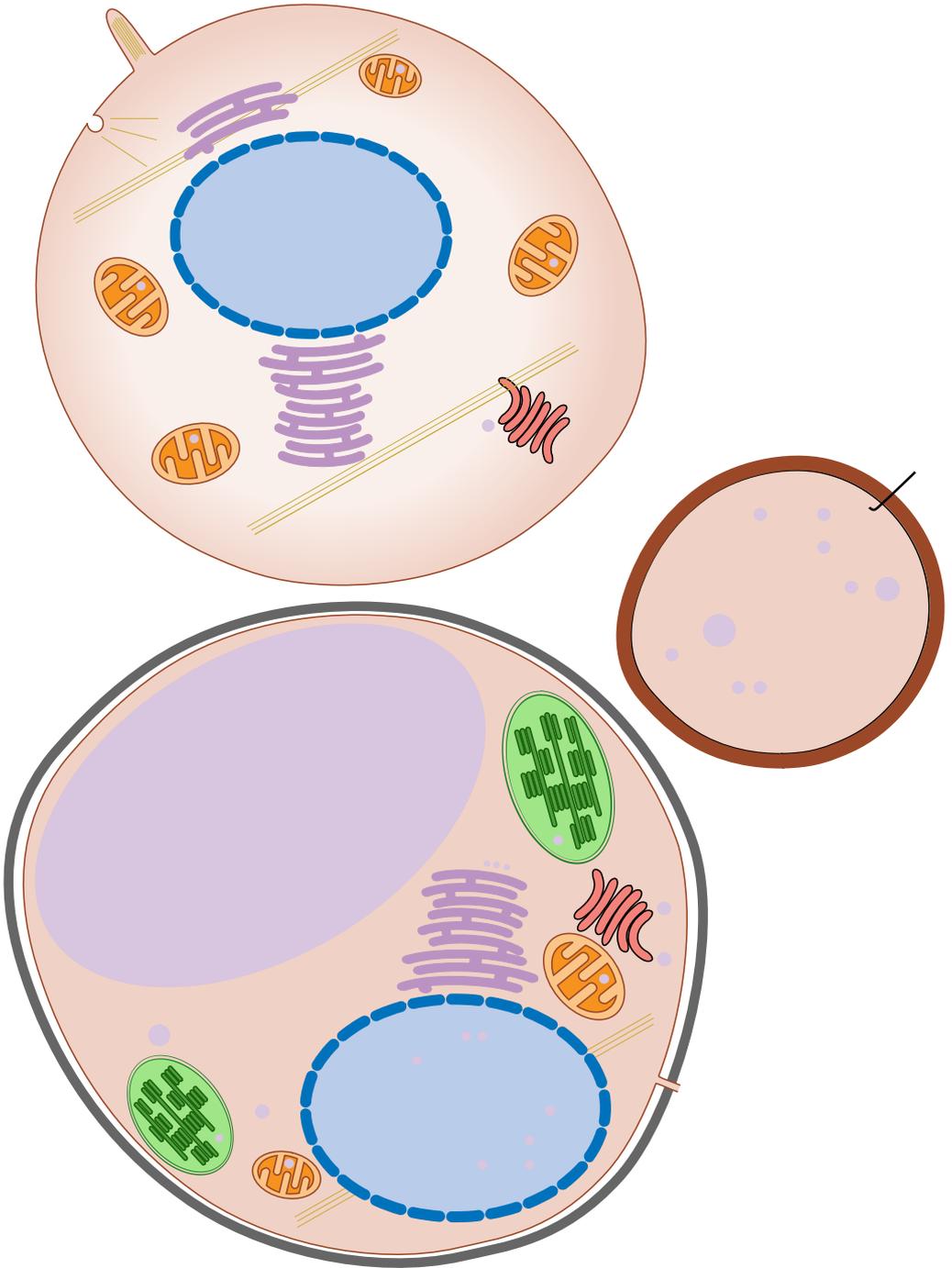
Figure 3.8. Animal, bacterial and plant cell.

3.4 Other Parts of the Cell

3.4.1 Protein Synthesis: from the Nucleus to the Ribosomes

The central dogma of molecular biology states that DNA will be converted into RNA by a process called **transcription** and RNA will be converted to protein by a process called **translation**. Translation in non-reversible whereas transcription could be reverted: there are viruses, such as HIV, that can make DNA from RNA with the enzyme called *reverse transcriptase*.

The nuclear envelope is built from a double-layered membrane. The inner and outer membranes of the nuclear envelope connect to form pores which are complicated structures controlling travel between the nucleus and the cytoplasm. Inside of the nuclear envelope there is the nucleoplasm.

Nuleoplasm contains chromatin (chromosomes). **Chromosomes** store genetic information in the form of DNA molecules. Each chromosome consists of a chain of nucleosomes, which are condensed long DNA molecules and their associated **histone** proteins. Chromatin is just another word for non-condensed chromosomes. Visible parts of chromatin (globules, filaments) correspond with non-functional DNA.

Ribosomes, which are particles that contain RNA and proteins, synthesize proteins. The **rough endoplasmic reticulum** (RER) has ribosomes along its surface, and the proteins they create are either secreted or incorporated into membranes in the cell. The **Golgi apparatus** (AG) is made of membranous sacs which are flattened and stacked, it modifies, packages, and sorts proteins and carbohydrates for the cell; this is not an essential component of cell.

3.4.2 Other Vesicles

Plant cells frequently have smaller vesicles: **lysosomes** which digest organic compounds and **peroxisomes** which, among other functions, help in photosynthesis (see above). In addition, many plant cells accumulate lipids as oil drops located directly in cytoplasm.

3.4.3 Cellular Skeleton

The cellular skeleton is a collection of protein filaments within the cytoplasm. **Microtubules** are key organelles in cell division, they form the basis for cilia and flagella and are guides for the construction of the cell wall. Cellulose fibers are parallel due to the microtubules. The movement in microtubules is based on tubulin-kinesin interactions. In contrast, the movement of **microfilaments** is based on actin-myosin interactions. Microfilaments guide the movement of organelles within the cell.

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Chapter 4

Multicellularity, the Cell Cycle and the Life Cycle

4.1   Mitosis and the Cell Cycle

Mitosis is a process of equal cell division, where each of the new cells receives the same number of chromosomes as the original cell. Mitosis does not change the cells' genotype. The goal of mitosis is to distribute pre-combined genetic material equally. Actually, mitosis is a kind of **karyokinesis**, or splitting of the nucleus, as opposed to **cytokinesis**, which is the splitting of the whole cell. Karyokinesis and cytokinesis are parts of the *cell cycle* (Fig. 4.3).

All prokaryotes (Monera) have a simple cell division called "binary fission". DNA duplicates (replication), segregates and then cell splits in two (Fig. 4.1).

Eukaryotes have much more DNA than prokaryotes. This is why their cell division is more complicated. There are four stages: prophase, metaphase, anaphase, and telophase. **Prophase** is the longest, nucleus disintegrates (except some protists like fungi) and the DNA is super-spiralized into chromosomes ("archived"). In **metaphase**, the chromosomes go to the cell equator, and every "double", "X-like" chromosome is then split in two halves which schematically can be shown as

$$X \rightarrow I + I$$

In **anaphase**, microtubules move these *I*-like chromosomes to different poles of the cell. In **telophase**, the endoplasmic reticulum will form nuclear envelopes and DNA despiralizes (Fig. 4.2).
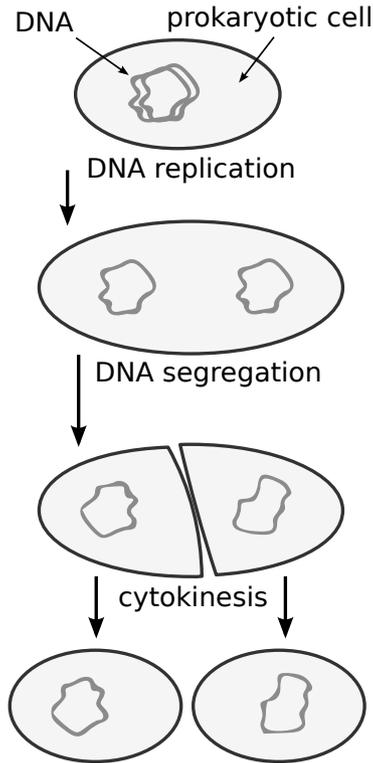
Figure 4.1. Binary fission of prokaryotes.

When mitosis is over, cell starts to divide (cytokinesis). Plant$_2$ cells use vesicles to form the border whereas many protists and animals form a constriction which finally separates two cells. Normally, chloroplasts and mitochodria are equally distributed between daughter cells along with the other cell content. Chloroplasts and mitochondria may also independently divide in "bacterial" (binary fission) way.

Mitosis is the part of the bigger **cell cycle** (Fig. 4.3). Cell cycle includes **pre-synthetic stage**, **synthetic stage**, **post-synthetic stage** (they are parts of **interphase**), karyokinesis (= mitosis) and finally cytokinesis. Apart from mitosis and cytokinesis, the most important stage of cell cycle is the **synthetic stage** (**S-stage**) when every DNA molecule (despiralized chromosome) duplicates:

$$I \to X$$

To simplify understanding of these numerous stages, one could use the following scheme. Cell cycle here has three main phases, and mitosis has four subphases:
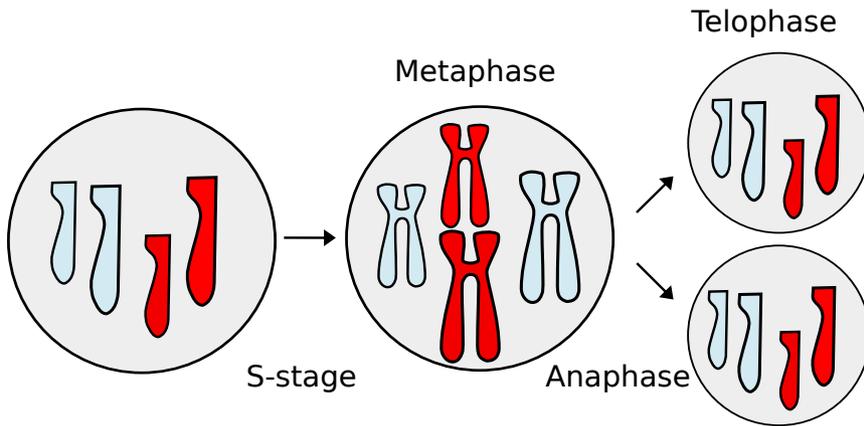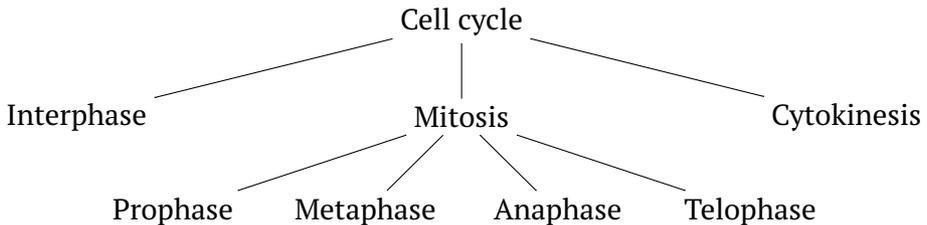
Figure 4.2. Principal scheme of mitosis.

4.2 Syngamy and Meiosis

4.2.1 Sexual Process and the Syngamy

A sexual process is important to the survival of a species. First, it makes the population more diverse, which allows more flexibility to adapt via natural selection. **Natural selection** means that all organisms are different, but if environmental conditions change, only most adapted will survive. If the population is uniform, it has less chance of survival. Second, it prevents lethal mutations from being transferred to the offspring, because those with the mutations will die instead of passing on these genes. The later happens when the mutated gene is either duplicated or alone in genotype.

(**Genotype** is a gene content of the organism. A **gene** is a piece of DNA, which is equal to one protein. A **mutation** is a "mistake" in DNA. A protein (many of them are enzymes) is made up of amino acids chained together. A **population** is a group of organisms which potentially may interbreed and have no isolation barriers.)
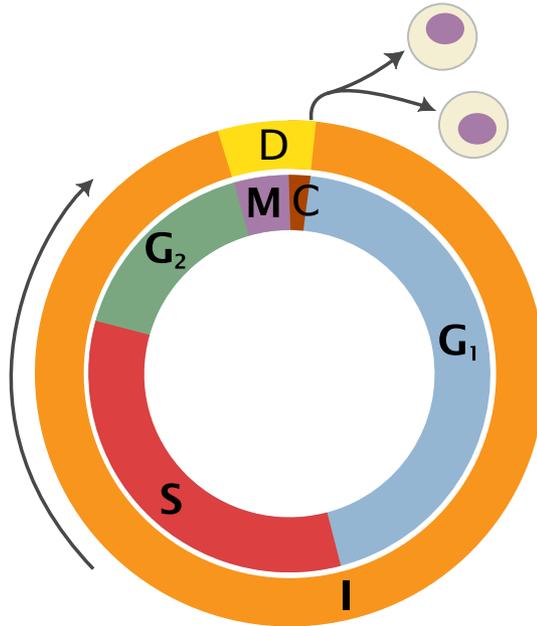
Figure 4.3. Cell cycle: I interphase, D cell division, G_1 pre-synthetic stage, S synthetic stage, G_2 post-synthetic stage, M mitosis (karyokinesis), C cytokinesis.

To make populations more diverse, organisms need to exchange DNA. One way that cells exchange genes is through syngamy. **Syngamy** (frequently labeled by "Y!"), is the fusion of two cells, resulting in a cell that has twice as many chromosomes. The two cells which are fused together are called **gametes**, and the resulting cell is a **zygote**. The goal of syngamy is the renovation of genetic material. The new cells have genotype different from the gametes. Continuous syngamy will increase the amount of DNA, so cells use meiosis (frequently labeled by "R!") to counterbalance this side-effect of syngamy:

$$Y! \rightarrow R!$$

Syngamy results in diploid cell:

$$X + X \rightarrow XX$$

In **diploid** organisms, chromosomes form pairs (these paired chromosomes are known as **homologous**), whereas in **halploid** organisms they remain single.

There are three types of syngamy (Fig. 4.4): isogamy, heterogamy, and oogamy. **Isogamy** happens when the gametes that fuse together are similar. To avoid self-

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fertilization, they must have an advanced system of recognition. Different genotypes (mating types) recognize each other with the help of surface proteins, like cells of immune system.

Heterogamy is when the gametes are of two different sizes. This difference makes recognition easier, but even more important is *division of labor*: the **female** is larger because it has resources to care for the offspring, whereas the **males** are smaller and can increase in number to allow competition and make fertilization more likely.

Oogamy is when the gametes also have different mobility. In oogamy, the non-motile female is known as the **oocyte**, and the flagellate male as the **spermatozoon**, which is only one mobile gamete here. In some organisms (red algae, sponges, crustaceans, most seed plants), spermatozoon become non-motile **spermatium** so it will need external agents to move it. Both spermatozoa and spermatia are called **sperms**.
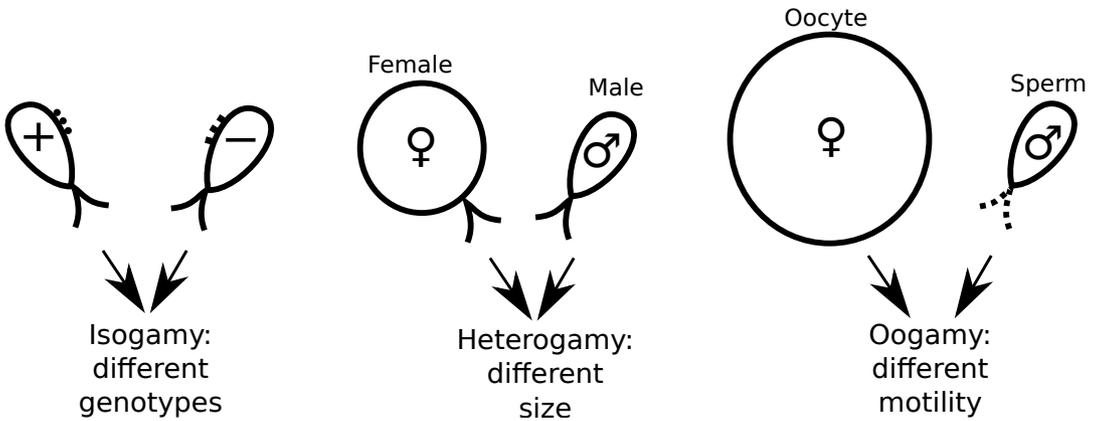

Figure 4.4. Three types of syngamy.

4.2.2 Meiosis

Syngamy is the way for organisms to become more genetically diverse, but since it increases the amount of chromosomes, it needs to be balanced by meiosis. Meiosis reduces the number of chromosomes, recombines the chromosomes, and allows chromosomes to exchange their genetic material.

Meiosis is a reductive form of cell division, where each new cell receives half of the original cell's chromosomes. Unlike mitosis, meiosis does change the genotype of cells because whole chromosomes are recombined and also exchanged their genetic material. Another difference is that in mitosis, **ploidy** ("twoness" of chromosomes) stays constant, while in meiosis, ploidy halves.

There are two problems of meiosis: first, how to find out which chromosomes are homologous; and second, how to split chromosomes which were already duplicated in S-phase. First problem is solving with "gluing" homologous chromosomes together; this happens because similar chains of DNA can attach each other. Second problem is usually solving with the second stage of meiosis which is quite similar to ordinary mitosis.

There are two stages of meiosis: a reductive division (meiosis I, unique) and an equal division (meiosis II, similar to mitosis). Each of these stages are divided into prophase, metaphase, anaphase, and telophase.

In prophase I, chromosomes *conjugate* (form **synapses**), and start to exchange DNA (crossing-over).

In anaphase I, chromosomes from each pair will *go independently to different poles*. *Independence* means that if we label "mother" and "father" chromosomes with, saying a and b, then two variants are possible:

$$X_a X_b + Y_a Y_b \rightarrow (X_a + Y_a) + (X_b + Y_b)$$

or

$$X_a X_b + Y_a Y_b \rightarrow (X_a + Y_b) + (X_a + Y_b)$$

because chromosomes do not know which is "father's" and which is "mother's".

Telophase I usually flows into prophase II. This second division of meiosis is very similar to mitosis *without synthetic stage* before it. Frequently, nuclei do not form until telophase II (Fig. 4.5).

In the first division, cell needs to split pairs of homologs to reduce ploidy. The second division of meiosis is necessary because DNA was already duplicated in the synthetic stage of the cell cycle. Consequently, every X-like chromosome needs to be split into two I-like chromosomes:

$$XX \rightarrow X + X \rightarrow I + I + I + I$$

This is why there are *two divisions* and *four cells* in the end (sometimes, however, only one of these four survives). If DNA would not be duplicated before, it is also possible for meiosis to happen in one stage instead of two. This kind of meiosis is described in some protists. Inverted meiosis, when reductive division is the second and equal the first, is rare but also exists in nature (e.g., in some rushes, bugs and butterflies).
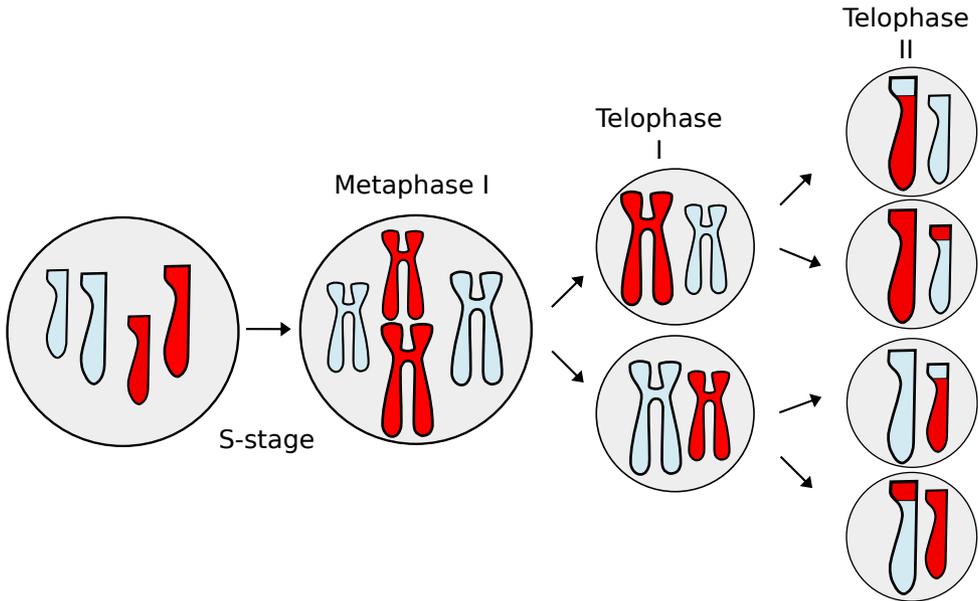
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Figure 4.5. Principal scheme of meiosis. Only one of two telophase I variants is shown.

It is possible that meiosis won't work properly, which results in a cell receiving a double set of chromosomes. If, in turn, that cell goes to syngamy, the resulting zygote will have 3 sets of chromosomes. Cells with more than two sets of chromosomes are called **polyploids**. Rarely, only some chromosome pairs do not want to split. In this case, after the syngamy, some chromosomes will be "triplicated" (**trisomy**). This is **aneuploidy**. One example of frequent ($^1/_{800}$ births) aneuploidy in humans is Down syndrome.

4.3   Life cycle of the Unicellular Eukaryote

The life cycle of a unicellular organism begins with syngamy: one cell unites with cell having different genotype. To recognize each other, cells which are going to fuse (**gametes**) frequently use surface proteins, like cells of our immune system. If these proteins are same (same genotype), gametes will not fuse. Two fused gametes form a zygote, new diploid organism. Many unicellular protists use a zygote as a wintering stage. On spring, zygote splits with meiosis, and four haploid **spores** start four new organisms which reproduce all summer with mitosis (vegetative reproduction, cloning):

$$X + X \rightarrow XX \rightarrow I + I + I + I \rightarrow X \rightarrow I + I \rightarrow \ldots$$
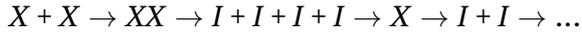
Despite its simplicity, this life cycle has all three possible ways of reproduction: **sexual** (ploidy doubles: syngamy), **asexual** (ploidy reduces: meiosis of zygote) and **vegetative** (ploidy does not change: mitotic divisions). To mark these ways of reproduction, we will use "**R!**" shortcut for the meiosis, and "**Y!**" shortcut for syngamy (Fig. 4.6). It should be noted that before every mitosis (and meiosis), cell DNA goes through duplication (S-stage of the cell cycle).
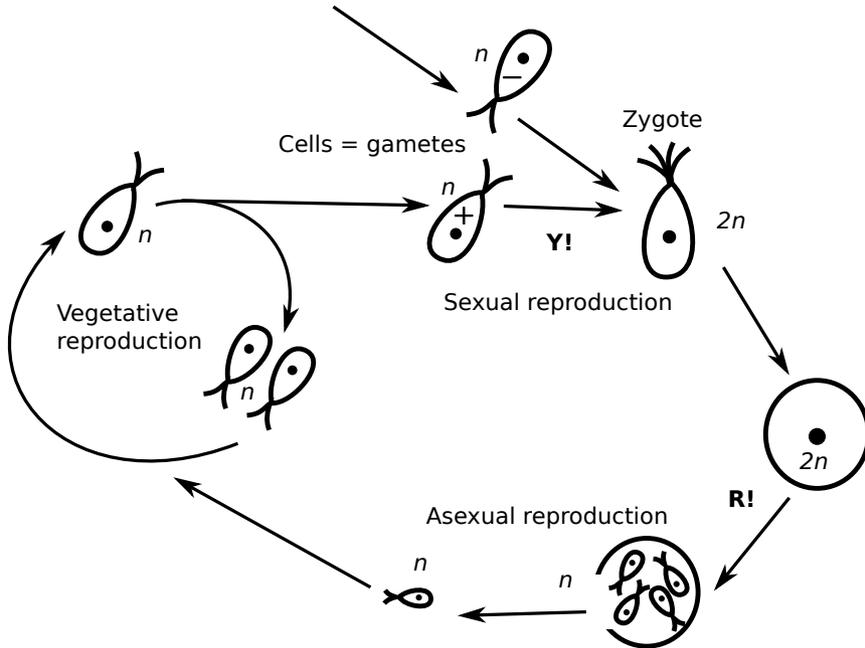
Figure 4.6. The life cycle of unicellular eukaryote.

4.4 Life cycle of the Multicellular Eukaryote

4.4.1 Origin of Death

Cells do not always part after mitosis, but sometimes stay together to form **multicellular organisms**. This increases their size, and hence provides a defense against predators. Unfortunately, it is not possible simply to increase the size of cell because the really big cell will have *less surface* (in relation to the volume), therefore it will have multiple difficulties with photosynthesis, respiration and other processes

which relate with surface of cell. But many cells together will make surface big enough (Fig. 4.7). Multicellular organism has two modes of growth: scaling the body and multiplying cells.
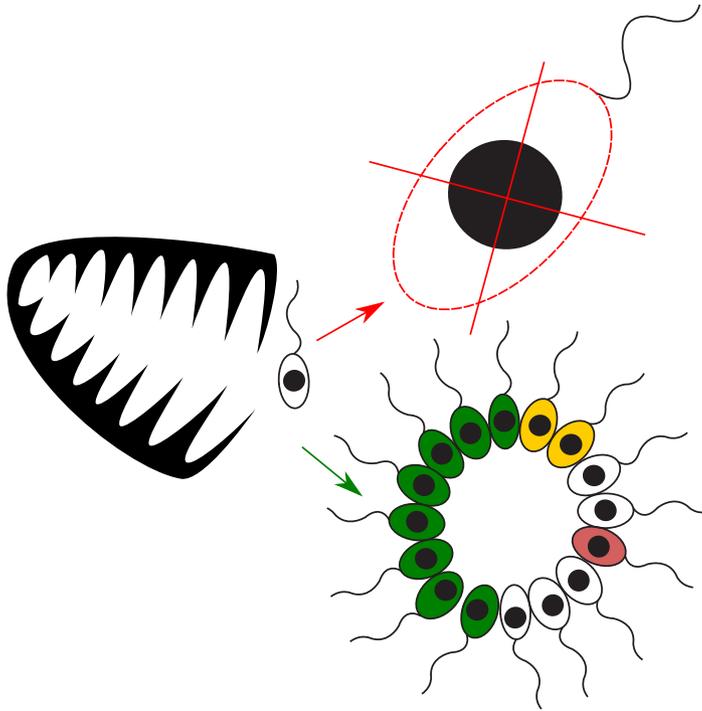

Figure 4.7. Origin of multicellularity. It is not feasible just to enlarge cell, surface is too small. But if cells do not part after mitosis, they might form the body which is big enough to escape from predators. This also provide with new mode of growth and possibility of the division of labor (colored cells).

Multicellularity allows these cells also to divide the labor and cooperate. This is extremely important for the future evolution.

Cells in the multicellular body are not connected forever. Sometimes, one or few cells escape and start a new body. This body will be exact copy (clone) of the previous one (*vegetative reproduction*). It is also possible that when these "escaped cells" go the different route: they become "sex delegates", *gametes*. All gametes want syngamy, and these cells will search for the partner of the same species but with another genotype. In case of heterogamy and oogamy, it is easy to recognize because genders will provide a hint: male will search for the female. In case of isogamy, gametes search for the partner with different surface proteins. After they finally mate, a diploid cell (zygote) appears. Zygote may winter and then divide meiotically. This is the simplest

life cycle of multicellular organism (Fig. 4.8), quite similar to the cycle discussed above for unicellular organism.

Figure 4.8. Most ancient life cycle of the multicellular organism. Zygote does not grow, it divides meiotically. Somatic ("grey") cells are going to die, only germ cells transfer their DNA to future generations.

However, frequently zygote starts to grow and divide mitotically, making the diploid body. There are two reasons to make multicellular body out of zygote without meiosis: (a) because in can and (b) because diploid is better. "It can" because zygote already contains DNA program about how to build multicellular body. Why diploid is better, explained in next section.

If multicellular organism consists of diploid cells ($2n$), we will use the neutral term **diplont**. Multicellular organisms with haploids cells (n) are **haplonts**.

"Escaped cells", "sex delegates", or mother cells of gametes from the above is a first stage of the division of labor when cells are separating into two types, **germ cells** and **somatic cells**. Somatic cells are those which will eventually die, but germ cells are capable of giving offspring. Having germ cells is not absolutely necessary for multicellular organisms, but most of them have well separated germ lines. Thus, origin of death is directly connected with this separation: somatic cells are not needed for

future generations. Unicellular organisms are potentially immortal, and same are cancer cells which also escape from organism (but they cannot make the new one).

Life cycle of multicellular organism could be described starting from haplont (Fig. 4.9). When environment conditions are favorable, it has vegetative reproduction. One variant of vegetative reproduction is that cell (**mitospore**) separates itself from a haplont, then divides into more cells and becomes a new haplont. Sometimes, whole chunks are separated and grow into new haplonts. When conditions change, haplont may start the sexual reproduction: syngamy. In syngamy, one gamete separates from the haplont and unites with a gamete from another haplont. Together, gametes form a zygote. This zygote might go straight to meiosis (as it happens in unicellular eukaryotes) but more frequently, zygote will grow, divide mitotically and finally becomes a diplont. This diplont might be superficially almost identical to haplont but every cell of it contains diploid nucleus (every chromosome has a pair). Diplont (similarly to haplont) may reproduce itself vegetatively (make clones): cell separates itself from a diplont, then divides mitotically into more cells and becomes a new diplont.

The diplont is also capable for asexual reproduction: there could be a cell separates itself from a diplont and divides with *meiosis* creating four spores, each of them will grow into *haplont*.
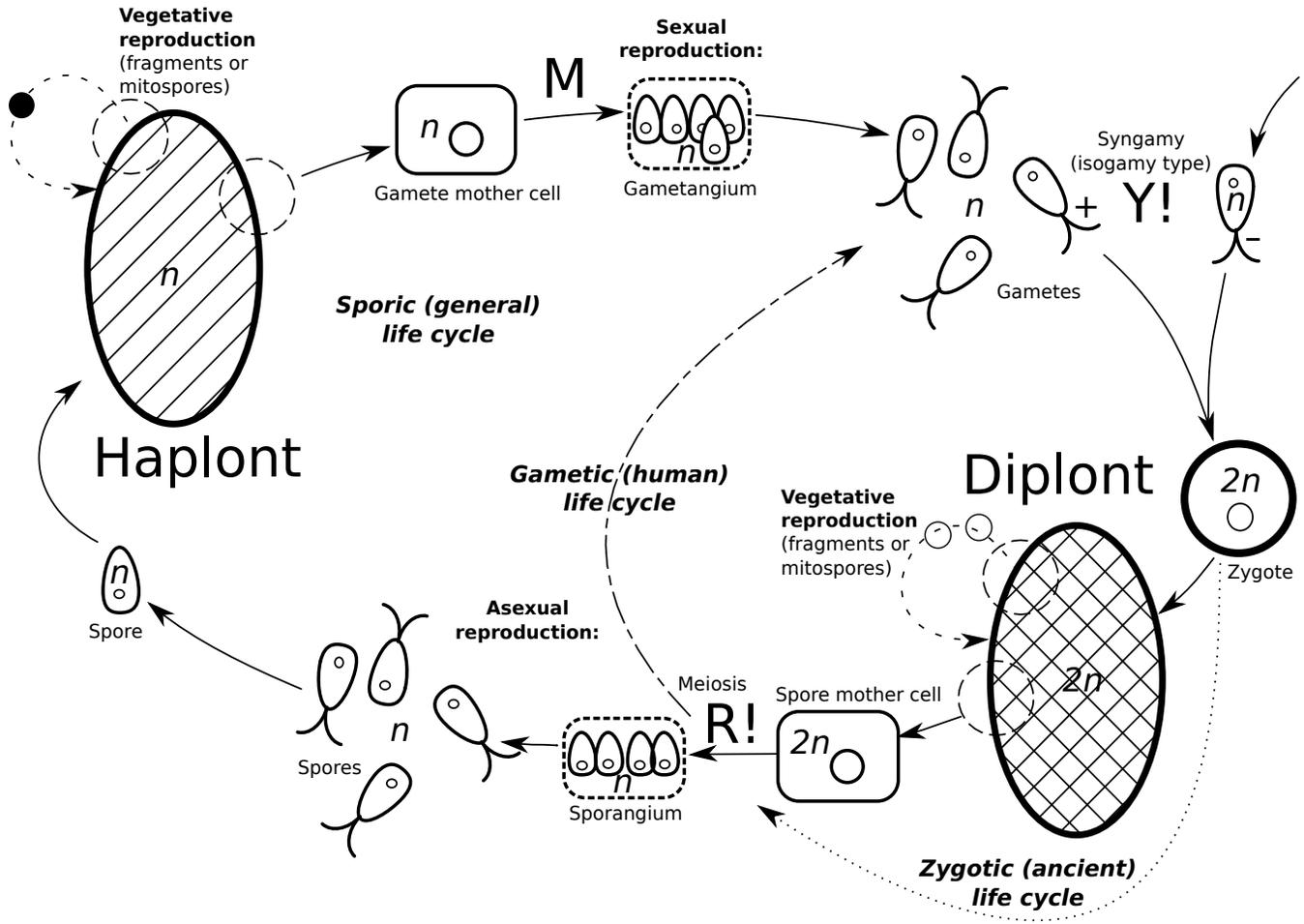
Figure 4.9. General life cycle. Haploid part is on the left, diploid on the right, syngamy on the top, meiosis on the bottom. "M" letter is used to label mitosis.

4.4.2 Sporic, Zygotic and Gametic Life Cycles

The life cycle described above is the **sporic** life cycle (Fig. 4.10). Organisms with sporic life cycle have both diplont and haplont, equally or unequally developed.
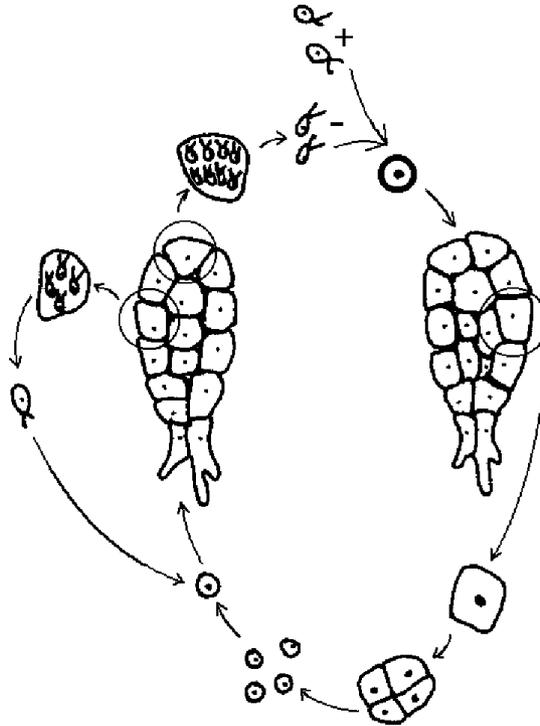
Figure 4.10. Sporic life cycle. Overview. Haploid part is on the left, diploid on the right, syngamy on the top, meiosis on the bottom.

In all, there are three types of life cycles: sporic, zygotic, which is the most similar to unicellular and most primitive; and gametic, which is used by animals and a few protists (Fig. 4.11). The **zygotic** life cycle starts with syngamy and goes to meiosis. It has no diplont. **Gametic** life cycle goes from meiosis to syngamy. It has no haplont.

Protists have all three types of life cycles whereas higher groups have only one. Animals exhibit gametic cycle, whereas plants$_2$ retained the more primitive sporic cycle.

4.4.3 Evolution of Life Cycles

The most striking difference between unicellular and multicellular life cycles is that zygote of multicellular organism may start to make diploid body (diplont) which sometimes is visually almost identical to haplont. This is because in the evolutionary

Figure 4.11. Schematic representation of three types of life cycle. The whole scheme is a sporic cycle; 1 zygotic cycle (Y!→R!); 2 gametic cycle (R!→Y!).

perspective, diplonts are "better" than haplonts. Frequent situation of gene dominance allows only one variant (allele) of the gene to work, that may save organism from lethal mutations. An increased number of genes could help to make more proteins. A third reason is that diplonts' genomes are more diverse. One gene may be able to withstand one group of conditions, and the other variant may have a different set of possible conditions. Therefore, diplont is able to take advantage of the capabilities of both genetic variants.

As a consequence, the evolution of life cycles goes from zygotic (similar to unicellular) to the sporic cycle (Fig. 4.12), and then to the more and more expressed domination of diplont, and finally to the complete reduction of haplont, gametic life cycle. It is still an open question how zygotic protists evolved to the sporic side. Most probably, zygote (which is diploid by definition) did not want to divide meiotically. Instead, it grows (which is seen in some protists) and divides mitotically, giving birth to the diplont. This is how first sporic cycle started. The last step of this evolutionary chain was a complete reduction of haplont: after meiosis, spores were replaced with gametes which immediately go to syngamy.

4.4.4 Life Cycle of Vegetabilia

Ancestors of Vegetabilia (plants$_2$) were green algae with zygotic life cycle. It could be imagined that their zygote started to grow because these organisms inhabited shallow waters and want their spores to be distributed with a wind. One way for this to happen is to have the spores on the stalk of the plant. This is probably the reason

Figure 4.12. The evolution of life cycles (green arrows represent five evolutionary transitions) from unicellular zygotic to multicellular gametic through different variants of sporic cycles.

of zygote growth: primordial diplonts of plants$_2$ were simply **sporangia**, structures bearing spores. Then the benefits of diploid condition described above started to appear, and these primitive plants went onto the road of haplont reduction. However, some Vegetabilia (liverworts, mosses and hornworts), still have haplont domination. This is probably because their haplonts are *poikilohydric* (it is explained in next chapters), adaptation which is beneficial for small plants.

Life cycle of plants$_2$ is sporic, but the science tradition uses plant-related names for the stages. The cycle (Fig. 4.13) begins with a diplont called a **sporophyte**, which produces spores. Sporophyte bears a **sporangium**, inside which **mother cell of spores** uses meiosis to make spores. The spores germinate and grow into haplont called **gametophyte**. Gametophyte produces gametes, specifically a spermatozoa (or simply "sperms") and an oocyte (egg cell). These gametes are developed in special organs—**gametangia**. Gametangium which contains male gametes (sperms) is called **antheridium**, and female gametangium is **archegonium**, the last normally contains only one egg cell (oocyte).

By syngamy (oogamy in this case), the two gametes form a zygote. Next, a *young sporophyte grows on the gametophyte*, and finally, the cycle starts again. Again, sporophyte of Vegetabilia starts its life as a parasite on gametophyte. Even flowering plants have this stage called **embryo**. Maybe, this is why the gametophyte of plants$_2$ has never been reduced completely to transform their cycle into gametic. Even in most advanced plant lineages, their male (which makes only sperms) and female gametophytes have minimum 3 and 4 cells, respectively, but not 0!

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Vegetative reproduction (fragments)

n Gamete mother cell

Male gametangium = antheridium

n

Spermatozoa

Sexual reproduction:

n

Gametes

Syngamy (oogamy type)

Y!

Female gametangium = archegonium

n

Oocyte (egg cell)

n

Zygote

2*n*

Haplont = Gametophyte

Spore

n

2*n*

Embryo (young sporophyte)

Vegetative reproduction (fragments)

2*n*

Spores

n

Meiosis

R!

Spore mother cell

2*n*

Sporangium

n

Asexual reproduction:

Diplont = Sporophyte

Figure 4.13. Life cycle of land plants. Red color is used for innovations, comparing with previous (general) life cycle scheme.

Chapter 5

Tissues and Organs; or how the Plant is built

5.1 Tissues

From now on, we will frequently use multiple names of plants$_2$ group, they are summarized on Figure 5.1, and in more details—on Fig.6.1.

plants$_2$ (Vegetabilia)			
mosses (Bryophyta)	seed plants (Spermatophyta)		
	"gymnosperms"	flowering plants, or angiosperms (Angiospermae)	
	conifers (Pinopsida)	"dicots" (Magnoliidae, Rosidae, Asteridae)	monocots (Liliidae)
ferns and allies (Pteridophyta)	other gymnosperms		
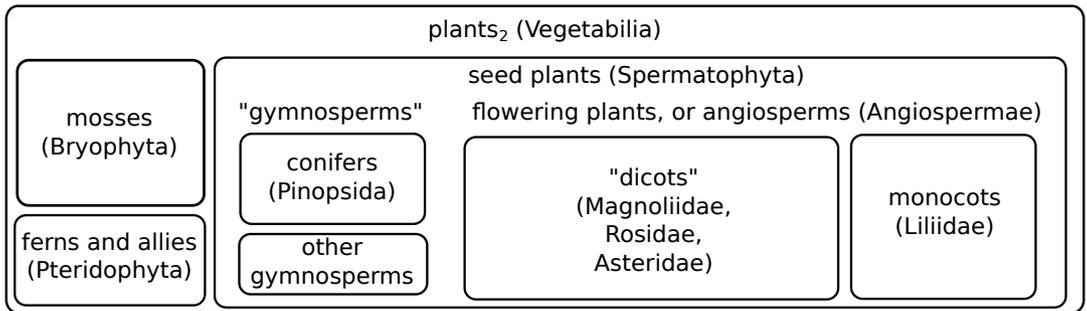
Figure 5.1. Plants$_2$ classification: overview.

5.1.1 Epidermis and Parenchyma

Why did plants go on land? In order to escape competition with other plants for resources like the sun and nutrients, but also to obtain much more sunlight that was otherwise seriously reduced underwater. The move to land also helped plants escape predators. Lastly, plants benefited from this change because they escaped

from the **temperature-gases conflict**: warmer temperatures are good for organisms but significantly decrease the amount of gases diluted in water.

Although this action solved several problems, it also raised new issues that needed to be dealt with. The most important was the risk of drying out. To combat this, plants developed their first **tissue**: **epidermis** covered with a **cuticle** which served a purpose similar to a plastic bag. For the really small (millimeters) plant it is enough because, in accordance to **surface / volume law**, they have high relative surface, and diffusion can serve for gas exchange.

However, bigger plants also need to exchange gases, and they developed **stomata** which served as a regulated pore system. The remaining cells became second tissue: **parenchyma** (or **ground tissue**, or **main tissue**).

Another response (Fig. 5.3) for drying was a development of *poikilohydricity* (see below), the ability to hibernate in (almost) dried condition. As hibernation is generally dangerous since it requires "system restart", that evolutionary route did not become the main.

Tissue is a union of cells which have common origin, function and similar morphology. Tissues belong to organs: **organ** is a union of different tissues which have common function(s) and origin. Plants have simple and complex tissues. The **simple tissues** are composed of the same type of cells; **complex tissues** are composed of more than one type of cell, these are unique to plants.

Parenchyma (Fig. 5.4) are spherical, elongated cells with a thin primary cell wall. It is a main component of young plant organs. The basic functions of parenchyma are *photosynthesis and storage*. Parenchyma cells are widespread in plant body. They fill the leaf, frequent in stem cortex and pith and is a component of complex vascular tissues (see below). Contrary to parenchyma (which is a simple tissue), **epidermis** is a complex tissue composed of epidermal and stomata cells. Its main functions are *transpiration, gas exchange and defense*.

As it seen here, plants acquired tissues in a way radically different from animals(Fig. 5.2) : while plants regulate gas and water exchange in response to terrestrial environment, animals actively hunt for food (using kinoblast tissues) and then digest it (with pagocytoblast tissue).

5.1.2 Supportive Tissues: Building Skyscrapers

When more and more plants began to move from the water to the land, competition once again became a problem (Fig. 5.3). To solve this, plants followed "Manhattan solution": they grew vertically in order to be able to escape competition for the sunlight and therefore must develop **supportive tissues**.
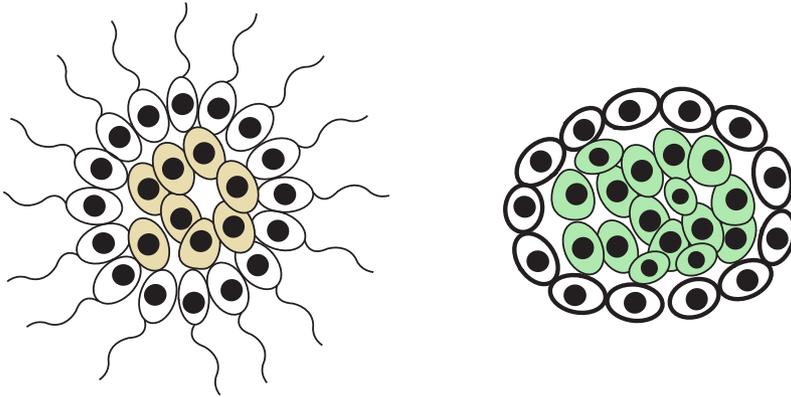
Figure 5.2. Phagocytella (proto-animal) with kinoblast and phagocytoblast *vs*. proto-plant with epidermis and ground tissue.

Collenchyma (Fig. 5.4) is living supportive tissue that has elongated cells and a thick primary cell wall. Its main function is the mechanical support of young stems and leaves via turgor.

Sclerenchyma (Fig. 5.4) is a dead supportive tissue that consists of long fibers or short, crystal-like cells. Each cell has a thick *secondary wall* that is rich in lignin. Its main function is a support of older plant organs, and also hardening different parts of plants (for example, make fruit inedible before ripeness so no one will take the fruit before seeds are ready to be distributed). Without sclerenchyma, if a plant isn't watered, the leaves will droop because the vacuoles will decrease in size which lowers the turgor. Fibers inside phloem (see below) are sometimes regarded as a separate sclerenchyma.

Three times in their evolution plants found the new application for lignin or similar polymers: at first, similar chemicals covered the spore wall which was an adaptation to the spore distribution with wind. Then similar chemicals were used to make cuticle, "epidermal plastic bag" to prevent transpiration outside of stomata. Finally, with acquiring of sclerenchyma, plants found how to use dead cells with completely lignified cell walls.

By the way, stomata likely had a similar fate, they historically appeared on sporangia to help them dry faster and release spores effectively. Regulation of transpiration is their second function.

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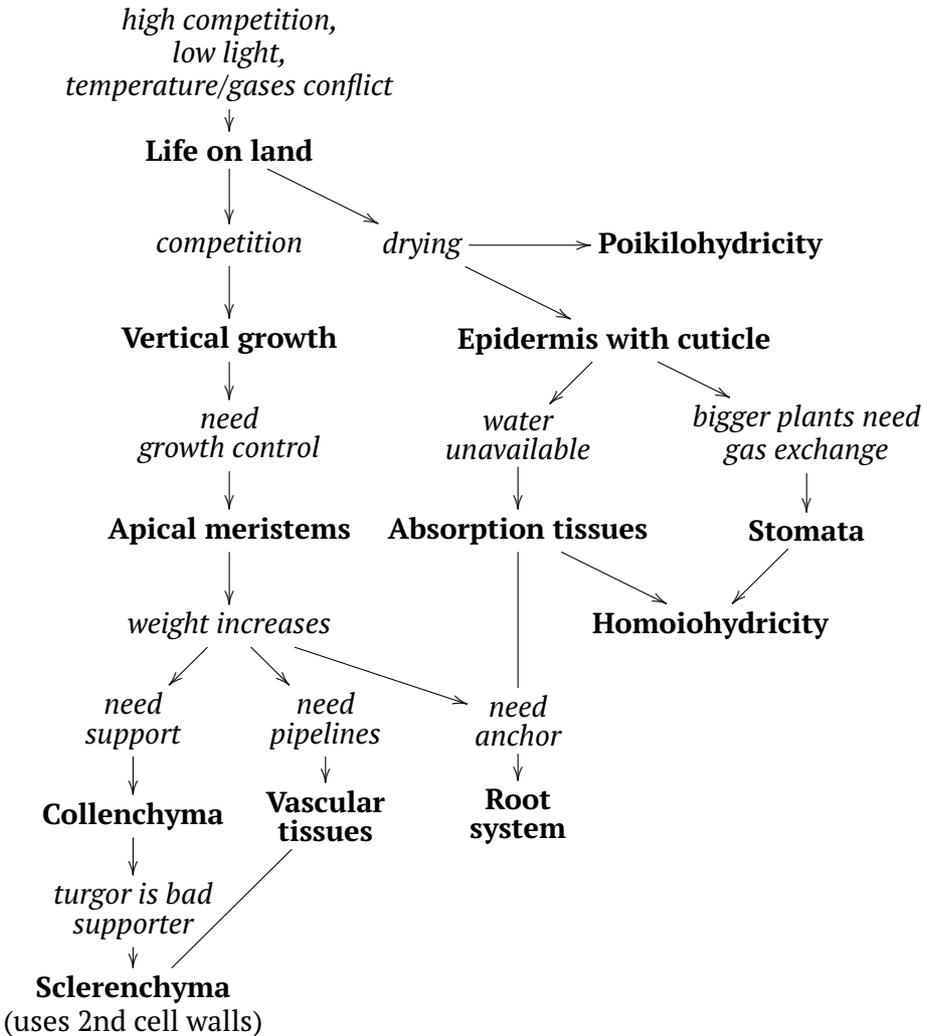
Figure 5.3. *Challenges* to land plants and their **responses**, part 1. Part 2 is on Fig. 7.14.
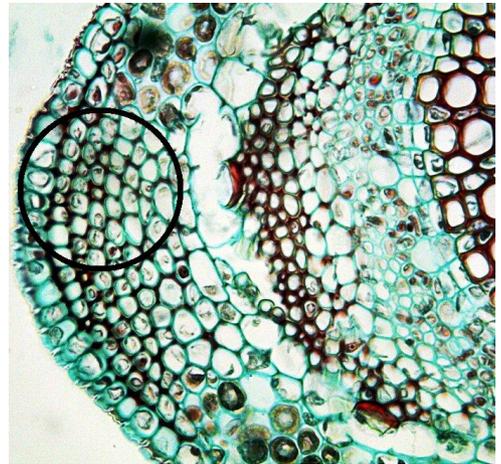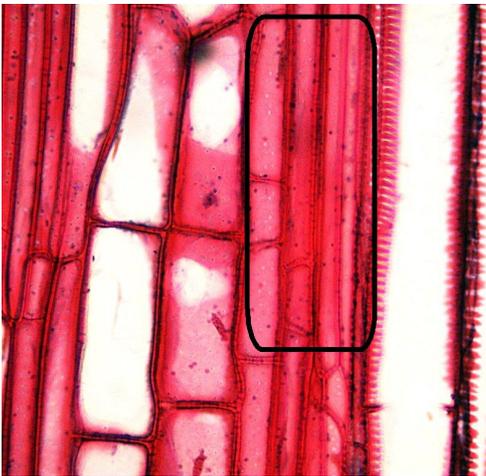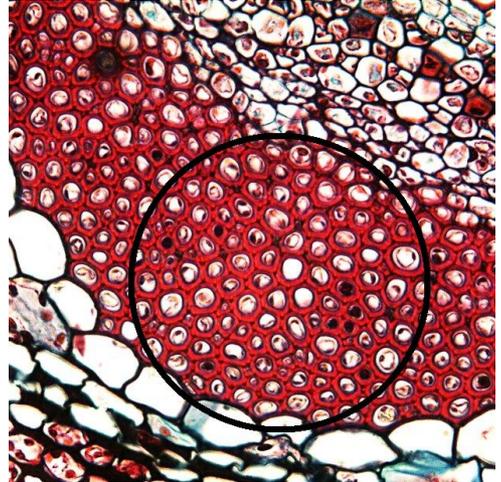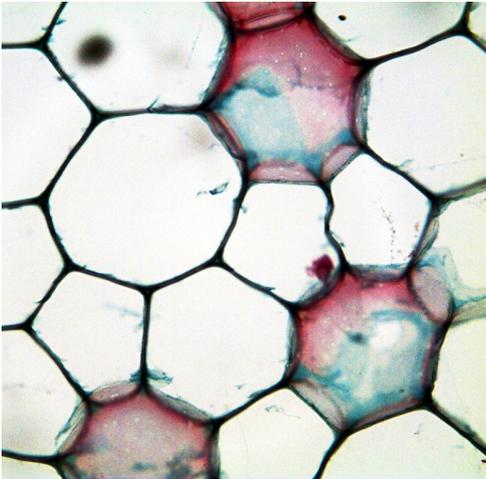
Figure 5.4. Left to right, top to bottom: parenchyma, sclerenchyma (cross- and longitudinal sections) and collenchyma. First three photos from the stem of *Helianthus*, fourth from *Medicago* stem. Magnification ×400.

Cell types and tissues

"Parenchyma" and "sclerenchyma" terms are freShoot systemquently used in two ways: first, to name tissues (or even classes of tissues) which occur in multiple places of the plant body, and second, to name the cell types which are components of tissues. Therefore, it is possible to say "parenchyma of stem", "parenchyma of stem pith", "parenchyma of xylem" and even "leaf mesophyll is a parenchyma".

5.1.3   Meristems: the Construction Sites

Plant growth requires centers of development which are **meristems**. **Apical meristems** are centers of plant development located on the very ends of roots (**RAM**) and stems (**SAM**). They produce intermediate meristems (like **procambium**) which form all **primary tissues**. The **lateral meristem** or **cambium** originates from the procambium which in turn originates from apical meristems. It usually arises between two vascular tissues and its main functions are thickening and producing **secondary vascular tissues** (Fig. 5.5).
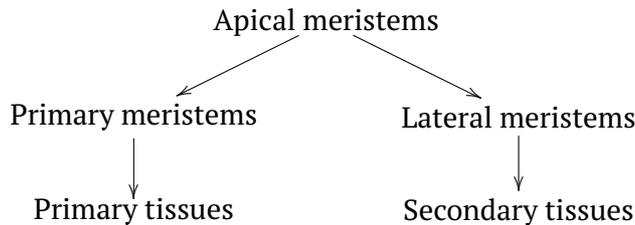
Figure 5.5. Meristems and tissues.

Other meristems include: **intercalary** which elongate stems from the "middle", **marginal** which are responsible for leaf development and **repair** meristems arising around wounds, they also control vegetative reproduction.

5.1.4   Vascular Tissues

Bigger plants escaped from competition and performed effective metabolism. However, with all the growth the plants went through, their size became too big for slow symplastic plasmodesmata connections. Another, filter paper-like apoplastic transport was also not powerful enough. The solution was to develop **vascular tissues**, xylem and phloem (Fig. 5.6, Fig. 5.29).

The main functions of xylem are the transportation of water and mechanical support. The **xylem** may be found either in a vascular bundle or a vascular cylinder. The three types of xylem cells are **tracheary elements** (these include **tracheids** and
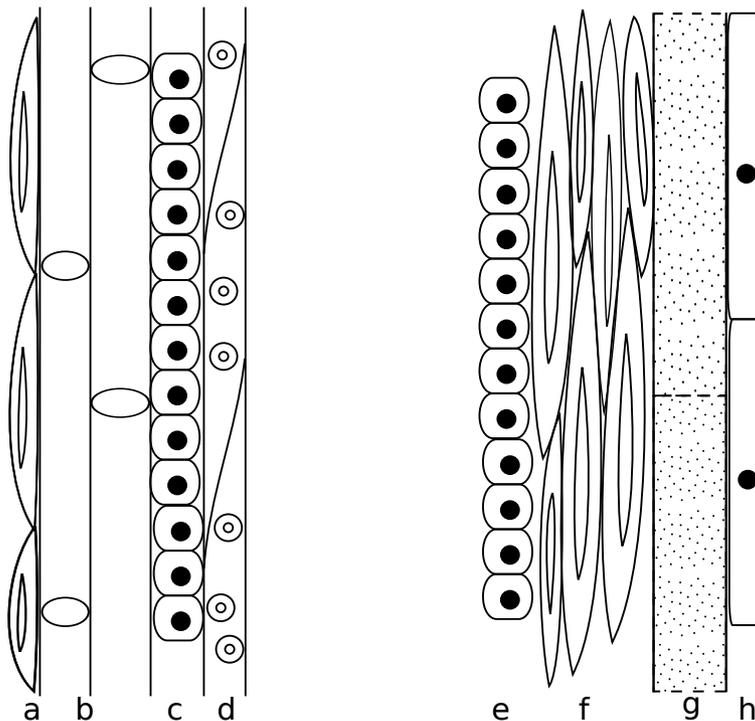
Figure 5.6. Cells of xylem (left, a–d) and phloem (right, e–h): a fibers, b vessels with open perforations, c parenchyma, d tracheids with pits, e parenchyma, f fibers, g sieve tubes, h companion cells.

vessel members), **fibers**, and **parenchyma**. Xylem elements, except for the parenchyma, are rich in lignin and are main components of wood. Tracheids are closed on both ends and connected with **pits** whereas vessel members are more or less open and connects via **perforations**. Tracheids, vessel members and fibers are dead cells. Xylem parenchyma, on the other hand, is alive.

Pits of tracheids consist of a pit membrane and the torus in a center, there are *no openings*. The presence of tracheids and/or vessel elements has evolutionary significance. Vessels (made of vessel members) are more effective; consequently, more "primitive" plants have more tracheids whereas more "advanced" have more vessel members. As an example, gymnosperms have only tracheids while most flowering plants have tracheids and vessel members. Individual development also mimics this evolutionary trend. Younger flowering plants have more tracheids whereas mature plants have more vessel members. Primary xylem mostly has tracheids and vessels with scalariform perforations whereas secondary xylem (which originates from cam-

bium) consists mostly of vessels with open perforations. The common name for secondary xylem is **wood**.

It is a mistake to think that tracheids are better than vessels. In fact, the main problem is frequently not too slow but too fast water transport. Tracheids have an advanced connection system (called torus) which has the ability to close pore if the water pressure is too high and therefore more controllable. Leaking would be less dangerous in tracheids. And in water-poor environments (like taiga in winter), plants with tracheids will have the advantage. Contrary, having vessels is like to have race car for ordinary life; only flowering plants "learned" how to use them effectively.

Dead cells are useful but hard to control. However, if xylem transport needs to be decreased, there is a way. Xylem parenchyma cells will make **tyloses** ("stoppers") which will grow into dead tracheary elements and stop water if needed. Many broadleaved trees use tyloses to lower xylem transport before the winter.

The **phloem** generally occurs adjacent, or right next to, the xylem, with the xylem facing the inner part of the plant and the phloem facing the outer part of the plant. The main functions of the phloem are the transportation of sugars and mechanical support. The four types of phloem cells are: **sieve tube cells**, **companion cells**, **fibers** (the only dead cells in phloem), and **parenchyma**. Sieve tube cells of flowering plants have cytoplasm flowing through perforations (sieve plates) between cells but do not contain nuclei. Companion cells will make proteins for them. However, in gymnosperms and more "primitive" plants there are no companion cells at all, so sieve tube cells do contain nuclei. This is comparable to red blood cells in vertebrates: while mammals have them anucleate, erythrocytes of other vertebrates contain nucleus. The secondary phloem generally has more fibers than the primary phloem.

This small table summarizes differences between xylem and phloem:

	Xylem	**Phloem**
Contains mostly	Dead cells	Living cells
Transports	Water	Sugar
Direction	Up	Down
Biomass	Big	Small

5.1.5 Periderm

Periderm is a secondary dermal tissue which arises inside the stem ground tissue, closer to the surface. Like the other dermal tissue (epidermis), it is a complex tissue. It includes three layers (starting from surface): **phellem** (**cork**), **phellogen** (**cork cambium**) and **phelloderm** (Fig. 5.7). Phellem consists of large dead cells with secondary walls saturated with suberin, and is the main, thickest component of periderm. Phellogen is a lateral meristem, like cambium; it often arises fragmentarily (and also temporarily) and does not cover the whole stem under-surface. But when phellem starts to grow, all peripheral tissues (like epidermis) will be separated from water transport and eventually die. Phellogen makes phellem towards the surface, and phelloderm towards the next layer (phloem). Phelloderm is a minute tissue, and does not play significant role in the periderm.
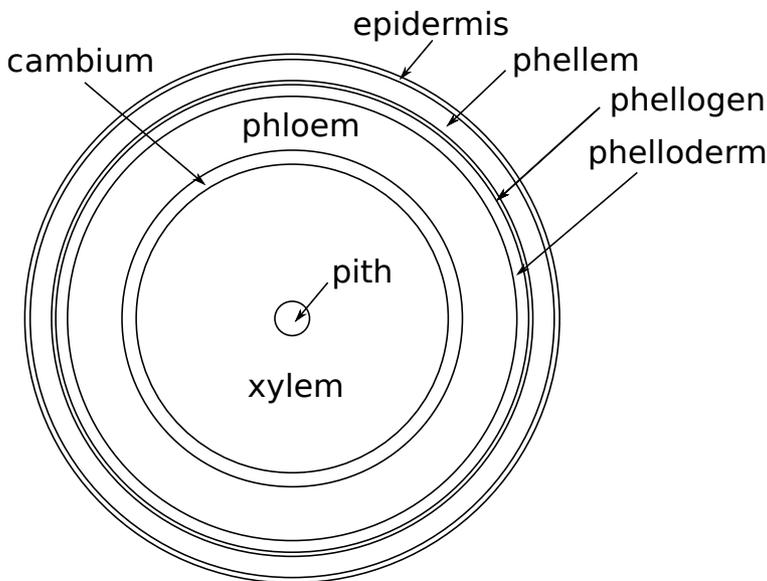
Figure 5.7. Principal location of stem tissues (simplified).

In older plants, phellogen arises deeper, sometimes inside phloem and separates outer layers of phloem from vascular cylinder. All this mixture of tissues (phellogen, phellem, phelloderm, epidermis and upper layers of phloem) considered as a **bark**.

5.1.6 Absorption Tissues

Poikilohydric plants do not save water and they can survive even complete desiccation because their cells will hibernate. An example of a poikilohydric plants would be mosses. **Homoiohydric** plants (which are majority of plants[2]), however, do save

water. They try to support the water content and do not survive complete desiccation. An example of a homoiohydric plant would be any "typical" plant, saying, corn. Somehow similar traits are comparable in poikilothermic animals, such as reptiles, and homoiothermic animals, such as birds and mammals, except in reference to body heat rather than water conservation.

Absorption tissues are always simple, primary tissues. Most important of them is **rhizodermis** (rhizoderm), or **root hairs**, which originates from protoderm (protoepidermis), but its lifespan is much shorter than of epidermis. There are other absorption tissues, for example, **velamen**, which originates from the root cortex and consists of large, empty, easy to get wet dead cells.

5.1.7   Other Tissues

Secretory tissues spread across the plant body, concentrating in leaves and young stems. These tissues may secrete latex, volatile oils, mucus and other chemicals. Its functions can be attraction or dis-attraction, communication or defense, and many others.

In addition to tissues, plant body may contain **idioblasts**, cells which are quite dissimilar from surrounding cells. Idioblasts used for accumulation of unusual (and possibly dangerous) compounds like **myrosinase**, protein splitting glucosinolates into sugars and toxic isothiocyanate (**mustard oil**). We use mustard oil as a spice but for the plant, it works like a binary chemical weapon against insect herbivores: when myrosinase-containing idioblasts are damaged, mustard oil kills damaging insects. Among plants, the whole order Brassicales from rosids is capable to produce myrosinase, examples are different cabbages (*Brassica* spp.), papaya (*Carica*), horseradish tree (*Moringa*) and many others.

5.2   Organs and Organ Systems

Vegetabilia (Fig. 6.1) have three different types of body construction (Fig. 5.8). The most primitive plants have thallus body, more advanced is the shoot (unipolar) plant body, and most land plants have the bipolar plant body. The **thallus** plant body is flat, similar to leaf but do not differentiated into particular organs. Most gametophytes (except true mosses) have this type, and also few sporophytes (which mostly are reduced water plants). **Shoot (unipolar) plant body** consists only of branching shoots, roots are absent. This is typical to all Bryophyta sporophytes, mosses (Bryopsida) gametophytes, and also to sporophytes of Psilotopsida (whisk ferns). Finally, **bipolar plant body** has both shoots and roots (Fig 5.11). Most bipolar plants have shoots consist of stems and leaves, but this is not an absolute requirement since young plant stems are normally green and can do photosynthesis.

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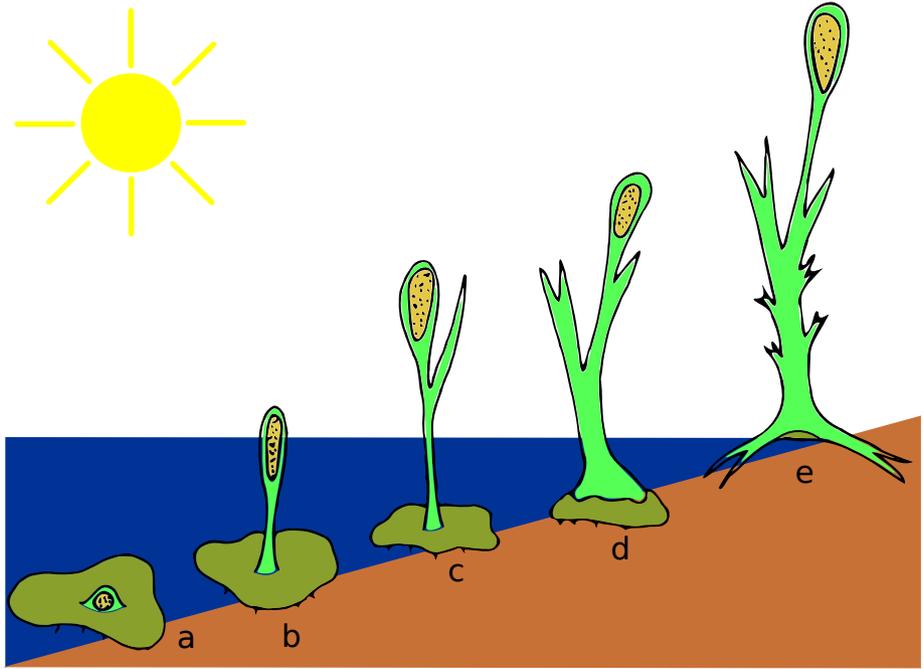
Figure 5.8. Evolution of plants$_2$ body types: a–e thallus gametophytes, a thallus sporophyte, b–d shoot sporophyte, e bipolar sporophyte.
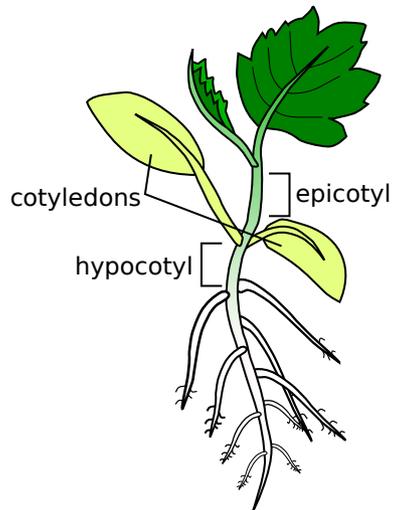
Figure 5.9. Young seedling with epicotyl and hypocotyl.

Typical organs of bipolar plant are stems (axial aerial organs with continuous growth), leaves (flat lateral organ with restricted growth), roots (axial soil organ modified for absorption) and **floral units (FU)** which are elements of the generative system (fructifications) such as a pine cone or any flower.

Buds, fruits, seeds and specific to seedlings hypocotyl and epicotyl are **non-organs** for different reasons: **buds** are just young shoos, **fruit** is the ripe flower, **hypocotyl** is a part of stem between first leaves of the seedling (cotyledons) and root (i.e., stem/root transition place), **epicotyl** is first internode of stem (Fig. 5.9), and finally, **seed** is a chimeric structure with three genotypes so it is impossible to call it "organ".

Root, stem, leaf and FU are *four basic plant organs* (Fig. 5.10) which in bipolar plant could be grouped in root and shoot system; the latter is frequently split into *generative shoot system* (bearing FU), and *vegetative shoot system* (without FU).
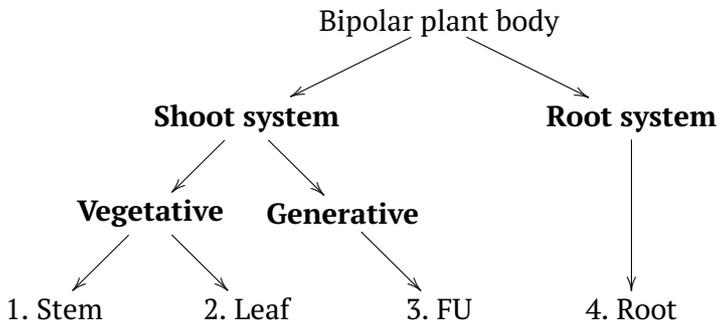
Figure 5.10. Bipolar plant: **organ systems** and four organs.

Vegetative shoot system usually consists of main and secondary shoots; shoots contain terminal buds, axillary (lateral) buds, stem (nodes and internodes) and leaves. We will start from leaves.

5.3   The Leaf

The first and ultimate goal of every plant is photosythesis. If a plant is multicellular, it usually develops relatively large, flat structures which goal is to catch sun rays. Terrestrial plants are no exception; most probably, they started to build their body with organs similar to present day leaves.

A **leaf** is *lateral photosynthetic organ of shoot with restricted growth*. Its functions are photosynthesis, respiration, transpiration, and synthesis of secondary chemicals. Features of a leaf (i.e., characters help to distinguish it) include having a bud in the

floral unit (FU)

terminal (apical) bud

stem

pedicel

node

internode

axial (lateral) bud

terminal bud on secondary shoot

secondary shoot

leaf blade

petiole

adventitious roots

hypocotyl

main root (taproot)

lateral roots

generative shoot system

vegetative shoot system

root system
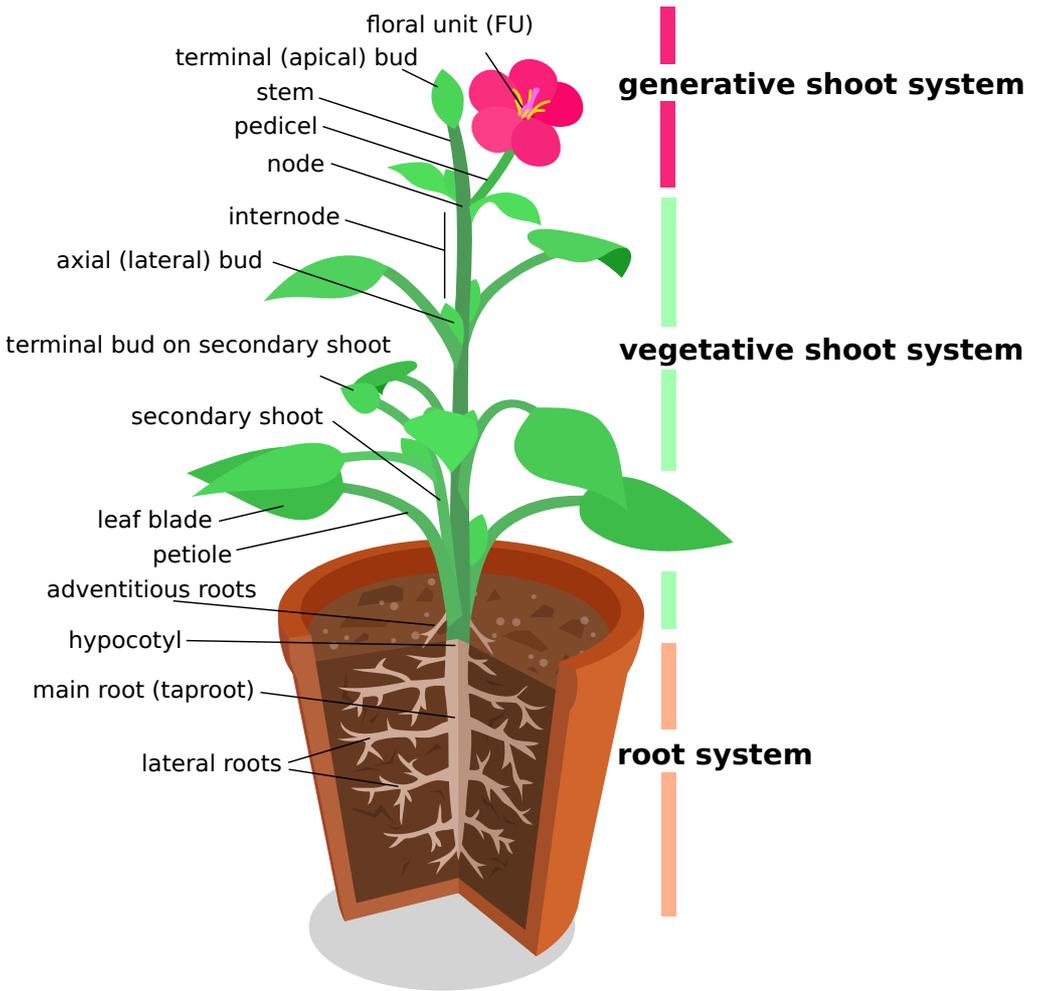
Figure 5.11. Systems of organs and organs of bipolar plant.
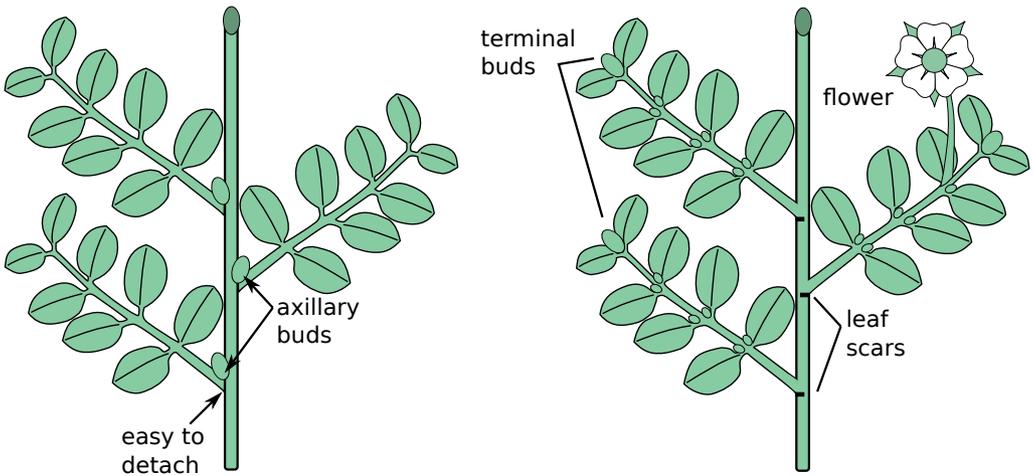
Figure 5.12. How to distinguish compound leaves (left) from branches (right).

axil, not growing by apex, not producing new leaves or shoots, and having *hierarchal morphology* (see below).

5.3.1 Morphology of the Leaf

Morphology means external, well visible structural features whereas **anatomy** needs tools like a microscope and/or scalpel. Leaves are very important in plant morphology. The ability to describe the leaf is a must even for novices in botany.

In all, *plants are fractal organisms*, like Sierpinski triange (Fig. 5.13). All fractals are self-similar (Fig. 5.14), and plants are no exception. Self-similarity, or "Russian doll effect" means that almost every part of plant may be a part of the bigger complex, this bigger one—the part of even bigger system, and so on. This is what we see in leaves as *levels of hierarchy*. **Simple leaves** have just one level of hierarchy whereas compound leaves have two or more levels of hierarchy. **Compound leaves** are sometimes mixed with branches but there are many other characteristics which allow to distinguish them (Fig. 5.12).

Figure 5.13. One of simple fractals: Sierpinski triangle.

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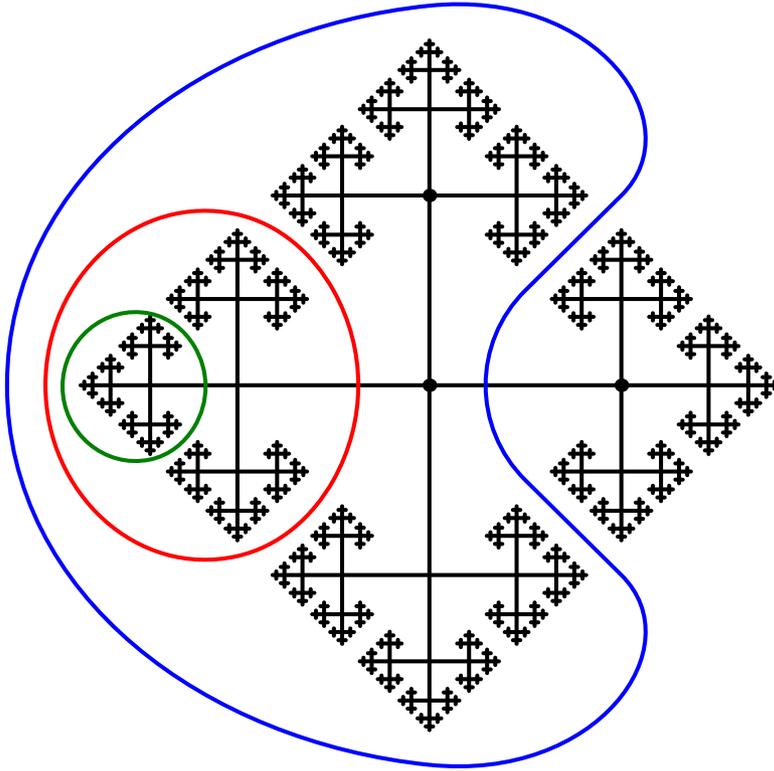
Figure 5.14. The example of self-similarity.

To describe leaves, one should always note the level of hierarchy like "on the first level of hierarchy, the shape is ..., on the second level of hierarchy, the shape is ..." As it was mentioned above, leaf hierarchy is similar to Russian dolls: every smaller doll has a bigger doll (next hierarchy level) outside. For example, if the leaf is compound (consists of multiple leaflets), the overall shape of it could be, saying, round (circular) but the shape of individual leaflet of the very same leaf could be ovate (Fig. 5.15). As a result, the description will say that on first level of hierarchy the leaf is ovate, and on the third level—circular.

There are three types of leaf characters: general, terminal, and repetitive. **General characters** are only applicable to the whole leaf. **Terminal characters** are only applicable to the terminal leaflets. Terminals are the end parts of leaves, they do not split in smaller terminals; clover leaf, for example, has 3 terminals. Lastly, repetitive characters repeat on each level of leaf hierarchy. General and terminal characters do not depend on hierarchy. **Repetitive characters** may be different on each step of hierarchy.

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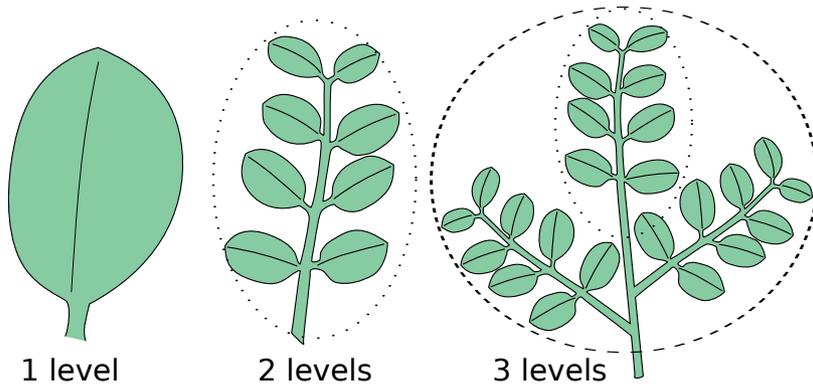
Figure 5.15. Leaves with one, two and three levels of hierarchy. Please note that the last leaf is ovate on the first and second level but circular on the third level of hierarchy.

General characters of leaf include **stipules** and other structures located near leaf base (Fig. 5.16): **sheath** (typical for grasses and other liliids) and **ocrea** (typical for buckwheat family, Polygonaceae).
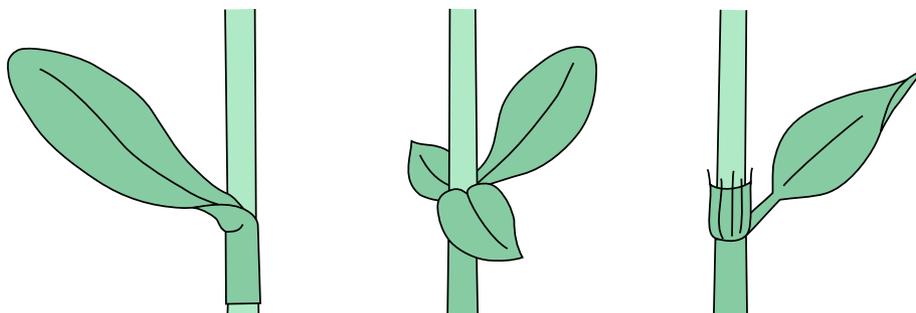
Figure 5.16. From left to right: sheath, stipules and ocrea.

Repetitive characters are the shape of the leaf (Fig. 5.17), leaf dissection, and whether the blade is stalked (has petiole) or not.

Terminal characters are applicable only to terminal leaflets of leaves. These characters (Fig. 5.19) are the shape of the leaf blade base, the leaf tip, the type of margin, the surface, and the venation. The base of the leaf blade could be **rounded**, **truncate** (straight), **cuneate**, and **cordate**. The leaf apex could be **rounded**, **mucronate**, **acute**, **obtuse**, and **acuminate**. Leaf margin variants are **entire** (smooth) and **toothed**: **dentate**, **serrate**, **double serrate** and **crenate**.

	Maximum width closer to leaf base	Maximum width in the middle	Maximum width closer to the apex
Length = width or slightly more	Deltate	Circular	Cuneate
Length > 1-1.5 x width	Ovate	Elliptic	Obovate
Length > 3-4 x width	Narrowly ovate	Lanceolate / Oblong	Narrowly obovate
Length > 5 x width		Linear	
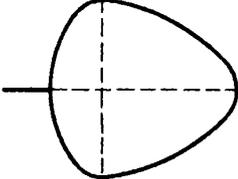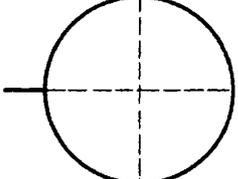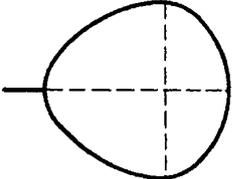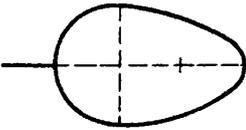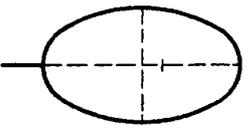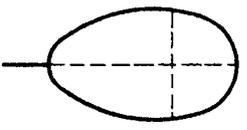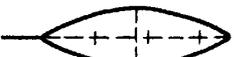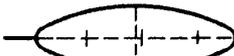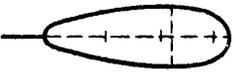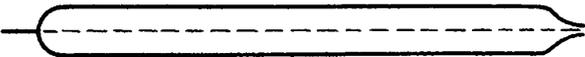
Figure 5.17. Leaf shapes.

		Two-, tri-	Palmately	Pinnately
Simple leaves	**Whole**			
	Lobed (from 1/4 to 3/4)			
	Dissected (from 3/4 to midrib)			

Compound leaves

(leaflets stalked, with joints)
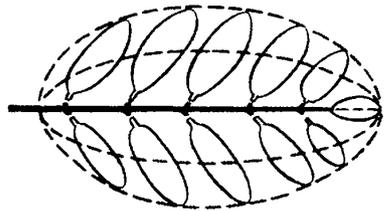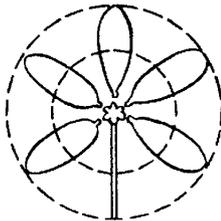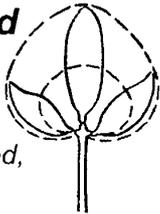
Figure 5.18. Leaf dissection.

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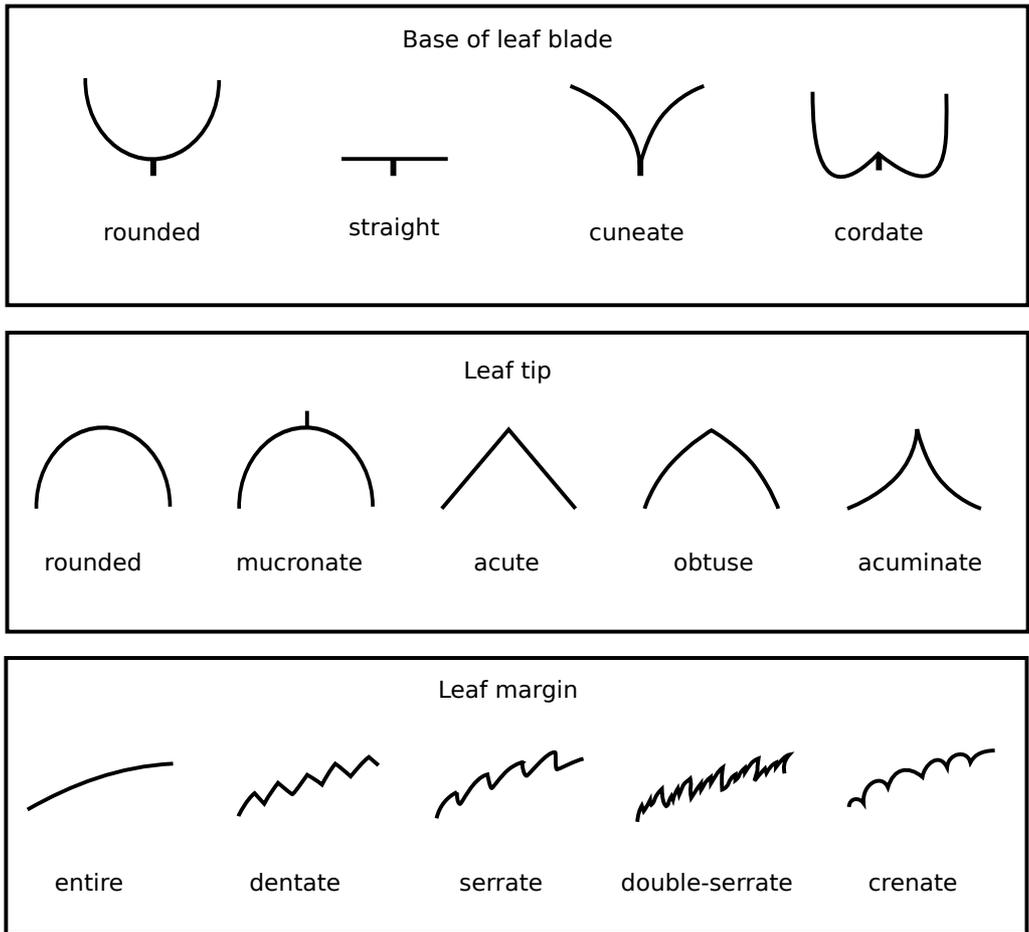
Figure 5.19. Terminal leaf characters.

Leaf veins are vascular bundles coming to the leaf from stem. Frequently, there is a **main vein** and **lateral veins** (veins of second order). There are multiple classifications of leaf venation; and example is shown on the Figure 5.20.

Note that in **dichotomous** venation, each vein divides into two similar parts which is known as dichotomous branching. The example of dichotomous venation is the leaf of maidenhair tree, ginkgo (*Ginkgo biloba*). Another frequently segregated type of venation is **parallellodromous**, but in essence, this is acrodromous venation in linear leaves (for example, leaves of grasses) where most of veins are almost parallel.

To characterize the whole leaf, one might use the following plan:

Main / Lateral	No	One	Several
No	Apodromous	Hyphodromous	Acrodromous
Several	Dichotomous	Pterodromous	Actinodromous
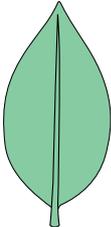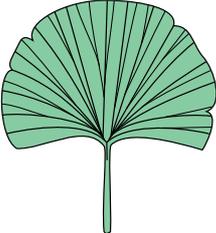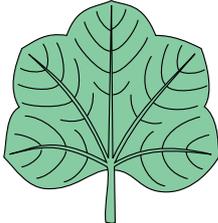
Figure 5.20. The simple classification of leaf venation.

1. General characters (leaf as a whole):
   (a) stipules (present / absent, deciduous / not, how many, size, shape);
   (b) base (sheath / no sheath, ocrea / no ocrea)
2. First level of hierarchy: repetitive characters:
   (a) symmetry (symmetrical / asymmetrical);
   (b) shape;
   (c) dissection;
   (d) petiole (presence and length)
3. Second level of hierarchy
4. Third level of hierarchy, and so on
5. Terminal characters (leaflets):
   (a) base of leaf blade (rounded, truncate, cuneate, cordate);

(b) apex (rounded, mucronate, acute, obtuse, acuminate);

(c) margin (whole, dentate, serrate, double serrate, crenate);

(d) surfaces (color, hairs etc.);

(e) venation (apo-, hypho-, acro-, ptero-, actinodromous)

* * *

Heterophylly refers to a plant having more than one kind of leaf. A plant can have both juvenile leaves and adult leaves, water leaves and air leaves, or sun leaves and shade leaves. A leaf mosaics refers to the distribution of leaves in a single plane perpendicular to light rays, this provides the least amount of shading for each leaf.

Leaves have seasonal lives; they arise from the SAM through **leaf primordia**, and grow via marginal meristems. The old leaves separate from the plant with an **abscission zone**.

* * *

The famous poet and writer Johann Wolfgang Goethe is also considered a founder of plant morphology. He is invented an idea of a "primordial plant" which he called "Urpflanze" where all organs were **modifications** of several primordial ones. In accordance to Goethe's ideas, plant morphology considers that many visible plant parts are just modifications of basic plant organs.

Modifications of the leaf include **spines** or **scales** for defense, **tendrils** for support, **traps**, "sticky tapes", or **urns** for interactions (in that case, catching insects), **plantlets** for expansion, and **succulent** leaves for storage. Plantlets are little mini plants that grow on the main plant and then fall off and grow into new plants; the most known example is *Kalanchoë* ("mother of thousands") which frequently uses plantlets to reproduce. Plants that have insect traps of various kinds are called carnivorous plants (in fact, they are still photoautotrophs and use insect bodied only as fertilizer). Several types of these are the cobra lily (*Darlingtonia*), various pitcher plants (*Nepenthes*, *Cephalotus*, *Sarracenia*), the butterwort (*Utricularia*), the sundew (*Drosera*), and the best known, the Venus flytrap (*Dionaea*).

5.3.2   Anatomy of the Leaf

Anatomically, leaves consist of epidermis with stomata, **mesophyll** (kind of parenchyma) and vascular bundles, or veins (Fig. 5.22). The mesophyll, in turn, has palisade and spongy variants. Palisade mesophyll is located in the upper layer and

serves to decrease the intensity of sunlight for the spongy mesophyll, and also catches slanted sun rays. The **palisade mesophyll** consists of long, thin, tightly arranged cells with chloroplasts mostly along the sides. The **spongy mesophyll** cells are roughly packed, they are rounded and have multiple chloroplasts (Fig. 5.21).
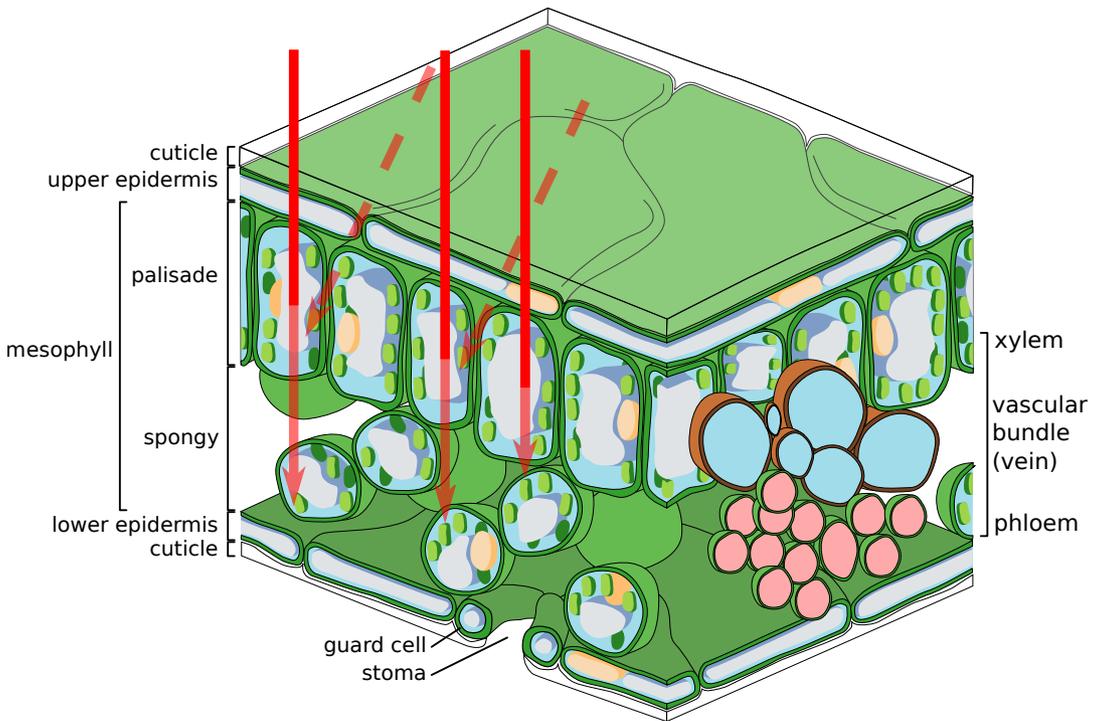

Figure 5.21. Leaf anatomy.

When a typical stem vascular bundle (which has xylem under phloem) enters the leaf, xylem usually faces upwards, whereas phloem faces downwards. Bundles of C_4-plants have additional bundle sheath cells in their vascular bundles.

The epidermis includes typical epidermal cells, stomata surrounded with guard cells (also optionally with subsidiary cells), and trichomes. Almost all epidermal cells are covered with waterproof cuticle, rich of lignin and waxes.

The stomata assists in gas exchange, cooling and water transpiration. There are two guard cells paired together on each side of the stoma. These guard cells are kidney beans shaped and have a thicker cell wall in the middle. The thicker cell wall on the inside makes use of the so-called "bacon effect" (when bacon slice curved on the frying pan) because thinner part of the cell wall is more flexible and therefore bends easier. The same curving effect might be seen in blowing air balloon with the piece
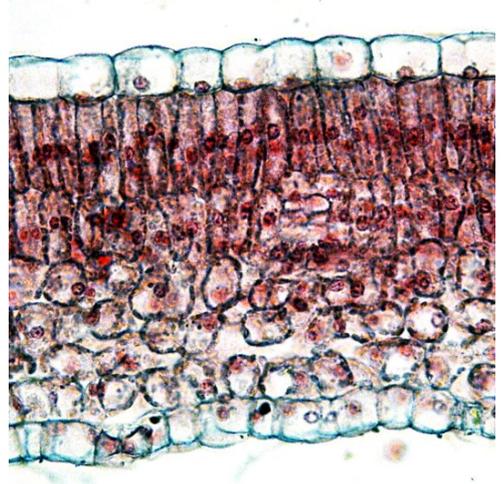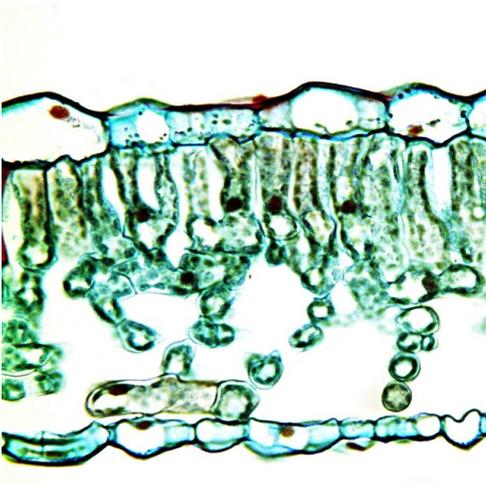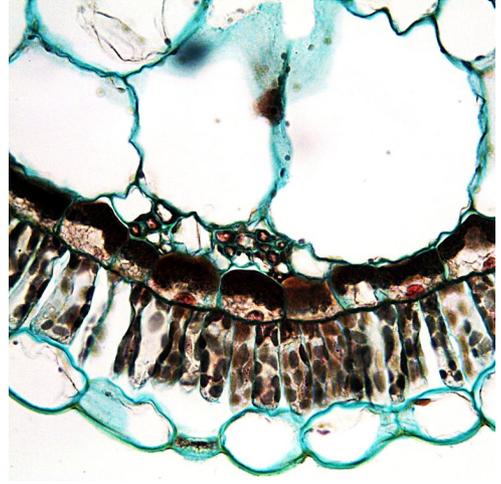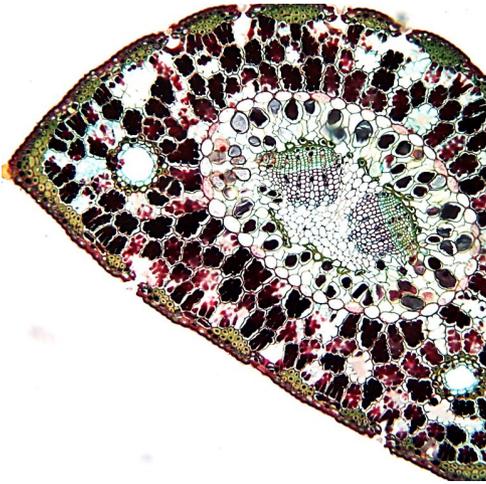
Figure 5.22. Left to right, top to bottom: leaf of sclerophyte *Pinus*, leaf of salt-avoiding (succulent-like) halophyte *Salsola* (epidermis is at the bottom), shade leaf of *Sambucus*, leaf of *Syringa* with guards cells (bottom left). Magnifications ×100 (first) and ×400 (others).

of scotch on one side. The opening of the stoma starts from K^+ accumulation, then osmosis inflates guard cells, and finally the uneven cell wall facilitates the opening of stoma. The stoma closes when the potassium ions exit the cell and water amount decreases in its vacuoles (Fig 5.23).
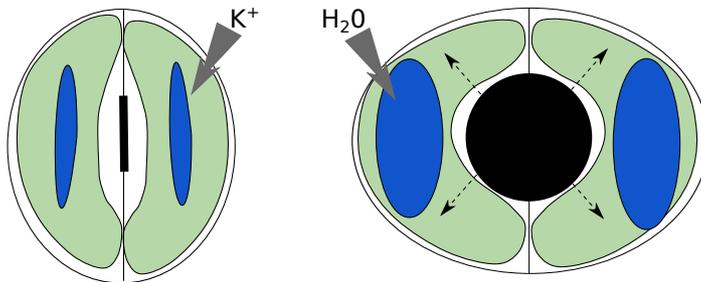
Figure 5.23. Closed and opened stoma. Cell walls are white, cytoplasm green, vacuoles blue.

In most cases, the lower epidermis contains more stomata than the upper epidermis because the bottom of the leaf is cooler and transpiration there is safer. A similar logic is applicable to trichomes (hairs): they are also more frequent on the lower side of the leaf.

5.3.3   Ecological Forms of Plants

When plants adapt to the particular environment conditions, leaves usually respond first. Conversely, one can estimate the ecology of plant simply looking on its leaves.

In regards to water, there are four main types of plants: xerophytes, mesophytes, hygrophytes, and hydrophytes. **Xerophytes** are adapted to the scarce water (Fig. 5.22), they could be **sclerophytes** (usually with prickly and/or rich of sclerenchyma leaves) and **succulents** (with water-accumulating stems or leaves). **Mesophytes** are typical plants which adapt to regular water. **Hygrophytes** live in constantly wet environment, their leaves adapted to high transpiration and sometimes even to guttation (excretion of water drops). **Hydrophytes** grow in water, their leaves are frequently highly dissected to access more gases dissolved in water, and their leaf petioles and stems have air canals to supply underwater organs with gases.

In regards to light, plants could be sciophytes or heliophytes. **Sciophytes** prefer the shade to sunlight, their leaves contain mostly spongy mesophyll. **Heliophytes** prefer the full sun and therefore have leaves filled with palisade mesophyll. The intermediate group are "partial shade" plants.

Halophytes, nitrate halophytes, oxylophytes, and calciphytes are ecological groups adapted to the over-presence of particular chemicals. **Halophyte** plants are fre-

quent, they accumulate (and look similarly to succulents), excrete or avoid (which looks like sclerophyte) sodium chloride (NaCl). They grow in salty places: sea shores, salt deserts and solonets prairies. **Nitrate halophyte** plants grow on soils rich in $NaNO_3$. **Oxylophytes** grow in acidic soils, whereas **calciphytes** grow in basic, chalk soils rich in $CaCO_3$.

Leaves will also reflect adaptations to the substrate, ecological forms named **psammophytes** (grow on sand), **petrophytes** (grow on rocks), and **rheophytes** (grow in fast springs). The latter plants frequently have serious simplifications in their body plan, their leaves and stems are often reduced to form a thallus-like body.

Parasitic plants could be classified in mycoparasites, hemiparasites, and phytoparasites. **Mycoparasitic** plants feed on soil fungi, **phytoparasitic** plants are either plant root parasites or plant stem parasites lacking chlorophyll and photosynthesis. **Hemiparasitic** plants are those which still have chloroplasts but take the significant part of water and even organic compounds from the host plant (like mistletoe, *Viscum*).

5.4 The Stem

The **stem** is an *axial organ of shoot*. It has functions of support, transportation, photosynthesis, and storage. Stem has radial structure, no root hairs and grows continuously.

5.4.1 Morphology of the Stem

Stem morphology is simple. Its components are **nodes** (places where leaves are/were attached) and **internodes**, long or short (in the last case, plant sometimes appears to be stemless, rosette-like).

Stems are different by the type of phyllotaxis. The **phyllotaxis** refers to the arrangement of leaves. If there is one leaf per node, it is a **spiral** (**alternate**) arrangement. Two leaves per node means **opposite** arrangement. Opposite leaves can be all in the same plane or each pair can rotate at $90°$. If there are more than two leaves per node, it is a **whorled** arrangement, and each whorl can also rotate.

Each type of spiral phyllotaxis has its own angle of divergence. Multiple types of spiral leaf arrangement mostly follow the **Fibonacci sequence**:

$$\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \cdots$$
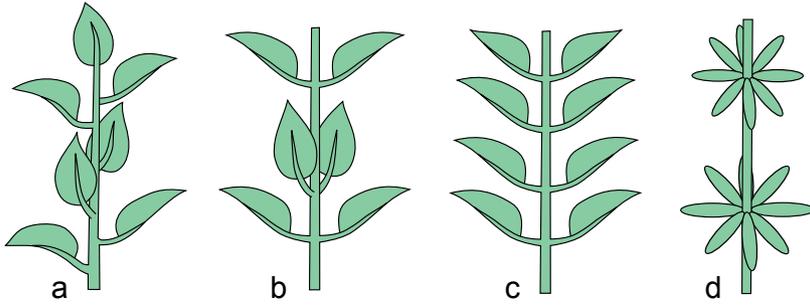
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Figure 5.24. Types of phyllotaxis (leaf arrangement): a spiral (alternate), b and c opposite, d whorled.

This sequence of numbers made with simple rule: in the every following fraction, the numerator and denominator are sums of two previous numerators and denominators, respectively. The sequence looks fairly theoretical but amazingly, it is fully applicable to plant science, namely to different types of spiral phyllotaxis (Fig. 5.25).
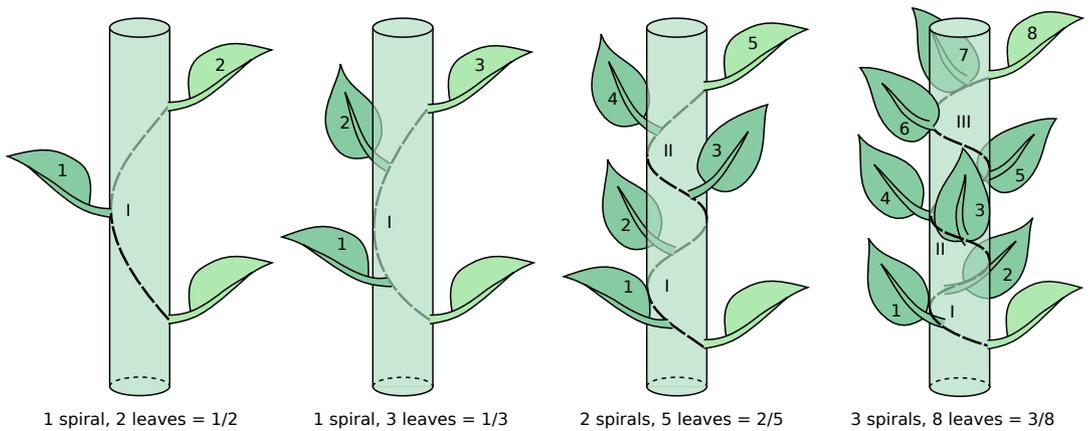

| 1 spiral, 2 leaves = 1/2 | 1 spiral, 3 leaves = 1/3 | 2 spirals, 5 leaves = 2/5 | 3 spirals, 8 leaves = 3/8 |

Figure 5.25. Four first Fibonacci types of spiral phyllotaxis: $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, and $\frac{3}{8}$.

To determine formula of spiral phyllotaxis, one needs to start with arbitrary leaf (or leaf scar) and then find the next (upper) one which is *directed the same way*, lays on the same virtual line. Then, the imaginary spiral should be drawn trough basements from the started leaf to the corresponding upper leaf.

This spiral should go through all intermediary leaves, there might be one, two or more intermediary leaves. Also, the spiral will go at least one time around the stem. (Instead of the imaginary spiral, it is sensible to use a thin thread). One needs to count all leaves in the spiral except the first, and also count number of rotations.

The number of leaves counted will be the denominator of the formula, and the number of rotations is the numerator. This is how Fibonacci numbers appear in plant morphology.

These phyllotaxis formulas are relatively stable and sometimes even taxon-specific. For example, grasses (Gramineae) have ½ phyllotaxis, sedges (*Carex*) ⅓, many Rosaceae (like apple, *Malus* or cherry, *Prunus*) have ⅖, willows frequently have ⅜, *et cetera*.

It is still not absolutely clear why the spiral phyllotaxis is under such a theoretical mathematical rule. The most feasible hypothesis emphasizes mathematical problem of circle packing and the competition between leaf primordia around SAM.

5.4.2 Anatomy of the Primary Stem

Plant evolution resulted first in the **primary stems** with no lateral meristems and secondary tissues. Only long after plants "learned" how to thicken their stems.
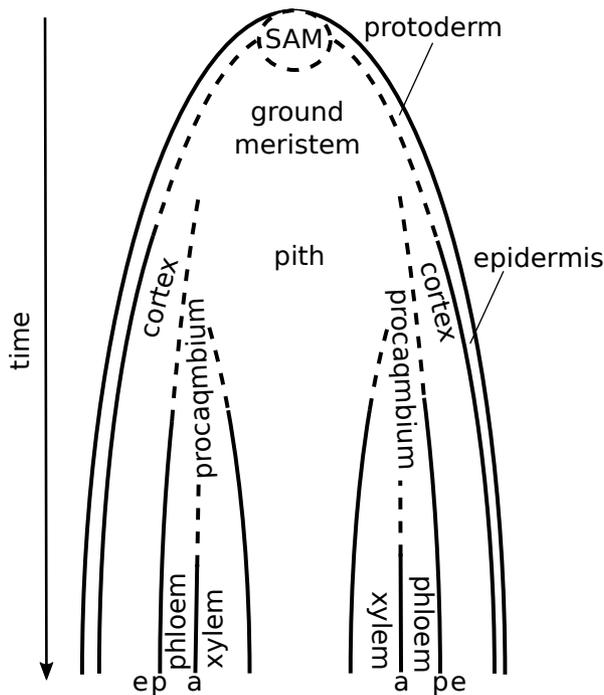
Figure 5.26. Developmental origin of stem tissues (simplified). Letters e, p, a show respectively where **e**ndoderm, **p**ericycle and v**a**scular **c**ambium might appear.

Development of stem starts from stem apical meristem (SAM) on the top of plant. The SAM produces three **primary meristems**: procambium, protoderm, and ground meristem. **Protoderm** cells differentiate into epidermal cells. The **ground meristem** differentiates into the **cortex** and **pith**. The **procambium** raises between the cortex and the pith. It forms **vascular bundles** or **vascular cylinder** (Fig. 5.26).
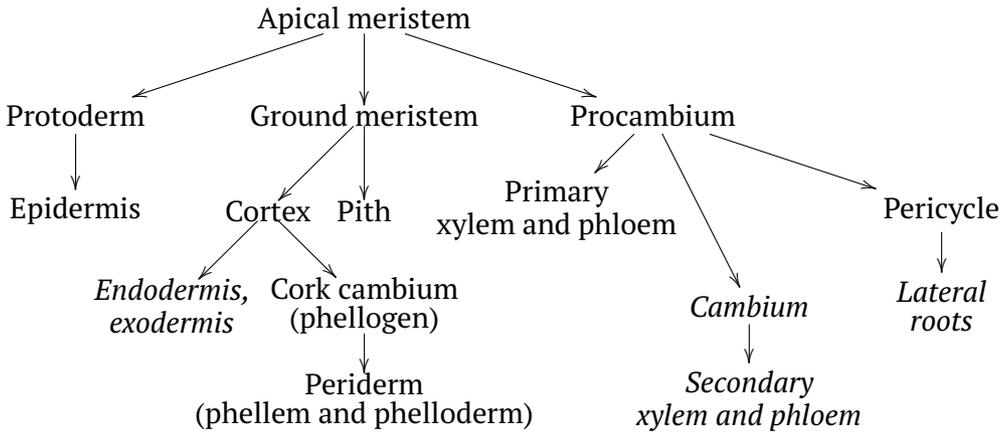
Figure 5.27. Developmental origin of stem tissues (detailed). Root tissues have similar ways of development.

The outer layers of the procambium form the *primary phloem*. The inner layers become the *primary xylem*. The middle layer can be entirely spent or will make cambium for the secondary thickening. At times, the layers of the outside of the procambium can form a **pericycle**. Sometimes the innermost layer of the cortex can form an **endodermis** (endoderm) (Fig. 5.28), and outermost layer makes the **exodermis** (exoderm). All these layers are some kind of the "border control" between functionally different layers of stem. Another frequent variant is the development of collenchyma in the cortex adjacent to epidermis.

Vascular bundles connect leaves and stems. In many plants, they form a ring on the cross-section of the stem. Parenchyma (ground tissue) between vascular bundles typically belongs to both cortex and pith. Another variant is a *vascular cylinder*, structure which fully encircles the stem. Liliid (monocot) stems generally have dispersed vascular bundles. These three variants are **steles**, overall configurations of the primary vascular system of the plant stem (Fig. 5.29). The most frequent kinds of steles are **eustele** (vascular bundles in a ring), **solenostele** (vascular cylinder) and **ataktostele** (dispersed vascular bundles).

All these types were probably originated from **protostele**, configuration where central xylem is surrounded with phloem and no pith is present (Fig. 5.30). While the
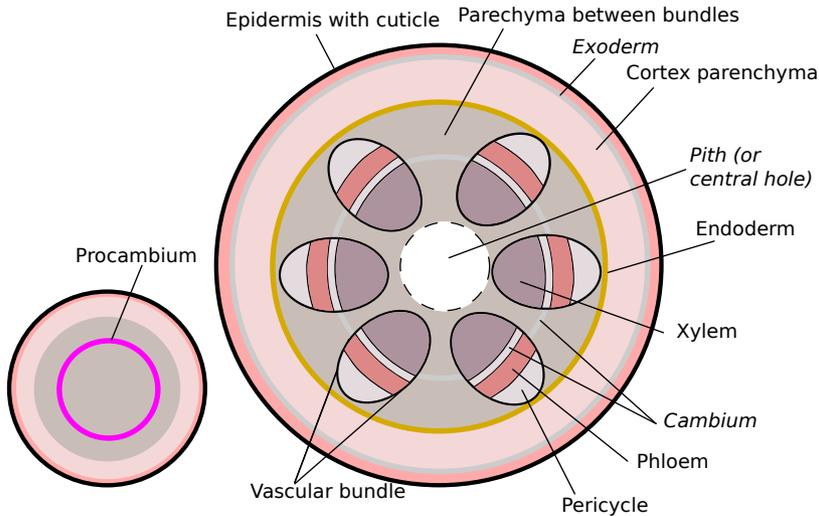
Figure 5.28. Anatomy of the primary stem (right). *Slanted font* is used for "optional" tissues. Small image on the left is the young stem consisted of epidermis, cortex, procambium and pith.

protostele was typical for many prehistoric plants, now only some lycophytes (*Huperzia*) have protostele in stems. Saying that, it is important to note that roots of most plants have vascular tissues arranged similarly to protostele.

5.5   The Root

Root is a latest evolutionary innovation in the vegetative plant anatomy. Many "primitive" plants (all mosses and even some ferns like *Psilotum*) do not have roots; some flowering water plants like the¿ rootless duckweed (*Wolffia*) or the coontail (*Ceratophyllum*) have also reduced their roots. However, large homoiohydric plants need the constant supply of water and minerals, and this evolutionary challenge was responded with appearance of the root system.

Root in *an axial organ of plant with geotropic growth*. One of root functions is to supply anchorage of the plant body in soil or on various surfaces. Other functions include water and mineral absorption and transport, food storage, and communication with other plants.
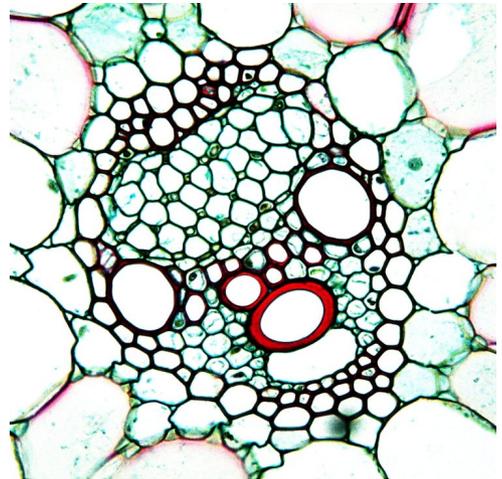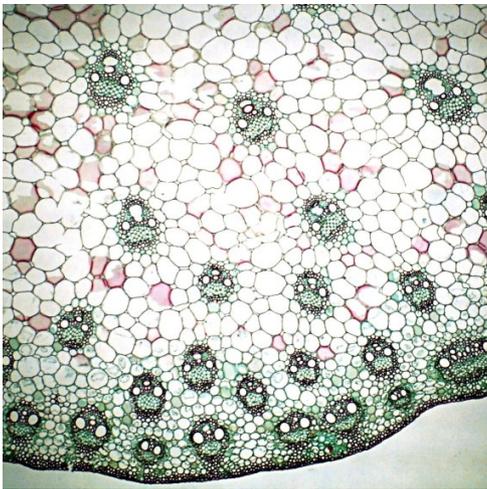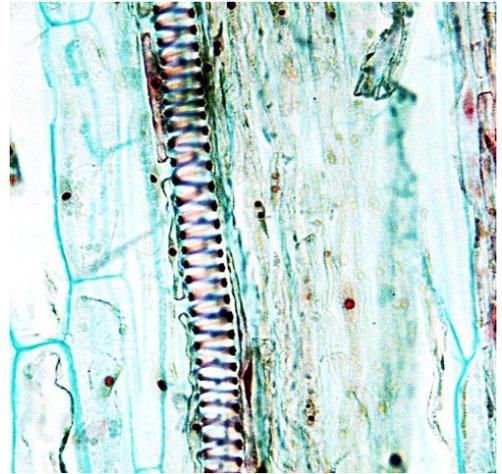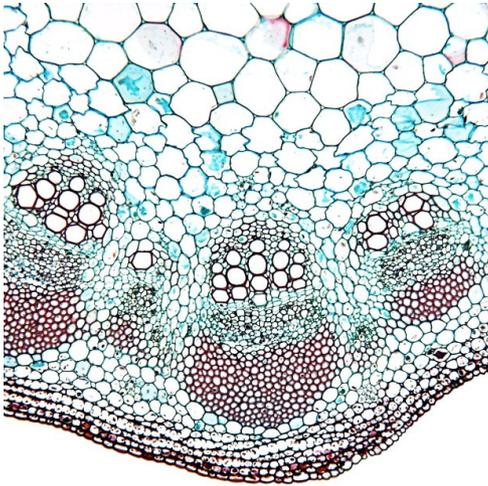
Figure 5.29. Left to right, top to bottom: eustele (stem segment), xylem vessel (longitudinal section) and ataktostele (stem segment and vascular bundle). First photo is from the stem of *Helianthus*, second from *Trifolium*, last two from the stem of *Zea*. Magnifications ×100 (first and third) and ×400 (second and fourth).
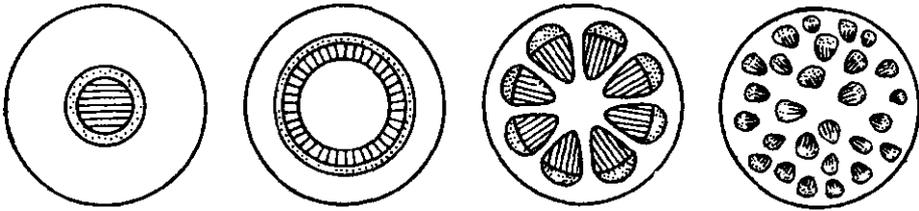
Figure 5.30. Steles (left to right): protostele, solenostele, eustele, ataktostele. Xylem is lined, phloem is dotted.

5.5.1 Morphology of the Root

There are two types of root systems. The first is a **fibrous root system** which has multiple big roots that branch and form a dense mass which does not have a visible primary root ("grass-like"). The other is the **tap root system** which has one main root that has branching into lateral roots ("carrot-like").

Along with having different systems, there are different types of roots: **primary root** originated from the root of the seedling, **secondary (lateral) roots** originate from the primary roots, and **adventitious roots** originate on stems (sometimes also on leaves), the example are prop roots of screw pine (*Pandanus*).

* * *

Roots employ many different modifications which help to protect, interact and storage. For example, roots of parasitic plants are modified into **haustoria** which sink themselves into the vascular tissue of a host plant and live off of the host plant's water and nutrients.

Roots of mangroves (plants growing in ocean coastal swamps) are frequently modified into *supportive aerial roots* ("legs"). Since these swamp plants need oxygen to allow cell respiration in underground parts, there are **pneumatophores**, specialized roots which grow upward (!) and passively catch the air via multiple pores. Plants which grow on sand (psammophytes, see above) have another problem: their substrate constantly disappears. To avoid this, plants developed **contractile roots** which may shorten and pull plant body deeper into the sand.

Some orchid roots are green and photosynthetic (Fig. 5.31)! However, as a rule, root is the heterotrophic organ, because root cells have no access to the light.

Root nodules present on the roots of nitrogen-fixing plants, they contain bacteria capable to deoxidize athmospheric nitrogen into ammonia: $N_2 \rightarrow NH_3$. Root nodules contain also hemoglobin-like proteins which facilitate nitrogen fixation by keep-

Figure 5.31. Photosynthetic roots of leafless orchid *Chiloschista segawai*.

ing oxygen concentration low. Nitrogen-fixing plants are especially frequent among *faboid rosids*: legumes (Leguminosae family) and many other genera (like alder, *Alnus*, or *Shepherdia*, buffaloberry) have root nodules with bacteria. Some other plants (mosquito fern, *Azolla* and dinosaur plant, *Gunnera*) employ cyanobacteria for the same purpose.

Mycorrhiza is a root modification started when fungus penetrates root and makes it more efficient in mineral and water absorption: it will exchange these for organic compounds. In addition to mycorrhizal fungi, **endophytic fungi** inhabit other plant organs and tissues.

5.5.2   Anatomy of the Root

On the *longitudinal section* of young growing root, there are different horizontal layers, zones: root cap covering *division zone*, *elongation zone*, *absorption zone*, and *maturation zone* (Fig. 5.32). The **root cap** protects the root apical meristem (RAM), which is a group of small regularly shaped cells. A small, centrally located part of the RAM is the **quiescent center** where initial cells divide and produce all other cells of root. Root cap is responsible for the geotropic growth, if the root tip comes into contact with a barrier, root cap will feel it and will grow on a different direction to go around it.

The **elongation zone** is where the cells start to elongate, giving it length. The **absorption zone** is where the rhizodermis tissue (root hairs) develops and where water and nutrients are absorbed and brought into the plant. Within the **maturation zone**,
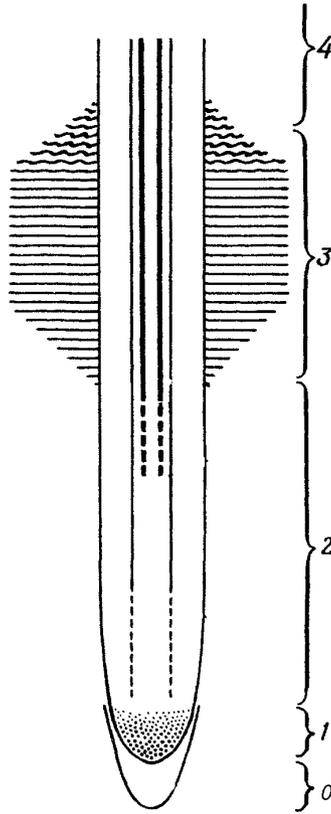
Figure 5.32. Root zones: 0 root cap, 1 division zone, 2 elongation zone, 3 absorption zone, 4 maturation zone.

root hairs degrade, many cells start to acquire secondary walls and lateral roots develop (Fig. 5.32).

On the *cross-section* of the root made within absorption zone, the first tissue is the rhizodermis, which is also known as the root epidermis, then cortex, which segregates external *exodermis* and internal *endodermis* one-cellular layers, and vascular cylinder (Fig. 5.33). Typically, roots have no pith. In some cases (for example, in orchids), cortex may give multi-layered *velamen* (see above), another absorption tissue.

Vascular cylinder is located in the center of the root, it contains the pericycle which is made of mostly parenchyma and bordering endodermis. Pericycle cells may be used for storage, they contribute to the vascular cambium, and initiate the development of lateral roots. Consequently, lateral roots are developing endogenously and break
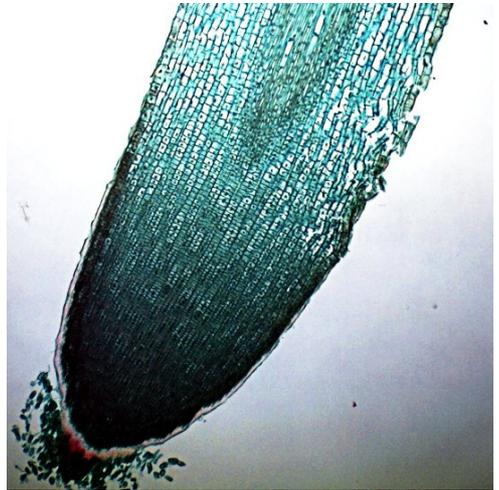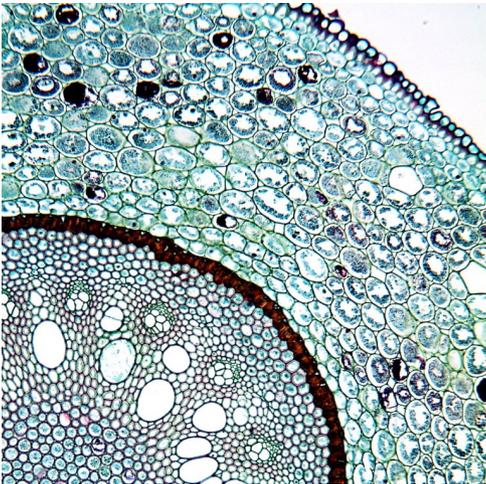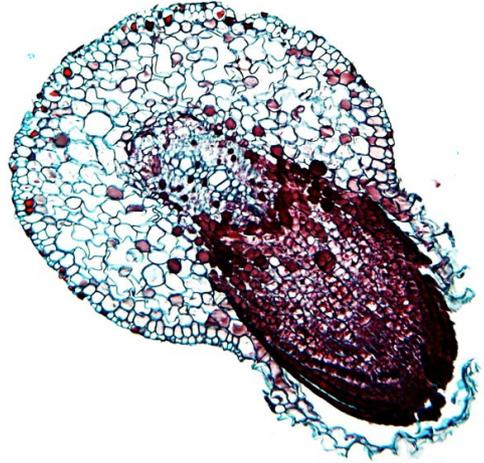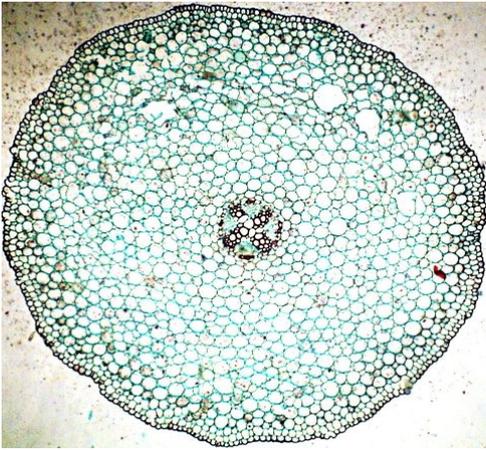
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Figure 5.33. Left to right, top to bottom: *Ranunculus* root with 4-rayed xylem, *Salix* root with the lateral root developing, *Smilax* root with visible Casparian stripes in the endodermis; *Zea* root longitudinal section with root cap, division and elongation zones. Magnifications ×100 (second) and ×40 (others).