SEMESTER-II
UNIT-II

Flowering plant

Flowering plants are plants that bear flowers and fruits, and form the clade **Angiospermae** (/ˌændʒiəˈspərmiː/),[5][6] commonly called **angiosperms**. They include all forbs (flowering plants without a woody stem), grasses and grass-like plants, a vast majority of broad-leaved trees, shrubs and vines, and most aquatic plants. The term "angiosperm" is derived from the Greek words ἀγγεῖον / *angeion* ('container, vessel') and σπέρμα / *sperma* ('seed'), meaning that the seeds are enclosed within a fruit. They are by far the most diverse group of land plants with 64 orders, 416 families, approximately 13,000 known genera and 300,000 known species.[7] Angiosperms were formerly called **Magnoliophyta** (/mæɡˌnoʊliˈɒfətə, -əˈfaɪtə/).[8]

Angiosperms are distinguished from the other seed-producing plants, the gymnosperms, by having flowers, xylem consisting of vessel elements instead of tracheids, endosperm within their seeds, and fruits that completely envelop the seeds. The ancestors of flowering plants diverged from the common ancestor of all living gymnosperms before the end of the Carboniferous, over 300 million years ago. In the Cretaceous, angiosperms diversified explosively, becoming the dominant group of plants across the planet.

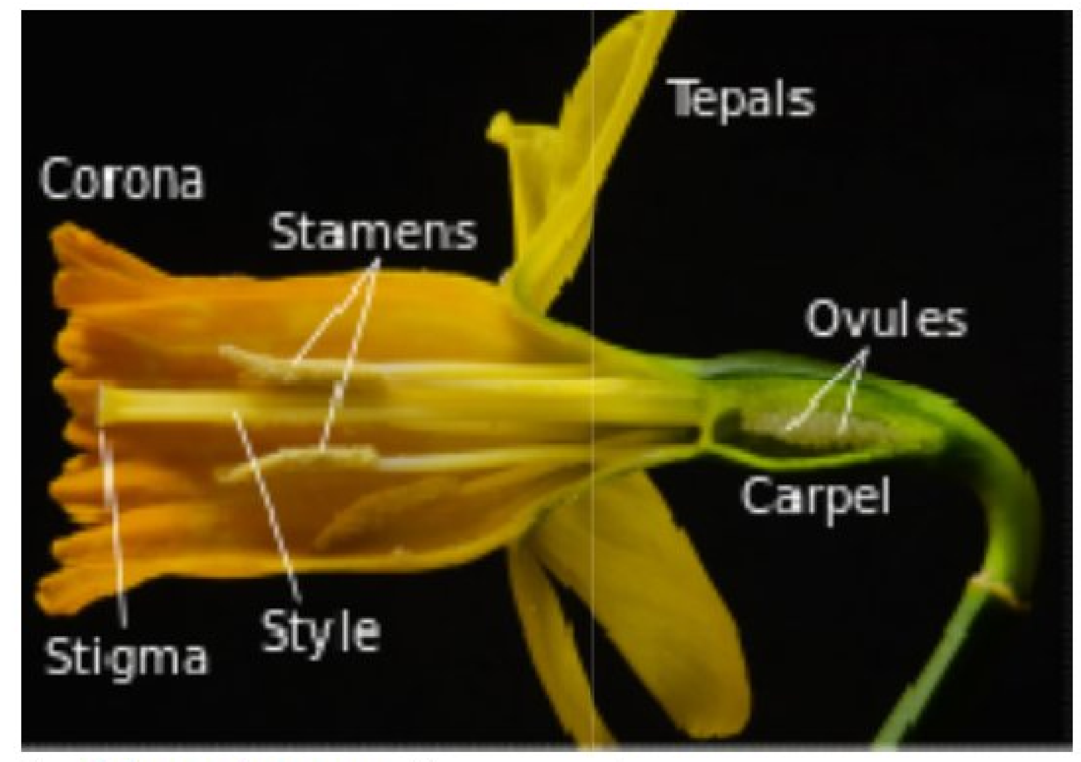
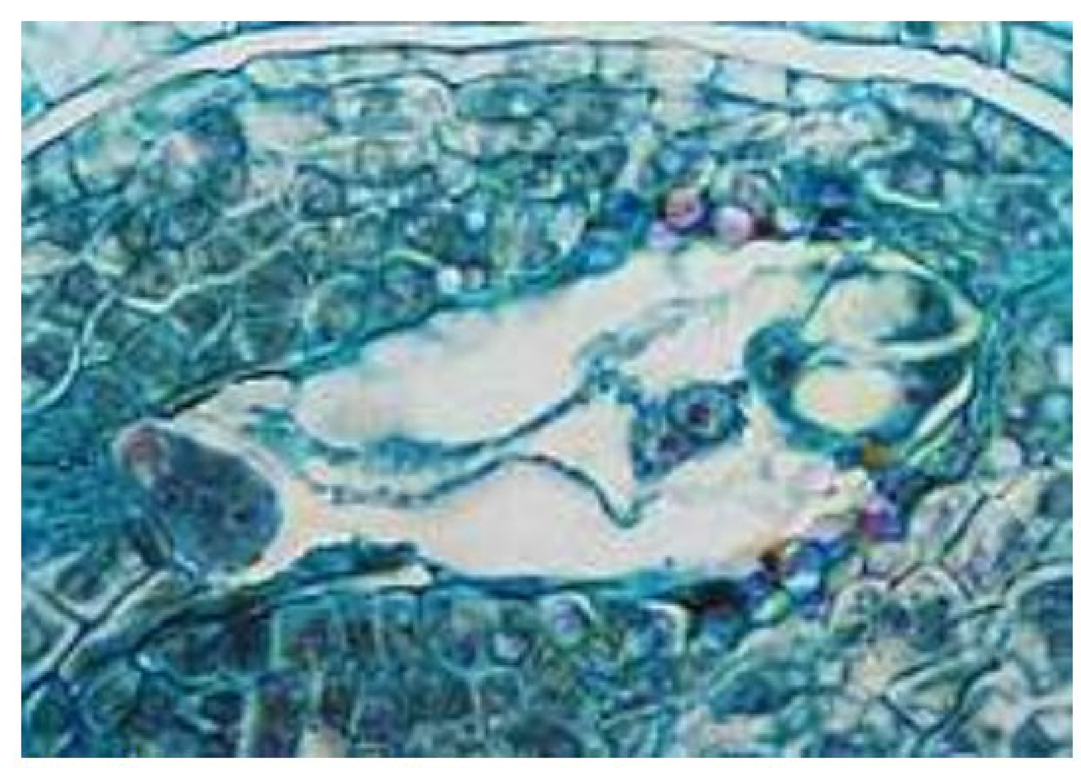
Agriculture is almost entirely dependent on angiosperms, and a small number of flowering plant families supply nearly all plant-based food and livestock feed. Rice, maize, and wheat provide half of the world's calorie intake, and all three plants are cereals from the Poaceae family (colloquially known as grasses). Other families provide materials such as wood, paper and cotton, and supply numerous ingredients for traditional and modern medicines. Flowering plants are also commonly grown for decorative purposes, with certain flowers playing a significant role in many cultures.

Out of the "Big Five" extinction events in Earth's history, only the Cretaceous–Paleogene extinction event had occurred while angiosperms dominated plant life on the planet. Today, the Holocene extinction affects all kingdoms of complex life on Earth, and conservation measures are necessary to protect plants in their habitats in the wild (*in situ*), or failing that, *ex situ* in seed banks or artificial habitats like botanic gardens. Otherwise, around 40% of plant species may become extinct due to human actions such as habitat destruction, introduction of invasive species, unsustainable logging and collection of medicinal or ornamental plants. Further, climate change is starting to impact plants and is likely to cause many species to become extinct by 2100.

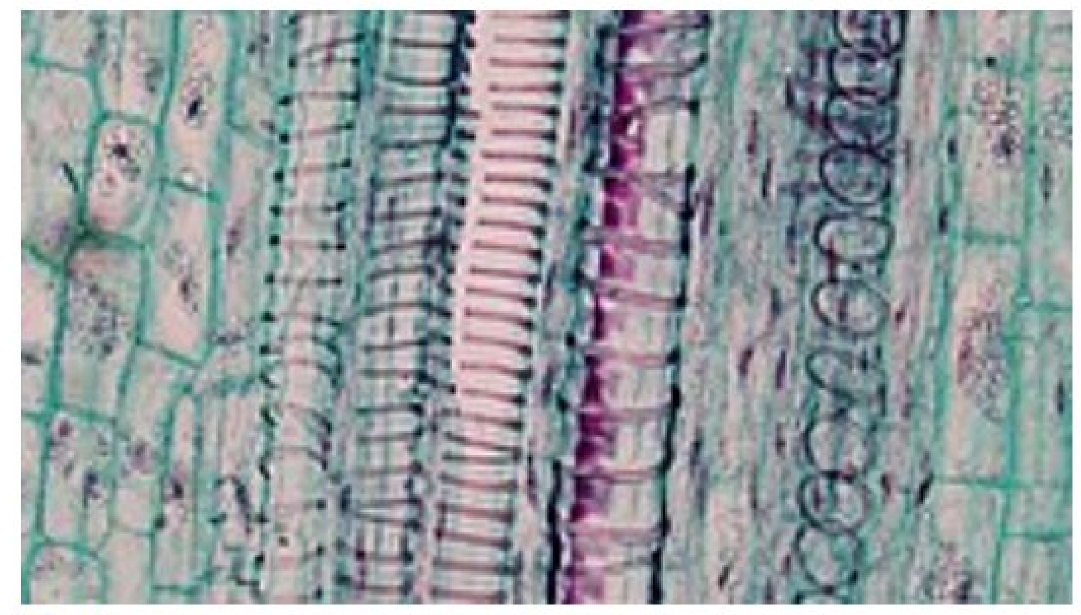
Distinguishing features

[edit]

Angiosperms are terrestrial vascular plants; like the gymnosperms, they have roots, stems, leaves, and seeds. They differ from other seed plants in several ways.

Feature	Description	Image
Flowers	The reproductive organs of flowering plants, not found in any other seed plants.[9]	 A *Narcissus* flower in section. Petals and sepals are replaced here by a fused tube, the corona, and tepals.
Reduced gametophytes, three cells in male, seven cells with eight nuclei in female (except for basal angiosperms)[10]	The gametophytes are smaller than those of gymnosperms.[11] The smaller size of the pollen reduces the time between pollination and fertilization, which in gymnosperms is up to a year.[12]	 Embryo sac is a reduced female gametophyte.
Endosperm	Endosperm forms after fertilization but before the zygote divides. It provides food for the developing embryo, the cotyledons, and sometimes the seedling.[13]	
Closed carpel enclosing the ovules.	Once the ovules are fertilised, the carpels, often with surrounding tissues, develop into fruits. Gymnosperms have unenclosed seeds.[14]	 Peas (seeds, from ovules) inside

pod (fruit, from fertilised carpel).

Xylem made of vessel elements	Open vessel elements are stacked end to end to form continuous tubes, whereas gymnosperm xylem is made of tapered tracheids connected by small pits.[15]	 Xylem vessels (long tubes).

Diversity

[edit]

Ecological diversity

[edit]

Further information: Plant ecology

- **Largest and smallest**
- 

Eucalyptus regnans,
a tree almost 100 m tall

- 

Wolffia arrhiza, a rootless floating freshwater plant under 2 mm across

The largest angiosperms are *Eucalyptus* gum trees of Australia, and *Shorea faguetiana*, dipterocarp rainforest trees of Southeast Asia, both of which can reach almost 100 metres (330 ft) in height.[16] The smallest are *Wolffia* duckweeds which float on freshwater, each plant less than 2 millimetres (0.08 in) across.[17]

- **Photosynthetic and parasitic**
- *Gunnera* captures sunlight for photosynthesis over the large surfaces of its leaves, which are supported by strong veins.

- 

Orobanche purpurea, a parasitic broomrape with no leaves, obtains all its food from other plants.

Considering their method of obtaining energy, some 99% of flowering plants are photosynthetic autotrophs, deriving their energy from sunlight and using it to create molecules such as sugars. The remainder are parasitic, whether on fungi like the orchids for part or all of their life-cycle,[18] or on other plants, either wholly like the broomrapes, *Orobanche*, or partially like the witchweeds, *Striga*.[19]

- **Hot, cold, wet, dry, fresh, salt**

- 

Carnegiea gigantea, the saguaro cactus, grows in hot dry deserts in Mexico and the southern United States.

- 

Dryas octopetala, the mountain avens, lives in cold arctic and montane habitats in the far north of America and Eurasia.

- 

Nelumbo nucifera, the sacred lotus, grows in warm freshwater across tropical and subtropical Asia.

- 

Zostera seagrass grows on the seabed in sheltered coastal waters.

In terms of their environment, flowering plants are cosmopolitan, occupying a wide range of habitats on land, in fresh water and in the sea. On land, they are the dominant plant group in every habitat except for frigid moss-lichen tundra and coniferous forest.[20] The seagrasses in the Alismatales grow in marine environments, spreading with rhizomes that grow through the mud in sheltered coastal waters.[21]

- **Acid, alkaline**
- 

Drosera anglica, a sundew, lives in nutrient-poor acid bogs, deriving nutrients from trapped insects.[22]

- 

Gentiana verna, the spring gentian, flourishes in dry limestone habitats.[23]

Some specialised angiosperms are able to flourish in extremely acid or alkaline habitats. The sundews, many of which live in nutrient-poor acid bogs, are carnivorous plants, able to derive nutrients such as nitrate from the bodies of trapped insects.[22] Other flowers such as *Gentiana verna*, the spring gentian, are adapted to the alkaline conditions found on calcium-rich chalk and limestone, which give rise to often dry topographies such as limestone pavement.[23]

- **Herbaceous, woody, climbing**
- 

Geranium robertianum, herb-Robert, is an annual or biennial herb of Europe and North America.

- 

Betula pendula, the silver birch, is a perennial deciduous tree of Eurasia.

- 

Lianas *Austrosteenisia*, *Parsonsia*, and *Sarcopetalum* climbing trees in Australia

As for their growth habit, the flowering plants range from small, soft herbaceous plants, often living as annuals or biennials that set seed and die after one growing season,[24] to large perennial woody trees that may live for many centuries and grow to many metres in height. Some species grow tall without being self-supporting like trees by climbing on other plants in the manner of vines or lianas.[25]

Taxonomic diversity

[edit]

The number of species of flowering plants is estimated to be in the range of 250,000 to 400,000.[26][27][28] This compares to around 12,000 species of moss[29] and 11,000 species of pteridophytes.[30] The APG system seeks to determine the number of families, mostly by molecular phylogenetics. In the 2009 APG III there were 415 families.[31] The 2016 APG IV added five new orders (Boraginales, Dilleniales, Icacinales, Metteniusales and Vahliales), along with some new families, for a total of 64 angiosperm orders and 416 families.[1]

The diversity of flowering plants is not evenly distributed. Nearly all species belong to the eudicot (75%), monocot (23%), and magnoliid (2%) clades. The remaining five clades contain a little over 250 species in total; i.e. less than 0.1% of flowering plant diversity, divided among nine families. The 25 most species-rich of 443 families,[32] containing over 166,000 species between them in their APG circumscriptions, are:

The 25 largest angiosperm families

Group	Family	English name	No. of spp.
Eudicot	Asteraceae or Compositae	daisy	22,750

The 25 largest angiosperm families

Group	Family	English name	No. of spp.
Monocot	Orchidaceae	orchid	21,950
Eudicot	Fabaceae or Leguminosae	pea, legume	19,400
Eudicot	Rubiaceae	madder	13,150 [33]
Monocot	Poaceae or Gramineae	grass	10,035
Eudicot	Lamiaceae or Labiatae	mint	7,175
Eudicot	Euphorbiaceae	spurge	5,735
Eudicot	Melastomataceae	melastome	5,005
Eudicot	Myrtaceae	myrtle	4,625
Eudicot	Apocynaceae	dogbane	4,555
Monocot	Cyperaceae	sedge	4,350
Eudicot	Malvaceae	mallow	4,225
Monocot	Araceae	arum	4,025
Eudicot	Ericaceae	heath	3,995
Eudicot	Gesneriaceae	gesneriad	3,870
Eudicot	Apiaceae or Umbelliferae	parsley	3,780
Eudicot	Brassicaceae or Cruciferae	cabbage	3,710
Magnoliid dicot	Piperaceae	pepper	3,600
Monocot	Bromeliaceae	bromeliad	3,540

The 25 largest angiosperm families

Group	Family	English name	No. of spp.
Eudicot	Acanthaceae	acanthus	3,500
Eudicot	Rosaceae	rose	2,830
Eudicot	Boraginaceae	borage	2,740
Eudicot	Urticaceae	nettle	2,625
Eudicot	Ranunculaceae	buttercup	2,525
Magnoliid dicot	Lauraceae	laurel	2,500

Evolution

[edit]

History of classification

[edit]

Main article: Plant taxonomy

From 1736, an illustration of Linnaean classification

The botanical term "angiosperm", from Greek words *angeíon* (ἀγγεῖον 'bottle, vessel') and *spérma* (σπέρμα 'seed'), was coined in the form "Angiospermae" by Paul Hermann in 1690, including only flowering plants whose seeds were enclosed in capsules.[34] The term angiosperm fundamentally changed in meaning in 1827 with Robert Brown, when angiosperm came to mean a seed plant with enclosed ovules.[35][36] In 1851, with Wilhelm Hofmeister's work on embryo-sacs, Angiosperm came to have its modern meaning of all the flowering plants including Dicotyledons and Monocotyledons.[36][37] The APG system[31] treats the flowering plants as an unranked clade without a formal Latin name (angiosperms). A formal classification was published alongside the 2009 revision in which the flowering plants rank as the subclass Magnoliidae.[38] From 1998, the Angiosperm Phylogeny Group (APG) has reclassified the angiosperms, with updates in the APG II system in 2003,[39] the APG III system in 2009,[31][40] and the APG IV system in 2016.[1]

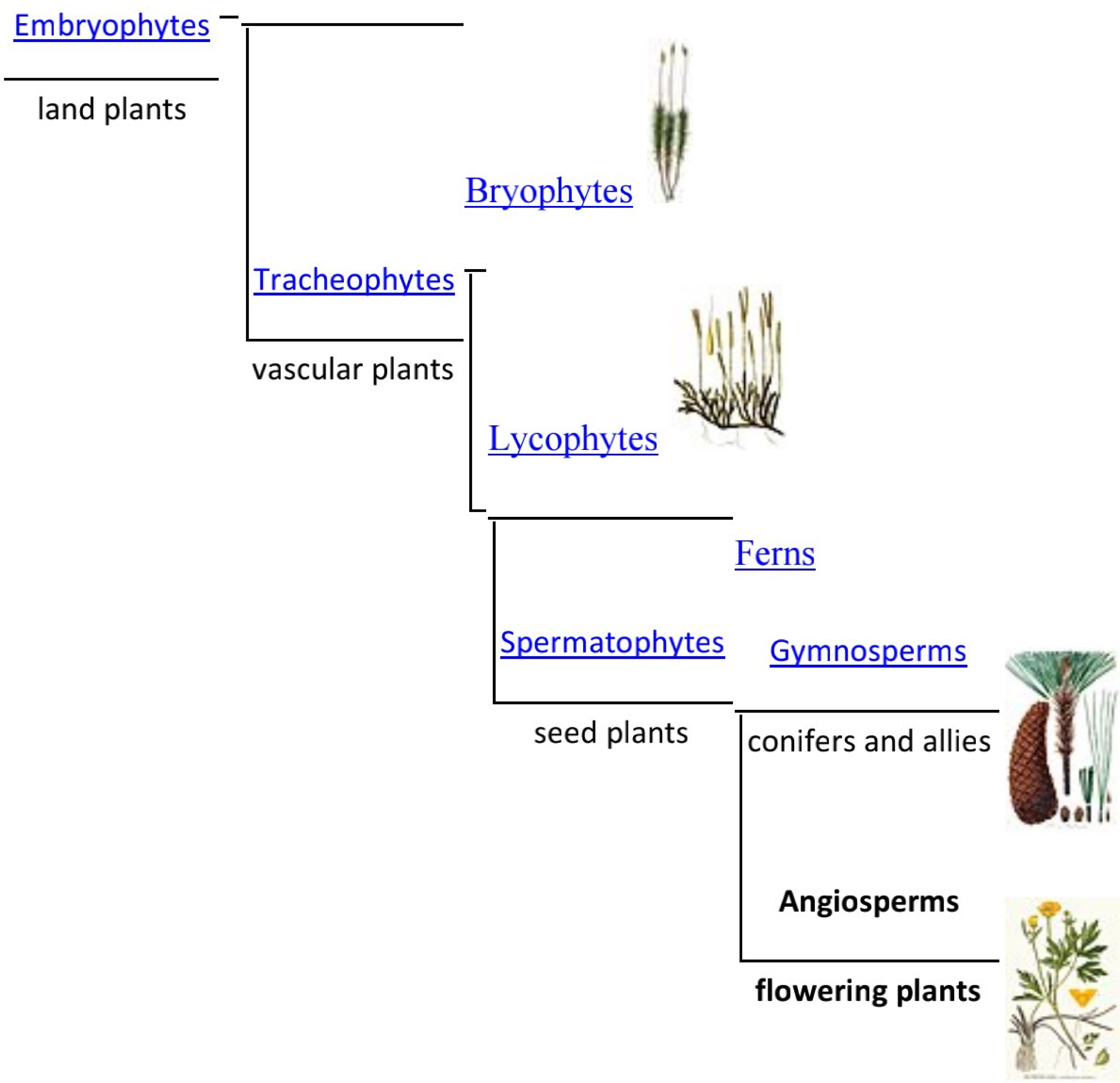
Phylogeny

[edit]

External

[edit]

In 2019, a molecular phylogeny of plants placed the flowering plants in their evolutionary context:[41]



Internal

[edit]

The main groups of living angiosperms are:[42][1]

Angiosperms

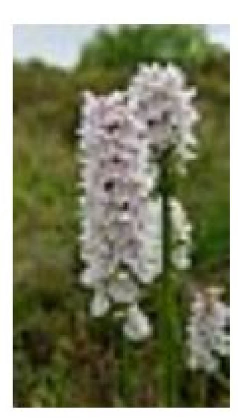
[Amborellales](#)  1 sp. New Caledonia shrub

Nymphaeales  c. 80 spp.[43] water lilies & allies

Austrobaileyales  c. 100 spp.[43] woody plants

Magnoliids  c. 10,000 spp.[43] 3-part flowers, 1-pore polle… nch-veined leaves

Chloranthales  77 spp.[44] Woody, apetalous

Monocots  c. 70,000 spp.[45] 3-part flowers, 1 cotyledon, 1-pore pollen, usu. parallel-veined leaves

Ceratophyllales  c. 6 spp.[43] aquatic plants

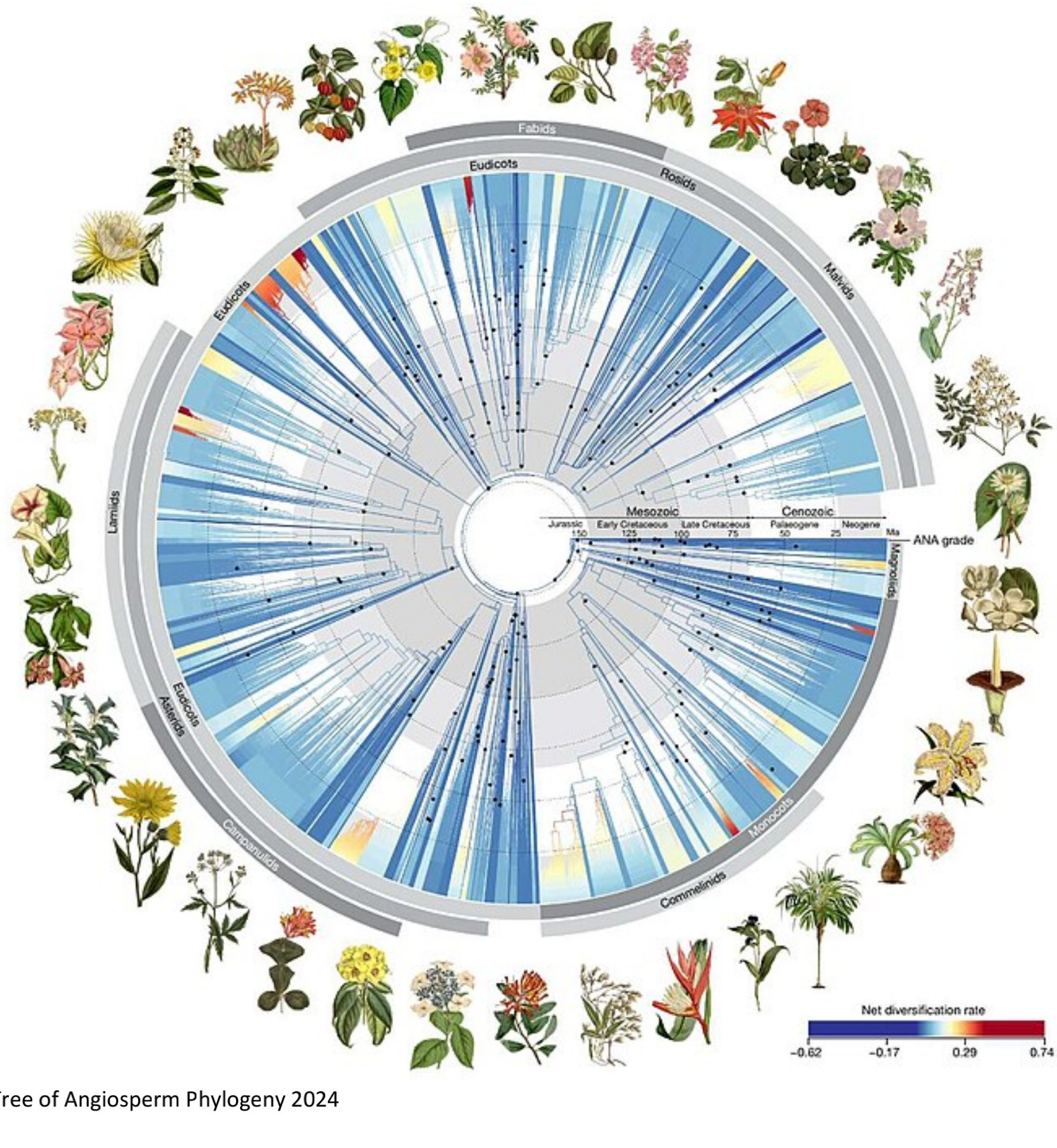
Eudicots  c. 175,000 spp.[43] 4- or 5-part flowers, 3-pore… u. branch-veined leaves

Basal angiosperms

Core angiosperms

showDetailed Cladogram of the 2016 Angiosperm Phylogeny Group (APG) IV classification.[1]

In 2024, Alexandre R. Zuntini and colleagues constructed a tree of some 6,000 flowering plant genera, representing some 60% of the existing genera, on the basis of analysis of 353 nuclear genes in each specimen. Much of the existing phylogeny is confirmed; the rosid phylogeny is revised.[46]



Tree of Angiosperm Phylogeny 2024

Fossil history

[edit]

Main article: Fossil history of flowering plants


Adaptive radiation in the Cretaceous created many flowering plants, such as *Sagaria* in the Ranunculaceae.

Fossilised spores suggest that land plants (embryophytes) have existed for at least 475 million years.[47] However, angiosperms appear suddenly and in great diversity in the fossil record in the Early Cretaceous (~130 mya).[48][49] Claimed records of flowering plants prior to this are not widely accepted.[50] Molecular evidence suggests that the ancestors of angiosperms diverged from the gymnosperms during the late Devonian, about 365 million years ago.[51] The origin time of the crown group of flowering plants remains contentious.[52] By the Late Cretaceous, angiosperms appear to have dominated environments formerly occupied by ferns and gymnosperms. Large canopy-forming trees replaced conifers as the dominant trees close to the end of the Cretaceous, 66 million years ago.[53] The radiation of herbaceous angiosperms occurred much later.[54]

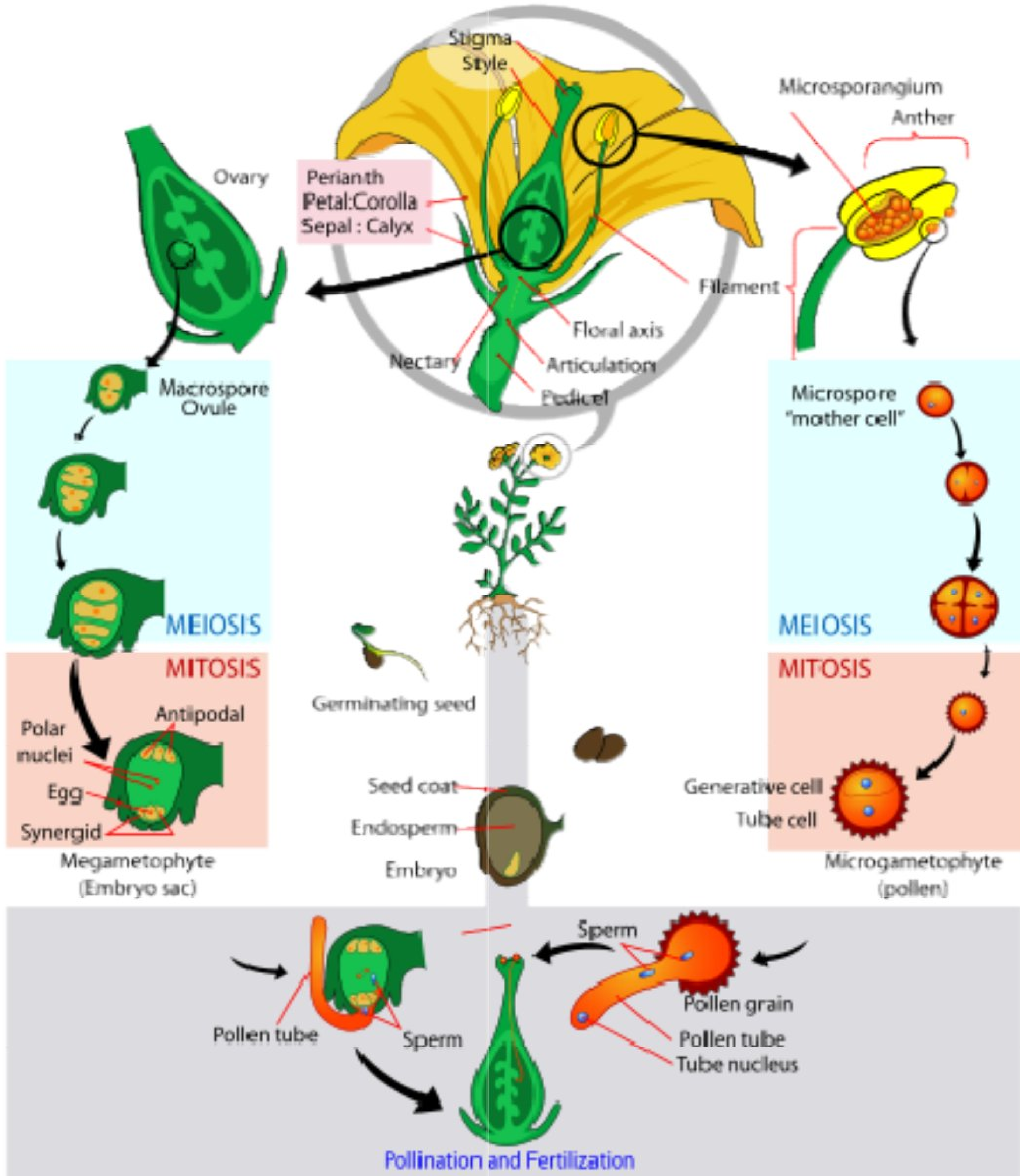
Reproduction

[edit]

Flowers

[edit]

Main articles: Flower and Plant reproductive morphology



Angiosperm flower showing reproductive parts and life cycle

The characteristic feature of angiosperms is the flower. Its function is to ensure fertilization of the ovule and development of fruit containing seeds.[55] It may arise terminally on a shoot or from the axil of a leaf.[56] The flower-bearing part of the plant is usually sharply distinguished from the leaf-bearing part, and forms a branch-system called an inflorescence.[37]

Flowers produce two kinds of reproductive cells. Microspores, which divide to become pollen grains, are the male cells; they are borne in the stamens.[57] The female cells, megaspores, divide to become the egg cell. They are contained in the ovule and enclosed in the carpel; one or more carpels form the pistil.[57]

The flower may consist only of these parts, as in wind-pollinated plants like the willow, where each flower comprises only a few stamens or two carpels.[37] In insect- or bird-pollinated plants, other structures protect the sporophylls and attract pollinators. The individual members of these surrounding structures are known as sepals and petals (or tepals in flowers such as *Magnolia* where sepals and petals are not distinguishable from each other). The outer series (calyx of sepals) is usually green and leaf-like, and functions to protect the rest of the flower, especially the bud.[58][59] The inner series (corolla of petals) is, in general, white or brightly colored, is more delicate in structure, and attracts pollinators by colour, scent, and nectar.[60][61]

Most flowers are hermaphroditic, producing both pollen and ovules in the same flower, but some use other devices to reduce self-fertilization. Heteromorphic flowers have carpels and stamens of differing lengths, so animal pollinators cannot easily transfer pollen between them. Homomorphic flowers may use a biochemical self-incompatibility to discriminate between self and non-self pollen grains. Dioecious plants such as holly have male and female flowers on separate plants.[62] Monoecious plants have separate male and female flowers on the same plant; these are often wind-pollinated,[63] as in maize,[64] but include some insect-pollinated plants such as *Cucurbita* squashes.[65][66]

Fertilisation and embryogenesis

[edit]

Main articles: Fertilization and Plant embryogenesis

Double fertilization requires two sperm cells to fertilise cells in the ovule. A pollen grain sticks to the stigma at the top of the pistil, germinates, and grows a long pollen tube. A haploid generative cell travels down the tube behind the tube nucleus. The generative cell divides by mitosis to produce two haploid (n) sperm cells. The pollen tube grows from the stigma, down the style and into the ovary. When it reaches the micropyle of the ovule, it digests its way into one of the synergids, releasing its contents including the sperm cells. The synergid that the cells were released into degenerates; one sperm makes its way to fertilise the egg cell, producing a diploid ($2n$) zygote. The second sperm cell fuses with both central cell nuclei, producing a triploid ($3n$) cell. The zygote develops into an embryo; the triploid cell develops into the endosperm, the embryo's food supply. The ovary develops into a fruit. and each ovule into a seed.[67]

Fruit and seed

[edit]


The fruit of the horse chestnut tree, showing the large seed inside the fruit, which is dehiscing or splitting open.

Main articles: Fruit and Seed

As the embryo and endosperm develop, the wall of the embryo sac enlarges and combines with the nucellus and integument to form the *seed coat*. The ovary wall develops to form the fruit or pericarp, whose form is closely associated with type of seed dispersal system.[68]

Other parts of the flower often contribute to forming the fruit. For example, in the apple, the hypanthium forms the edible flesh, surrounding the ovaries which form the tough cases around the seeds.[69]

Apomixis, setting seed without fertilization, is found naturally in about 2.2% of angiosperm genera.[70] Some angiosperms, including many citrus varieties, are able to produce fruits through a type of apomixis called nucellar embryony.[71]

Sexual selection

[edit]

This section is an excerpt from Sexual selection in flowering plants.[edit]

Sexual selection is described as natural selection arising through preference by one sex for certain characteristics in individuals of the other sex. Sexual selection is a common concept in animal evolution but, with plants, it is often overlooked because many plants are hermaphrodites. Flowering plants show many characteristics that are often sexually selected for. For example, flower symmetry, nectar production, floral structure, and inflorescences are just a few of the many secondary sex characteristics acted upon by sexual selection. Sexual dimorphisms and reproductive organs can also be affected by sexual selection in flowering plants.[72]

Adaptive function of flowers

[edit]

Charles Darwin in his 1878 book The Effects of Cross and Self-Fertilization in the Vegetable Kingdom[73] in the initial paragraph of chapter XII noted "The first and most important of the conclusions which may be drawn from the observations given in this volume, is that generally cross-fertilisation is beneficial and self-fertilisation often injurious, at least with the plants on which I experimented." Flowers emerged in plant evolution as an adaptation for the promotion of cross-fertilisation (outcrossing), a process that allows the masking of deleterious mutations in the genome of progeny. The masking effect is known as genetic complementation.[74] This beneficial effect of cross-fertilisation on progeny is also referred to as hybrid vigor or heterosis. Once flowers became established in a lineage as an evolutionary adaptation to promote cross-fertilization, subsequent switching to inbreeding usually becomes disadvantageous, in large part because it allows expression of the previously masked deleterious recessive mutations, i.e. inbreeding depression.

Also, Meiosis in flowering plants provides a direct mechanism for repairing DNA through genetic recombination in reproductive tissues.[75] Sexual reproduction appears to be required for maintaining long-term genomic integrity and only infrequent combinations of extrinsic and intrinsic factors permit shifts to asexuality.[75] Thus the two fundamental aspects of sexual reproduction in flowering plants, cross-fertilization (outcrossing) and meiosis appear to be maintained respectively by the advantages of genetic complementation and recombinational repair.[74]

Interactions with humans

[edit]

Main article: Human uses of plants

Practical uses

[edit]


Harvesting rice in Arkansas, 2020


Food from plants: a dish of *Dal tadka*, Indian lentil soup

Agriculture is almost entirely dependent on angiosperms, which provide virtually all plant-based food and livestock feed. Much of this food derives from a small number of flowering plant families.[76] For instance, half of the world's calorie intake is supplied by just three plants – wheat, rice and maize.[77]

Major food-providing families[76]

Family	English	Example foods from that family
Poaceae	Grasses, cereals	Most feedstocks, inc. rice, maize, wheat, barley, rye, oats, pearl millet, sugar cane, sorghum
Fabaceae	Legumes, pea family	Peas, beans, lentils; for animal feed, clover, alfalfa

Solanaceae	Nightshade family	Potatoes, tomatoes, peppers, aubergines
Cucurbitaceae	Gourd family	Squashes, cucumbers, pumpkins, melons
Brassicaceae	Cabbage family	Cabbage and its varieties, e.g. Brussels sprout, broccoli; mustard; oilseed rape
Apiaceae	Parsley family	Parsnip, carrot, parsley, coriander, fennel, cumin, caraway
Rutaceae	Rue family[78]	Oranges, lemons, grapefruits
Rosaceae	Rose family[79]	Apples, pears, cherries, apricots, plums, peaches

Flowering plants provide a diverse range of materials in the form of wood, paper, fibers such as cotton, flax, and hemp, medicines such as digoxin and opioids, and decorative and landscaping plants. Coffee and hot chocolate are beverages from flowering plants.[76]

Cultural uses

[edit]


Bird-and-flower painting: *Kingfisher and iris kachō-e* woodblock print by Ohara Koson (late 19th century)

Both real and fictitious plants play a wide variety of roles in literature and film.[80] Flowers are the subjects of many poems by poets such as William Blake, Robert Frost, and Rabindranath Tagore.[81] Bird-and-flower painting (*Huaniaohua*) is a kind of Chinese painting that celebrates the beauty of flowering plants.[82] Flowers have been used in literature to convey meaning by authors including William Shakespeare.[83] Flowers are used in a variety of art forms which arrange cut or living plants, such as bonsai, ikebana, and flower arranging. Ornamental plants have sometimes changed the course of history, as in tulipomania.[84] Many countries and regions have floral emblems; a survey of 70 of these found that the most popular flowering plant family for such emblems is Orchidaceae at 15.7% (11 emblems), followed by Fabaceae at 10% (7 emblems), and Asparagaceae, Asteraceae, and Rosaceae all at 5.7% (4 emblems each).[85]

Conservation

[edit]

Further information: Conservation biology and Effects of climate change on plant biodiversity

Viola calcarata, a species highly vulnerable to climate change.[86]

Human impact on the environment has driven a range of species extinct and is threatening even more today. Multiple organizations such as IUCN and Royal Botanic Gardens, Kew suggest that around 40% of plant species are threatened with extinction.[87] The majority are threatened by habitat loss, but activities such as logging of wild timber trees and collection of medicinal plants, or the introduction of non-native invasive species, also play a role.[88]

Relatively few plant diversity assessments currently consider climate change,[87] yet it is starting to impact plants as well. About 3% of flowering plants are very likely to be driven extinct within a century at 2 °C (3.6 °F) of global warming, and 10% at 3.2 °C (5.8 °F).[89] In worst-case scenarios, half of all tree species may be driven extinct by climate change over that timeframe.[87]

Conservation in this context is the attempt to prevent extinction, whether *in situ* by protecting plants and their habitats in the wild, or *ex situ* in seed banks or as living plants.[88] Some 3000 botanic gardens around the world maintain living plants, including over 40% of the species known to be threatened, as an "insurance policy against extinction in the wild."[90] The United Nations' Global Strategy for Plant Conservation asserts that "without plants, there is no life".[91] It aims to "halt the continuing loss of plant diversity" throughout the world.[91]

Leaf

A **leaf** (pl.: **leaves**) is a principal appendage of the stem of a vascular plant,[1] usually borne laterally aboveground and specialized for photosynthesis. Leaves are collectively called **foliage**, as in "autumn foliage",[2][3] while the leaves, stem, flower, and fruit collectively form the shoot system.[4] In most leaves, the primary photosynthetic tissue is the palisade mesophyll and is located on the upper side of the blade or lamina of the leaf[1] but in some species, including the mature foliage of *Eucalyptus*,[5] palisade mesophyll is present on both sides and the leaves are said to be isobilateral. Most leaves are flattened and have distinct upper (adaxial) and lower (abaxial) surfaces that differ in color, hairiness, the number of stomata (pores that intake and output gases), the amount and structure of epicuticular wax and other features. Leaves are mostly green in color due to the presence of a compound called chlorophyll which is essential for photosynthesis as it absorbs light energy from the sun. A leaf with lighter-colored or white patches or edges is called a variegated leaf.

Leaves can have many different shapes, sizes, textures and colors. The broad, flat leaves with complex venation of flowering plants are known as *megaphylls* and the species that bear them, the majority, as broad-leaved or megaphyllous plants, which also include acrogymnosperms and ferns. In the lycopods, with different evolutionary origins, the leaves are simple (with only a single vein) and are known as *microphylls*.[6] Some leaves, such as bulb scales, are not above ground. In many aquatic species, the leaves are submerged in water. Succulent plants often have thick juicy leaves, but some leaves are without major photosynthetic function and may be dead at maturity, as in some cataphylls and spines. Furthermore, several kinds of leaf-like structures found in vascular plants are not totally homologous with them. Examples include flattened plant stems called phylloclades and cladodes, and flattened leaf stems called phyllodes which differ from leaves both in their structure and origin.[3][7] Some structures of non-vascular plants look and function much like leaves. Examples include the phyllids of mosses and liverworts.

General characteristics

[edit]

3D rendering of a computed tomography scan of a leaf

Leaves are the most important organs of most vascular plants.[8] Green plants are autotrophic, meaning that they do not obtain food from other living things but instead create their own food by photosynthesis. They capture the energy in sunlight and use it to make simple sugars, such as glucose and sucrose, from carbon dioxide and water. The sugars are then stored as starch, further processed by chemical synthesis into more complex organic molecules such as proteins or cellulose, the basic structural material in plant cell walls, or metabolized by cellular respiration to provide chemical energy to run cellular processes. The leaves draw water from the ground in the transpiration stream through a vascular conducting system known as xylem and obtain carbon dioxide from the atmosphere by diffusion through openings called stomata in the outer covering layer of the leaf (epidermis), while leaves are orientated to maximize their exposure to sunlight. Once sugar has been synthesized, it needs to be transported to areas of active growth such as the plant shoots and roots. Vascular plants transport sucrose in a special tissue called the phloem. The phloem and xylem are parallel to each other, but the transport of materials is usually in opposite directions. Within the leaf these vascular systems branch (ramify) to form veins which supply as much of the leaf as possible, ensuring that cells carrying out photosynthesis are close to the transportation system.[9]

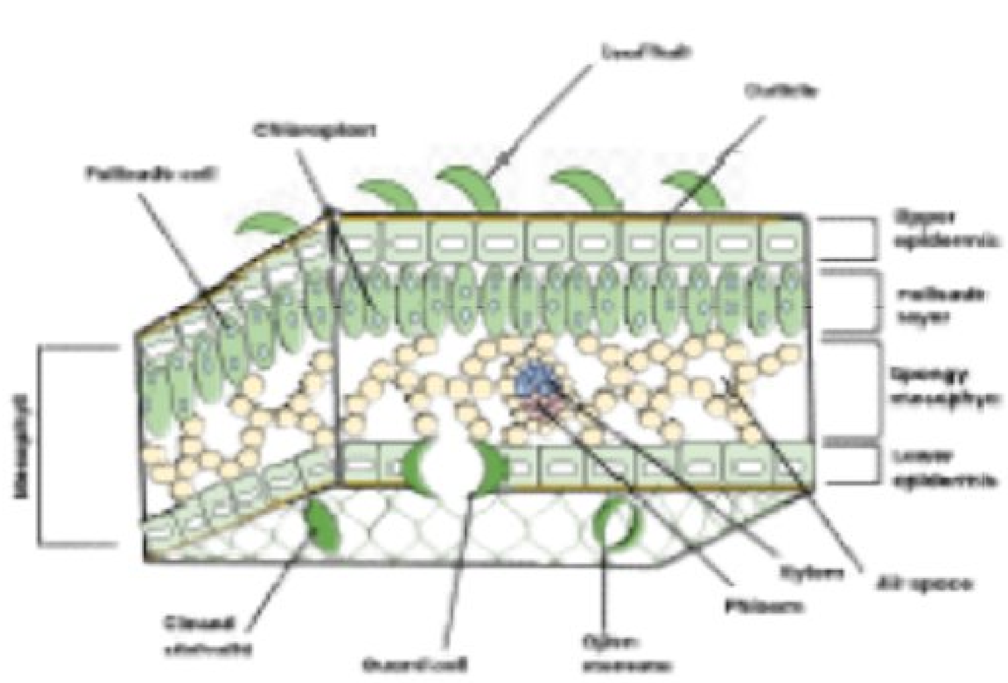
Typically leaves are broad, flat and thin (dorsiventrally flattened), thereby maximising the surface area directly exposed to light and enabling the light to penetrate the tissues and reach the chloroplasts, thus promoting photosynthesis. They are arranged on the plant so as to expose their surfaces to light as efficiently as possible without shading each other, but there are many exceptions and complications. For instance, plants adapted to windy conditions may have pendent leaves, such as in many willows and eucalypts. The flat, or laminar, shape also maximizes thermal contact with the surrounding air, promoting cooling. Functionally, in addition to carrying out photosynthesis, the leaf is the principal site of transpiration, providing the energy required to draw the transpiration stream up from the roots, and guttation.

Many conifers have thin needle-like or scale-like leaves that can be advantageous in cold climates with frequent snow and frost.[10] These are interpreted as reduced from megaphyllous leaves of their Devonian ancestors.[6] Some leaf forms are adapted to modulate the amount of light they absorb to avoid or mitigate excessive heat, ultraviolet damage, or desiccation, or to sacrifice light-absorption efficiency in favor of protection from herbivory. For xerophytes the major constraint is not light flux or intensity, but drought.[11] Some window plants such as *Fenestraria* species and some *Haworthia* species such as *Haworthia tesselata* and *Haworthia truncata* are examples of xerophytes.[12] and *Bulbine mesembryanthemoides*.[13]

Leaves also function to store chemical energy and water (especially in succulents) and may become specialized organs serving other functions, such as tendrils of peas and other legumes, the protective spines of cacti and the insect traps in carnivorous plants such as *Nepenthes* and *Sarracenia*.[14] Leaves are the fundamental structural units from which cones are constructed in gymnosperms (each cone scale is a modified megaphyll leaf known as a sporophyll)[6]:408 and from which flowers are constructed in flowering plants.[6]:445


Vein skeleton of a leaf. Veins contain lignin that make them harder to degrade for microorganisms.

The internal organization of most kinds of leaves has evolved to maximize exposure of the photosynthetic organelles, the chloroplasts, to light and to increase the absorption of carbon dioxide while at the same time controlling water loss. Their surfaces are waterproofed by the plant cuticle and gas exchange between the mesophyll cells and the atmosphere is controlled by minute (length and width measured in tens of μm) openings called stomata which open or close to regulate the rate exchange of carbon dioxide(CO_2), oxygen(O_2) and water vapor into and out of the internal intercellular space system. Stomatal opening is controlled by the turgor pressure in a pair of guard cells that surround the stomatal aperture. In any square centimeter of a plant leaf, there may be from 1,000 to 100,000 stomata.[15]



Near the ground these *Eucalyptus* saplings have juvenile dorsiventral foliage from the previous year, but this season their newly sprouting foliage is isobilateral, like the mature foliage on the adult trees above

The shape and structure of leaves vary considerably from species to species of plant, depending largely on their adaptation to climate and available light, but also to other factors such as grazing animals (such as deer), available nutrients, and ecological competition from other plants. Considerable changes in leaf type occur within species, too, for example as a plant matures; as a case in point *Eucalyptus* species commonly have isobilateral, pendent leaves when mature and dominating their neighbors; however, such trees tend to have erect or horizontal dorsiventral leaves as seedlings, when their growth is limited by the available light.[16] Other factors include the need to balance water loss at high temperature and low humidity against the need to absorb atmospheric carbon dioxide. In most plants, leaves also are the primary organs responsible for transpiration and guttation (beads of fluid forming at leaf margins).

Leaves can also store food and water, and are modified accordingly to meet these functions, for example in the leaves of succulent plants and in bulb scales. The concentration of photosynthetic structures in leaves requires that they be richer in protein, minerals, and sugars than, say, woody stem tissues. Accordingly, leaves are prominent in the diet of many animals.

A leaf shed in autumn

Correspondingly, leaves represent heavy investment on the part of the plants bearing them, and their retention or disposition are the subject of elaborate strategies for dealing with pest pressures, seasonal conditions, and protective measures such as the growth of thorns and the production of phytoliths, lignins, tannins and poisons.

Deciduous plants in frigid or cold temperate regions typically shed their leaves in autumn, whereas in areas with a severe dry season, some plants may shed their leaves until the dry season ends. In either case, the shed leaves may be expected to contribute their retained nutrients to the soil where they fall.

New pomegranate leaves

In contrast, many other non-seasonal plants, such as palms and conifers, retain their leaves for long periods; *Welwitschia* retains its two main leaves throughout a lifetime that may exceed a thousand years.

The leaf-like organs of bryophytes (e.g., mosses and liverworts), known as phyllids, differ heavily morphologically from the leaves of vascular plants. In most cases, they lack vascular tissue, are only a single cell thick, and have no cuticle, stomata, or internal system of intercellular spaces. (The phyllids of the moss family Polytrichaceae are notable exceptions.) The phyllids of bryophytes are only present on the gametophytes, while in contrast the leaves of vascular plants are only present on the sporophytes. These can further develop into either vegetative or reproductive structures.[14]

Simple, vascularized leaves (microphylls), such as those of the early Devonian lycopsid *Baragwanathia*, first evolved as enations, extensions of the stem. True leaves or euphylls of larger size and with more complex venation did not become widespread in other groups until the Devonian period, by which time the carbon dioxide concentration in the atmosphere had dropped significantly. This occurred independently in several separate lineages of vascular plants, in progymnosperms like *Archaeopteris*, in Sphenopsida, ferns and later in the gymnosperms and angiosperms. Euphylls are also referred to as macrophylls or megaphylls (large leaves).[6]

Morphology

[edit]

See also: Glossary of leaf morphology

Animated zoom into the leaf of a *Sequoia sempervirens* (California redwood)

Rosa canina: Petiole, two stipules, rachis, five leaflets

Citrus leaves with translucent glands[17]

A structurally complete leaf of an angiosperm consists of a petiole (leaf stalk), a lamina (leaf blade), stipules (small structures located to either side of the base of the petiole) and a sheath. Not every species produces leaves with all of these structural components. The proximal stalk or petiole is called a stipe in ferns. The lamina is the expanded, flat component of the leaf which contains the chloroplasts. The sheath is a structure, typically at the base that fully or partially clasps the stem above the node, where the leaf is attached. Leaf sheathes typically occur in Poaceae (grasses) and Apiaceae (umbellifers). Between the sheath and the lamina, there may be a pseudopetiole, a petiole like structure. Pseudopetioles occur in some monocotyledons including bananas, palms and bamboos.[18] Stipules may be conspicuous (e.g. beans and roses), soon falling or otherwise not obvious as in Moraceae or absent altogether as in the Magnoliaceae. A petiole may be absent (apetiolate), or the blade may not be laminar (flattened). The petiole mechanically links the leaf to the plant and provides the route for transfer of water and sugars to and from the leaf. The lamina is typically the location of the majority of photosynthesis. The upper (adaxial) angle between a leaf and a stem is known as the axil of the leaf. It is often the location of a bud. Structures located there are called "axillary".

External leaf characteristics, such as shape, margin, hairs, the petiole, and the presence of stipules and glands, are frequently important for identifying plants to family, genus or species levels, and botanists have developed a rich terminology for describing leaf characteristics. Leaves almost always have determinate growth. They grow to a specific pattern and shape and then stop. Other plant parts like stems or roots have non-determinate growth, and will usually continue to grow as long as they have the resources to do so.

The type of leaf is usually characteristic of a species (monomorphic), although some species produce more than one type of leaf (dimorphic or polymorphic). The longest leaves are those of the Raffia palm, *R. regalis* which may be up to 25 m (82 ft) long and 3 m (9.8 ft) wide.[19] The terminology associated with the description of leaf morphology is presented, in illustrated form, at Wikibooks.


Prostrate leaves in *Crossyne guttata*

Where leaves are basal, and lie on the ground, they are referred to as prostrate.

Basic leaf types

[edit]


Whorled leaf pattern of the American tiger lily

Perennial plants whose leaves are shed annually are said to have deciduous leaves, while leaves that remain through winter are evergreens. Leaves attached to stems by stalks (known as petioles) are called petiolate, and if attached directly to the stem with no petiole they are called sessile.[20]

- Ferns have fronds.
- Conifer leaves are typically needle- or awl-shaped or scale-like, they are usually evergreen, but can sometimes be deciduous. Usually, they have a single vein.

- Flowering plant (Angiosperm) leaves: the standard form includes stipules, a petiole, and a lamina.
- Lycophytes have microphylls.
- Sheath leaves are the type found in most grasses and many other monocots.
- Other specialized leaves include those of *Nepenthes*, a pitcher plant.

Dicot leaves have blades with pinnate venation (where major veins diverge from one large mid-vein and have smaller connecting networks between them). Less commonly, dicot leaf blades may have palmate venation (several large veins diverging from petiole to leaf edges). Finally, some exhibit parallel venation.[20]

Monocot leaves in temperate climates usually have narrow blades, and usually parallel venation converging at leaf tips or edges. Some also have pinnate venation.[20]

Arrangement on the stem

[edit]

Main article: Phyllotaxis

The arrangement of leaves on the stem is known as phyllotaxis.[21] A large variety of phyllotactic patterns occur in nature:


The leaves on this plant are arranged in pairs opposite one another, with successive pairs at right angles to each other (*decussate*) along the red stem. Note the developing buds in the axils of these leaves.


The leaves on this plant (*Senecio angulatus*) are alternately arranged.

Alternate

One leaf, branch, or flower part attaches at each point or node on the stem, and leaves alternate direction, to a greater or lesser degree, along the stem.

Basal

Arising from the base of the plant.

Cauline

Attached to the aerial stem.

Opposite

Two leaves, branches, or flower parts attach at each point or node on the stem. Leaf attachments are paired at each node.

Decussate

An opposite arrangement in which each successive pair is rotated 90° from the previous.

Whorled, or verticillate

Three or more leaves, branches, or flower parts attach at each point or node on the stem. As with opposite leaves, successive whorls may or may not be decussate, rotated by half the angle between the leaves in the whorl (i.e., successive whorls of three rotated 60°, whorls of four rotated 45°, etc.). Opposite leaves may appear whorled near the tip of the stem. **Pseudoverticillate** describes an arrangement only appearing whorled, but not actually so.

Rosulate

Leaves form a rosette.

Rows

The term, *distichous*, literally means *two rows*. Leaves in this arrangement may be alternate or opposite in their attachment. The term, *2-ranked*, is equivalent. The terms, *tristichous* and *tetrastichous*, are sometimes encountered. For example, the "leaves" (actually microphylls) of most species of ***Selaginella*** are tetrastichous, but not decussate.

In the simplest mathematical models of phyllotaxis, the apex of the stem is represented as a circle. Each new node is formed at the apex, and it is rotated by a constant angle from the previous node. This angle is called the *divergence angle*. The number of leaves that grow from a node depends on the plant species. When a single leaf grows from each node, and when the stem is held straight, the leaves form a helix.

The divergence angle is often represented as a fraction of a full rotation around the stem. A rotation fraction of 1/2 (a divergence angle of 180°) produces an alternate arrangement, such as in Gasteria or the fan-aloe Kumara plicatilis. Rotation fractions of 1/3 (divergence angles of 120°) occur in beech and hazel. Oak and apricot rotate by 2/5, sunflowers, poplar, and pear by 3/8, and in willow and almond the fraction is 5/13.[22] These arrangements are periodic. The denominator of the rotation fraction indicates the number of leaves in one period, while the numerator indicates the number of complete turns or *gyres* made in one period. For example:

- 180° (or $\frac{1}{2}$): two leaves in one circle (alternate leaves)
- 120° (or $\frac{1}{3}$): three leaves in one circle
- 144° (or $\frac{2}{5}$): five leaves in two gyres

- 135° (or $\frac{3}{8}$): eight leaves in three gyres.

Most divergence angles are related to the sequence of Fibonacci numbers F_n. This sequence begins 1, 1, 2, 3, 5, 8, 13; each term is the sum of the previous two. Rotation fractions are often quotients F_n / F_{n+2} of a Fibonacci number by the number two terms later in the sequence. This is the case for the fractions 1/2, 1/3, 2/5, 3/8, and 5/13. The ratio between successive Fibonacci numbers tends to the golden ratio $\varphi = (1 + \sqrt{5})/2$. When a circle is divided into two arcs whose lengths are in the ratio $1{:}\varphi$, the angle formed by the smaller arc is the golden angle, which is $1/\varphi^2 \times 360° \approx 137.5°$. Because of this, many divergence angles are approximately $137.5°$.

In plants where a pair of opposite leaves grows from each node, the leaves form a double helix. If the nodes do not rotate (a rotation fraction of zero and a divergence angle of 0°), the two helices become a pair of parallel lines, creating a distichous arrangement as in maple or olive trees. More common in a decussate pattern, in which each node rotates by 1/4 (90°) as in the herb basil. The leaves of tricussate plants such as Nerium oleander form a triple helix.

The leaves of some plants do not form helices. In some plants, the divergence angle changes as the plant grows.[23] In orixate phyllotaxis, named after *Orixa japonica*, the divergence angle is not constant. Instead, it is periodic and follows the sequence 180°, 90°, 180°, 270°.[24]

Divisions of the blade

[edit]


A leaf with laminar structure and pinnate venation

Two basic forms of leaves can be described considering the way the blade (lamina) is divided. A **simple leaf** has an undivided blade. However, the leaf may be *dissected* to form lobes, but the gaps between lobes do not reach to the main vein. A **compound leaf** has a fully subdivided blade, each leaflet of the blade being separated along a main or secondary vein. The leaflets may have petiolules and stipels, the equivalents of the petioles and stipules of leaves. Because each leaflet can appear to be a simple leaf, it is important to recognize where the petiole occurs to identify a compound leaf. Compound leaves are a characteristic of some families of higher plants, such as the Fabaceae. The middle vein of a compound leaf or a frond, when it is present, is called a rachis.

Palmately compound

The leaflets all have a common point of attachment at the end of the petiole, radiating like fingers of a hand; for example, *Cannabis* (hemp) and *Aesculus* (buckeyes).

Pinnately compound

Leaflets are arranged either side of the main axis, or rachis.

Odd pinnate

With a terminal leaflet; for example, *Fraxinus* (ash).

Even pinnate

Lacking a terminal leaflet; for example, *Swietenia* (mahogany). A specific type of even pinnate is bifoliolate, where leaves only consist of two leaflets; for example, *Hymenaea*.

Bipinnately compound

Leaves are twice divided: the leaflets (technically "subleaflets") are arranged along a secondary axis that is one of several branching off the rachis. Each leaflet is called a *pinnule*. The group of pinnules on each secondary vein forms a *pinna*; for example, *Albizia* (silk tree).

Trifoliate (or trifoliolate)

A pinnate leaf with just three leaflets; for example, *Trifolium* (clover), *Laburnum* (laburnum), and some species of *Toxicodendron* (for instance, poison ivy).

Pinnatifid

Pinnately dissected to the central vein, but with the leaflets not entirely separate; for example, *Polypodium*, some *Sorbus* (whitebeams). In pinnately veined leaves the central vein is known as the *midrib*.

Characteristics of the petiole

[edit]


The overgrown petioles of rhubarb (*Rheum rhabarbarum*) are edible.

Leaves which have a petiole (leaf stalk) are said to be *petiolate*.

Sessile (epetiolate) leaves have no petiole and the blade attaches directly to the stem. Subpetiolate leaves are nearly petiolate or have an extremely short petiole and may appear to be sessile.

In **clasping** or decurrent leaves, the blade partially surrounds the stem.

When the leaf base completely surrounds the stem, the leaves are said to be **perfoliate**, such as in *Eupatorium perfoliatum*.

In peltate leaves, the petiole attaches to the blade inside the blade margin.

In some *Acacia* species, such as the koa tree (*Acacia koa*), the petioles are expanded or broadened and function like leaf blades; these are called phyllodes. There may or may not be normal pinnate leaves at the tip of the phyllode.

A stipule, present on the leaves of many dicotyledons, is an appendage on each side at the base of the petiole, resembling a small leaf. Stipules may be lasting and not be shed (a stipulate leaf, such as in roses and beans), or be shed as the leaf expands, leaving a stipule scar on the twig (an exstipulate leaf). The situation, arrangement, and structure of the stipules is called the "stipulation".

Free, lateral

As in *Hibiscus*.

Adnate

Fused to the petiole base, as in *Rosa*.

Ochreate

Provided with ochrea, or sheath-formed stipules, as in Polygonaceae; e.g., rhubarb.

Encircling the petiole base

Interpetiolar

Between the petioles of two opposite leaves, as in Rubiaceae.

Intrapetiolar

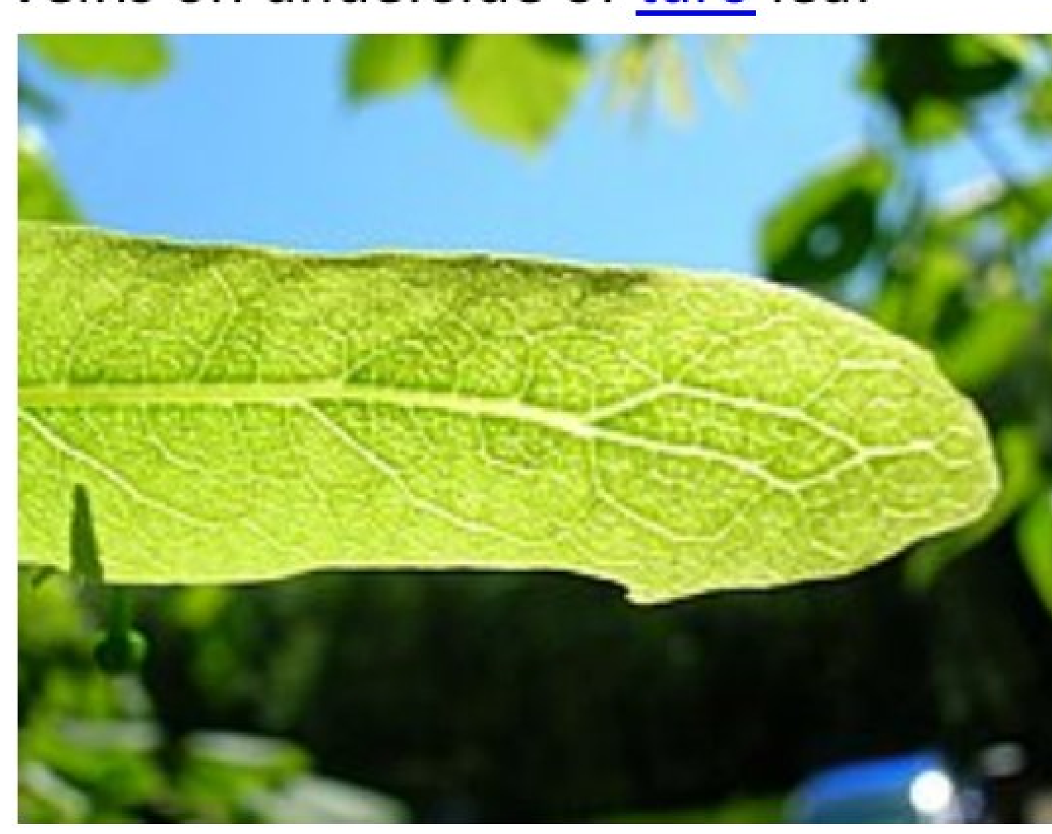
Between the petiole and the subtending stem, as in Malpighiaceae.

Veins

[edit]

See also: § Venation, and § Vascular tissue

Branching veins on underside of taro leaf



The venation within the bract of a linden


Micrograph of a leaf skeleton

Veins (sometimes referred to as nerves) constitute one of the most visible features of leaves. The veins in a leaf represent the vascular structure of the organ, extending into the leaf via the petiole and providing transportation of water and nutrients between leaf and stem, and play a crucial role in the maintenance of leaf water status and photosynthetic capacity. They also play a role in the mechanical support of the leaf.[25][26] Within the lamina of the leaf, while some vascular plants possess only a single vein, in most this vasculature generally divides (ramifies) according to a variety of patterns (venation) and form cylindrical bundles, usually lying in the median plane of the mesophyll, between the two layers of epidermis.[27] This pattern is often specific to taxa, and of which angiosperms possess two main types, parallel and reticulate (net like). In general, parallel venation is typical of monocots, while reticulate is more typical of eudicots and magnoliids ("dicots"), though there are many exceptions.[28][27][29]

The vein or veins entering the leaf from the petiole are called primary or first-order veins. The veins branching from these are secondary or second-order veins. These primary and secondary veins are considered major veins or lower order veins, though some authors include third order.[30] Each subsequent branching is sequentially numbered, and these are the higher order veins, each branching being associated with a narrower vein diameter.[31]

In parallel veined leaves, the primary veins run parallel and equidistant to each other for most of the length of the leaf and then converge or fuse (anastomose) towards the apex. Usually, many smaller minor veins interconnect these primary veins, but may terminate with very fine vein endings in the mesophyll. Minor veins are more typical of angiosperms, which may have as many as four higher orders.[30]

In contrast, leaves with reticulate venation have a single (sometimes more) primary vein in the centre of the leaf, referred to as the midrib or costa, which is continuous with the vasculature of the petiole. The secondary veins, also known as second order veins or lateral veins, branch off from the midrib and extend toward the leaf margins. These often terminate in a hydathode, a secretory organ, at the margin. In turn, smaller veins branch from the secondary veins, known as tertiary or third order (or higher order) veins, forming a dense reticulate pattern. The areas or islands of mesophyll lying between the higher order veins, are called areoles. Some of the smallest veins (veinlets) may have their endings in the areoles, a process known as areolation.[31] These minor veins act as the sites of exchange between the mesophyll and the plant's vascular system.[26] Thus, minor veins collect the products of photosynthesis (photosynthate) from the cells where it takes place, while major veins are responsible for its transport outside of the leaf. At the same time water is being transported in the opposite direction.[32][28][27]

The number of vein endings is very variable, as is whether second order veins end at the margin, or link back to other veins.[29] There are many elaborate variations on the patterns that the leaf veins form, and these have functional implications. Of these, angiosperms have the greatest diversity.[30] Within these the major veins function as the support and distribution network for leaves and are correlated with leaf shape. For instance, the parallel venation found in most monocots correlates with their elongated leaf shape and wide leaf base, while reticulate venation is seen in simple entire leaves, while digitate leaves typically have venation in which three or more primary veins diverge radially from a single point.[33][26][31][34]

In evolutionary terms, early emerging taxa tend to have dichotomous branching with reticulate systems emerging later. Veins appeared in the Permian period (299–252 mya), prior to the appearance of angiosperms in the Triassic (252–201 mya), during which vein hierarchy appeared enabling higher function, larger leaf size and adaption to a wider variety of climatic conditions.[30] Although it is the more complex pattern, branching veins appear to be plesiomorphic and in some form were present in ancient seed plants as long as 250 million years ago. A pseudo-reticulate venation that is actually a highly modified penniparallel one is an autapomorphy of some Melanthiaceae, which are monocots; e.g., *Paris quadrifolia* (True-lover's Knot). In leaves with reticulate venation, veins form a scaffolding matrix imparting mechanical rigidity to leaves.[35]

Morphology changes within a single plant

[edit]

Homoblasty
: Characteristic in which a plant has small changes in leaf size, shape, and growth habit between juvenile and adult stages, in contrast to;

Heteroblasty
: Characteristic in which a plant has marked changes in leaf size, shape, and growth habit between juvenile and adult stages.

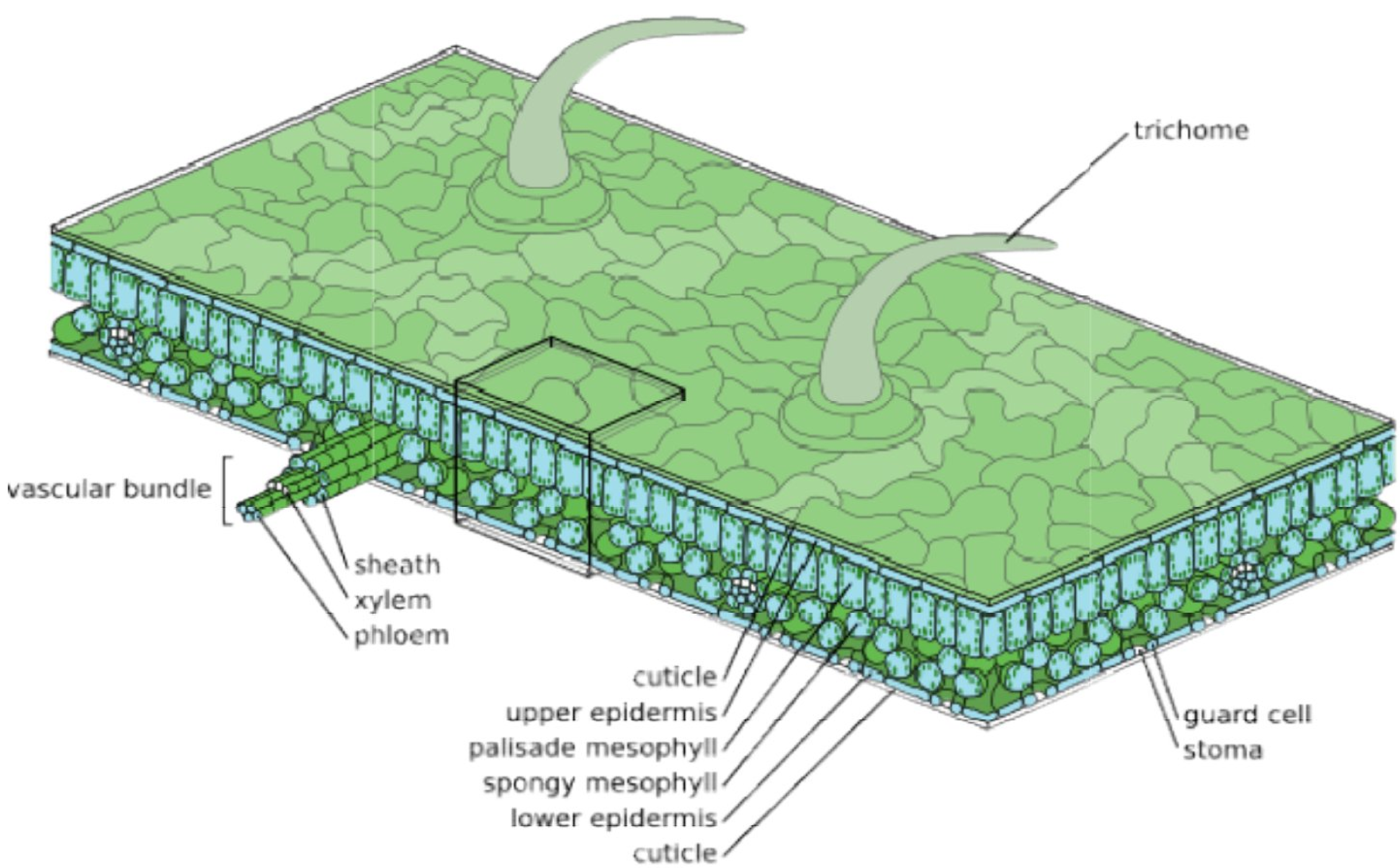
Anatomy

[edit]

Medium-scale features

[edit]

Leaves are normally extensively vascularized and typically have networks of vascular bundles containing xylem, which supplies water for photosynthesis, and phloem, which transports the sugars produced by photosynthesis. Many leaves are covered in trichomes (small hairs) which have diverse structures and functions.



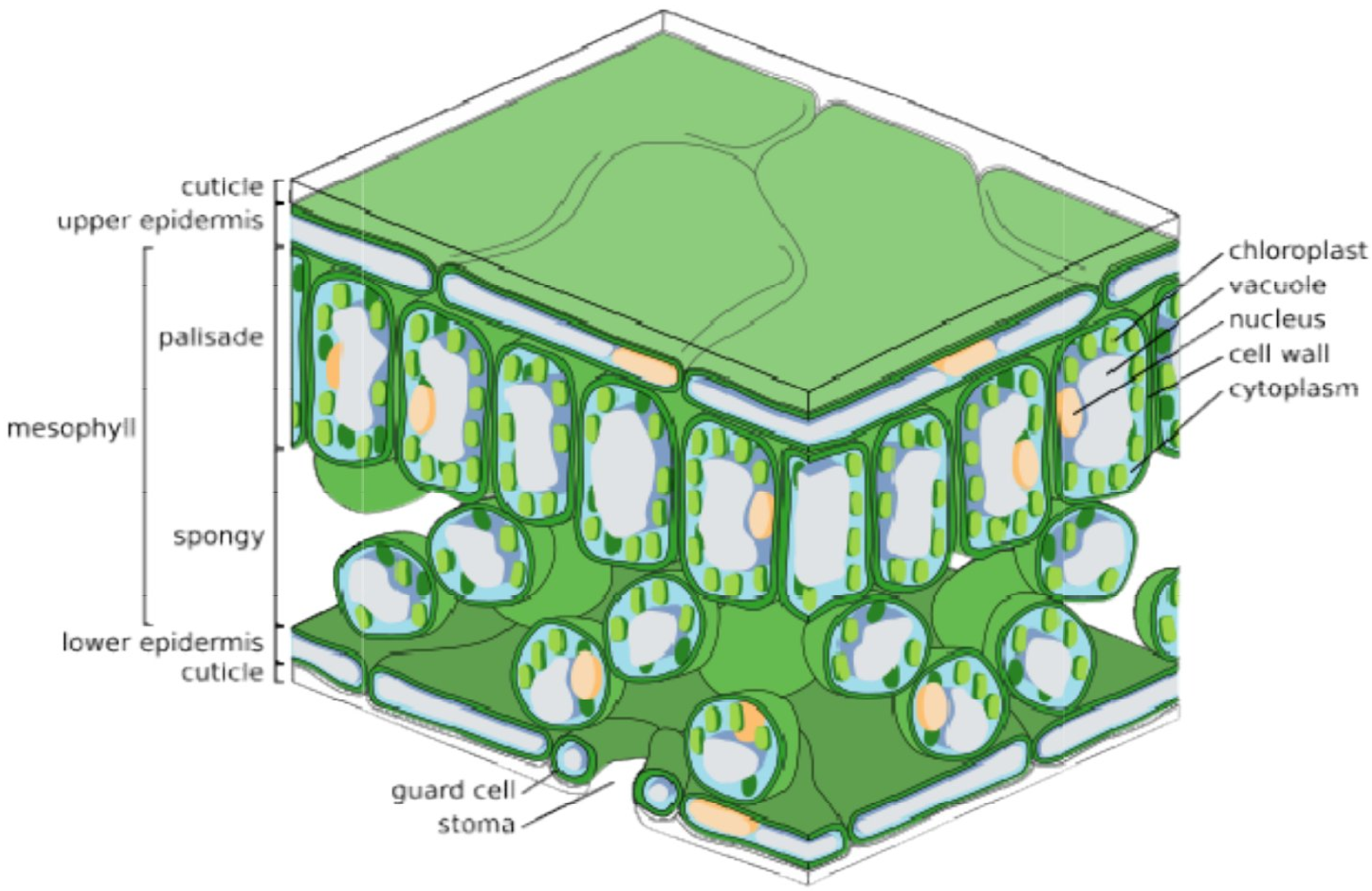
Small-scale features

[edit]

The major tissue systems present are

- The **epidermis**, which covers the upper and lower surfaces
- The **mesophyll tissue**, which consists of photosynthetic cells rich in chloroplasts. (also called **chlorenchyma**)
- The arrangement of **veins** (the vascular tissue)

These three tissue systems typically form a regular organization at the cellular scale. Specialized cells that differ markedly from surrounding cells, and which often synthesize specialized products such as crystals, are termed **idioblasts**.[36]



Major leaf tissues

[edit]

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Cross-section of a leaf

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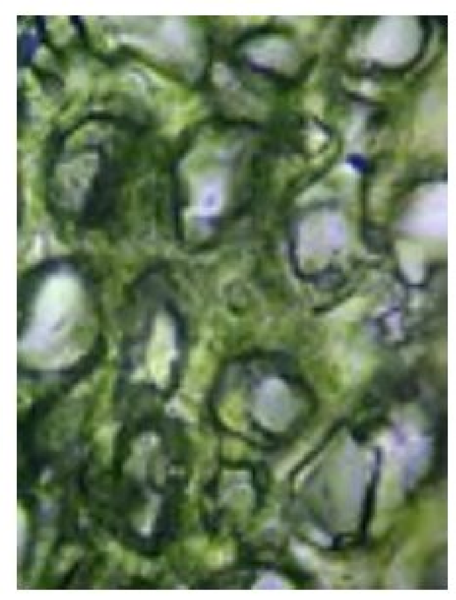
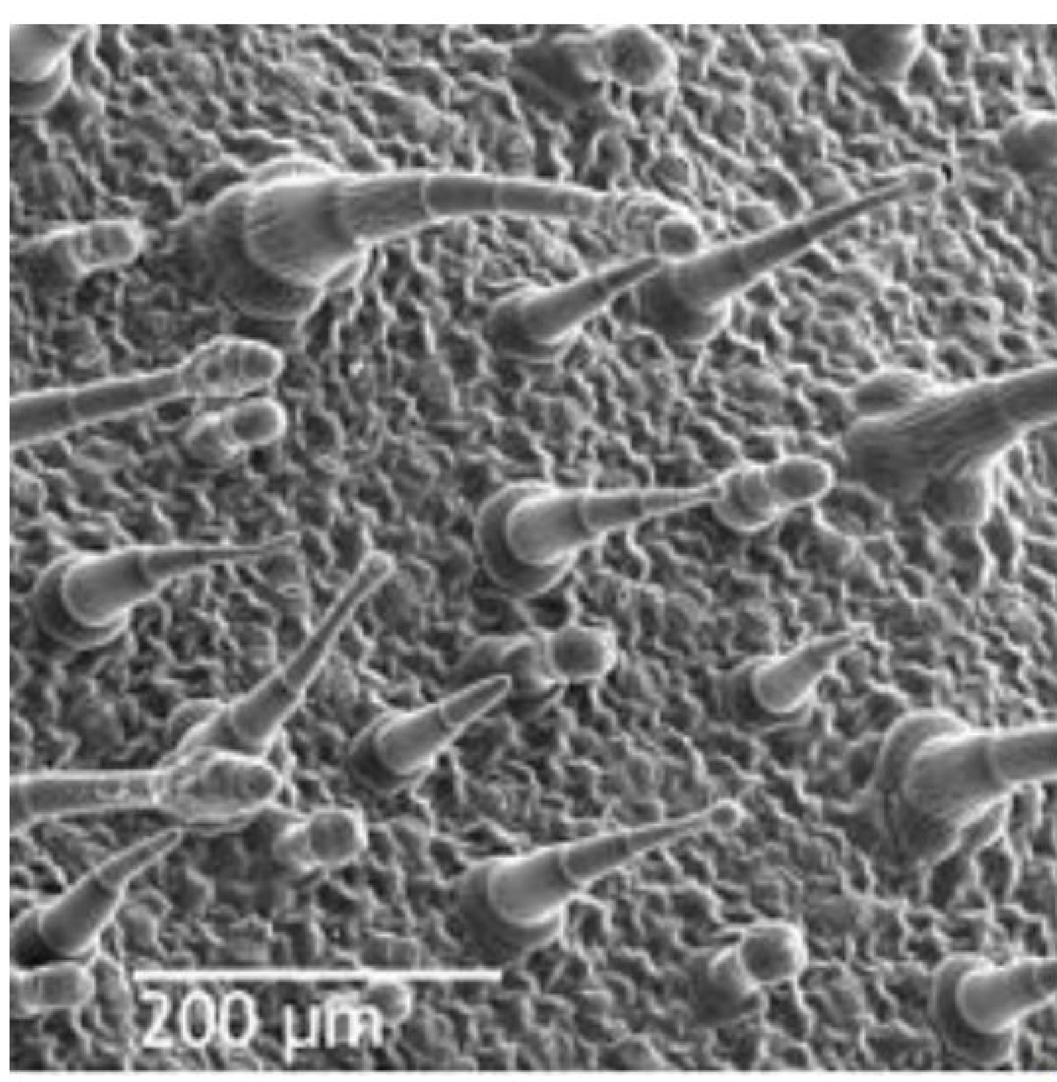
Epidermal cells

- 

Spongy mesophyll cells

Epidermis
[edit]



SEM image of the leaf epidermis of *Nicotiana alata*, showing trichomes (hair-like appendages) and stomata (eye-shaped slits, visible at full resolution).

The epidermis is the outer layer of cells covering the leaf. It is covered with a waxy cuticle which is impermeable to liquid water and water vapor and forms the boundary separating the plant's inner cells from the external world. The cuticle is in some cases thinner on the lower epidermis than on the upper epidermis, and is generally thicker on leaves from dry climates as compared with those from wet climates.[37] The epidermis serves several functions: protection against water loss by way of transpiration, regulation of gas exchange and secretion of metabolic compounds. Most leaves show dorsoventral anatomy: The upper (adaxial) and lower (abaxial) surfaces have somewhat different construction and may serve different functions.

The epidermis tissue includes several differentiated cell types; epidermal cells, epidermal hair cells (trichomes), cells in the stomatal complex; guard cells and subsidiary cells. The epidermal cells are the most numerous, largest, and least specialized and form the majority of the epidermis. They are typically more elongated in the leaves of monocots than in those of dicots.

Chloroplasts are generally absent in epidermal cells, the exception being the guard cells of the stomata. The stomatal pores perforate the epidermis and are surrounded on each side by chloroplast-containing guard cells, and two to four subsidiary cells that lack chloroplasts, forming a specialized cell group known as the stomatal complex. The opening and closing of the stomatal aperture is controlled by the stomatal complex and regulates the exchange of gases and water vapor between the outside air and the interior of the leaf. Stomata therefore play the important role in allowing photosynthesis without letting the leaf dry out. In a typical leaf, the stomata are more numerous over the abaxial (lower) epidermis than the adaxial (upper) epidermis and are more numerous in plants from cooler climates.

Mesophyll

[edit]

For the term Mesophyll *in the size classification of leaves, see Leaf size.*

Most of the interior of the leaf between the upper and lower layers of epidermis is a *parenchyma* (ground tissue) or *chlorenchyma* tissue called the **mesophyll** (Greek for "middle leaf"). This assimilation tissue is the primary location of photosynthesis in the plant. The products of photosynthesis are called "assimilates".

In ferns and most flowering plants, the mesophyll is divided into two layers:

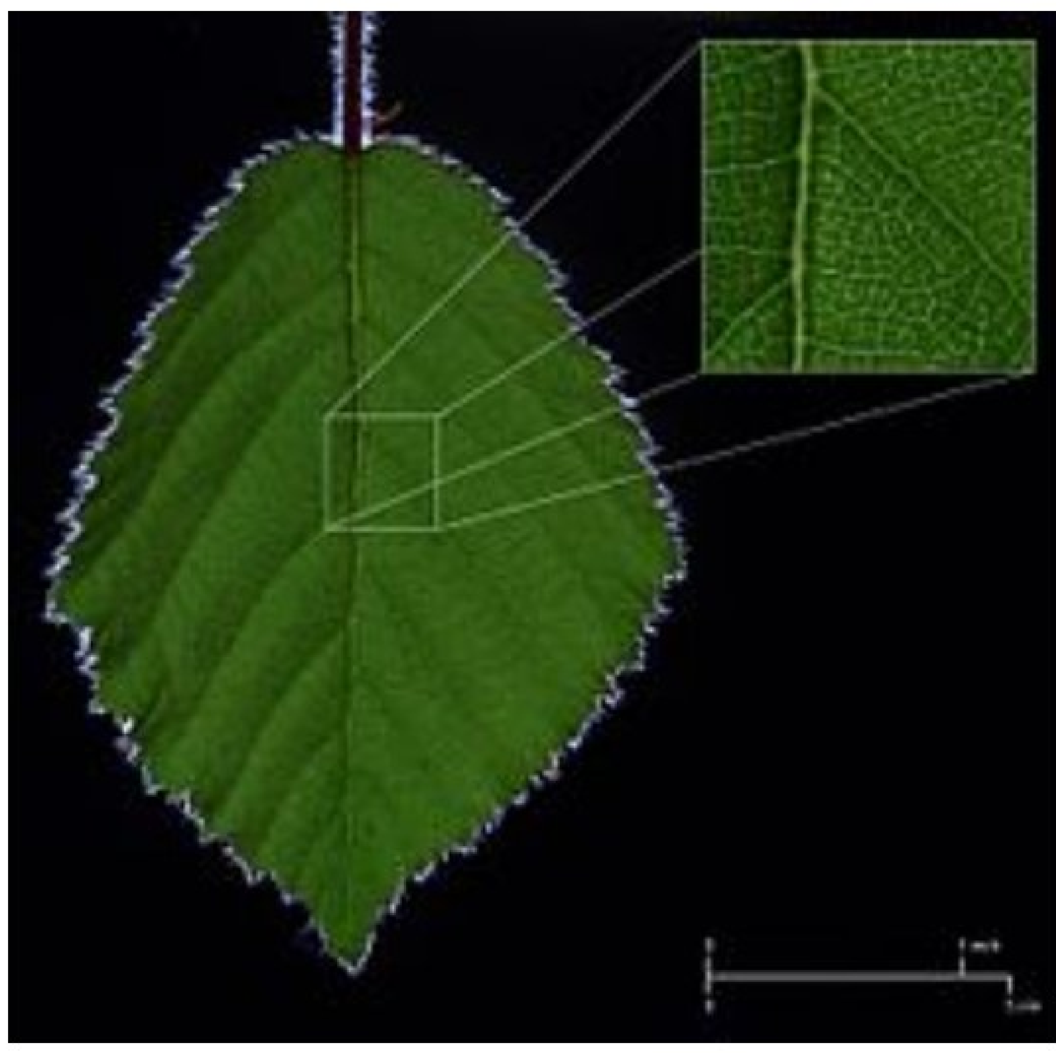
- An upper **palisade layer** of vertically elongated cells, one to two cells thick, directly beneath the adaxial epidermis, with intercellular air spaces between them. Its cells contain many more chloroplasts than the spongy layer. Cylindrical cells, with the *chloroplasts* close to the walls of the cell, can take optimal advantage of light. The slight separation of the cells provides maximum absorption of carbon dioxide. Sun leaves have a multi-layered palisade layer, while shade leaves or older leaves closer to the soil are single-layered.
- Beneath the palisade layer is the **spongy layer**. The cells of the spongy layer are more branched and not so tightly packed, so that there are large intercellular air spaces between them. The pores or *stomata* of the epidermis open into substomatal chambers, which are connected to the intercellular air spaces between the spongy

and palisade mesophyll cell, so that oxygen, carbon dioxide and water vapor can diffuse into and out of the leaf and access the mesophyll cells during respiration, photosynthesis and transpiration.

Leaves are normally green, due to chlorophyll in chloroplasts in the mesophyll cells. Some plants have leaves of different colours due to the presence of accessory pigments such as carotenoids in their mesophyll cells.

Vascular tissue

[edit]



The veins of a bramble leaf

The **veins** are the vascular tissue of the leaf and are located in the spongy layer of the mesophyll. The pattern of the veins is called venation. In angiosperms the venation is typically parallel in monocotyledons and forms an interconnecting network in broad-leaved plants. They were once thought to be typical examples of pattern formation through ramification, but they may instead exemplify a pattern formed in a stress tensor field.[38][39][40]

A vein is made up of a vascular bundle. At the core of each bundle are clusters of two distinct types of conducting cells:

Xylem

Cells that bring water and minerals from the roots into the leaf.

Phloem

Cells that usually move sap, with dissolved sucrose (glucose to sucrose) produced by photosynthesis in the leaf, out of the leaf.

The xylem typically lies on the adaxial side of the vascular bundle and the phloem typically lies on the abaxial side. Both are embedded in a dense parenchyma tissue, called the sheath, which usually includes some structural collenchyma tissue.

Leaf development

[edit]

According to Agnes Arber's partial-shoot theory of the leaf, leaves are partial shoots,[41] being derived from leaf primordia of the shoot apex. Early in development they are dorsiventrally flattened with both dorsal and ventral surfaces.[14] Compound leaves are closer to shoots than simple leaves. Developmental studies have shown that compound leaves, like shoots, may branch in three dimensions.[42][43] On the basis of molecular genetics, Eckardt and Baum (2010) concluded that "it is now generally accepted that compound leaves express both leaf and shoot properties."[44] Many dicotyledonous leaves show endogenously driven daily rhythmicity in growth.[45][46][47]

Ecology

[edit]

Biomechanics

[edit]

Plants respond and adapt to environmental factors, such as light and mechanical stress from wind. Leaves need to support their own mass and align themselves in such a way as to optimize their exposure to the sun, generally more or less horizontally. However, horizontal alignment maximizes exposure to bending forces and failure from stresses such as wind, snow, hail, falling debris, animals, and abrasion from surrounding foliage and plant structures. Overall leaves are relatively flimsy with regard to other plant structures such as stems, branches and roots.[48]

Both leaf blade and petiole structure influence the leaf's response to forces such as wind, allowing a degree of repositioning to minimize drag and damage, as opposed to resistance. Leaf movement like this may also increase turbulence of the air close to the surface of the leaf, which thins the boundary layer of air immediately adjacent to the surface, increasing the capacity for gas and heat exchange, as well as photosynthesis. Strong wind forces may result in diminished leaf number and surface area, which while reducing drag, involves a trade off of also reducing photosynthesis. Thus, leaf design may involve compromise between carbon gain, thermoregulation and water loss on the one hand, and the cost of sustaining both static and dynamic loads. In vascular plants, perpendicular forces are spread over a larger area and are relatively flexible in both bending and torsion, enabling elastic deforming without damage.[48]

Many leaves rely on hydrostatic support arranged around a skeleton of vascular tissue for their strength, which depends on maintaining leaf water status. Both the mechanics and architecture of the leaf reflect the need for transportation and support. Read and Stokes (2006) consider two basic models, the "hydrostatic" and "I-beam leaf" form (see Fig 1).[48] Hydrostatic leaves such as in *Prostanthera lasianthos* are large and thin, and may involve the need for multiple leaves rather single large leaves because of the amount of veins needed to support the periphery of large leaves. But large leaf size favors efficiency in photosynthesis and water conservation, involving further trade offs. On the other hand, I-beam leaves such as *Banksia marginata* involve specialized structures to stiffen them. These I-beams are formed from bundle sheath extensions of sclerenchyma meeting stiffened sub-epidermal layers. This shifts the balance from reliance on hydrostatic pressure to structural support, an obvious advantage where water is relatively scarce. [48] Long narrow leaves bend more easily than ovate leaf blades of the same area. Monocots typically have such linear leaves that maximize surface area while minimising self-shading. In these a high proportion of longitudinal main veins provide additional support.[48]

Interactions with other organisms

[edit]

Some insects, like *Kallima inachus*, mimic leaves.

Although not as nutritious as other organs such as fruit, leaves provide a food source for many organisms. The leaf is a vital source of energy production for the plant, and plants have evolved protection against animals that consume leaves, such as tannins, chemicals which hinder the digestion of proteins and have an unpleasant taste. Animals that are specialized to eat leaves are known as folivores.

Some species have cryptic adaptations by which they use leaves in avoiding predators. For example, the caterpillars of some leaf-roller moths will create a small home in the leaf by folding it over themselves. Some sawflies similarly roll the leaves of their food plants into tubes. Females of the Attelabidae, so-called leaf-rolling weevils, lay their eggs into leaves that they then roll up as means of protection. Other herbivores and their predators mimic the appearance of the leaf. Reptiles such as some chameleons, and insects such as some katydids, also mimic the oscillating movements of leaves in the wind, moving from side to side or back and forth while evading a possible threat.

Seasonal leaf loss

[edit]


Leaves shifting color in autumn (fall)

Main article: Autumn leaf color

Leaves in temperate, boreal, and seasonally dry zones may be seasonally deciduous (falling off or dying for the inclement season). This mechanism to shed leaves is called abscission. When the leaf is shed, it leaves a leaf scar on the twig. In cold autumns, they sometimes change color, and turn yellow, bright-orange, or red, as various accessory pigments (carotenoids and xanthophylls) are revealed when the tree responds to cold and reduced sunlight by curtailing chlorophyll production. Red anthocyanin pigments are now thought to be produced in the leaf as it dies, possibly to mask the yellow hue left when the chlorophyll is lost—yellow leaves appear to attract herbivores such as aphids.[49] Optical masking of chlorophyll by anthocyanins reduces risk of photo-oxidative damage to leaf cells as they senesce, which otherwise may lower the efficiency of nutrient retrieval from senescing autumn leaves.[50]

Evolutionary adaptation

[edit]


Poinsettia bracts are leaves which have evolved red pigmentation in order to attract insects and birds to the central flowers, an adaptive function normally served by petals (which are themselves leaves highly modified by evolution).

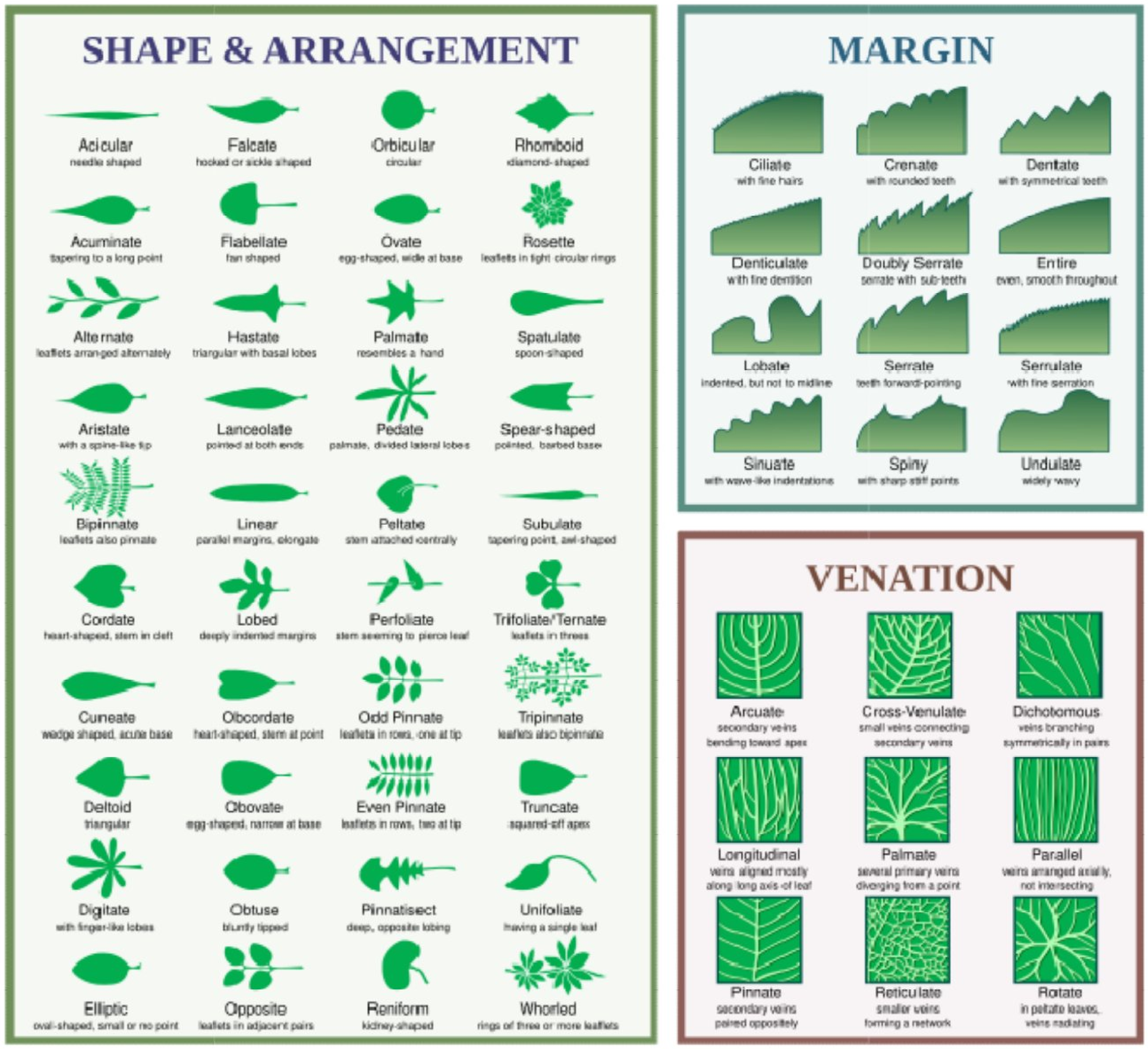
In the course of evolution, leaves have adapted to different environments in the following ways:[citation needed]

- Waxy micro- and nanostructures on the surface reduce wetting by rain and adhesion of contamination (*See Lotus effect*).
- Divided and compound leaves reduce wind resistance and promote cooling.
- Hairs on the leaf surface trap humidity in dry climates and create a boundary layer reducing water loss.
- Waxy plant cuticles reduce water loss.
- Large surface area provides a large area for capture of sunlight.
- In harmful levels of sunlight, specialized leaves, opaque or partly buried, admit light through a translucent leaf window for photosynthesis at inner leaf surfaces (e.g. *Fenestraria*).
- Kranz leaf anatomy in plants which perform C_4 carbon fixation
- Succulent leaves store water and organic acids for use in CAM photosynthesis.
- Aromatic oils, poisons or pheromones produced by leaf borne glands deter herbivores (e.g. eucalypts).
- Inclusions of crystalline minerals deter herbivores (e.g. silica phytoliths in grasses, raphides in Araceae).
- Petals attract pollinators.
- Spines protect the plants from herbivores (e.g. cacti).
- Stinging hairs to protect against herbivory, e.g. in *Urtica dioica* and *Dendrocnide moroides* (Urticaceae).
- Special leaves on carnivorous plants are adapted for trapping food, mainly invertebrate prey, though some species trap small vertebrates as well (see carnivorous plants).
- Bulbs store food and water (e.g. onions).
- Tendrils allow the plant to climb (e.g. peas).
- Bracts and pseudanthia (false flowers) replace normal flower structures when the true flowers are greatly reduced (e.g. spurges, spathes in the Araceae and floral heads in the Asteraceae).

Terminology

[edit]

See also: Glossary of leaf morphology, Glossary of plant morphology, and Glossary of botanical terms



Leaf morphology terms

Shape

[edit]

Main article: Glossary of leaf morphology § Leaf and leaflet shapes

Leaves showing various morphologies (clockwise from upper left): tripartite lobation, elliptic with serrulate margin, palmate venation, acuminate odd-pinnate (center), pinnatisect, lobed, elliptic with entire margin

Edge (margin)

[edit]

The *edge* or *margin* is the outside perimeter of a leaf. The terms are interchangeable.

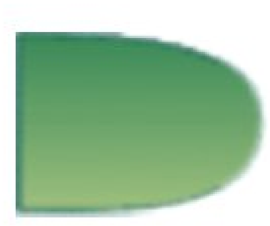
Image	Term	Latin	Description
	Entire	*Forma integra*	Even; with a smooth margin; without toothing
	Ciliate	*ciliatus*	Fringed with hairs
	Crenate	*crenatus*	Wavy-toothed; dentate with rounded teeth
	crenulate	*crenulatus*	Finely crenate
	crisped	*crispus*	Curly

Image	Term	Latin	Description
	Dentate	*dentatus*	Toothed; may be **coarsely dentate**, having large teeth or **glandular dentate**, having teeth which bear glands
	Denticulate	*denticulatus*	Finely toothed
	Doubly serrate	*duplicato-dentatus*	Each tooth bearing smaller teeth
	Serrate	*serratus*	Saw-toothed; with asymmetrical teeth pointing forward
	Serrulate	*serrulatus*	Finely serrate
	Sinuate	*sinuosus*	With deep, wave-like indentations; coarsely crenate
	Lobate	*lobatus*	Indented, with the indentations not reaching the center
	Undulate	*undulatus*	With a wavy edge, shallower than sinuate
	Spiny or pungent	*spiculatus*	With stiff, sharp points such as thistles

Apex (tip)

[edit]

Image	Term	Latin	Description
	Acuminate	–	Long-pointed, prolonged into a narrow, tapering point in a concave manner

Image	Term	Latin	Description
	Acute	_	Ending in a sharp, but not prolonged point
	Cuspidate	_	With a sharp, elongated, rigid tip; tipped with a cusp
	Emarginate	_	Indented, with a shallow notch at the tip
	Mucronate	_	Abruptly tipped with a small short point
	Mucronulate	_	Mucronate, but with a noticeably diminutive spine
	Obcordate	_	Inversely heart-shaped
	Obtuse	_	Rounded or blunt
	Truncate	_	Ending abruptly with a flat end

Base

[edit]