Kingdom Plantae

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Chapter- 1

Plant

Plants Temporal range: Early Cambrian to recent, 520–0 Ma

Scientific classification
Domain: Eukaryota
(unranked): Archaeplastida
Kingdom: **Plantae** Haeckel, 1866
Divisions

Green algae

- Chlorophyta
- Charophyta

Land plants (embryophytes)

- **Non-vascular land plants (bryophytes)**
  - Marchantiophyta—liverworts
  - Anthocerotophyta—hornworts
  - Bryophyta—mosses
  - †Horneophytopsida
- **Vascular plants (tracheophytes)**
  - †Rhyniophyta—rhyniophytes
  - †Zosterophyllophyta—zosterophylls
  - Lycopodiophyta—clubmosses
  - †Trimerophytophyta—trimerophytes
  - Pteridophyta—ferns and horsetails
  - †Progymnospermophyta
  - **Seed plants (spermatophytes)**
    - †Pteridospermatophyta—seed ferns
    - Pinophyta—conifers
    - Cycadophyta—cycads
    - Ginkgophyta—ginkgo
    - Gnetophyta—gnetae
    - Magnoliophyta—flowering plants

†Nematophytes

Plants are living organisms belonging to the kingdom **Plantae**. They include familiar organisms such as trees, flowers, herbs, bushes, grasses, vines, ferns, mosses, and green algae. The scientific study of plants, known as botany, has identified about 350,000 extant species of plants, defined as seed plants, bryophytes, ferns and fern allies. As of 2004, some 287,655 species had been identified, of which 258,650 are flowering and 18,000 bryophytes. **Green plants**, sometimes called **Viridiplantae**, obtain most of their energy from sunlight via a process called photosynthesis.

Definition

Aristotle divided all living things between plants (which generally do not move), and animals (which often are mobile to catch their food). In Linnaeus' system, these became the Kingdoms Vegetabilia (later Metaphyta or Plantae) and Animalia (also called Metazoa). Since then, it has become clear that the Plantae as originally defined included several unrelated groups, and the fungi and several groups of algae were removed to new kingdoms. However, these are still often considered plants in many contexts, both technical and popular.

Current definitions of Plantae

When the name Plantae or plant is applied to a specific taxon, it is usually referring to one of three concepts. From least to most inclusive, these three groupings are:

Name(s)	Scope	Description
Land plants, also known as Embryophyta or Metaphyta.	Plantae *sensu strictissimo*	This group includes the liverworts, hornworts, mosses, and vascular plants, as well as fossil plants similar to these surviving groups.
Green plants - also known as **Viridiplantae**, **Viridiphyta** or **Chlorobionta**	Plantae *sensu stricto*	Includes the land plants plus Charophyta (i.e. stoneworts), and Chlorophyta (i.e., other green algae such as sea lettuce). Viridiplantae encompass a group of organisms that possess chlorophyll *a* and *b*, have plastids that are bound by only two membranes, are capable of storing starch, and have cellulose in their cell walls.
Archaeplastida, Plastida or Primoplantae	Plantae *sensu lato*	Comprises the green plants above plus Rhodophyta (red algae) and Glaucophyta (glaucophyte algae). This clade includes the organisms that eons ago acquired their chloroplasts directly by engulfing cyanobacteria.

Outside of formal scientific contexts, the term "plant" implies an association with certain traits, such as multicellularity, cellulose, and photosynthesis. Many of the classification controversies involve organisms that are rarely encountered and are of minimal apparent economic significance, but are crucial in developing an understanding of the evolution of modern flora.

Algae

Green algae from Ernst Haeckel's *Kunstformen der Natur*, 1904

Most algae are no longer classified within the Kingdom Plantae. The algae comprise several different groups of organisms that produce energy through photosynthesis, each of which arose independently from separate non-photosynthetic ancestors. Most conspicuous among the algae are the seaweeds, multicellular algae that may roughly resemble terrestrial plants, but are classified among the green, red, and brown algae. Each of these algal groups also includes various microscopic and single-celled organisms.

The two groups of green algae are the closest relatives of land plants (embryophytes). The first of these groups is the Charophyta (desmids and stoneworts), from which the

embryophytes developed. The sister group to the combined embryophytes and charophytes is the other group of green algae, Chlorophyta, and this more inclusive group is collectively referred to as the green plants or Viridiplantae. The Kingdom Plantae is often taken to mean this monophyletic grouping. With a few exceptions among the green algae, all such forms have cell walls containing cellulose, have chloroplasts containing chlorophylls *a* and *b*, and store food in the form of starch. They undergo closed mitosis without centrioles, and typically have mitochondria with flat cristae.

The chloroplasts of green plants are surrounded by two membranes, suggesting they originated directly from endosymbiotic cyanobacteria. The same is true of two additional groups of algae: the Rhodophyta (red algae) and Glaucophyta. All three groups together are generally believed to have a common origin, and so are classified together in the taxon Archaeplastida. In contrast, most other algae (e.g. heterokonts, haptophytes, dinoflagellates, and euglenids) have chloroplasts with three or four surrounding membranes. They are not close relatives of the green plants, presumably acquiring chloroplasts separately from ingested or symbiotic green and red algae.

Fungi

The classification of fungi has been controversial until quite recently in the history of biology. Linnaeus' original classification placed the fungi within the Plantae, since they were unquestionably not animalian; this being the only other alternative. With later developments in microbiology, in the 19th century Ernst Haeckel felt that a third kingdom was required to classify newly discovered micro-organisms. The introduction of the new kingdom Protista as an alternative to Animalia, led to uncertainty as to whether fungi truly were best placed in the Plantae or whether they ought to be reclassified as protists. Haeckel himself found it difficult to decide and it was not until 1969 that a solution was found whereby Robert Whittaker proposed the creation of the kingdom Fungi. Molecular evidence has since shown that the concestor (last common ancestor) of the Fungi was probably more similar to that of the Animalia than of any other kingdom, including the Plantae.

Whittaker's original reclassification was based on the fundamental difference in nutrition between the Fungi and the Plantae. Unlike plants, which are generally autotrophic multicellular phototrophs which gain carbon through photosynthesis, fungi are generally heterotrophic uni- or multi-cellular saprotrophs, obtaining carbon by breaking down and absorbing surrounding materials. In addition, the substructure of multicellular fungi takes the form of many chitinous microscopic strands called hyphae, which may be further subdivided into cells or may form a syncytium containing many eukaryotic nuclei. Fruiting bodies, of which mushrooms are most familiar example, are the reproductive structures of fungi.

Diversity

About 350,000 species of plants, defined as seed plants, bryophytes, ferns and fern allies, are estimated to exist currently. As of 2004, some 287,655 species had been identified, of

which 258,650 are flowering plants, 16,000 bryophytes, 11,000 ferns and 8,000 green algae.

Diversity of living plant divisions			
Informal group	**Division name**	**Common name**	**No. of living species**
Green algae	**Chlorophyta**	green algae (chlorophytes)	3,800
	Charophyta	green algae (desmids & charophytes)	4,000 - 6,000
Bryophytes	**Marchantiophyta**	liverworts	6,000 - 8,000
	Anthocerotophyta	hornworts	100 - 200
	Bryophyta	mosses	12,000
Pteridophytes	**Lycopodiophyta**	club mosses	1,200
	Pteridophyta	ferns, whisk ferns & horsetails	11,000
Seed plants	**Cycadophyta**	cycads	160
	Ginkgophyta	ginkgo	1
	Pinophyta	conifers	630
	Gnetophyta	gnetophytes	70
	Magnoliophyta	flowering plants	258,650

The naming of plants is governed by the International Code of Botanical Nomenclature and International Code of Nomenclature for Cultivated Plants.

Evolution

The evolution of plants has resulted in increasing levels of complexity, from the earliest algal mats, through bryophytes, lycopods, ferns to the complex gymnosperms and angiosperms of today. While the groups which appeared earlier continue to thrive, especially in the environments in which they evolved, each new grade of organisation has eventually become more "successful" than its predecessors by most measures.

Evidence suggests that an algal scum formed on the land 1,200 million years ago, but it was not until the Ordovician Period, around 450 million years ago, that land plants appeared. These began to diversify in the late Silurian Period, around 420 million years ago, and the fruits of their diversification are displayed in remarkable detail in an early Devonian fossil assemblage from the Rhynie chert. This chert preserved early plants in cellular detail, petrified in volcanic springs. By the middle of the Devonian Period most of the features recognised in plants today are present, including roots, leaves and secondary wood, and by late Devonian times seeds had evolved. Late Devonian plants had thereby reached a degree of sophistication that allowed them to form forests of tall trees. Evolutionary innovation continued after the Devonian period. Most plant groups were relatively unscathed by the Permo-Triassic extinction event, although the structures

of communities changed. This may have set the scene for the evolution of flowering plants in the Triassic (~200 million years ago), which exploded in the Cretaceous and Tertiary. The latest major group of plants to evolve were the grasses, which became important in the mid Tertiary, from around 40 million years ago. The grasses, as well as many other groups, evolved new mechanisms of metabolism to survive the low CO_2 and warm, dry conditions of the tropics over the last 10 million years.

Embryophytes

Dicksonia antarctica, a species of tree fern

The plants that are likely most familiar to us are the multicellular land plants, called embryophytes. They include the vascular plants, plants with full systems of leaves, stems,

and roots. They also include a few of their close relatives, often called *bryophytes*, of which mosses and liverworts are the most common.

All of these plants have eukaryotic cells with cell walls composed of cellulose, and most obtain their energy through photosynthesis, using light and carbon dioxide to synthesize food. About three hundred plant species do not photosynthesize but are parasites on other species of photosynthetic plants. Plants are distinguished from green algae, which represent a mode of photosynthetic life similar to the kind modern plants are believed to have evolved from, by having specialized reproductive organs protected by non-reproductive tissues.

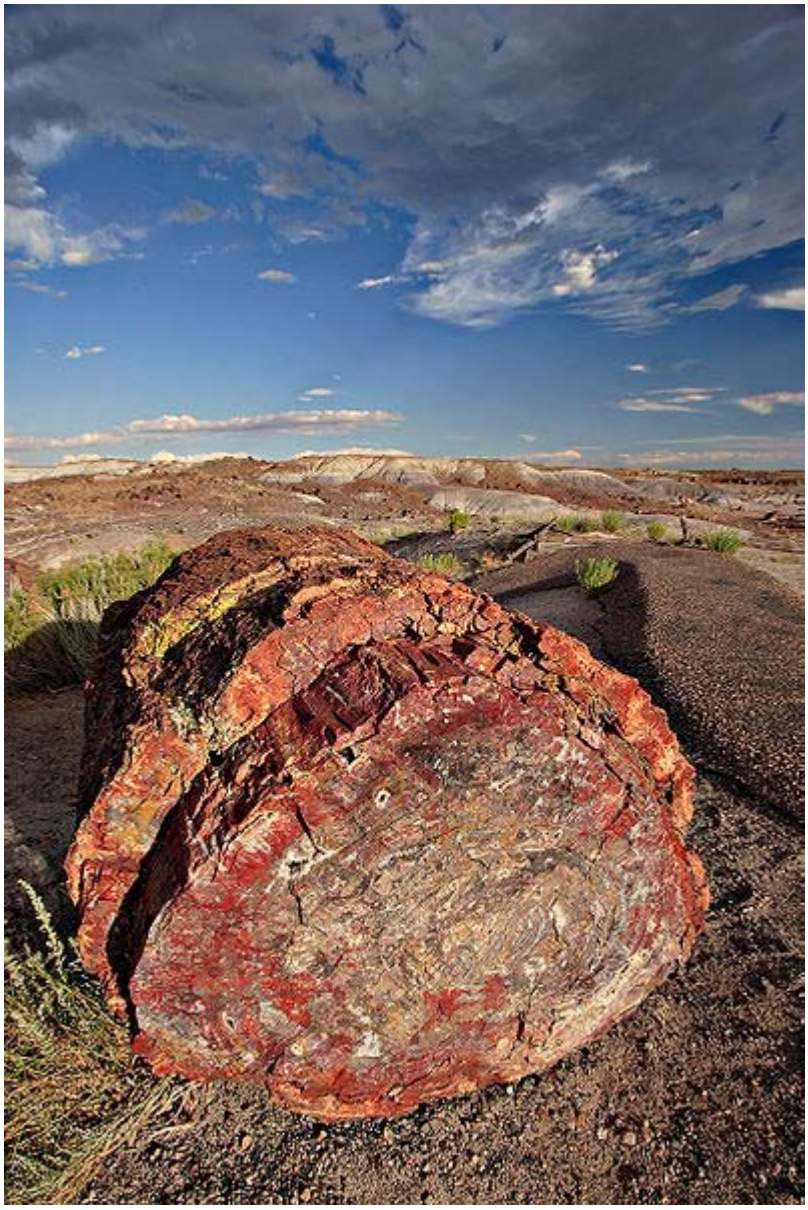
Bryophytes first appeared during the early Paleozoic. They can only survive where moisture is available for significant periods, although some species are desiccation tolerant. Most species of bryophyte remain small throughout their life-cycle. This involves an alternation between two generations: a haploid stage, called the gametophyte, and a diploid stage, called the sporophyte. The sporophyte is short-lived and remains dependent on its parent gametophyte.

Vascular plants first appeared during the Silurian period, and by the Devonian had diversified and spread into many different land environments. They have a number of adaptations that allowed them to overcome the limitations of the bryophytes. These include a cuticle resistant to desiccation, and vascular tissues which transport water throughout the organism. In most the sporophyte acts as a separate individual, while the gametophyte remains small.

The first primitive seed plants, Pteridosperms (seed ferns) and Cordaites, both groups now extinct, appeared in the late Devonian and diversified through the Carboniferous, with further evolution through the Permian and Triassic periods. In these the gametophyte stage is completely reduced, and the sporophyte begins life inside an enclosure called a seed, which develops while on the parent plant, and with fertilisation by means of pollen grains. Whereas other vascular plants, such as ferns, reproduce by means of spores and so need moisture to develop, some seed plants can survive and reproduce in extremely arid conditions.

Early seed plants are referred to as gymnosperms (naked seeds), as the seed embryo is not enclosed in a protective structure at pollination, with the pollen landing directly on the embryo. Four surviving groups remain widespread now, particularly the conifers, which are dominant trees in several biomes. The angiosperms, comprising the flowering plants, were the last major group of plants to appear, emerging from within the gymnosperms during the Jurassic and diversifying rapidly during the Cretaceous. These differ in that the seed embryo (angiosperm) is enclosed, so the pollen has to grow a tube to penetrate the protective seed coat; they are the predominant group of flora in most biomes today.

Fossils



A petrified log in Petrified Forest National Park

Plant fossils include roots, wood, leaves, seeds, fruit, pollen, spores, phytoliths, and amber (the fossilized resin produced by some plants). Fossil land plants are recorded in terrestrial, lacustrine, fluvial and nearshore marine sediments. Pollen, spores and algae (dinoflagellates and acritarchs) are used for dating sedimentary rock sequences. The remains of fossil plants are not as common as fossil animals, although plant fossils are locally abundant in many regions worldwide.

The earliest fossils clearly assignable to Kingdom Plantae are fossil green algae from the Cambrian. These fossils resemble calcified multicellular members of the Dasycladales.

Earlier Precambrian fossils are known which resemble single-cell green algae, but definitive identity with that group of algae is uncertain.

The oldest known fossils of embryophytes date from the Ordovician, though such fossils are fragmentary. By the Silurian, fossils of whole plants are preserved, including the lycophyte *Baragwanathia longifolia*. From the Devonian, detailed fossils of rhyniophytes have been found. Early fossils of these ancient plants show the individual cells within the plant tissue. The Devonian period also saw the evolution of what many believe to be the first modern tree, *Archaeopteris*. This fern-like tree combined a woody trunk with the fronds of a fern, but produced no seeds.

The Coal measures are a major source of Paleozoic plant fossils, with many groups of plants in existence at this time. The spoil heaps of coal mines are the best places to collect; coal itself is the remains of fossilised plants, though structural detail of the plant fossils is rarely visible in coal. In the Fossil Forest at Victoria Park in Glasgow, Scotland, the stumps of *Lepidodendron* trees are found in their original growth positions.

The fossilized remains of conifer and angiosperm roots, stems and branches may be locally abundant in lake and inshore sedimentary rocks from the Mesozoic and Cenozoic eras. Sequoia and its allies, magnolia, oak, and palms are often found.

Petrified wood is common in some parts of the world, and is most frequently found in arid or desert areas where it is more readily exposed by erosion. Petrified wood is often heavily silicified (the organic material replaced by silicon dioxide), and the impregnated tissue is often preserved in fine detail. Such specimens may be cut and polished using lapidary equipment. Fossil forests of petrified wood have been found in all continents.

Fossils of seed ferns such as *Glossopteris* are widely distributed throughout several continents of the Southern Hemisphere, a fact that gave support to Alfred Wegener's early ideas regarding Continental drift theory.

Structure, growth, and development

Most of the solid material in a plant is taken from the atmosphere. Through a process known as photosynthesis, most plants use the energy in sunlight to convert carbon dioxide from the atmosphere, plus water, into simple sugars. Parasitic plants, on the other hand, use the resources of its host to grow. These sugars are then used as building blocks and form the main structural component of the plant. Chlorophyll, a green-colored, magnesium-containing pigment is essential to this process; it is generally present in plant leaves, and often in other plant parts as well.

Plants usually rely on soil primarily for support and water (in quantitative terms), but also obtain compounds of nitrogen, phosphorus, and other crucial elemental nutrients. Epiphytic and lithophytic plants often depend on rainwater or other sources for nutrients and carnivorous plants supplement their nutrient requirements with insect prey that they capture. For the majority of plants to grow successfully they also require oxygen in the

atmosphere and around their roots for respiration. However, some plants grow as submerged aquatics, using oxygen dissolved in the surrounding water, and a few specialized vascular plants, such as mangroves, can grow with their roots in anoxic conditions.

The leaf is usually the primary site of photosynthesis in plants

There is no photosynthesis in deciduous leaves in autumn

Factors affecting growth

The genotype of a plant affects its growth. For example, selected varieties of wheat grow rapidly, maturing within 110 days, whereas others, in the same environmental conditions, grow more slowly and mature within 155 days.

Growth is also determined by environmental factors, such as temperature, available water, available light, and available nutrients in the soil. Any change in the availability of these external conditions will be reflected in the plants growth.

Biotic factors are also capable of affecting plant growth. Plants compete with other plants for space, water, light and nutrients. Plants can be so crowded that no single individual

produces normal growth, causing etiolation and chlorosis. Optimal plant growth can be hampered by grazing animals, suboptimal soil composition, lack of mycorrhizal fungi, and attacks by insects or plant diseases, including those caused by bacteria, fungi, viruses, and nematodes.

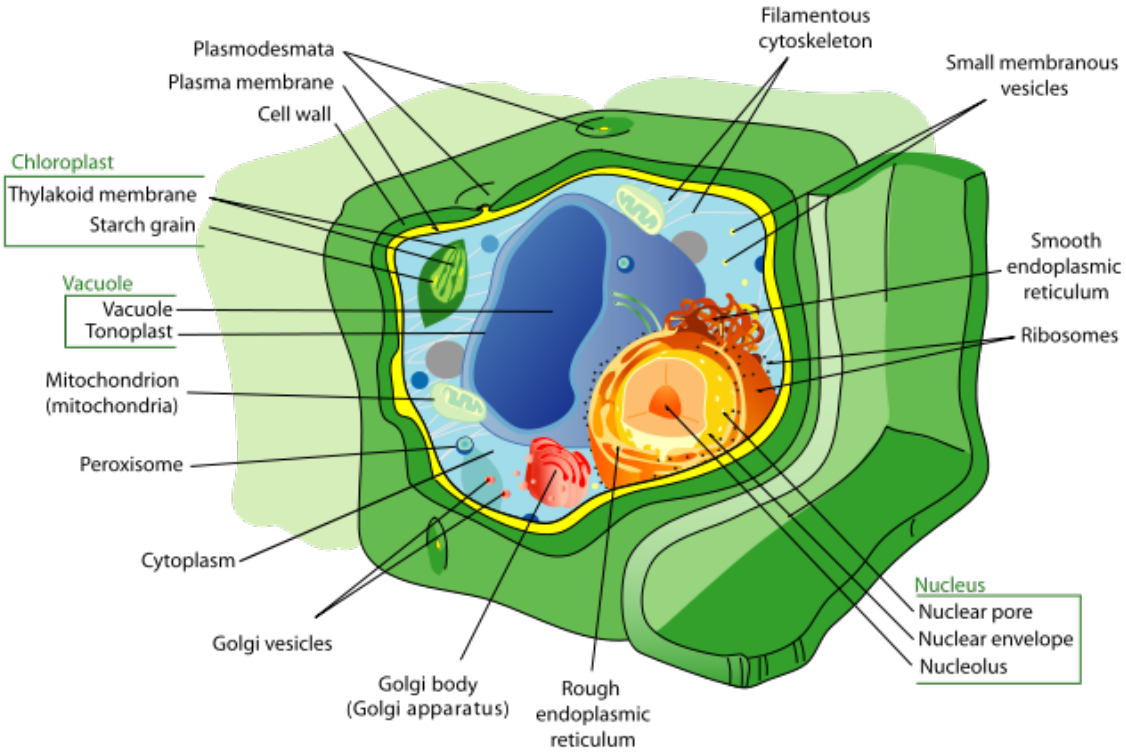
Simple plants like algae may have short life spans as individuals, but their populations are commonly seasonal. Other plants may be organized according to their seasonal growth pattern: annual plants live and reproduce within one growing season, biennial plants live for two growing seasons and usually reproduce in second year, and perennial plants live for many growing seasons and continue to reproduce once they are mature. These designations often depend on climate and other environmental factors; plants that are annual in alpine or temperate regions can be biennial or perennial in warmer climates. Among the vascular plants, perennials include both evergreens that keep their leaves the entire year, and deciduous plants which lose their leaves for some part of it. In temperate and boreal climates, they generally lose their leaves during the winter; many tropical plants lose their leaves during the dry season.

The growth rate of plants is extremely variable. Some mosses grow less than 0.001 millimeters per hour (mm/h), while most trees grow 0.025-0.250 mm/h. Some climbing species, such as kudzu, which do not need to produce thick supportive tissue, may grow up to 12.5 mm/h.

Dried dead plants

Plants protect themselves from frost and dehydration stress with antifreeze proteins, heat-shock proteins and sugars (sucrose is common). LEA (Late Embryogenesis Abundant) protein expression is induced by stresses and protects other proteins from aggregation as a result of desiccation and freezing.

Plant cell



Plant cell structure

Plant cells are typically distinguished by their large water-filled central vacuole, chloroplasts, and rigid cell walls that are made up of cellulose, hemicellulose, and pectin. Cell division is also characterized by the development of a phragmoplast for the construction of a cell plate in the late stages of cytokinesis. Just as in animals, plant cells differentiate and develop into multiple cell types. Totipotent meristematic cells can differentiate into vascular, storage, protective (e.g. epidermal layer), or reproductive tissues, with more primitive plants lacking some tissue types.

Physiology

Photosynthesis

Plants are photosynthetic, which means that they manufacture their own food molecules using energy obtained from light. The primary mechanism plants have for capturing light energy is the pigment chlorophyll. All green plants contain two forms of chlorophyll, chlorophyll *a* and chlorophyll *b*. The latter of these pigments is not found in red or brown algae.

Immune system

By means of cells that behave like nerves, plants receive and distribute within their systems information about incident light intensity and quality. Incident light which stimulates a chemical reaction in one leaf, will cause a chain reaction of signals to the entire plant via a type of cell termed a *"bundle sheath cell"*. Researchers from the Warsaw University of Life Sciences in Poland, found that plants have a specific memory for varying light conditions which prepares their immune systems against seasonal pathogens.

Internal distribution

Vascular plants differ from other plants in that they transport nutrients between different parts through specialized structures, called xylem and phloem. They also have roots for taking up water and minerals. The xylem moves water and minerals from the root to the rest of the plant, and the phloem provides the roots with sugars and other nutrient produced by the leaves.

Ecology

The photosynthesis conducted by land plants and algae is the ultimate source of energy and organic material in nearly all ecosystems. Photosynthesis radically changed the composition of the early Earth's atmosphere, which as a result is now 21% oxygen. Animals and most other organisms are aerobic, relying on oxygen; those that do not are confined to relatively rare anaerobic environments. Plants are the primary producers in most terrestrial ecosystems and form the basis of the food web in those ecosystems. Many animals rely on plants for shelter as well as oxygen and food.

Land plants are key components of the water cycle and several other biogeochemical cycles. Some plants have coevolved with nitrogen fixing bacteria, making plants an important part of the nitrogen cycle. Plant roots play an essential role in soil development and prevention of soil erosion.

Distribution

Plants are distributed worldwide in varying numbers. While they inhabit a multitude of biomes and ecoregions, few can be found beyond the tundras at the northernmost regions of continental shelves. At the southern extremes, plants have adapted tenaciously to the prevailing conditions.

Plants are often the dominant physical and structural component of habitats where they occur. Many of the Earth's biomes are named for the type of vegetation because plants are the dominant organisms in those biomes, such as grasslands and forests.

Ecological relationships

The Venus flytrap, a species of carnivorous plant

Numerous animals have coevolved with plants. Many animals pollinate flowers in exchange for food in the form of pollen or nectar. Many animals disperse seeds, often by eating fruit and passing the seeds in their feces. Myrmecophytes are plants that have coevolved with ants. The plant provides a home, and sometimes food, for the ants. In exchange, the ants defend the plant from herbivores and sometimes competing plants. Ant wastes provide organic fertilizer.

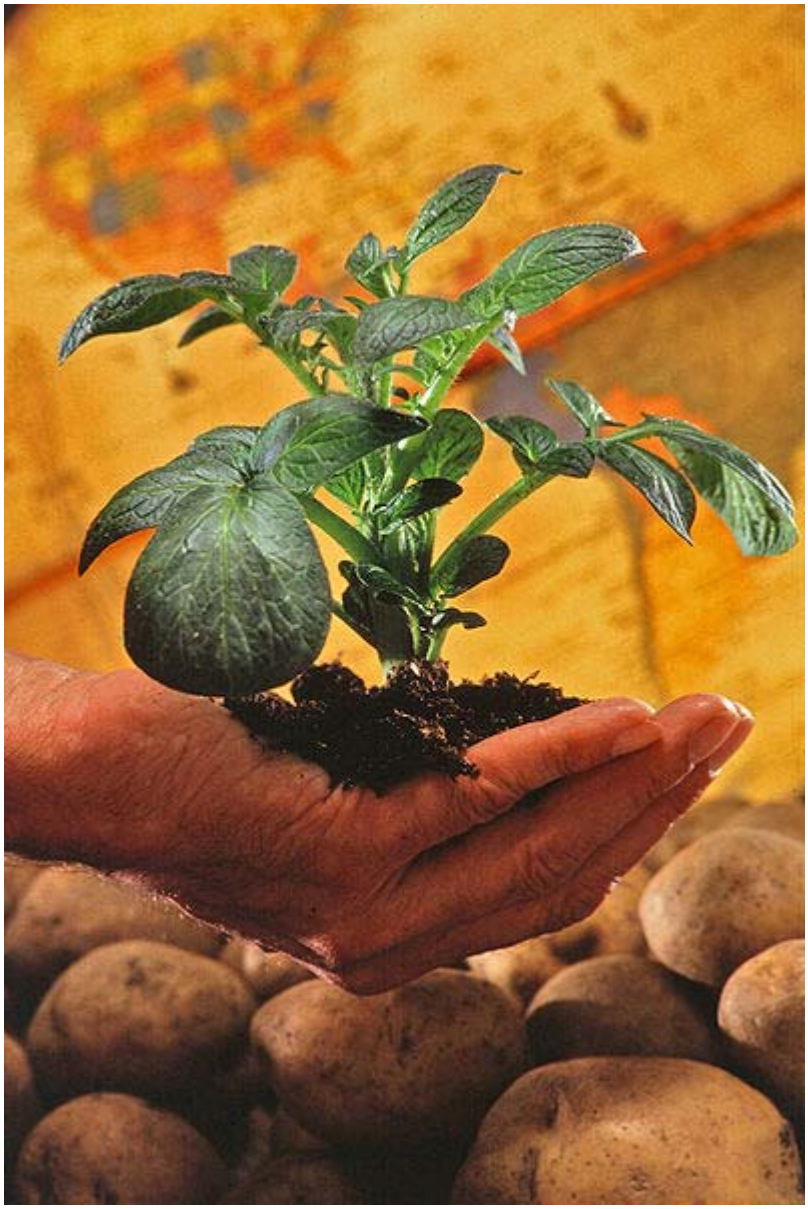
The majority of plant species have various kinds of fungi associated with their root systems in a kind of mutualistic symbiosis known as mycorrhiza. The fungi help the plants gain water and mineral nutrients from the soil, while the plant gives the fungi carbohydrates manufactured in photosynthesis. Some plants serve as homes for endophytic fungi that protect the plant from herbivores by producing toxins. The fungal endophyte, *Neotyphodium coenophialum*, in tall fescue (*Festuca arundinacea*) does tremendous economic damage to the cattle industry in the U.S.

Various forms of parasitism are also fairly common among plants, from the semi-parasitic mistletoe that merely takes some nutrients from its host, but still has photosynthetic leaves, to the fully parasitic broomrape and toothwort that acquire all their nutrients through connections to the roots of other plants, and so have no chlorophyll. Some plants, known as myco-heterotrophs, parasitize mycorrhizal fungi, and hence act as epiparasites on other plants.

Many plants are epiphytes, meaning they grow on other plants, usually trees, without parasitizing them. Epiphytes may indirectly harm their host plant by intercepting mineral nutrients and light that the host would otherwise receive. The weight of large numbers of epiphytes may break tree limbs. Hemiepiphytes like the strangler fig begin as epiphytes but eventually set their own roots and overpower and kill their host. Many orchids, bromeliads, ferns and mosses often grow as epiphytes. Bromeliad epiphytes accumulate water in leaf axils to form phytotelmata, complex aquatic food webs.

Approximately 630 plants are carnivorous, such as the Venus Flytrap (*Dionaea muscipula*) and sundew (*Drosera* species). They trap small animals and digest them to obtain mineral nutrients, especially nitrogen and phosphorus.

Importance



Potato plant. Potatoes spread to the rest of the world after European contact with the Americas in the late 15th and early 16th centuries and have since become an important field crop.

Timber in storage for later processing at a sawmill

A section of a Yew branch showing 27 annual growth rings, pale sapwood and dark heartwood, and pith (centre dark spot). The dark radial lines are longitudinal sections of small branches which became included by growth of the tree.

The study of plant uses by people is termed economic botany or ethnobotany; some consider economic botany to focus on modern cultivated plants, while ethnobotany focuses on indigenous plants cultivated and used by native peoples. Human cultivation of plants is part of agriculture, which is the basis of human civilization. Plant agriculture is subdivided into agronomy, horticulture and forestry.

Food

Much of human nutrition depends on land plants, either directly or indirectly.
Human nutrition depends to a large extent on cereals, especially maize (or corn), wheat and rice. Other staple crops include potato, cassava, and legumes. Human food also includes vegetables, spices, and certain fruits, nuts, herbs, and edible flowers.
Beverages produced from plants include coffee, tea, wine, beer and alcohol.
Sugar is obtained mainly from sugar cane and sugar beet.
Cooking oils and margarine come from maize, soybean, rapeseed, safflower, sunflower, olive and others.
Food additives include gum arabic, guar gum, locust bean gum, starch and pectin.

Livestock animals including cows, pigs, sheep, and goats are all herbivores; and feed primarily or entirely on cereal plants, particularly grasses.

Nonfood products

Wood is used for buildings, furniture, paper, cardboard, musical instruments and sports equipment. Cloth is often made from cotton, flax or synthetic fibers derived from cellulose, such as rayon and acetate. Renewable fuels from plants include firewood, peat and many other biofuels. Coal and petroleum are fossil fuels derived from plants. Medicines derived from plants include aspirin, taxol, morphine, quinine, reserpine, colchicine, digitalis and vincristine. There are hundreds of herbal supplements such as ginkgo, Echinacea, feverfew, and Saint John's wort. Pesticides derived from plants include nicotine, rotenone, strychnine and pyrethrins. Drugs obtained from plants include opium, cocaine and marijuana. Poisons from plants include ricin, hemlock and curare. Plants are the source of many natural products such as fibers, essential oils, natural dyes, pigments, waxes, tannins, latex, gums, resins, alkaloids, amber and cork. Products derived from plants include soaps, paints, shampoos, perfumes, cosmetics, turpentine, rubber, varnish, lubricants, linoleum, plastics, inks, chewing gum and hemp rope. Plants are also a primary source of basic chemicals for the industrial synthesis of a vast array of organic chemicals. These chemicals are used in a vast variety of studies and experiments.

Aesthetic uses

Thousands of plant species are cultivated for aesthetic purposes as well as to provide shade, modify temperatures, reduce wind, abate noise, provide privacy, and prevent soil erosion. People use cut flowers, dried flowers and houseplants indoors or in greenhouses. In outdoor gardens, lawn grasses, shade trees, ornamental trees, shrubs, vines, herbaceous perennials and bedding plants are used. Images of plants are often used in art, architecture, humor, language, and photography and on textiles, money, stamps, flags and coats of arms. Living plant art forms include topiary, bonsai, ikebana and espalier. Ornamental plants have sometimes changed the course of history, as in tulipomania. Plants are the basis of a multi-billion dollar per year tourism industry which includes travel to arboretums, botanical gardens, historic gardens, national parks, tulip festivals, rainforests, forests with colorful autumn leaves and the National Cherry Blossom Festival. Venus Flytrap, sensitive plant and resurrection plant are examples of plants sold as novelties.

Scientific and cultural uses

Tree rings are an important method of dating in archeology and serve as a record of past climates. Basic biological research has often been done with plants, such as the pea plants used to derive Gregor Mendel's laws of genetics. Space stations or space colonies may one day rely on plants for life support. Plants are used as national and state emblems, including state trees and state flowers. Ancient trees are revered and many are famous. Numerous world records are held by plants. Plants are often used as memorials, gifts and to mark special occasions such as births, deaths, weddings and holidays. Plants figure

prominently in mythology, religion and literature. The field of ethnobotany studies plant use by indigenous cultures which helps to conserve endangered species as well as discover new medicinal plants. Gardening is the most popular leisure activity in the U.S. Working with plants or horticulture therapy is beneficial for rehabilitating people with disabilities. Certain plants contain psychotropic chemicals which are extracted and ingested, including tobacco, cannabis (marijuana), and opium.

Negative effects

Weeds are plants that grow where people do not want them. People have spread plants beyond their native ranges and some of these introduced plants become invasive, damaging existing ecosystems by displacing native species. Invasive plants cause billions of dollars in crop losses annually by displacing crop plants, they increase the cost of production and the use of chemical means to control them affects the environment.

Plants may cause harm to people and animals. Plants that produce windblown pollen invoke allergic reactions in people who suffer from hay fever. A wide variety of plants are poisonous to people and/or animals. Toxalbumins are plant poisons fatal to most mammals and act as a serious deterrent to consumption. Several plants cause skin irritations when touched, such as poison ivy. Certain plants contain psychotropic chemicals, which are extracted and ingested or smoked, including tobacco, cannabis (marijuana), cocaine and opium. Smoking causes damage to health or even death, while some drugs may also be harmful or fatal to people. Both illegal and legal drugs derived from plants may have negative effects on the economy, affecting worker productivity and law enforcement costs. Some plants cause allergic reactions in people and animals when ingested, while other plants cause food intolerances that negatively affect health.

Chapter- 2

Embryophyte

Land plants Temporal range: Late Silurian–Recent (Spores from Dapingian (early Middle Ordovician)

Fern Leaf

Scientific classification	
Kingdom:	Plantae
Subkingdom:	**Embryophyta**

Divisions

- **Non-vascular land plants (bryophytes)**
  - Marchantiophyta - liverworts
  - Bryophyta - mosses
  - Anthocerotophyta - hornworts
  - †Horneophytopsida
- **Vascular plants (tracheophytes)**
  - †Rhyniophyta—rhyniophytes
  - †Zosterophyllophyta—zosterophylls
  - Lycopodiophyta—clubmosses
  - †Trimerophytophyta—trimerophytes
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    - †Pteridospermatophyta - seed ferns
    - Pinophyta - conifers
    - Cycadophyta - cycads
    - Ginkgophyta - ginkgo

- Gnetophyta - gnetae
- Magnoliophyta - flowering plants

The **land plants** or **embryophytes**, more formally **Embryophyta** or **Metaphyta**, are the most familiar group of plants. They are called 'land plants' because they live primarily in terrestrial habitats, in contrast with the related green algae that are primarily aquatic. The embryophytes include trees, flowers, ferns, mosses, and various other **green land plants**. All are complex multicellular eukaryotes with specialized reproductive organs. With very few exceptions, embryophytes obtain their energy through photosynthesis (that is, by absorbing light); and they synthesize their food from carbon dioxide.

Description

The evolutionary origins of the embryophytes are discussed further below, but they are believed to have evolved from within a group of complex green algae during the Paleozoic era (which started around 540 million years ago). The Charales or stoneworts appear to be the best living illustration of that developmental step. Embryophytes are primarily adapted for life on land, although some are secondarily aquatic. Accordingly, they are often called *land plants* or *terrestrial plants*.

On a microscopic level, the cells of embryophytes remain very similar to those of green algae. They are eukaryotic, with a cell wall composed of cellulose and plastids surrounded by two membranes. The latter usually take the form of chloroplasts, which conduct photosynthesis and store food in the form of starch, and are characteristically pigmented with chlorophylls *a* and *b*, generally giving them a bright green color. Embryophyte cells also generally have an enlarged central vacuole or tonoplast, which maintains cell turgor and keeps the plant rigid. They lack flagella and centrioles except in certain gametes.

Embryophytes have three features related to their reproduction which collectively distinguish them from all other plant lineages. Firstly, they have a life cycle which involves 'alternation of generations'. A multicellular generation with a single set of chromosomes – the haploid gametophyte – produces sperm and eggs which fuse and grow into a multicellular generation with twice the number of chromosomes – the diploid sporophyte. The mature sporophyte produces spores which grow into a gametophyte, thus completing the cycle. Secondly, their gametophytes produce sperm and eggs in multicellular structures (called 'antheridia' and 'archegonia' respectively) containing sterile tissue (i.e. non-reproducing tissue). Thirdly, the fertilized egg (the zygote) initially develops within the archegonium where it is protected and provided with nutrition. This last feature is the origin of the term 'embryophyte' – the fertilized egg develops into a protected embryo, rather than dispersing as a single cell.

Embryophytes also differ from algae in having metamers. Metamers are repeated units of development, in which each unit derives from a single cell, but the resulting product tissue or part is largely the same for each cell. The whole organism is thus constructed

from similar, repeating parts or *metamers*. Accordingly, these plants are sometimes termed 'metaphytes' and classified as the group Metaphyta.

Phylogeny and classification

All green algae and land plants are now known to form a single evolutionary lineage or clade, one name for which is Viridiplantae (i.e. 'green plants'). According to several molecular clock estimates the Viridiplantae split 1,200 million years ago to 725 million years ago into two clades: chlorophytes and streptophytes. The chlorophytes are considerably more diverse (with around 700 genera) and were originally marine, although some groups have since spread into fresh water. The streptophyte algae (i.e. the streptophyte clade minus the land plants) are less diverse (with around 122 genera) and adapted to fresh water very early in their evolutionary history. They have not spread into marine environments (only a few stoneworts, which belong to this group, tolerate brackish water). Some time during the Ordovician period (which started around 490 million years ago) one or more streptophytes invaded the land and began the evolution of the embryophyte land plants.

Becker and Marin speculate that land plants evolved from streptophytes rather than any other group of algae because streptophytes were adapted to living in fresh water. This prepared them to tolerate a range of environmental conditions found on land. Fresh water living made them tolerant of exposure to rain; living in shallow pools required tolerance to temperature variation, high levels of ultra-violet light and seasonal dehydration.

Relationships between the groups making up Viridiplantae are still being elucidated; views have changed considerably since 2000 and classifications have not yet caught up. However, the division between chlorophytes and streptophytes and the evolution of embryophytes from within the latter group, as shown in the cladogram below, are well established. Three approaches to classification are shown. Older classifications, as on the left, treated all green algae as a single division of the plant kingdom under the name Chlorophyta. Land plants were then placed in separate divisions. All the streptophyte algae can be grouped into one paraphyletic taxon, as in the middle, allowing the embryophytes to form a taxon at the same level. Alternatively, the embryophytes can be sunk into a monophyletic taxon comprising all the streptophytes, as on the right. A variety of names have been used for the different groups which result from these approaches; those used below are only one of a number of possibilities. The higher-level classification of the Viridiplantae varies considerably, resulting in widely different ranks being assigned to the embryophytes.

Studies based on morphology rather than on genes and proteins have regularly reached different conclusions; for example that neither the monilophytes (ferns and horsetails) nor the gymnosperms are a natural or monophyletic group.

There is considerable variation in how these relationships are converted into a formal classification. Consider the angiosperms or flowering plants. Many botanists, following Lindley in 1830, have treated the angiosperms as a division. Researchers concerned with

fossil plants have usually followed Banks in treating the tracheophytes or vascular plants as a division, so that the angiosperms become a class or even a subclass. Two very different systems are shown below. The classification on the left is a traditional one, in which ten living groups are treated as separate divisions; the classification on the right (based on Kenrick and Crane's 1997 treatment) sharply reduces the rank of groups such as the flowering plants. (More complex classifications are needed if extinct plants are included.)

Two contrasting classifications of living land plants

Liverworts	Marchiantiophyta	Marchiantiophyta
Mosses	Bryophyta	Bryophyta
Hornworts	Anthocerotophyta	Anthocerotophyta
		Tracheophyta
Lycophytes	Lycopodiophyta	Lycophytina
		Euphyllophytina
Ferns and horsetails	Pteridophyta	Moniliformopses
		Radiatopses
Cycads	Cycadophyta	Cycadatae
Conifers	Pinophyta	Coniferophytatae
Ginkgo	Ginkgophyta	Ginkgoatae
Gnetophytes	Gnetophyta	Anthophytatae
Flowering plants	Magnoliophyta	

Diversity

Bryophytes

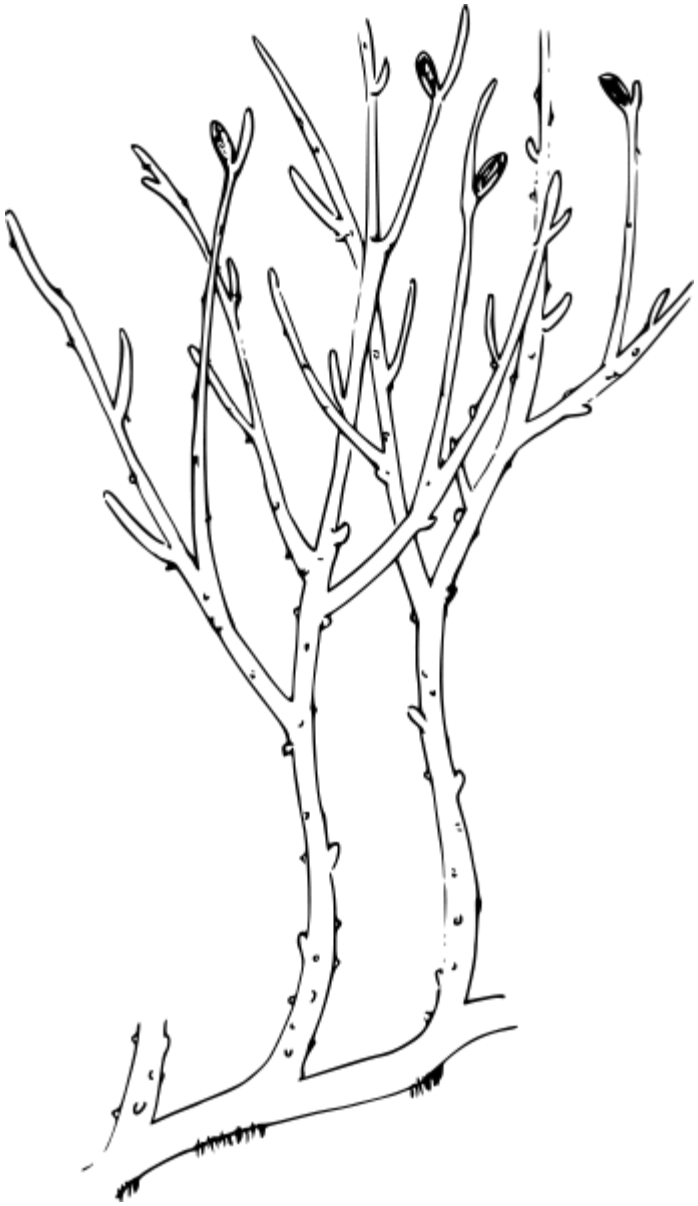
Mosses are one group of 'bryophytes'

According to the phylogeny shown above, the first diverging embryophytes were the group informally called the 'bryophytes'. Their life-cycle is strongly dominated by the gametophyte generation. Their sporophytes are very different in structure and function, remaining small and dependent on the parent gametophyte for their entire brief life. There are three surviving groups:

- Marchantiophyta (liverworts)
- Bryophyta (mosses)
- Anthocerotophyta (hornworts)

All of them are relatively small and are usually confined to moist environments, relying on water to disperse their spores. Although some mosses have quite complex water-conducting vessels, bryophytes lack true vascular tissue.

Rise of vascular plants



Reconstruction of a plant of *Rhynia*

During the Silurian and Devonian periods (around 440 to 360 million years ago), plants evolved which possessed true vascular tissue, including cells with walls strengthened by lignin (tracheids). Some extinct early plants appear to be between the grade of organization bryophytes and that of true vascular plants (eutracheophytes). Genera such as *Horneophyton* have water-conducting tissue more like that of mosses, but a different life-cycle in which the sporophyte is more developed than the gametophyte. Genera such as *Rhynia* have a similar life-cycle but have simple tracheids and so are a kind of vascular plant.

During the Devonian period, vascular plants diversified and spread to many different land environments. In addition to vascular tissues which transport water throughout the body, tracheophytes have an outer layer or cuticle that resists drying out. The sporophyte is the dominant generation, and in modern species develops leaves, stems and roots, while the gametophyte remains very small.

Lycophytes and euphyllophytes

Selaginella species, a lycophyte

All the vascular plants which disperse through spores were once thought to be related (and were often grouped as 'ferns and allies'). However, recent research suggests that leaves evolved quite separately in two different lineages. The lycophytes or lycopodiophytes – modern clubmosses, spikemosses and quillworts – make up less than 1% of living vascular plants. They have small leaves, often called 'microphylls' or 'lycophylls', which are borne all along the stems in the clubmosses and spikemosses, and which effectively grow from the base, via an intercalary meristem. It is believed that microphylls evolved from outgrowths on stems, such as spines, which later acquired veins (vascular traces).

Although the living lycophytes are all relatively small and inconspicuous plants, more common in the moist tropics than in temperate regions, during the Carboniferous period tree-like lycophytes (such as *Lepidodendron*) formed huge forests that dominated the landscape.

The euphyllophytes, making up more than 99% of living vascular plant species, have large 'true' leaves (megaphylls), which effectively grow from the sides or the apex, via marginal or apical meristems. One theory is that megaphylls developed from three-dimensional branching systems by first 'planation' – flattening to produce a two dimensional branched structure – and then 'webbing' – tissue growing out between the flattened branches. Others have questioned whether megaphylls developed in the same way in different groups.

Ferns and horsetails

Athyrium filix-femina, unrolling young frond

Euphyllophytes are divided into two lineages: the ferns and horsetails (monilophytes) and the seed plants (spermatophytes). Like all the preceding groups, the monilophytes continue to use spores as their main method of dispersal. Traditionally, whisk ferns and horsetails were treated as distinct from 'true' ferns. Recent research suggests that they all belong together, although there are differences of opinion on the exact classification to be used. Living whisk ferns and horsetails do not have the large leaves (megaphylls) which would be expected of euphyllophytes. However, this has probably resulted from

reduction, as evidenced by early fossil horsetails, in which the leaves are broad with branching veins.

Ferns are a large and diverse group, with some 12,000 species. A stereotypical fern has broad, much divided leaves, which grow by unrolling.

Seed plants

Large seed of a horse chestnut, *Aesculus hippocastanum*

Seed plants, which first appeared in the fossil record towards the end of the Paleozoic era, reproduce using desiccation-resistant capsules called seeds. Starting from a plant which disperses by spores, highly complex changes are needed to produce seeds. The sporophyte has two kinds of spore-forming organs (sporangia). One kind, the megasporangium, produces only a single large spore (a megaspore). This sporangium is surrounded by one or more sheathing layers (integuments) which form the seed coat. Within the seed coat, the megaspore develops into a tiny gametophyte, which in turn produces one or more egg cells. Before fertilization, the sporangium and its contents plus its coat is called an 'ovule'; after fertilization a 'seed'. In parallel to these developments, the other kind of sporangium, the microsporangium, produces microspores. A tiny gametophyte develops inside the wall of a microspore, producing a pollen grain. Pollen grains are physically transferred between plants by the wind or by insects. When a pollen grain reaches an ovule, it enters via a microscopic gap in the coat (the micropyle). The

tiny gametophyte inside the pollen grain then produces sperm cells which move to the egg cell and fertilize it.

Conifer forest in Northern California

Seed plants include two groups with living members, the gymnosperms and the angiosperms or flowering plants. In gymnosperms, the ovules or seeds are not further enclosed. In angiosperms, they are enclosed in ovaries. A split ovary with a visible seed can be seen in the image to the right. Angiosperms typically also have other, secondary structures, such as petals, which together form a flower.

Extant seed plants are divided into five groups:

Gymnosperms

- Pinophyta - conifers
- Cycadophyta - cycads
- Ginkgophyta - ginkgo
- Gnetophyta - gnetophytes

Angiosperms

- Magnoliophyta – flowering plants

Chapter- 3

Bryophyte

Marchantia, a liverwort

Bryophyte is a traditional name used to refer to all embryophytes (land plants) that do not have true vascular tissue and are therefore called 'non-vascular plants'. Some bryophytes do have specialized tissues for the transport of water; however since these do not contain lignin, they are not considered to be true vascular tissue. Currently bryophytes are thought not to be a natural or monophyletic group; however the name is convenient and remains in use as a collective term. Bryophytes produce enclosed reproductive structures (gametangia and sporangia), but they produce neither flowers nor

seeds, reproducing via spores. The term *bryophyte* comes from Greek *βρύον* - *bryon*, "tree-moss, oyster-green" + *φυτόν* - *fyton* "plant".

Bryophyte classification and phylogeny

Mosses are one group of bryophytes

Hornworts are the third group of bryophytes

Traditionally, all living land plants without vascular tissues were classified in a single taxonomic group, often a division (or phylum). More recently, phylogenetic research has questioned whether the bryophytes form a monophyletic group and thus whether they should form a single taxon. A broad consensus among systematists has recently emerged that bryophytes as a whole are not a natural group (i.e. are paraphyletic), although each of the three extant (living) groups is monophyletic. The three lineages are Marchantiophyta (liverworts), Bryophyta (mosses) and Anthocerotophyta (hornworts).

The vascular plants or tracheophytes are the fourth lineage of living land plants. Currently there is some uncertainty over the exact evolutionary relationships among these four lineages, although this may be nearing resolution as data on a variety of coding and non-coding DNA sequences from all three genomes (chloroplast, mitochondrion and nucleus) in addition to protein sequences are brought to bear on the problem. Although a 2005 study supported the traditional view that the bryophytes form a monophyletic group, the preponderance of currently available evidence suggests that the hornworts are sister to vascular plants and liverworts are sister to all other land plants.

When extinct plants are taken into account, the picture is slightly altered. There are extinct land plants, such as the horneophytes, which are not bryophytes, but also are not vascular plants since like bryophytes they do not have true vascular tissue. A different distinction is needed. In bryophytes, the sporophyte is a simple unbranched structure with a single spore-forming organ (sporangium). In all other land plants, the polysporangiophytes, the sporophyte is branched and carries many sporangia. It has been argued that this contrast between bryophytes and other land plants is less misleading than

the traditional one of non-vascular versus vascular plant, since many mosses have well-developed water-conducting vessels.

The term "bryophyte" thus refers to a grade of lineages defined primarily by what they lack: compared to other living land plants, they lack vascular tissue containing lignin; compared to all other land plants, they lack branched sporophytes bearing multiple sporangia. The prominence of the gametophyte in the life cycle is also a shared feature of the three bryophyte lineages (extant vascular plants are all sporophyte dominant).

Bryophyte life cycle

Like all land plants (embryophytes), bryophytes show 'alternation of generations'. A haploid gametophyte, each of whose cells contains a fixed number of unpaired chromosomes, gives rise to a diploid sporophyte, each of whose cells contains twice the number of paired chromosomes. Gametophytes produce sperm and eggs which fuse and grow into sporophytes. Sporophytes produce spores which grow into gametophytes.

Bryophytes are gametophyte dominant, meaning that the more prominent, longer-lived plant is the haploid gametophyte. The diploid sporophytes appear only occasionally and typically remain attached to and nutritionally dependent on the gametophyte. They produce a single sporangium (spore producing structure), with, in many cases, a complex capsule aiding in dispersal of the spores.

Liverworts, mosses and hornworts spend most of their lives as gametophytes. Archegonia and antheridia are produced on the gametophytes. These are sometimes at the tips of shoots, in the axils of leaves or hidden under thalli. Some bryophytes create elaborate structures that bear gametangia called gametangiophores. Sperm are flagellated and must swim from antheridia to archegonia. Arthropods may assist in transfer of sperm. Fertilized eggs become zygotes, which develop into sporophyte embryos inside the archegonia. Mature sporophytes do not branch and remain attached to the gametophyte. They consist of a stalk called a seta and a capsule enclosing a single sporangium. Inside the sporangium, spores are produced by meiosis. These are dispersed presumably by wind and if they land in a suitable environment can develop into a new gametophyte. Thus bryophytes disperse by a combination of swimming sperm and spores, in a manner similar to lycophytes and ferns.

Bryophyte sexuality

Individual liverwort, moss and hornwort plants can be unisexual or bisexual. The terms for this are as follows:

- Dioicous bryophytes produce only antheridia (sperm producing structures) or archegonia (egg producing structures) on a single plant body.
- Monoicous bryophytes produce both antheridia and archegonia on the same plant body.

Notice that these terms are *not* the same as monoecious and dioecious, which refer to whether or not a sporophyte plant bears megasporangia, microsporangia or both. Those terms generally apply only to seed plants.

Some bryophyte species may be either monoicous or dioicous depending on environmental conditions. Other species are exclusively unisexual or bisexual.

Chapter- 4

Vascular Plant

Vascular Plants
Temporal range: Mid-Silurian - Recent

Scientific classification

Kingdom: Plantae

Divisions

- Non-seed-bearing plants
  - †Rhyniophyta
  - †Zosterophyllophyta
  - Lycopodiophyta

    - †Trimerophytophyta
    - Pteridophyta
- Superdivision Spermatophyta
    - †Pteridospermatophyta
    - Pinophyta
    - Cycadophyta
    - Ginkgophyta
    - Gnetophyta
    - Magnoliophyta

Vascular plants (also known as **tracheophytes** or **higher plants**) are those plants that have lignified tissues for conducting water, minerals, and photosynthetic products through the plant. Vascular plants include the ferns, clubmosses, flowering plants, conifers and other gymnosperms. Scientific names for the group include *Tracheophyta* and *Tracheobionta*, but neither name is very widely used.

Characteristics

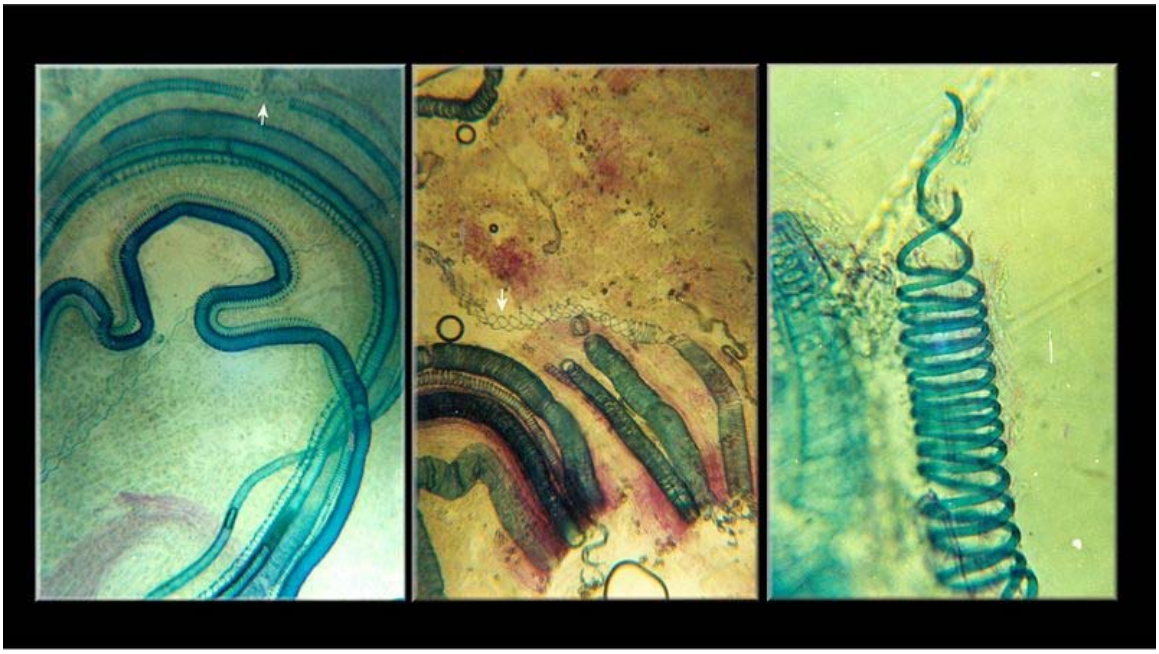
Vascular plants are distinguished by two primary characteristics:

1. Vascular plants have vascular tissues, which circulate resources through the plant. This feature allows vascular plants to evolve to a larger size than non-vascular plants, which lack these specialized conducting tissues and are therefore restricted to relatively small sizes.
2. In vascular plants, the principal generation phase is the *sporophyte*, which is usually diploid with two sets of chromosomes per cell. Only the germ cells and gametophytes are haploid. By contrast, the principal generation phase in non-vascular plants is usually the *gametophyte*, which is haploid with one set of chromosomes per cell. In these plants, generally only the spore stalk and capsule are diploid.

One possible mechanism for the presumed switch from emphasis on the haploid generation to emphasis on the diploid generation is the greater efficiency in spore dispersal with more complex diploid structures. In other words, elaboration of the spore stalk enabled the production of more spore and the ability to release it higher and to broadcast it farther. Such developments may include more photosynthetic area for the spore-bearing structure, the ability to grow independent roots, woody structure for support, and more branching.

Water transport happens in either xylem or phloem: xylem carries water and inorganic solutes upward toward the leaves from the roots, while phloem carries organic solutes throughout the plant.

Nutrient distribution



Photographs showing xylem elements in the shoot of a fig tree (*Ficus alba*): crushed in hydrochloric acid, between slides and cover slips.

Nutrients and water from the soil and the organic compounds produced in leaves are distributed to specific areas in the plant through the xylem and phloem. The xylem draws water and nutrients up from the roots to the upper sections of the plant's body, and the phloem conducts other materials, such as the sucrose produced during photosynthesis, which gives the plant energy to keep growing and seeding.

The xylem consists of tracheids, which are dead hard-walled hollow cells arranged to form tiny tubes to function in water transport. A tracheid cell wall usually contains the polymer lignin. The phloem however consists of living cells called sieve-tube members. Between the sieve-tube members are sieve plates, which have pores to allow molecules to pass through. Sieve-tube members lack such organs as nuclei or ribosomes, but cells next to them, the companion cells, function to keep the sieve-tube members alive.

The movement of nutrients, water and sugars is affected by transpiration, conduction and absorption of water.

Transpiration

The most abundant compound in all plants, as in all life, is water which serves an important role in the various processes taking place. Transpiration is the main process a plant can call upon to move compounds within its tissues. The basic minerals and

nutrients a plant is composed of remain, generally, within the plant. Water is constantly lost from the plant through its stomata to the atmosphere.

Water is transpired from the plants leaves via stomata, carried there via leaf veins and vascular bundles within the plants cambium layer. The movement of water out of the leaf stomata creates, when the leaves are considered collectively, a transpiration pull. The pull is created through water surface tension within the plant cells. The draw of water upwards is assisted by the movement of water into the roots via osmosis. This process also assists the plant in absorbing nutrients from the soil as soluble salts, a process known as absorption. Surprisingly, the movement of water upwards requires very little or no energy from the plant. Hydrogen bonds exist between water molecules, causing them to line up; as the molecules at the top of the plant evaporate, each pulls the next one up to replace it, which in turn pulls on the next one in line.

Absorption

Xylem vessels allow the movement of water and nutrients upwards towards the shoots and leaves through the roots and fine root hairs from the soil. Living root cells passively absorb water in the absence of transpiration pull via osmosis creating root pressure. It is possible for there to be no evapotranspiration and therefore no pull of water towards the shoots and leaves. This is usually due to high temperatures, high humidity, darkness or drought.

Conduction

Xylem and phloem tissues are involved in the conduction processes within plants. Sugars are conducted throughout the plant in the phloem and other nutrients through the xylem. Conduction occurs from a source to a sink for each separate nutrient. Sugars are produced in the leaves (a source) by photosynthesis and transported to the roots (a sink) for use in cellular respiration or storage. Minerals are absorbed in the roots (a source) and transported to the shoots to allow cell division and growth.

Chapter- 5

Marchantiophyta

Liverworts
Temporal range: 472–0 Ma
Mid-Ordovician to recent

"Hepaticae" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification

Kingdom: Plantae

Division: **Marchantiophyta**
Stotler & Stotl.-Crand., 1977 emend. 2000

Classes and Orders

Haplomitriopsida Stotler & Stotl.-Crand.

- Haplomitriales (Calobryales)
- Treubiales

Jungermanniopsida Stotler & Stotl.-Crand.

- Metzgeriales (simple thalloids)
- Jungermanniales (leafy liverworts)

Marchantiopsida Stotler & Stotl.-Crand.

- Blasiales
- Sphaerocarpales (bottle liverworts)
- Marchantiales (complex thalloids)

The **Marchantiophyta** are a division of bryophyte plants commonly referred to as **hepatics** or **liverworts**. Like other bryophytes, they have a gametophyte-dominant life cycle, in which cells of the plant carry only a single set of genetic information.

It is estimated that there are 6000 to 8000 species of liverworts, though when neotropical regions are better studied this number may approach 10,000. Some of the more familiar species grow as a flattened leafless thallus, but most species are leafy with a form very much like a flattened moss. Leafy species can be distinguished from the apparently similar mosses on the basis of a number of features, including their single-celled rhizoids. Leafy liverworts also differ from most (but not all) mosses in that their leaves never have a costa (present in many mosses) and may bear marginal cilia (very rare in mosses). Other differences are not universal for all mosses and liverworts, but the occurrence of leaves arranged in three ranks, the presence of deep lobes or segmented leaves, or a lack of clearly differentiated stem and leaves all point to the plant being a liverwort.

Liverworts are typically small, usually from 2–20 mm wide with individual plants less than 10 cm long, and are therefore often overlooked. However, certain species may cover large patches of ground, rocks, trees or any other reasonably firm substrate on which they occur. They are distributed globally in almost every available habitat, most often in humid locations although there are desert and arctic species as well. Some species can be a nuisance in shady green-houses or a weed in gardens.

Physical characteristics

Description

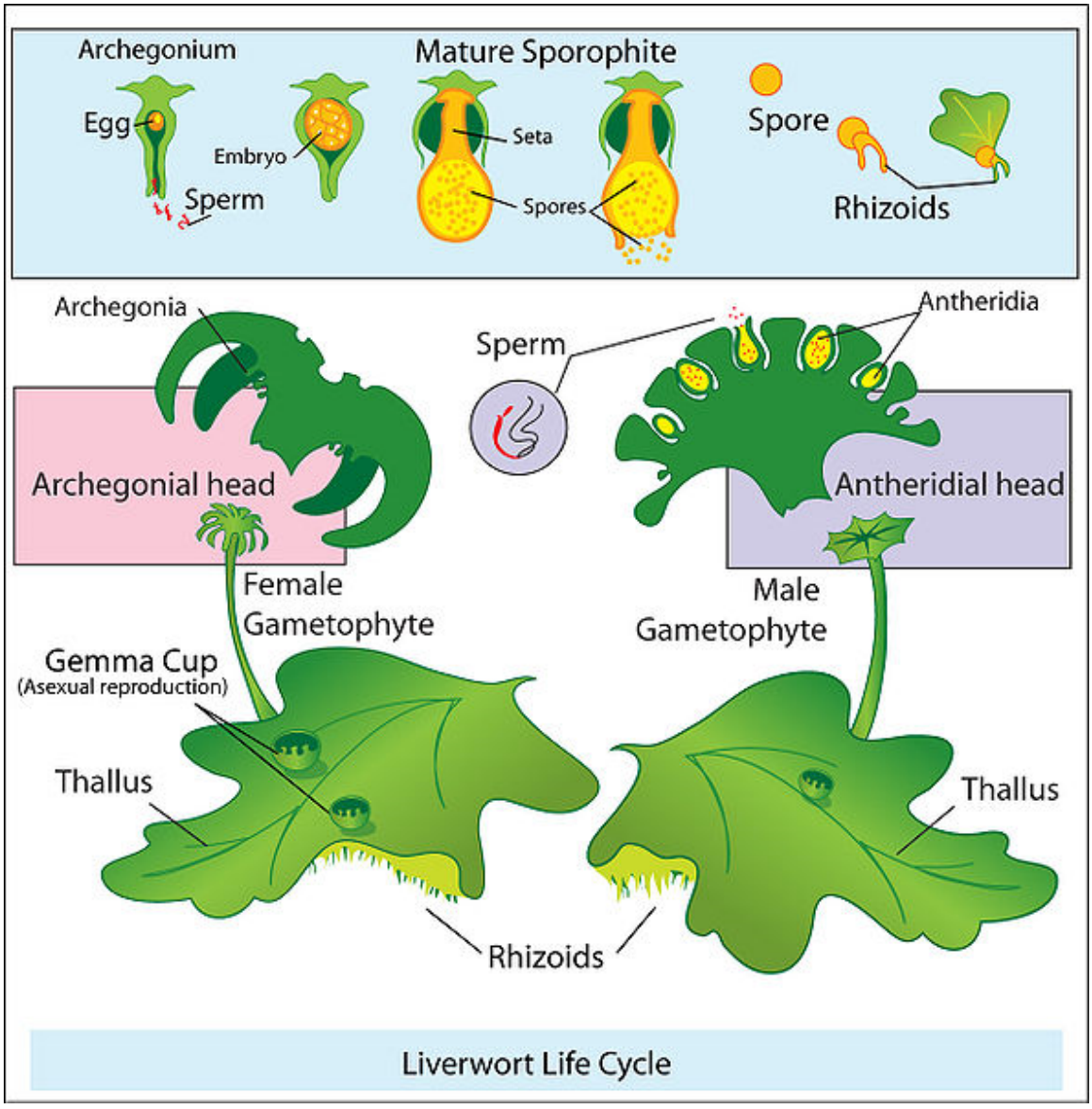
Most liverworts are small, usually from 2–20 millimetres (0.08–0.8 in) wide with individual plants less than 10 centimetres (4 in) long, so they are often overlooked. The most familiar liverworts consist of a prostrate, flattened, ribbon-like or branching structure called a thallus (plant body); these liverworts are termed *thallose liverworts*. However, most liverworts produce flattened stems with overlapping scales or leaves in two or more ranks, the middle rank is often conspicuously different from the outer ranks; these are called *leafy liverworts* or *scale liverworts*.

A thallose liverwort, *Lunularia cruciata*

Liverworts can most reliably be distinguished from the apparently similar mosses by their single-celled rhizoids. Other differences are not universal for all mosses and all liverworts; but the lack of clearly differentiated stem and leaves in thallose species, or in leafy species the presence of deeply lobed or segmented leaves and the presence of leaves arranged in three ranks, all point to the plant being a liverwort. In addition, 90% of liverworts contain oil bodies in at least some of their cells, and these cellular structures are absent from most other bryophytes and from all vascular plants. The overall physical similarity of some mosses and leafy liverworts means that confirmation of the identification of some groups can be performed with certainty only with the aid of microscopy or an experienced bryologist.

Liverworts have a gametophyte-dominant life cycle, with the sporophyte dependent on the gametophyte. Cells in a typical liverwort plant each contain only a single set of genetic information, so the plant's cells are haploid for the majority of its life cycle. This contrasts sharply with the pattern exhibited by nearly all animals and by most other plants. In the more familiar seed plants, the haploid generation is represented only by the tiny pollen and the ovule, while the diploid generation is the familiar tree or other plant. Another unusual feature of the liverwort life cycle is that sporophytes (i.e. the diploid body) are very short-lived, withering away not long after releasing spores. Even in other bryophytes, the sporophyte is persistent and disperses spores over an extended period.

Life cycle



Life cycle of a typical liverwort

The life of a liverwort starts from the germination of a haploid spore to produce a protonema, which is either a mass of thread-like filaments or else a flattened thallus. The protonema is a transitory stage in the life of a liverwort, from which will grow the mature gametophore ("gamete-bearer") plant that produces the sex organs. The male organs are known as antheridia (*singular:* antheridium) and produce the sperm cells. Clusters of antheridia are enclosed by a protective layer of cells called the **perigonium** (*plural:* perigonia). As in other land plants, the female organs are known as archegonia (*singular:* archegonium) and are protected by the thin surrounding **perichaetum** (*plural:* perichaeta). Each archegonium has a slender hollow tube, the "neck", down which the sperm swim to reach the egg cell.

Liverwort species may be either dioicous or monoicous. In dioicious liverworts, female and male sex organs are borne on different and separate gametophyte plants. In monoicious liverworts, the two kinds of reproductive structures are borne on different branches of the same plant. In either case, the sperm must move from the antheridia where they are produced to the archegonium where the eggs are held. The sperm of liverworts is *biflagellate*, i.e. they have two tail-like flagellae that enable them to swim short distances, provided that at least a thin film of water is present. Their journey may be assisted by the splashing of raindrops. In 2008, Japanese researchers discovered that some liverworts are able to fire sperm-containing water up to 15 cm in the air, enabling them to fertilize female plants growing more than a metre from the nearest male.

When sperm reach the archegonia, fertilisation occurs, leading to the production of a diploid sporophyte. After fertilisation, the immature sporophyte within the archegonium develops three distinct regions: (1) a **foot**, which both anchors the sporophyte in place and receives nutrients from its "mother" plant, (2) a spherical or ellipsoidal **capsule**, inside which the spores will be produced for dispersing to new locations, and (3) a **seta** (stalk) which lies between the other two regions and connects them. When the sporophyte has developed all three regions, the seta elongates, pushing its way out of the archegonium and rupturing it. While the foot remains anchored within the parent plant, the capsule is forced out by the seta and is extended away from the plant and into the air. Within the capsule, cells divide to produce both elater cells and spore-producing cells. The elaters are spring-like, and will push open the wall of the capsule to scatter themselves when the capsule bursts. The spore-producing cells will undergo meiosis to form haploid spores to disperse, upon which point the life cycle can start again.

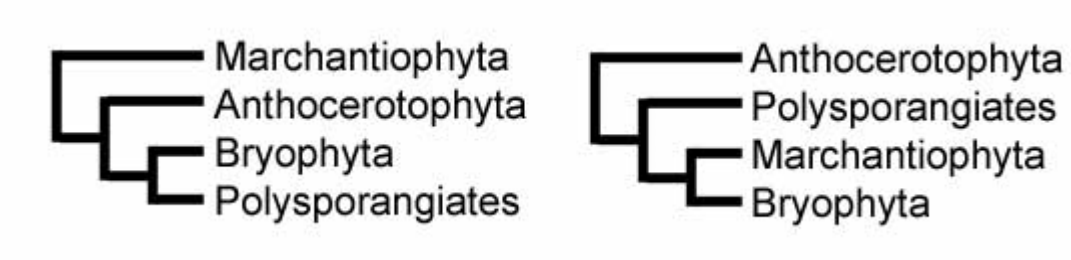
Ecology

Today, liverworts can be found in many ecosystems across the planet except the sea and excessively dry environments, or those exposed to high levels of direct solar radiation. As with most groups of living plants, they are most common (both in numbers and species) in moist tropical areas. Liverworts are more commonly found in moderate to deep shade, though desert species may tolerate direct sunlight and periods of total desiccation.

Classification

Relationship to other plants

Traditionally, the liverworts were grouped together with other bryophytes (mosses and hornworts) in the Division Bryophyta, within which the liverworts made up the class **Hepaticae** (also called Marchantiopsida). However, since this grouping makes the Bryophyta paraphyletic, the liverworts are now usually given their own division. The use of the division name Bryophyta *sensu lato* is still found in the literature, but more frequently the Bryophyta now is used in a restricted sense to include only the mosses.



Two hypotheses on the phylogeny of land plants (embryophyta).

Another reason that liverworts are now classified separately is that they appear to have diverged from all other embryophyte plants near the beginning of their evolution. The strongest line of supporting evidence is that liverworts are the only living group of land plants that do not have stomata on the sporophyte generation. Among the earliest fossils believed to be liverworts are compression fossils of *Pallaviciniites* from the Upper Devonian of New York. These fossils resemble modern species in the Metzgeriales. Another Devonian fossil called *Protosalvinia* also looks like a liverwort, but its relationship to other plants is still uncertain, so it may not belong to the Marchantiophyta. In 2007, the oldest fossils assignable to the liverworts were announced, *Metzgeriothallus sharonae* from the Givetian (Middle Devonian) of New York, USA. However, in 2010, five different types of fossilized liverwort spores were found in Argentina, dating to the much earlier Middle Ordovician, around 470 million years ago.

Internal classification

Bryologists classify liverworts in the division **Marchantiophyta**. This divisional name is based on the name of the most universally recognized liverwort genus *Marchantia*. In addition to this taxon-based name, the liverworts are often called **Hepaticophyta**. This name is derived from their common Latin name as Latin was the language in which botanists published their descriptions of species. This name has led to some confusion, partly because it appears to be a taxon-based name derived from the genus *Hepatica* which is actually a flowering plant of the buttercup family Ranunculaceae. In addition, the name Hepaticophyta is frequently misspelled in textbooks as **Hepatophyta**, which only adds to the confusion.

Although there is no consensus among bryologists as to the classification of liverworts above family rank, the Marchantiophyta may be subdivided into three classes:

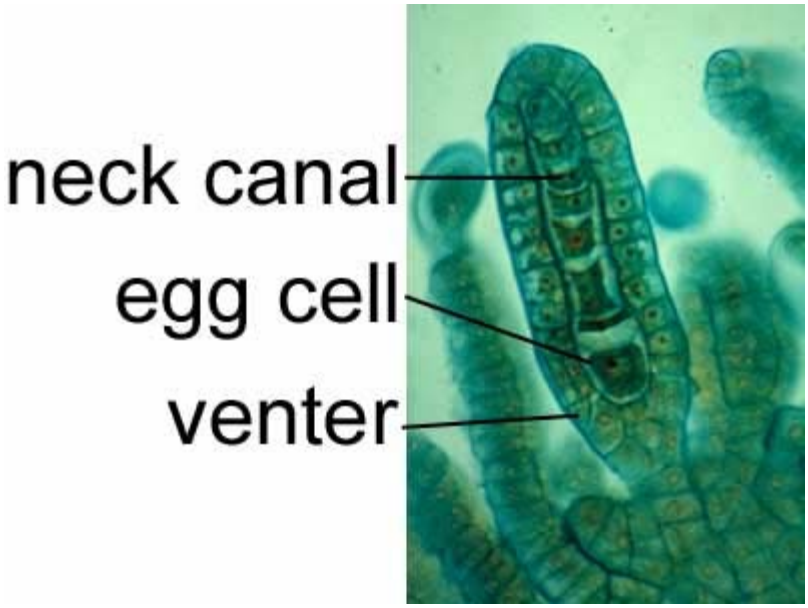
- The **Jungermanniopsida** includes the two orders Metzgeriales (simple thalloids) and Jungermanniales (leafy liverworts).
- The **Marchantiopsida** includes the three orders Marchantiales (complex-thallus liverworts), and Sphaerocarpales (bottle hepatics), as well as the Blasiales (previously placed among the Metzgeriales). It also includes the problematic genus *Monoclea*, which is sometimes placed in its own order Monocleales.
- A third class, the **Haplomitriopsida** is newly recognized as a basal sister group to the other liverworts; it comprises the genera *Haplomitrium*, *Treubia*, and *Apotreubia*.

Economic importance

In ancient times, it was believed that liverworts cured diseases of the liver, hence the name. In Old English, the word liverwort literally means *liver plant*. This probably stemmed from the superficial appearance of some thalloid liverworts (which resemble a liver in outline), and led to the common name of the group as *hepatics*, from the Latin word *hēpaticus* for "belonging to the liver". An unrelated flowering plant, *Hepatica*, is sometimes also referred to as liverwort because it was once also used in treating diseases of the liver. This archaic relationship of plant form to function was based in the "Doctrine of Signatures".

Liverworts have little direct economic importance today. Their greatest impact is indirect, through the reduction of erosion along streambanks, their collection and retention of water in tropical forests, and the formation of soil crusts in deserts and polar regions. However, a few species are used by humans directly. A few species, such as *Riccia fluitans*, are aquatic thallose liverworts sold for use in aquariums. Their thin, slender branches float on the water's surface and provide habitat for both small invertebrates and the fish that feed on them.

Marchantia polymorpha, with antheridial and archegonial stalks



The archegonium of *Porella*

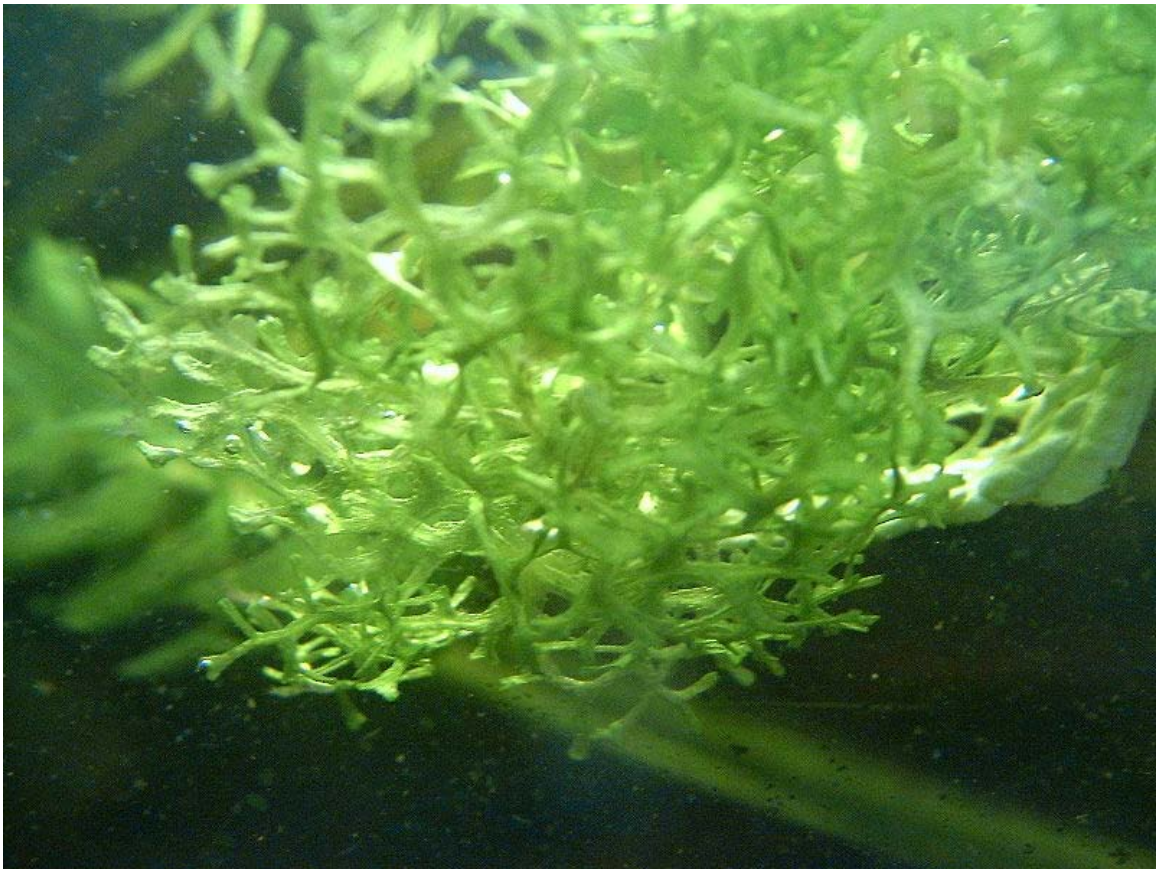
A sporophyte emerging from its archegonium

Porella platyphylla clump growing on a tree

Pellia epiphylla, growing on moist soil

Plagiochila asplenioides, a leafy liverwort

Conocephalum conicum, a large thallose liverwort



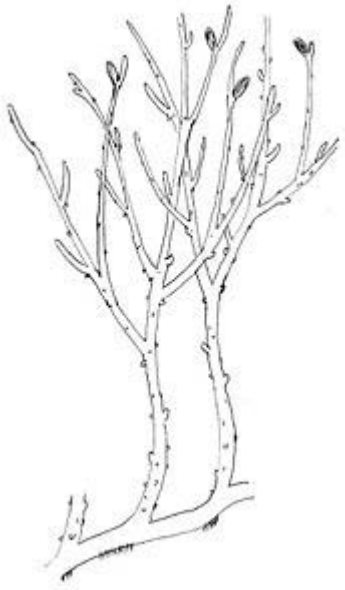
Riccia fluitans, an aquatic thallose liverwort

Chapter- 6

Rhyniopsida and Zosterophyllopsida

Rhyniopsida

Rhyniopsida
Temporal range: Early Devonian



Reconstruction of *Rhynia gwynne-vaughanii*

Scientific classification

Kingdom:	Plantae
Subkingdom:	Embryophyta
clade:	Polysporangiophyta
Division:	Tracheophyta
Class:	**†Rhyniopsida**

Families

Rhyniaceae

Rhyniopsida is a class of extinct early vascular plants, with one family, **Rhyniaceae**, found in the Early Devonian (around 416 to 398 million years ago). They are polysporangiophytes, since their sporophytes consisted of branched stems bearing sporangia (spore-forming organs). They lacked leaves or true roots but did have simple vascular tissue. The group was first placed in a subdivision of the division Tracheophyta under the name **Rhyniophytina**. This group was found not to be monophyletic since some specimens which had been included are now known to lack vascular tissue. Some former members have been placed in the class Horneophytopsida, which is defined as lacking true vascular tissue. Currently, Rhyniopsida includes the genera *Huvenia*, *Rhynia*, and *Stockmansella*, all from the Devonian.

One of the most important radiations for land plants occurred in the early Devonian (Pragian), when the first rhyniophytes appear in the fossil record, making this rich fossil discovery of major importance to paleobotany.

Phylogeny

In 2004, Crane et al. published a cladogram for the polysporangiophytes in which the Rhyniacae are shown as the sister group of all other tracheophytes (vascular plants). The other former "rhyniophytes", such as *Horneophyton* and *Aglaophyton*, are placed outside the tracheophyte clade, as they did not possess true vascular tissue (in particular did not have tracheids).

Rhynie flora

The general term **"rhyniophytes"** or **"rhyniophytoids"** is sometimes used for the assemblage of plants found in the Rhynie chert Lagerstätte - rich fossil beds in Aberdeenshire, Scotland, and roughly coeval sites with similar flora. Used in this way, these terms refer to a floristic assemblage of more or less related early landplants, not a taxon. Though the rhyniophytes are well-represented, plants with simpler anatomy, like *Aglaophyton*, are also common.

The Rhynie flora is unusual for the excellent preservation of early vascular plants, in addition to plants transitional between vascular and non-vascular. The fossils contain sufficient internal detail to determine vascular organization and to distinguish sporangia and gametangia. This has led to the recognition of species which apparently had an isomorphic alternation of generations (gametophytes and sporophytes of similar prominence), a condition unknown among land plants today. Because the plants were buried in situ, rather than after transport to a distant location, important morphological details and ecological information can be obtained. The site also preserves other organisms such as arthropods and fungi that lived in the Rhynie ecosystem.

Zosterophyllopsida

Zosterophyllopsida
Temporal range: Ludlow to Devonian

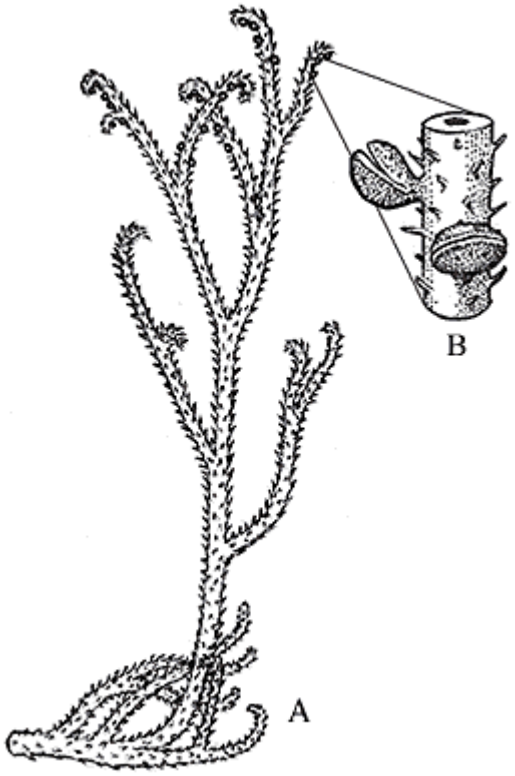
Zosterophyllum species fossils

Scientific classification

Kingdom: Plantae
Division: Tracheophyta
Subdivision: Lycophytina
Class: **†Zosterophyllopsida**

The **Zosterophylls** are a group of extinct plants. The taxon was first established by Banks in 1968 as the subdivision **Zosterophyllophytina**; they have since also been treated as the division **Zosterophyllophyta** and the class **Zosterophyllopsida**. They were among the first vascular plants in the fossil record, and had a world-wide distribution. They were probably stem-group lycophytes, forming a sister group to the ancestors of the living lycophytes. By the late Silurian (late Ludlovian, about 420 million years ago) a diverse assemblage of species existed, examples of which have been found fossilised in what is now Bathurst Island in Arctic Canada.

Morphology



Reconstruction of the zosterophyll *Sawdonia ornata*

The stems of zosterophylls were either smooth or covered with small spines known as enations, branched dichotomously, and grew at the ends by unrolling, a process known as circinate vernation. The stems had a central vascular column in which the protoxylem was exarch, and the metaxylem developed centripetally. The sporangia were kidney-shaped (reniform), with conspicuous lateral dehiscence and were borne laterally in a fertile zone towards the tips of the branches.

The zosterophylls were named after the aquatic flowering plant *Zostera* from a mistaken belief that the two groups were related. David P. Penhallow's generic description of the type genus *Zosterophyllum* refers to "Aquatic plants with creeping stems, from which arise narrow dichotomous branches and narrow linear leaves of the aspect of *Zostera*." *Zosterophyllum rhenanum* was reconstructed as aquatic, the lack of stomata on the lower axes giving support to this interpretation. However, current opinion is that the Zosterophylls were terrestrial plants, and Penhallow's "linear leaves" are interpreted as the aerial stems of the plant that had become flattened during fossilization.

Stomata were present, particularly on the upper axes. Their absence on the lower portions of the axes suggests that this part of the plants may have been submerged, and that the plants dwelt in boggy ground or even shallow water. In many fossils these appear to

consist of a slit-like opening in the middle of a single elongated guard cell, leading to comparison with the stomata of some mosses. However, this is now thought to result from the loss of the wall separating paired guard cells during fossilisation.

Taxonomy

At first most of the fossilized early land plants other than bryophytes were placed in the class Psilophyta, established in 1917 by Kidston and Lang. As additional fossils were discovered and described, it became apparent that the Psilophyta were not a homogeneous group of plants and in 1975 Banks formalized his earlier proposal to split it into three groups, which he put at the rank of subdivision. One of these was the subdivision Zosterophyllophytina, named after the genus *Zosterophyllum*. Subsequently others have treated this group of plants as a division (phylum) Zosterophyllophyta or a class Zosterophyllopsida. For Banks, zosterophyllophytes or zosterophylls comprised plants with lateral sporangia which released their spores by splitting distally (i.e. away from their attachment), and which had exarch strands of xylem.

The class has been divided into orders and families, e.g. the Zosterophyllales containing the Zosterophyllaceae and the Sawdoniales containing the Sawdoniaceae. A major work published in 1997 by Kenrick and Crane presented a cladistic study of land plants. This concluded that although there was a monophyletic clade of zosterophylls, some genera previously included in a broad grouping of zosterophylls fell outside this clade (e.g. *Hicklingia*, *Nothia*), and that the genus *Zosterophyllum* itself was paraphyletic, thus casting doubt on divisions of the class, which have not been used in recent works such as the 2009 paleobotany textbook by Taylor et al.

Phylogeny and Genera

In 2004, Crane et al. published a unified cladogram for the polysporangiophytes (plants with branched stems bearing sporangia), based on cladistic analyses of morphological features. This suggests that the zosterophylls were a paraphyletic stem group, related to the ancestors of modern lycophytes.

Genera which are included at or around the zosterophyll position in the cladogram or have otherwise been included in the group, and hence may be considered zosterophylls in the broad sense, are listed below.

- *Adoketophyton*
- *Anisophyton*
- *Barinophyton*
- *Bathurstia* (B)
- *Crenaticaulis* (B)
- *Deheubarthia*
- *Discalis*
- *Distichophytum* (B)

- *Gosslingia* (B)
- *Gumuia*
- *Hicklingia*
- *Hsua*
- *Huia*
- *Konioria*
- *Nothia*
- *Oricilla*
- *Protobarinophyton*
- *Rebuchia*
- *Sawdonia* (B)
- *Serrulacaulis*
- *Tarella*
- *Thrinkophyton*
- *Ventarura*
- *Zosterophyllum* (B)

B = included by Banks in his 1975 description of Zosterophyllophytina.

Genera may not be assigned to this group by other authors; for example, *Adoketophyton* was regarded by Hao et al., who named the genus, as having evolved separately from the lycopsids, so that its taxonomic placement was uncertain.

Chapter- 7

Lycopodiophyta

Lycopodiophyta
Temporal range: 428 Ma
Silurian to recent

Lycopodiella cernua

Scientific classification

Kingdom: Plantae

Division: **Lycopodiophyta** Cronquist, Takht. & W.Zimm. [P.D. Cantino & M.J. Donoghue]

Classes

Lycopodiopsida - clubmosses
Isoetopsida - spikemosses, quillworts, scale trees

† Zosterophyllopsida -
zosterophylls

The Division **Lycopodiophyta** (sometimes called **Lycophyta** or **Lycopods**) is a tracheophyte subdivision of the Kingdom Plantae. It is the oldest extant (living) vascular plant division at around 410 million years old, and includes some of the most "primitive" extant species. These species reproduce by shedding spores and have macroscopic alternation of generations, although some are homosporous while others are heterosporous. Members of Lycopodiophyta bear a protostele, and the sporophyte generation is dominant. They differ from all other vascular plants in having microphylls, leaves that have only a single vascular trace (vein) rather than the much more complex megaphylls found in ferns and seed plants.

Classification

There are around 1,200 living (extant) species of Lycopodiophyta which are generally divided into three orders (Lycopodiales, Isoetales, and Selaginellales); in addition there are extinct groups. There is some variation in how the extant orders are grouped into classes: they may be put into a single class; they may be put into two classes, with the Isoetales and Selaginellales combined into one class; or they may be put into three classes, one order in each. The system which uses two classes for extant species is:

- Class Lycopodiopsida (or Lycopsida) – clubmosses and firmosses
- Class Isoetopsida – quillworts, scale trees, and spikemosses
- Class † Zosterophyllopsida – extinct zosterophylls.

Evolution

The members of this division have a long evolutionary history, and fossils are abundant worldwide, especially in coal deposits. In fact, most known genera are extinct. The Silurian species *Baragwanathia longifolia* represents the earliest identifable Lycopodiophyta, while some *Cooksonia* seem to be related.

Fossils ascribed to the Lycopodiophyta first appear in the Silurian period, along with a number of other vascular plants. Phylogenetic analysis places them at the base of the vascular plants; they are distinguished by their microphylls and by transverse dehiscence of their sporangia (as contrasted with longitudinal in other vascular plants). Sporangia of living species are borne on the upper surfaces of microphylls (called sporophylls). In some groups, these sporophylls are clustered into strobili.

During the Carboniferous Period, tree-like Lycopodiophyta (such as *Lepidodendron*) formed huge forests that dominated the landscape. The complex ecology of these tropical rainforests collapsed during the mid Pennsylvanian due to a change in climate.

Unlike modern trees, leaves grew out of the entire surface of the trunk and branches, but would fall off as the plant grew, leaving only a small cluster of leaves at the top. Their remains formed many fossil coal deposits. In Fossil Park, Glasgow, Scotland, fossilized Lycopodiophyta trees can be found in sandstone. The trees are marked with diamond-shaped scars where they once had leaves.

Characteristics

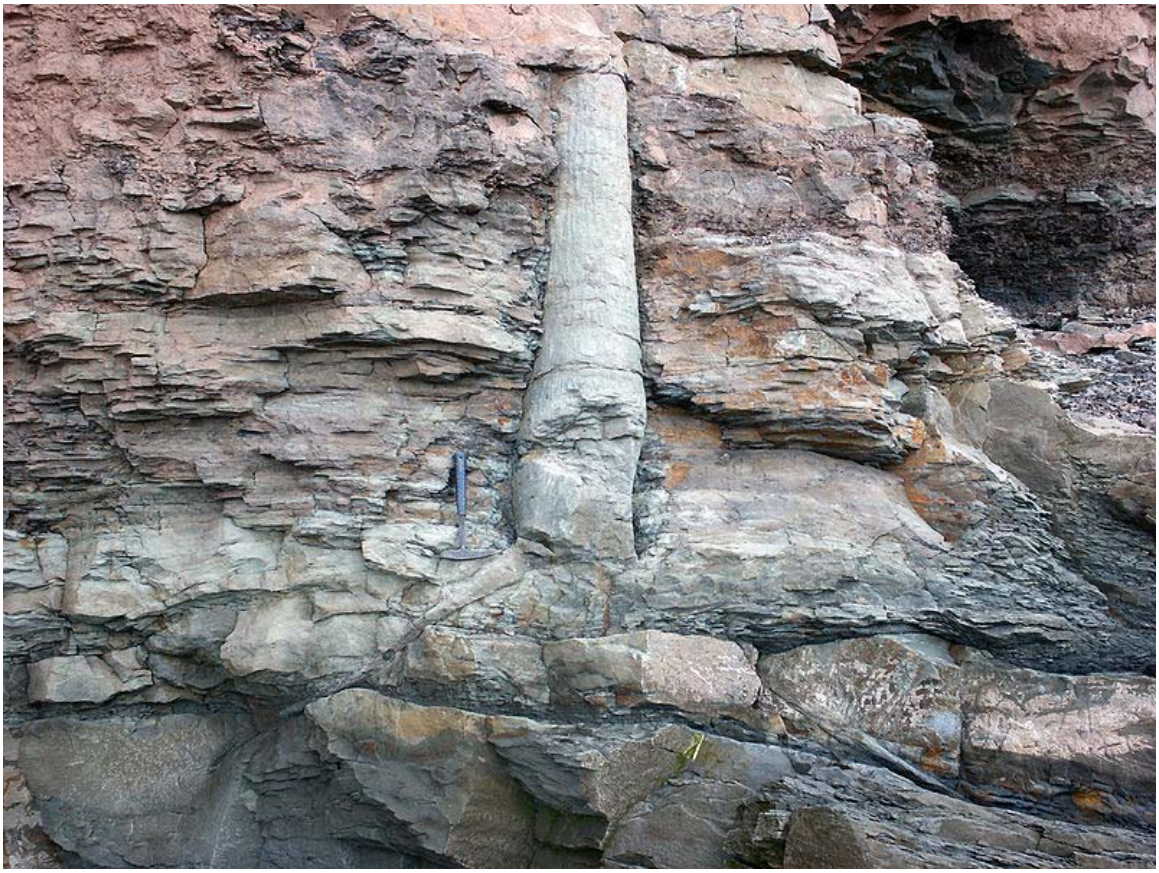
Club-mosses are *homosporous*, but spike-mosses and quillworts are *heterosporous*, with female spores larger than the male, and gametophytes forming entirely within the spore walls.

The spores of Lycopodiophyta are highly flammable and so have been used in fireworks. Currently, huperzine, a chemical isolated from a Chinese clubmoss, is under investigation as a possible treatment for Alzheimer's disease.

Lycopodites, an early lycopod-like fossil

External mold of *Lepidodendron* from the Upper Carboniferous of Ohio

Base of a fossil lycopsid showing connection with stigmarian roots



Fossil *in situ* lycopsid, probably *Sigillaria*, with attached stigmarian roots

Chapter- 8

Fern

Ferns (Badz) Temporal range: Mid Devonian—Recent

Athyrium filix-femina unrolling young frond
Scientific classification
Kingdom: Plantae
Division: **Pteridophyta**
Classes
• †Cladoxylopsida • Psilotopsida • Equisetopsida (*alias* Sphenopsida) • Marattiopsida • Polypodiopsida (*alias* Pteridopsida, Filicopsida)

A **fern** is any one of a group of about 12,000 species of plants. Unlike mosses, they have xylem and phloem (making them vascular plants). They have stems, leaves, and roots like other vascular plants. Ferns do not have either seeds or flowers (they reproduce via spores).

By far the largest group of ferns are the leptosporangiate ferns, but ferns as defined here (also called **monilophytes**) include horsetails, whisk ferns, marattioid ferns, and ophioglossoid ferns. The term **pteridophyte** also refers to ferns. A pteridologist is a specialist in the study of ferns and lycophytes.

Ferns first appear in the fossil record 360 million years ago in the Carboniferous but many of the current families and species did not appear until roughly 145 million years ago in the late Cretaceous (after flowering plants came to dominate many environments).

Ferns are not of major economic importance, but some are grown or gathered for food, as ornamental plants, or for remediating contaminated soils. Some are significant weeds. They also featured in mythology, medicine, and art.

Life cycle

Gametophyte (thalloid green mass) and sporophyte (ascendent frond) of *Onoclea sensibilis*

Ferns are vascular plants differing from lycophytes by having true leaves (megaphylls). They differ from seed plants (gymnosperms and angiosperms) in their mode of reproduction—lacking flowers and seeds. Like all other vascular plants, they have a life cycle referred to as alternation of generations, characterized by a diploid sporophytic and a haploid gametophytic phase. Unlike the gymnosperms and angiosperms, the ferns' gametophyte is a free-living organism.

Life cycle of a typical fern:

1. A sporophyte (diploid) phase produces haploid spores by meiosis.
2. A spore grows by mitosis into a gametophyte, which typically consists of a photosynthetic prothallus.
3. The gametophyte produces gametes (often both sperm and eggs on the same prothallus) by mitosis.
4. A mobile, flagellate sperm fertilizes an egg that remains attached to the prothallus.
5. The fertilized egg is now a diploid zygote and grows by mitosis into a sporophyte (the typical "fern" plant).

Fern ecology

Ferns at Muir Woods, California

The stereotypic image of ferns growing in moist shady woodland nooks is far from being a complete picture of the habitats where ferns can be found growing. Fern species live in a wide variety of habitats, from remote mountain elevations, to dry desert rock faces, to bodies of water or in open fields. Ferns in general may be thought of as largely being specialists in marginal habitats, often succeeding in places where various environmental factors limit the success of flowering plants. Some ferns are among the world's most serious weed species, including the bracken fern growing in the Scottish highlands, or the mosquito fern (*Azolla*) growing in tropical lakes, both species forming large aggressively spreading colonies. There are four particular types of habitats that ferns are found in: moist, shady forests; crevices in rock faces, especially when sheltered from the full sun; acid wetlands including bogs and swamps; and tropical trees, where many species are epiphytes (something like a quarter to a third of all fern species).

Many ferns depend on associations with mycorrhizal fungi. Many ferns only grow within specific pH ranges; for instance, the climbing fern (*Lygodium*) of eastern North America will only grow in moist, intensely acid soils, while the bulblet bladder fern (*Cystopteris bulbifera*), with an overlapping range, is only found on limestone.

The spores are rich in lipids, protein and calories, so some vertebrates eat these. The European woodmouse (*Apodemus sylvaticus*) has been found to eat the spores of *Culcita macrocarpa* and the bullfinch (*Pyrrhula murina*) and the New Zealand lesser short-tailed bat (*Mystacina tuberculata*) also eat fern spores.

Fern structure

Ferns at the Royal Melbourne Botanical Gardens

Tree ferns, probably *Dicksonia antarctica,* growing in Nunniong, Australia

Like the sporophytes of seed plants, those of ferns consist of:

- Stems: Most often an underground creeping rhizome, but sometimes an above-ground creeping stolon (e.g., Polypodiaceae), or an above-ground erect semi-woody trunk (e.g., Cyatheaceae) reaching up to 20 m in a few species (e.g., *Cyathea brownii* on Norfolk Island and *Cyathea medullaris* in New Zealand).
- Leaf: The green, photosynthetic part of the plant. In ferns, it is often referred to as a frond, but this is because of the historical division between people who study ferns and people who study seed plants, rather than because of differences in structure. New leaves typically expand by the unrolling of a tight spiral called a

crozier or fiddlehead. This uncurling of the leaf is termed circinate vernation. Leaves are divided into three types:
    - Trophophyll: A leaf that does not produce spores, instead only producing sugars by photosynthesis. Analogous to the typical green leaves of seed plants.
    - Sporophyll: A leaf that produces spores. These leaves are analogous to the scales of pine cones or to stamens and pistil in gymnosperms and angiosperms, respectively. Unlike the seed plants, however, the sporophylls of ferns are typically not very specialized, looking similar to trophophylls and producing sugars by photosynthesis as the trophophylls do.
    - Brophophyll: A leaf that produces abnormally large amounts of spores. Their leaves are also larger than the other leaves but bear a resemblance to trophophylls.
- Roots: The underground non-photosynthetic structures that take up water and nutrients from soil. They are always fibrous and are structurally very similar to the roots of seed plants.

The gametophytes of ferns, however, are very different from those of seed plants. They typically consist of:

- Prothallus: A green, photosynthetic structure that is one cell thick, usually heart or kidney shaped, 3–10 mm long and 2–8 mm broad. The prothallus produces gametes by means of:
    - Antheridia: Small spherical structures that produce flagellate sperm.
    - Archegonia: A flask-shaped structure that produces a single egg at the bottom, reached by the sperm by swimming down the neck.
- Rhizoids: root-like structures (not true roots) that consist of single greatly elongated cells, water and mineral salts are absorbed over the whole structure. Rhizoids anchor the prothallus to the soil.

One difference between sporophytes and gametophytes might be summed up by the saying that "Nothing eats ferns, but everything eats gametophytes." This is an over-simplification, but it is true that gametophytes are often difficult to find in the field because they are far more likely to be food than are the sporophytes.

Evolution and classification

Ferns first appear in the fossil record in the early-Carboniferous period. By the Triassic, the first evidence of ferns related to several modern families appeared. The "great fern radiation" occurred in the late-Cretaceous, when many modern families of ferns first appeared.

One problem with fern classification is the problem of cryptic species. A cryptic species is a species that is morphologically similar to another species, but differs genetically in ways that prevent fertile interbreeding. A good example of this is the currently designated

species *Asplenium trichomanes*, the maidenhair spleenwort. This is actually a species complex that includes distinct diploid and tetraploid races. There are minor but unclear morphological differences between the two groups, which prefer distinctly differing habitats. In many cases such as this, the species complexes have been separated into separate species, thus raising the number of overall fern species. Possibly many more cryptic species are yet to be discovered and designated.

Ferns have traditionally been grouped in the Class Filices, but modern classifications assign them their own phylum or division in the plant kingdom, called Pteridophyta, also known as Filicophyta. The group is also referred to as Polypodiophyta, (or Polypodiopsida when treated as a subdivision of tracheophyta (vascular plants), although Polypodiopsida sometimes refers to only the leptosporangiate ferns). The term "pteridophyte" has traditionally been used to describe all seedless vascular plants, making it synonymous with "ferns and fern allies". This can be confusing since members of the fern phylum Pteridophyta are also sometimes referred to as pteridophytes. The study of ferns and other pteridophytes is called pteridology, and one who studies ferns and other pteridophytes is called a pteridologist.

Traditionally, three discrete groups of plants have been considered ferns: two groups of eusporangiate ferns—families Ophioglossaceae (adders-tongues, moonworts, and grape-ferns) and Marattiaceae—and the leptosporangiate ferns. The Marattiaceae are a primitive group of tropical ferns with a large, fleshy rhizome, and are now thought to be a sibling taxon to the main group of ferns, the leptosporangiate ferns. Several other groups of plants were considered "fern allies": the clubmosses, spikemosses, and quillworts in the Lycopodiophyta, the whisk ferns in Psilotaceae, and the horsetails in the Equisetaceae. More recent genetic studies have shown that the Lycopodiophyta are more distantly related to other vascular plants, having radiated evolutionarily at the base of the vascular plant clade, while both the whisk ferns and horsetails are as much "true" ferns as are the Ophioglossoids and Marattiaceae. In fact, the whisk ferns and Ophioglossoids are demonstrably a clade, and the horsetails and Marattiaceae are arguably another clade. Molecular data—which remain poorly constrained for many parts of the plants' phylogeny — have been supplemented by recent morphological observations supporting the inclusion of *Equisetaceae* within the ferns, notably relating to the construction of their sperm, and peculiarities of their roots. However, there are still differences of opinion about the placement of the Equisetum species. One possible means of treating this situation is to consider only the leptosporangiate ferns as "true" ferns, while considering the other three groups as "fern allies". In practice, numerous classification schemes have been proposed for ferns and fern allies, and there has been little consensus among them.

A 2006 classification by Smith *et al.* is based on recent molecular systematic studies, in addition to morphological data. Their phylogeny is a consensus of a number of studies, and is shown below (to the level of orders).

Smith's Classification

The complete classification scheme proposed by Smith *et al.* (2006) is shown below (alternative names in brackets).

- Class Psilotopsida
  - Order Ophioglossales
    - Family Ophioglossaceae (incl. Botrychiaceae, Helminthostachyaceae)
  - Order Psilotales
    - Family Psilotaceae (incl. Tmesipteridaceae)
- Class Equisetopsida [=Sphenopsida]
  - Order Equisetales
    - Family Equisetaceae
- Class Marattiopsida
  - Order Marattiales
    - Family Marattiaceae (incl. Angiopteridaceae, Christenseniaceae, Danaeaceae, Kaulfussiaceae)
- Class Pteridopsida [=Filicopsida, Polypodiopsida]
  - Order Osmundales
    - Family Osmundaceae
  - Order Hymenophyllales
    - Family Hymenophyllaceae (incl. Trichomanaceae)
  - Order Gleicheniales
    - Family Gleicheniaceae (incl. Dicranopteridaceae, Stromatopteridaceae)
    - Family Dipteridaceae (incl. Cheiropleuriaceae)
    - Family Matoniaceae
  - Order Schizaeales
    - Family Lygodiaceae
    - Family Anemiaceae (incl. Mohriaceae)
    - Family Schizaeaceae
  - Order Salviniales
    - Family Marsileaceae (incl. Pilulariaceae)
    - Family Salviniaceae (incl. Azollaceae)
  - Order Cyatheales
    - Family Thyrsopteridaceae
    - Family Loxsomataceae
    - Family Culcitaceae
    - Family Plagiogyriaceae
    - Family Cibotiaceae
    - Family Cyatheaceae (incl. Alsophilaceae, Hymenophyllopsidaceae)
    - Family Dicksoniaceae (incl. Lophosoriaceae)
    - Family Metaxyaceae
  - Order Polypodiales

Adiantum lunulatum from Family Pteridaceae

- Family Lindsaeaceae (incl. Cystodiaceae, Lonchitidaceae)
- Family Saccolomataceae
- Family Dennstaedtiaceae (incl. Hypolepidaceae, Monachosoraceae, Pteridiaceae)
- Family Pteridaceae (incl. Pellaeaceae, Adiantaceae, Ceratopteridaceae, Cryptogrammaceae)
- Family Aspleniaceae
- Family Thelypteridaceae
- Family Woodsiaceae (incl. Athyriaceae, Cystopteridaceae)
- Family Blechnaceae (incl. Stenochlaenaceae)
- Family Onocleaceae
- Family Dryopteridaceae (incl. Aspidiaceae, Bolbitidaceae, Elaphoglossaceae, Hypodematiaceae, Peranemataceae)
- Family Oleandraceae
- Family Davalliaceae
- Family Lomariopsidaceae (incl. Nephrolepis)

- Family Polypodiaceae (incl. Drynariaceae, Grammitidaceae, Gymnogrammitidaceae, Loxogrammaceae, Platyceriaceae, Pleurisoriopsidaceae)
- Family Tectariaceae

Uses

Ferns are not as important economically as seed plants but have considerable importance in some societies. Some ferns are used for food, including the fiddleheads of bracken, *Pteridium aquilinum*, ostrich fern, *Matteuccia struthiopteris*, and cinnamon fern, *Osmunda cinnamomea*. *Diplazium esculentum* is also used by some tropical peoples as food. Tubers from the King Fern or *para* (*Ptisana salicina*) are a traditional food in New Zealand and the South Pacific. Fern tubers were used for food 30,000 years ago in Europe. Fern tubers were used by the Guanches to make gofio in the Canary Islands. Licorice fern rhizomes were chewed by the natives of the Pacific Northwest for their flavor.

Ferns of the genus *Azolla* are very small, floating plants that do not resemble ferns. Called mosquito fern, they are used as a biological fertilizer in the rice paddies of southeast Asia, taking advantage of their ability to fix nitrogen from the air into compounds that can then be used by other plants.

Many ferns are grown in horticulture as landscape plants, for cut foliage and as houseplants, especially the Boston fern (*Nephrolepis exaltata*) and other members of the genus Nephrolepis. The Bird's Nest Fern (*Asplenium nidus*) is also popular, as is the staghorn ferns (genus *Platycerium*). Perennial (also known as hardy) ferns planted in gardens in the northern hemisphere also have a considerable following.

Several ferns are noxious weeds or invasive species, including Japanese climbing fern (*Lygodium japonicum*), mosquito fern and sensitive fern (*Onoclea sensibilis*). Giant water fern (*Salvinia molesta*) is one of the world's worst aquatic weeds. The important fossil fuel coal consists of the remains of primitive plants, including ferns.

Ferns have been studied and found to be useful in the removal of heavy metals, especially arsenic, from the soil. Other ferns with some economic significance include:

- *Dryopteris filix-mas* (male fern), used as a vermifuge, and formerly in the US Pharmacopeia; also, this fern accidentally sprouting in a bottle resulted in Nathaniel Bagshaw Ward's 1829 invention of the terrarium or Wardian case
- *Rumohra adiantiformis* (floral fern), extensively used in the florist trade
- *Microsorum pteropus* (Java fern), one of the most popular freshwater aquarium plants.
- *Osmunda regalis* (royal fern) and *Osmunda cinnamomea* (cinnamon fern), the root fiber being used horticulturally; the fiddleheads of *O. cinnamomea* are also used as a cooked vegetable

- *Matteuccia struthiopteris* (ostrich fern), the fiddleheads used as a cooked vegetable in North America
- *Pteridium aquilinum or Pteridium esculentum* (bracken), the fiddleheads used as a cooked vegetable in Japan and are believed to be responsible for the high rate of stomach cancer in Japan. It is also one of the world's most important agricultural weeds, especially in the British highlands, and often poisons cattle and horses.
- *Diplazium esculentum* (vegetable fern), a source of food for some native societies
- *Pteris vittata* (brake fern), used to absorb arsenic from the soil
- *Polypodium glycyrrhiza* (licorice fern), roots chewed for their pleasant flavor
- Tree ferns, used as building material in some tropical areas
- *Cyathea cooperi* (Australian tree fern), an important invasive species in Hawaii
- *Ceratopteris richardii*, a model plant for teaching and research, often called C-fern

Cultural connotations

Blätter des Manns Walfarn. by Alois Auer, Vienna: Imperial Printing Office, 1853

Ferns figure in folklore, for example in legends about mythical flowers or seeds. In Slavic folklore, ferns are believed to bloom once a year, during the Ivan Kupala night. Although alleged to be exceedingly difficult to find, anyone who sees a "fern flower" is thought to be guaranteed to be happy and rich for the rest of their life. Similarly, Finnish tradition holds that one who finds the "seed" of a fern in bloom on Midsummer night will, by possession of it, be guided and be able to travel invisibly to the locations where eternally blazing Will o' the wisps called aarnivalkea mark the spot of hidden treasure. These spots are protected by a spell that prevents anyone but the fern-seed holder from ever knowing their locations.

"Pteridomania"' is a term for the Victorian era craze of fern collecting and fern motifs in decorative art including pottery, glass, metals, textiles, wood, printed paper, and sculpture "appearing on everything from christening presents to gravestones and memorials." The fashion for growing ferns indoors led to the development of the Wardian case, a glazed cabinet that would exclude air pollutants and maintain the necessary humidity.

Barnsley fern created using chaos game, through an Iterated function system (IFS)

The dried form of ferns was also used in other arts, being used as a stencil or directly inked for use in a design. The botanical work, *The Ferns of Great Britain and Ireland*, is a notable example of this type of nature printing. The process, patented by the artist and publisher Henry Bradbury, impressed a specimen on to a soft lead plate. The first

publication to demonstrate this was Alois Auer's *The Discovery of the Nature Printing-Process*.

Misunderstood names

Several non-fern plants are called "ferns" and are sometimes confused with true ferns. These include:

- "Asparagus fern"—This may apply to one of several species of the monocot genus *Asparagus*, which are flowering plants.
- "Sweetfern"—A flowering shrub of the genus *Comptonia*.
- "Air fern"—A group of animals called hydrozoan that are distantly related to jellyfish and corals. They are harvested, dried, dyed green, and then sold as a "plant" that can "live on air". While it may look like a fern, it is merely the skeleton of this colonial animal.
- "Fern bush"—*Chamaebatiaria millefolium*—a rose family shrub with fern-like leaves.

In addition, the book *Where the Red Fern Grows* has elicited many questions about the mythical "red fern" named in the book. There is no such known plant, although there has been speculation that the oblique grape-fern, *Sceptridium dissectum*, could be referred to here, because it is known to appear on disturbed sites and its fronds may redden over the winter.

Adiantum lunulatum

Fern leaf, probably *Blechnum nudum*

A tree fern unrolling a new frond

Tree fern, probably *Dicksonia antarctica*

Tree ferns, probably *Dicksonia antarctica*

Unidentified tree fern in Oaxaca

Tree Fern Spores San Diego, CA

Leaf of fern

Unidentified fern with spores showing in Rotorua, NZ

Ferns in one of many natural Coast Redwood undergrowth settings Santa Cruz, CA.

A young, newly-formed fern frond

Fern fronds

Fern bed under a forest canopy in woods near Franklin, Virginia

Chapter- 9

Pinophyta

Pinophyta
Temporal range: Late Carboniferous - Recent

Conifer forest in Northern California

Scientific classification

Kingdom: Plantae
Division: **Pinophyta**
Class: **Pinopsida**

Orders & Families

Cordaitales †
Pinales
  Pinaceae - Pine family
  Araucariaceae - Araucaria family
  Podocarpaceae - Yellow-wood family
  Sciadopityaceae - Umbrella-pine family
  Cupressaceae - Cypress family
  Cephalotaxaceae - Plum-yew family
  Taxaceae - Yew family

Vojnovskyales †
Voltziales †

Synonyms

Coniferophyta
Coniferae

The **conifers**, division **Pinophyta**, also known as division **Coniferophyta** or **Coniferae**, are one of 13 or 14 division level taxa within the Kingdom Plantae. Pinophytes are gymnosperms. They are cone-bearing seed plants with vascular tissue; all extant conifers are woody plants, the great majority being trees with just a few being shrubs. Typical examples of conifers include cedars, Douglas-firs, cypresses, firs, junipers, kauris, larches, pines, hemlocks, redwoods, spruces, and yews. The division contains approximately eight families, 68 genera, and 630 living species. Although the total number of species is relatively small, conifers are of immense ecological importance. They are the dominant plants over huge areas of land, most notably the boreal forests of the northern hemisphere, but also in similar cool climates in mountains further south. Boreal conifers have many winter time adaptations. The narrow conical shape of northern conifers, and their downward-drooping limbs help them shed snow. Many of them seasonally alter their biochemistry to make them more resistant to freezing, called "hardening". While tropical rain forests have more biodiversity and turnover, the immense conifer forests of the world represent the largest terrestrial carbon sink, i.e. where carbon is bound as organic compounds. They are also of great economic value, primarily for timber and paper production; the wood of conifers is known as softwood.

Evolution

The earliest conifers in the fossil record date to the late Carboniferous (Pennsylvanian) period (about 300 million years ago), possibly arising from *Cordaites*, a seed-bearing plant with cone-like fertile structures. This plant resembled the modern *Araucaria*. Pinophyta, Cycadophyta, and Ginkgophyta all developed at this time. An important adaptation of these gymnosperms was allowing plants to live without being so dependent on water. Other adaptations are pollen (allowing fertilization to occur without water) and the seed, which allows the embryo to be transported and developed elsewhere.

Conifers appear to be one of the taxa that benefitted from the Permo-Triassic extinction event. Some speculation has been noted as saying it might be a relative species of the Mitchellius Hamiltonuis variety of plants.

Taxonomy and naming

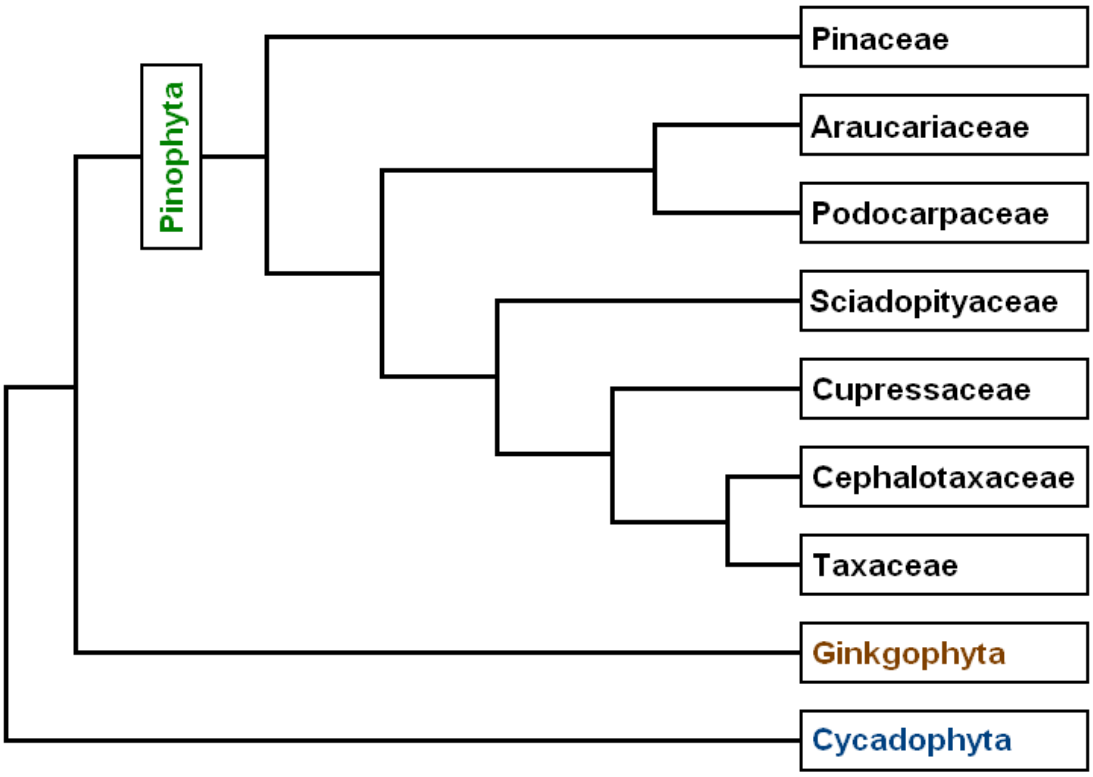
The division name Pinophyta conforms to the rules of the *ICBN*, which state (Article 16.1) that the names of higher taxa in plants (above the rank of family) are either formed from the name of an included family (usually the most common and/or representative), in this case Pinaceae (the pine family), or are descriptive. In the latter case the name for the conifers (at whatever rank is chosen) is **Coniferae** (Art 16 Ex 2), which is also in

widespread use. Older scientific names (no longer allowed) are Coniferophyta and Coniferales.

According to the *ICBN* it is possible to use a name formed by replacing the termination -*aceae* in the name of an included family, in this case preferably Pinaceae, by the appropriate termination, in the case of this division -*ophyta*. Alternatively, "descriptive botanical names" may also be used at any rank above family. Both are allowed.

This means that if the conifers are regarded to be a division they may be called Pinophyta or Coniferae (if regarded as a class they may be called Pinopsida or Coniferae; if regarded as an order they may be called Pinales or Coniferae).

Commonly the conifers are considered equivalent to the Gymnosperms, particularly in areas with a temperate climate where they may be the only commonly occurring gymnosperms. However, these are two different levels of grouping: conifers are the largest and economically most important component group of the gymnosperms, but nevertheless they comprise only one of the four groups. The division Pinophyta consists of just one class, Pinopsida, which includes both living and fossil taxa. Subdivision of the living conifers into two or more orders has been proposed from time to time. The most commonly seen in the past was a split into two orders, Taxales (Taxaceae only) and Pinales (the rest), but recent research into DNA sequences suggests that this interpretation leaves the Pinales without Taxales as paraphyletic, and the latter order is no longer regarded as distinct. A more accurate subdivision would be to split the class into three orders, Pinales containing only Pinaceae, Araucariales containing Araucariaceae and Podocarpaceae, and Cupressales containing the remaining families (including Taxaceae), but there has not been any significant support for such a split, with the majority of opinion preferring retention of all the families within a single order Pinales, despite their antiquity and diverse morphology.



Phylogeny of the Pinophyta based on cladistic analysis of molecular data

The conifers are now accepted as comprising six to eight families, with a total of 65-70 genera and 600-630 species (696 accepted names). The seven most distinct families are linked in the box above right and phylogenetic diagram left. In other interpretations, the Cephalotaxaceae may be better included within the Taxaceae, and some authors additionally recognize Phyllocladaceae as distinct from Podocarpaceae (in which it is included here). The family Taxodiaceae is here included in family Cupressaceae, but was widely recognized in the past and can still be found in many field guides.

The conifers are an ancient group, with a fossil record extending back about 300 million years to the Paleozoic in the late Carboniferous period; even many of the modern genera are recognizable from fossils 60-120 million years old. Other classes and orders, now long extinct, also occur as fossils, particularly from the late Paleozoic and Mesozoic eras. Fossil conifers included many diverse forms, the most dramatically distinct from modern conifers being some herbaceous conifers with no woody stems. Major fossil orders of conifers or conifer-like plants include the Cordaitales, Vojnovskyales, Voltziales and perhaps also the Czekanowskiales (possibly more closely related to the Ginkgophyta).

Morphology

All living conifers are woody plants, and most are trees, the majority having monopodial growth form (a single, straight trunk with side branches) with strong apical dominance.

Many conifers have distinctly scented resin, secreted to protect the tree against insect infestation and fungal infection of wounds. Fossilized resin hardens into amber. The size of mature conifers varies from less than one meter, to over 100 meters. The world's tallest, largest, thickest and oldest living things are all conifers. The tallest is a Coast Redwood (*Sequoia sempervirens*), with a height of 115.55 meters. The largest is a Giant Sequoia (*Sequoiadendron giganteum*), with a volume 1486.9 cubic meters. The thickest, or tree with the greatest trunk diameter, is a Montezuma Cypress (*Taxodium mucronatum*), 11.42 meters in diameter. The oldest is a Great Basin Bristlecone Pine (*Pinus longaeva*), 4,700 years old.

Foliage

Pinaceae: needle leaves and bud of Coast Douglas-fir (*Pseudotsuga menziesii*)

Araucariaceae: Awl-like leaves of Cook Pine (*Araucaria columnaris*)

Cupressaceae: scale leaves of Lawson's Cypress (*Chamaecyparis lawsoniana*); scale in mm

Since most conifers are evergreens, the leaves of many conifers are long, thin and have a needle-like appearance, but others, including most of the Cupressaceae and some of the

Podocarpaceae, have flat, triangular scale-like leaves. Some, notably *Agathis* in Araucariaceae and *Nageia* in Podocarpaceae, have broad, flat strap-shaped leaves. Others such as Araucaria columnaris have leaves that are awl-shaped. In the majority of conifers, the leaves are arranged spirally, exceptions being most of Cupressaceae and one genus in Podocarpaceae, where they are arranged in decussate opposite pairs or whorls of 3 (-4). In many species with spirally arranged leaves, the leaf bases are twisted to present the leaves in a very flat plane for maximum light capture. Leaf size varies from 2 mm in many scale-leaved species, up to 400 mm long in the needles of some pines (e.g. Apache Pine *Pinus engelmannii*). The stomata are in lines or patches on the leaves, and can be closed when it is very dry or cold. The leaves are often dark green in colour which may help absorb a maximum of energy from weak sunshine at high latitudes or under forest canopy shade. Conifers from hotter areas with high sunlight levels (e.g. Turkish Pine *Pinus brutia*) often have yellower-green leaves, while others (e.g. Blue Spruce *Picea pungens*) have a very strong glaucous wax bloom to reflect ultraviolet light. In the great majority of genera the leaves are evergreen, usually remaining on the plant for several (2-40) years before falling, but five genera (*Larix*, *Pseudolarix*, *Glyptostrobus*, *Metasequoia* and *Taxodium*) are deciduous, shedding the leaves in autumn and leafless through the winter. The seedlings of many conifers, including most of the Cupressaceae, and *Pinus* in Pinaceae, have a distinct juvenile foliage period where the leaves are different, often markedly so, from the typical adult leaves.

Reproduction

Pinaceae: cone of a Norway Spruce (*Picea abies*)

Taxaceae: the fleshy aril which surrounds each seed in the European Yew(*Taxus baccata*) is a highly modified seed cone scale

Pinaceae: pollen cone of a Japanese Larch (*Larix kaempferi*)

Most conifers are monoecious, but some are subdioecious or dioecious; all are wind-pollinated. Conifer seeds develop inside a protective cone called a strobilus. The cones take from four months to three years to reach maturity, and vary in size from 2 mm to 600 mm long.

In Pinaceae, Araucariaceae, Sciadopityaceae and most Cupressaceae, the cones are woody, and when mature the scales usually spread open allowing the seeds to fall out and be dispersed by the wind. In some (e.g. firs and cedars), the cones disintegrate to release the seeds, and in others (e.g. the pines that produce pine nuts) the nut-like seeds are dispersed by birds (mainly nutcrackers and jays) which break up the specially adapted softer cones. Ripe cones may remain on the plant for a varied amount of time before falling to the ground; in some fire-adapted pines, the seeds may be stored in closed cones for up to 60–80 years, being released only when a fire kills the parent tree.

In the families Podocarpaceae, Cephalotaxaceae, Taxaceae, and one Cupressaceae genus (*Juniperus*), the scales are soft, fleshy, sweet and brightly colored, and are eaten by fruit-eating birds, which then pass the seeds in their droppings. These fleshy scales are (except in *Juniperus*) known as arils. In some of these conifers (e.g. most Podocarpaceae), the cone consists of several fused scales, while in others (e.g. Taxaceae), the cone is reduced to just one seed scale or (e.g. Cephalotaxaceae) the several scales of a cone develop into individual arils, giving the appearance of a cluster of berries.

The male cones have structures called microsporangia which produce yellowish pollen through meiosis. Pollen is released and carried by the wind to female cones. Pollen grains from living pinophyte species produce pollen tubes, much like those of angiosperms. When a pollen grain lands near a female gametophyte, it undergoes fertilization of the female gametophyte. Alternatively, the gymnosperm male gametophytes are carried by wind to a female cone and are drawn into a tiny opening on the ovule called the micropyle. It is within the ovule that germination occurs. From here, a pollen tube seeks out the female gametophyte and if successful, fertilization will occur. In both cases, the resulting zygote develops into an embryo, which along with its surrounding integument, becomes a seed. Eventually the seed may fall to the ground and, if conditions permit, grows into a new plant.

In forestry, the terminology of flowering plants has commonly though inaccurately been applied to cone-bearing trees as well. The male cone and unfertilized female cone are called "male flower" and "female flower", respectively. After fertilization, the female cone is termed "fruit", which undergoes "ripening" (maturation).

Life cycle

1. To fertilize the ovum, the male cone releases pollen that is carried on the wind to the female cone. (Male and female cones can be found on the same plant)
2. The pollen fertilizes the female gamete (located in the female cone).*
3. A fertilized female gamete (called a zygote) develops into an embryo.

4. Along with integument cells surrounding the embryo, a seed develops containing the embryo. This is an evolutionary characteristic of the gymnosperms.
5. Mature seed drops out of cone onto the ground.
6. Seed germinates and seedling grows into a mature plant.
7. When the plant is mature, the adult plant produces cones and the cycle continues.

Invasive species

A number of conifers have become invasive species in parts of New Zealand. These "wilding conifers" are a serious environmental issue causing problems for pastoral farming and for conservation.

Chapter- 10

Cycad

Cycadophyta
Temporal range: Early Permian–Recent

Cycas rumphii with old and new male cones.

Scientific classification

Kingdom:	Plantae
Division:	**Cycadophyta**
Class:	**Cycadopsida**
Order:	**Cycadales** Dumortier

Families

Cycadaceae cycas family
Stangeriaceae stangeria family
Zamiaceae zamia family

Cycads are seed plants characterized by a large crown of compound leaves and a stout trunk. They are evergreen, dioecious plants having large pinnately compound leaves. They are frequently confused with and mistaken for palms or ferns, but are only distantly related to both, and instead belong to the division **Cycadophyta**.

Cycads are found across much of the subtropical and tropical parts of the world. They are found in South and Central America (where the greatest diversity occurs), Mexico, the Antilles, southeastern United States, Australia, Melanesia, Micronesia, Japan, China, Southeast Asia, India, Sri Lanka, Madagascar, and southern and tropical Africa, where at least 65 species occur. Some are renowned for survival in harsh semidesert climates, and can grow in sand or even on rock. They are able to grow in full sun or shade, and some are salt tolerant. Though they are a minor component of the plant kingdom today, during the Jurassic period they were extremely common.

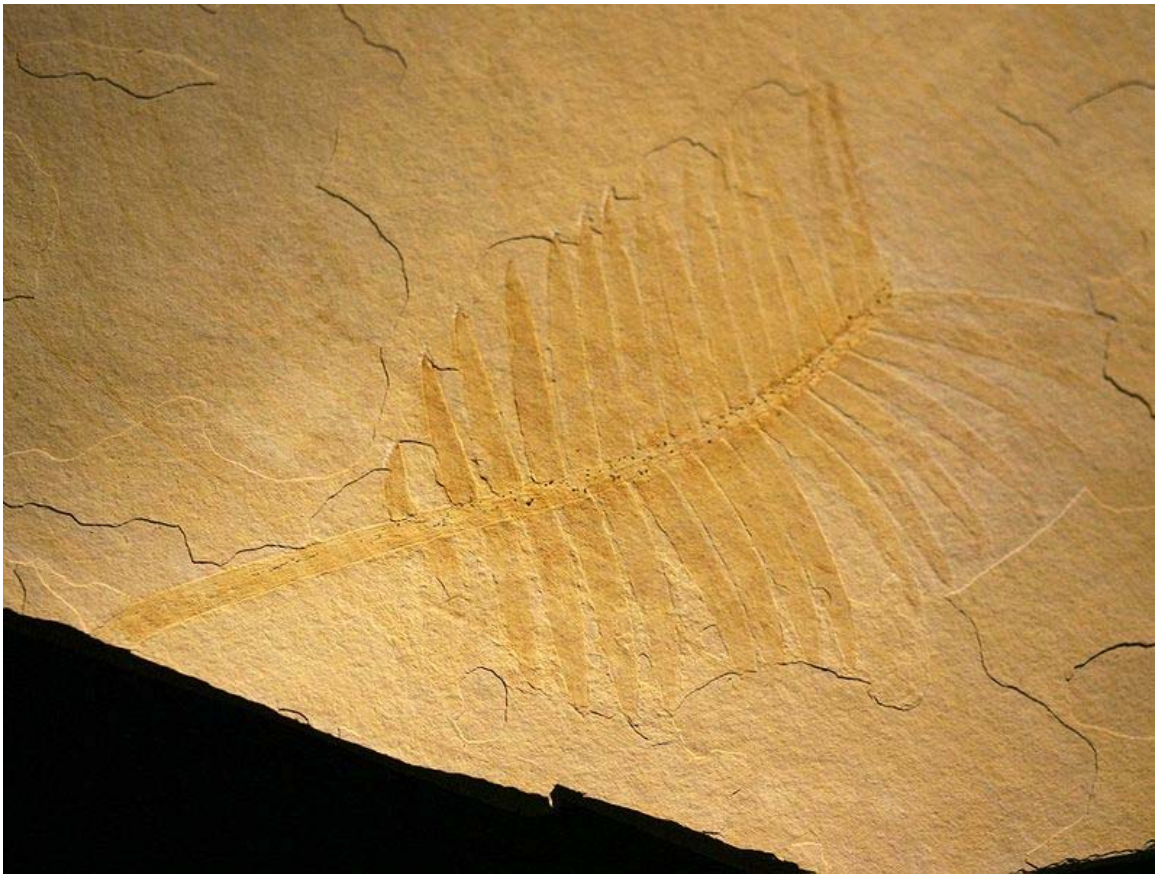
They have very specialized pollinators and have been reported to fix nitrogen in association with a cyanobacterium living in the roots. These blue-green algae produce a neurotoxin called BMAA that is found in the seeds of cycads.

Origins

The cycad fossil record dates to the early Permian, 280 mya. There is controversy over older cycad fossils that date to the late Carboniferous period, 300–325 mya. One of the first colonizers of terrestrial habitats, this clade probably diversified extensively within its first few million years, although the extent to which it radiated is unknown because relatively few fossil specimens have been found. The regions to which cycads are restricted probably indicate their former distribution in the Pangea before supercontinents Laurasia and Gondwana separated (Hermsen et al. 2006).

The family Stangeriaceae (named for Dr. William Stanger, 1812(?)–1854), consisting of only three extant species, is thought to be of Gondwanan origin, as fossils have been found in Lower Cretaceous deposits in Argentina, dating to 70–135 mya. Zamiaceae is more diverse, with a fossil record extending from the middle Triassic to the Eocene (54–200 mya) in North and South America, Europe, Australia, and Antarctica, implying that the family was present before the break-up of Pangea. Cycadaceae are thought to be early offshoots from other cycads, with fossils from Eocene deposits (38–54 mya) in Japan and China, indicating that this family originated in Laurasia. *Cycas* is the only genus in the family and contains 99 species, the most of any cycad genus. Molecular data have recently shown that *Cycas* species in Australasia and the east coast of Africa are recent arrivals, suggesting adaptive radiation may have occurred. The current distribution of cycads may be due to radiations from a few ancestral types sequestered on Laurasia and Gondwana, or could be explained by genetic drift following the separation of already evolved genera. Both explanations account for the strict endemism across present continental lines.

Leaves and cone of *Encephalartos sclavoi*



The fossil Cycad *Zamites feneonis*

Taxonomy

There are about 305 described species, in 10–12 genera and 2–3 families of cycads (depending on taxonomic viewpoint). The classification below, proposed by Dennis Stevenson in 1992, is based upon a hierarchical structure based on cladistic analyses of morphological, anatomical, karyological, physiological and phytochemical data.

The number of species in the clade is low compared to the number of species in most other plant phyla. However, paleobotanical and molecular research indicates that diversity was higher in the history of the phylum. Fossil evidence shows that structural diversity in Mesozoic cycad pollen "considerably exceeds that seen in surviving genera today". The impacts of extinction on diversity are highlighted below. The disparity in molecular sequences is very high between the three main lineages of cycads, implying that genetic diversity in the clade was once high, but this fact has led to major disagreements about the divisions within the Cycadales.

The number of described cycad species has doubled in the past 25 years, mostly due to improved sampling and further exploration. Experts infer there may still be about 100 undescribed species, based on the rate of discovery. These are likely to be in Asia and

South America, where areas of endemism are highest. Diversity hotspots also occur in Australia, South Africa, Mexico, China and Vietnam, which together account for more than 70% of the world's cycad species. The taxonomy of the Cycadophyta is, however, now stabilizing.

Cycad systematists reject the biological species concept, because some clearly defined cycad species can interbreed and produce fertile offspring; this character is thus not disproportionately weighted when determining species barriers. The phenetic species concept, which states that a species is defined based on overall similarities with other individuals of the same species combined with a significant gap in variation with other species, is also rejected. Most cycad taxonomists agree on a modified version of the evolutionary species concept, The classification below is taken from Stevenson (1992).

Suborder Cycadineae
- Family Cycadaceae
- Subfamily Cycadoideae
- *Cycas*. About 105 species in the Old World from Africa east to southern Japan, Australia and the western Pacific Ocean islands; type: *C. circinalis* L.

Suborder Zamiineae
- Family Stangeriaceae
- Subfamily Stangerioideae
- *Stangeria*. One species in southern Africa; type: *S. eriopus* (Kunze) Baillon
- Subfamily Bowenioideae
- *Bowenia*. Two species in Queensland, Australia; type: *B. spectabilis* Hook. ex Hook. f.
- Family Zamiaceae
- Subfamily Encephalartoideae
- Tribe Diooeae
- *Dioon*. 13 species in Mexico and Central America; type: *D. edule* Lindley
- Tribe Encephalarteae
- Subtribe Encephalartinae
- *Encephalartos*. About 66 species in southeast Africa; type: *E. friderici-guilielmi* Lehmann, *E. transvenosus (Modjadji cycad)*
- Subtribe Macrozamiinae
- *Macrozamia*. About 41 species in Australia; type: *M. riedlei* (Fischer ex Gaudichaud) C.A. Gardner
- *Lepidozamia*. Two species in eastern Australia; type: *L. peroffskyana* Regel
- Subfamily Zamioideae
- Tribe Ceratozamieae
- *Ceratozamia*. 26 species in southern Mexico and Central America; type: *C. mexicana* Brongn.
- Tribe Zamieae
- Subtribe Microcycadinae
- *Microcycas*. One species in Cuba; type: *M. calocoma* (Miquel) A. DC.
- Subtribe Zamiinae
- *Chigua*. Two species in Colombia; type: *C. restrepoi* E. Stevenson

Zamia. About 65 species in the New World from Georgia, USA south to Bolivia; type: *Z. pumila* L..

History

Modern knowledge about cycads began in the 9th century with the recording by two Arab naturalists that the genus *Cycas* was used as a source of flour in India. Later, in the 16th century, Antonio Pigafetta, Fernao Lopez de Castanheda and Francis Drake found *Cycas* plants in the Moluccas, where the seeds were eaten. The first report of cycads in the New World was by Giovanni Lerio in his 1576 trip to Brazil, where he observed a plant named *ayrius* by the indigenous people; this species is now classified in the genus *Zamia*.

Cycads belonging to the genus *Encephalartos* were first described by Johann Georg Christian Lehmann in 1834. The name is derived from the Greek articles "en", meaning "in", "cephale", meaning "head", and "artos", meaning "bread".

Throughout the 18th-19th centuries, discoveries of several species were reported by numerous naturalist researchers and discoverers traveling throughout the world. One of the most notable researchers of cycads was American botanist C.J. Chamberlain whose work is noteworthy for the quantity of data and the novelty of his approach to studying cycads. His 15 years of travel throughout Africa, the Americas and Australia to observe cycads in their natural habitat resulted in his 1919 publication of *The Living Cycads* which remains current in its synthesis of taxonomy, morphology and reproductive biology of cycads, most of which was obtained from his original research. His 1940s monograph on the Cycadales, though never published (most likely because of his death) was never used by botanists. The most recent complete work on the cycads is the book by Norstog and Nicholls entitled "the Biology of the Cycads" published in 1998.

Uses

The generic name refers to the starch obtained from the stems, which was used as food by some indigenous tribes. Tribal people grind and soak the seeds to remove the nerve toxin, making the food source generally safe to eat, although often not all the toxin is removed. In addition, consumers of bush meat may face a health threat as the meat comes from game which may have eaten cycad seeds and carry traces of the toxin in body fat.

Cycad, known as *sotetsu* (Jap. ソテツ, Kanji: 蘇鉄) in Japanese, was traditionally a famine food in Okinawa - a last resort to turn to for sustenance during particularly difficult times. A period of particularly devastating poverty and famine in the 1920s, caused in large part by Japanese economic policies in the island prefecture, is known as "cycad hell" or *sotetsu jigoku*.

Cycad known as *Eenthu* in Malayalam is a common food in Kerala.The seeds were cut and kept in sun or kept near the hearth in kitchen during rainy season to get dried. Drying is to reduce the toxin content of the seed.Outer shell is then removed and the collected

inner portion is ground into power.Properly dried cycad seed powder can be stored for years together.

Food items like *Puttu,Eenthu kanji,Eenthu payasam* etc are made out of cycad seed power.These food items are particularly prepared in heavy rainy seasons in Kerala.

Cycad leaves are used to decorate venues during festivals, marriages and other community celebrations.

There is some indication that the regular consumption of starch derived from cycads is a factor in the development of Lytico-Bodig disease, a neurological disease with symptoms similar to those of Parkinson's disease and ALS. Lytico-Bodic and its potential connection to cycasin ingestion is one of the subjects explored in Oliver Sacks' 1997 book *Island of the Colourblind.* Cattle that graze in pastures containing cycads may ingest the leaves and seeds and develop the neurologic syndrome of cycad toxicosis known as zamia staggers.

Distribution

Approximate world distribution of living Cycadales

Overall species diversity peaks at 17° 15"N and 28° 12"S, with a minor peak at the equator. There is therefore not a latitudinal diversity gradient towards the equator but towards the tropics. However, the peak in the northern tropics is largely due to *Cycas* in Asia and *Zamia* in the New World, whereas the peak in the southern tropics is due to *Cycas* again, and also to the diverse genus *Encephalartos* in southern and central Africa and *Macrozamia* in Australia. Thus, the distribution pattern of cycad species with latitude appears to be an artifact of the geographical isolation of cycad genera, and is dependent on the remaining species in each genus that did not follow the extinction pattern of their

ancestors. *Cycas* is the only genus that has a broad geographical range and can thus be used to infer that cycads tend to live in the upper and lower tropics. This is probably because these areas have a drier climate with relatively cool winters; while cycads require some rainfall, they appear to be partly xerophytic. Potted specimens are found and thrive in global locations such as Canada, Russia, Finland and Chile.

Speciation

There are no documented cases of sympatric speciation in cycads and allopatry appears to be the most common form of speciation in the group. This is difficult to study. as they are long-lived plants, so natural experiments have been investigated. One example is *Cycas seemannii*, which occurs only in Fiji, New Caledonia, Tonga and Vanuatu. Genetic diversity within populations was found to be significantly lower than between islands, suggesting that genetic drift is a likely mechanism for speciation, and is probably currently occurring between the isolated populations. Allopatry has also been proposed as the mechanism of speciation in *Dioon*, which predominantly occurs in Mexico. The many rivers that have shaped the region, and repeated glaciation and consequent disjunction, are thought to have been important in reproductive isolation not only in *Dioon* but in many other plant and animal taxa. Parapatric speciation may also have occurred, especially as cycads are pollinated by insects rather than by wind (Stevenson et al. 1998). As the range of the species grows, the individuals furthest apart are prevented from interbreeding, as insects have relatively small ranges and will not pollinate between these plants. If sympatric speciation has occurred in cycads, this would most likely be because of a host shift in pollinators, due to the very fact that cycads are uniformly dioecious.

Extinction

The probable former range of cycads can be inferred from their global distribution. For example, the family Stangeriaceae only contains three extant species in Africa and Australia. Diverse fossils of this family have been dated to 135 mya, indicating that diversity may have been much greater before the Jurassic and late Triassic mass extinction events. However, the cycad fossil record is generally poor and little can be deduced about the effects of each mass extinction event on their diversity.

Instead, correlations can be made between the number of extant gymnosperms and angiosperms. It is likely that cycad diversity was affected more by the great angiosperm radiation in the mid-Cretaceous than by extinctions. Very slow cambial growth was first used to define cycads, and because of this characteristic the group could not compete with the rapidly growing, relatively short-lived angiosperms, which now number over 250,000 species, compared to the 947 remaining gymnosperms. It is surprising that the cycads are still extant, having been faced with extreme competition and five major extinctions. The ability of cycads to survive in relatively dry environments where plant diversity is generally lower, and their great longevity may explain their long persistence.

Conservation

Encephalartos woodii is extinct in the wild, and all living specimens are clones of the type

In recent years, many cycads have been dwindling in numbers and may face risk of extinction because of theft and unscrupulous collection from their natural habitats, as well as from habitat destruction.

About 23% of the 305 extant cycad species are either critically endangered or endangered, and 15% are vulnerable. Thus, 38% of cycads are on the IUCN Red List (2004), and the other 62% are in the Least concern or Near Threatened category (i.e. not

actually on the Red List), or are data deficient. This value has changed dramatically within the past few years; 46% of cycads were on the 1978 Red List, and this rose to 82% in 1997. This was largely due to the recent discovery of over 150 new species, disagreements about classification, and uncertainty. This has not been helpful for conservation planning for the group.

Zamia in the New World, *Cycas* in Asia and *Encephalartos* in Africa are the most threatened genera. This pattern reflects the pressures on species in these regions. At least two species, *Encephalartos woodii* and *Encephalartos relictus* (both from Africa), are confirmed extinct in the wild. Cycads are long-lived with infrequent reproduction, and most populations are small, putting them at risk of extinction from habitat destruction and stochastic environmental events. Regionally, Australian cycads are the least at risk, as they are locally common and habitat fragmentation is low. However, land management with fire is thought to be a threat to Australian species. African cycads are rare and are thought to be naturally decreasing due to small population sizes, and there is controversy over whether to let natural extinction processes act on these cycads.

All cycads are in the CITES appendix appearing under the heading Plant Kingdom and under three family names, Cycadaceae, Stangeriaceae and Zamiaceae.

All cycads are CITES APPENDIX II except the following, in APPENDIX I:

- *Cycas beddomei*
- *Stangeria eriopus*
- All *Ceratozamia*
- All *Chigua*
- All *Encephalartos*
- *Microcycas calocoma*

Cycad seeds from species on APPENDIX II are not CITES regulated. APPENDIX I seeds are treated the same as the plants.

Horticulture

A Sago Cycad (*Cycas revoluta*) growing in England as a houseplant

Cycads can be cut into pieces to make new plants, or by direct planting of the seeds. Propagation by seeds is the preferred method of growth, and two unique risks to their germination exist. One is that the seeds have no dormancy, so the embryo is biologically required to maintain growth and development, which means if the seed dries out, it dies. The second is that the emerging radicle and embryo can be very susceptible to fungal diseases in its early stages, when in unhygienic or excessively wet conditions. Thus, many cycad growers pregerminate the seeds in moist, sterile media such as vermiculite or perlite. However pregermination is not necessary, and many report success by directly planting the seeds in regular potting soil. As with many plants, a combination of well-drained soil, sunlight, water and nutrients will help it to prosper. Although, because of their hardy nature, cycads do not necessarily require the most tender or careful treatment, they can grow in almost any medium, including soilless ones. One of the most common causes of cycad death is from rotting stems and roots due to over-watering.

Some insects, particularly scale insects, some weevils and chewing insects can damage cycads, though the pests are susceptible to insecticides such as the horticulture soluble oil white oil. Sometimes bacterial preparations may be used to control insect infestation on cycads. When some of the mature plants prepare for reproduction, though, the presence of weevils has been shown to help accomplish pollination.

While the cycads have a reputation of slow growth, it is not always well-founded, and some actually grow quite fast, achieving reproductive maturity in 2–3 years (as with some *Zamia* species), while others in 15 years (as with some *Cycas*, Australian *Macrozamia* and *Lepidozamia*).

Chapter- 11

Gnetophyta

Gnetophyta

Welwitschia mirabilis

Scientific classification

Kingdom:	Plantae
Division:	**Gnetophyta**
Class:	**Gnetopsida**

Families & Genera

Gnetaceae
Gnetum
Welwitschiaceae
Welwitschia
Ephedraceae
Ephedra

Distribution, separated by genus:
Green – *Welwitschia*
Blue – *Gnetum*

Red – *Ephedra*
Purple – *Gnetum* and *Ephedra* range overlap

The plant division **Gnetophyta** or gnetophytes consists of three genera of woody plants grouped in the gymnosperms. The living Gnetophyta are in the genera *Gnetum* (family Gnetaceae), *Welwitschia* (family Welwitschiaceae), and *Ephedra* (family Ephedraceae).

The gnetophytes differ from other gymnosperms (conifers, cycads, and ginkgos) in having vessel elements as in the flowering plants. In some classifications, all three genera are placed in a single order (Gnetales) but in others distributed among three orders, each containing a single family and genus. Most morphological and molecular studies confirm that *Gnetum* and *Welwitschia* diverged from each other more recently than from *Ephedra*.

Ecology and Morphology

The three genera of the gnetophytes are highly specialized to their respective environments, making it difficult to identify homologous characters. The three extant genera of gnetophytes, a "bizarre and enigmatic" trio, are likely aberrant members of the group, which was diverse and dominant in the Tertiary. Some synapomorphies of the gnetophytes include enveloping bracts around the ovules and microsporangia, and a micropylar projection of the outer membrane of the ovule that produces a pollination droplet.

Gnetum species are mostly woody climbers in tropical forests. However, the most well-known member of this group, *Gnetum gnemon*, is a tree. Its seeds are used to produce a crispy *krupuk* snack known as *emping* or *krupuk belinjo*.

Welwitschia comprises only one species, *Welwitschia mirabilis*. It grows only in the deserts of Namibia and Angola. This strange species has only two large strap-like leaves that grow continuously from the base throughout the plant's life.

Plants of the genus *Ephedra* are known as jointfirs because they have long slender branches which bear tiny scale-like leaves at their nodes. *Ephedra* has been traditionally used as a stimulant, but is a controlled substance today in many jurisdictions because of the risk of harmful or even fatal overdosing.

Knowledge of fossils of the gnetophytes has increased greatly since the 1980s. There are fossils from the Permian, the Triassic, and the Jurassic which may belong to the gnetophytes, but this is uncertain. The fossil record is richer starting in the early Cretaceous, with fossils of plants as well as seeds and pollen which can be clearly assigned to the gnetophytes.

Classification

The evolutionary relationships among the seed plants are highly unresolved, and the gnetophytes have played an important role in the formation of phylogenetic hypotheses. Molecular phylogenies of extant gymnosperms have conflicted with morphological characters with regard to whether the gymnosperms as a whole (including gnetophytes) comprise a monophyletic group or a paraphyletic one that gave rise to angiosperms. At issue is whether the Gnetophyta are the sister group of angiosperms, or whether they are sister to, or nested within, other extant gymnosperms. Numerous fossil gymnosperm clades once existed that are morphologically at least as distinctive as the four living gymnosperm groups, such as Bennettitales, *Caytonia* and the glossopterids. When these gymnosperm fossils are considered, the question of gnetophyte relationships to other seed plants becomes even more complicated. Several hypotheses, illustrated below, have been presented to explain seed plant evolution.

Anthophyte hypothesis

From the early twentieth century, the anthophyte hypothesis was the prevailing explanation for seed plant evolution, based on shared morphological characters between the gnetophytes and angiosperms. In this hypothesis, the gnetophytes, along with the extinct order Bennettitales, are sister to the angiosperms, forming the "anthophytes". Some morphological characters that were suggested to unite the anthophytes include vessels in wood, net-veined leaves (in *Gnetum* only), lignin chemistry, the layering of cells in the apical meristem, pollen and megaspore features (including thin megaspore wall), short cambial initials, and lignin syringal groups. However, most genetic studies have rejected the anthophyte hypothesis. Several of these studies have suggested that the gnetophytes and angiosperms have independently derived characters, including flower-like reproductive structures and tracheid vessel elements, that appear shared but are actually the result of parallel evolution.

Gnetifer hypothesis

In the gnetifer hypothesis, the gnetophytes are sister to the conifers, and the gymnosperms are a monophyletic group, sister to the angiosperms. The gnetifer hypothesis first formally emerged in the mid-twentieth century, when vessel elements in the gnetophytes were interpreted as being derived from tracheids with circular bordered pits, as in conifers. It did not gain strong support, however, until the emergence of molecular data in the late 1990s. Although the morphological evidence still largely supports the anthophyte hypothesis, there are some morphological commonalities between the gnetophytes and conifers that lend support to the gnetifer hypothesis. These shared traits include: tracheids with scalariform pits with tori interspersed with annular thickenings, absence of scalariform pitting in primary xylem, scale-like and strap-shaped leaves of *Ephedra* and *Welwitschia*; and reduced sporophylls.

Gnepine hypothesis

The gnepine hypothesis is a modification of the gnetifer hypothesis, and suggests that the gnetophytes belong within the conifers as a sister group to the Pinaceae. According to this hypothesis, the conifers as currently defined are not a monophyletic group, in contrast with molecular findings that support its monophyly. All existing evidence for this hypothesis comes from molecular studies within the last decade. However, the morphological evidence remains difficult to reconcile with the gnepine hypothesis. If the gnetophytes are nested within conifers, they must have lost several shared derived characters of the conifers (or these characters must have evolved in parallel in the other conifer lineages): narrowly triangular leaves (gnetophytes have diverse leaf shapes), resin canals, a tiered proembryo, and flat woody ovuliferous cone scales.

Gnetophyte-sister hypothesis

Some partitions of the genetic data suggest that the gnetophytes are sister to all of the other extant seed plant groups. However, there is no morphological evidence nor evidence in the fossil record to support the gnetophyte-sister hypotheses.

Chapter- 12

Flowering Plant

Flowering plants
Temporal range: Early Cretaceous — Recent

Magnolia virginiana
Sweet Bay

Scientific classification

Kingdom: Plantae

Division: **Angiospermae**
Lindley [P.D. Cantino & M.J. Donoghue]

Clades

Amborellaceae
Nymphaeales
Austrobaileyales
Mesangiospermae

- Ceratophyllaceae
- Chloranthaceae
- Eudicotyledoneae (eudicots)

- Magnoliidae
- Monocotyledoneae (monocots)

Synonyms

Anthophyta
Magnoliophyta Cronquist, Takht. & W.Zimm., 1966

The **flowering plants** (**angiosperms**), also known as **Angiospermae** or **Magnoliophyta**, are the most diverse group of land plants. Angiosperms are seed-producing plants like the gymnosperms and can be distinguished from the gymnosperms by a series of synapomorphies (derived characteristics). These characteristics include flowers, endosperm within the seeds, and the production of fruits that contain the seeds.

The ancestors of flowering plants diverged from gymnosperms around 245–202 million years ago, and the first flowering plants known to exist are from 140 million years ago. They diversified enormously during the Lower Cretaceous and became widespread around 100 million years ago, but replaced conifers as the dominant trees only around 60-100 million years ago.

Angiosperm derived characteristics

- Flowers

The flowers, which are the reproductive organs of flowering plants, are the most remarkable feature distinguishing them from other seed plants. Flowers aid angiosperms by enabling a wider range of adaptability and broadening the ecological niches open to them. This has allowed flowering plants to largely dominate terrestrial ecosystems.

- Stamens with two pairs of pollen sacs

Stamens are much lighter than the corresponding organs of gymnosperms and have contributed to the diversification of angiosperms through time with adaptations to specialized pollination syndromes, such as particular pollinators. Stamens have also become modified through time to prevent self-fertilization, which has permitted further diversification, allowing angiosperms eventually to fill more niches.

- Reduced male parts, three cells

The male gametophyte in angiosperms is significantly reduced in size compared to those of gymnosperm seed plants. The smaller pollen decreases the time from pollination — the pollen grain reaching the female plant — to fertilization of the ovary; in gymnosperms fertilization can occur up to a year after pollination, while in angiosperms the fertilization begins very soon after pollination. The shorter time leads to angiosperm

plants setting seeds sooner and faster than gymnosperms, which is a distinct evolutionary advantage.

- Closed carpel enclosing the ovules (carpel or carpels and accessory parts may become the fruit)

The closed carpel of angiosperms also allows adaptations to specialized pollination syndromes and controls. This helps to prevent self-fertilization, thereby maintaining increased diversity. Once the ovary is fertilized, the carpel and some surrounding tissues develop into a fruit. This fruit often serves as an attractant to seed-dispersing animals. The resulting cooperative relationship presents another advantage to angiosperms in the process of dispersal.

- Reduced female gametophyte, seven cells with eight nuclei

The reduced female gametophyte, like the reduced male gametophyte, may be an adaptation allowing for more rapid seed set, eventually leading to such flowering plant adaptations as annual herbaceous life cycles, allowing the flowering plants to fill even more niches.

- Endosperm

Endosperm formation generally begins after fertilization and before the first division of the zygote. Endosperm is a highly nutritive tissue that can provide food for the developing embryo, the cotyledons, and sometimes for the seedling when it first appears.

These distinguishing characteristics taken together have made the angiosperms the most diverse and numerous land plants and the most commercially important group to humans. The major exception to the dominance of terrestrial ecosystems by flowering plants is the coniferous forest.

Evolution

Flowers of *Malus sylvestris* (crab apple)

Land plants have existed for about 425 million years. Early land plants reproduced sexually with flagellated, swimming sperm, like the green algae from which they evolved. An adaptation to terrestrialization was the development of upright meiosporangia for dispersal by spores to new habitats. This feature is lacking in the descendants of their nearest algal relatives, the Charophycean green algae. A later terrestrial adaptation took place with retention of the delicate, avascular sexual stage, the gametophyte, within the tissues of the vascular sporophyte. This occurred by spore germination within sporangia rather than spore release, as in non-seed plants. A current

example of how this might have happened can be seen in the precocious spore germination in *Sellaginella*, the spike-moss. The result for the ancestors of angiosperms was enclosing them in a case, the seed. The first seed bearing plants, like the ginkgo, and conifers (such as pines and firs), did not produce flowers. Interestingly, the pollen grains (males) of *Ginkgo* and cycads produce a pair of flagellated, mobile sperm cells that "swim" down the developing pollen tube to the female and her eggs.

The apparently sudden appearance of relatively modern flowers in the fossil record initially posed such a problem for the theory of evolution that it was called an "*abominable mystery*" by Charles Darwin. However, the fossil record has considerably grown since the time of Darwin, and recently discovered angiosperm fossils such as *Archaefructus*, along with further discoveries of fossil gymnosperms, suggest how angiosperm characteristics may have been acquired in a series of steps. Several groups of extinct gymnosperms, particularly seed ferns, have been proposed as the ancestors of flowering plants but there is no continuous fossil evidence showing exactly how flowers evolved. Some older fossils, such as the upper Triassic *Sanmiguelia*, have been suggested. Based on current evidence, some propose that the ancestors of the angiosperms diverged from an unknown group of gymnosperms during the late Triassic (245–202 million years ago). A close relationship between angiosperms and gnetophytes, proposed on the basis of morphological evidence, has more recently been disputed on the basis of molecular evidence that suggest gnetophytes are instead more closely related to other gymnosperms.

The earliest known macrofossil confidently identified as an angiosperm, *Archaefructus liaoningensis*, is dated to about 125 million years BP (the Cretaceous period), while pollen considered to be of angiosperm origin takes the fossil record back to about 130 million years BP. However, one study has suggested that the early-middle Jurassic plant *Schmeissneria*, traditionally considered a type of ginkgo, may be the earliest known angiosperm, or at least a close relative. Additionally, circumstantial chemical evidence has been found for the existence of angiosperms as early as 250 million years ago. Oleanane, a secondary metabolite produced by many flowering plants, has been found in Permian deposits of that age together with fossils of gigantopterids. Gigantopterids are a group of extinct seed plants that share many morphological traits with flowering plants, although they are not known to have been flowering plants themselves.

Recent DNA analysis based on molecular systematics showed that *Amborella trichopoda*, found on the Pacific island of New Caledonia, belongs to a sister group of the other flowering plants, and morphological studies suggest that it has features that may have been characteristic of the earliest flowering plants.

The great angiosperm radiation, when a great diversity of angiosperms appears in the fossil record, occurred in the mid-Cretaceous (approximately 100 million years ago). However, a study in 2007 estimated that the division of the five most recent (the genus *Ceratophyllum*, the family Chloranthaceae, the eudicots, the magnoliids, and the monocots) of the eight main groups occurred around 140 million years ago. By the late Cretaceous, angiosperms appear to have dominated environments formerly occupied by

ferns and cycadophytes, but large canopy-forming trees replaced conifers as the dominant trees only close to the end of the Cretaceous 65 millions years ago or even later, at the beginning of the Tertiary. The radiation of herbaceous angiosperm occurred much later. Yet, many fossil plants recognizable as belonging to modern families (including beech, oak, maple, and magnolia) appeared already at late Cretaceous.

Two bees on a flower head of Creeping Thistle, *Cirsium arvense*

It is generally assumed that the function of flowers, from the start, was to involve mobile animals in their reproduction processes. That is, pollen can be scattered even if the flower is not brightly colored or oddly shaped in a way that attracts animals; however, by expending the energy required to create such traits, angiosperms can enlist the aid of animals and thus reproduce more efficiently.

Island genetics provides one proposed explanation for the sudden, fully developed appearance of flowering plants. Island genetics is believed to be a common source of speciation in general, especially when it comes to radical adaptations that seem to have required inferior transitional forms. Flowering plants may have evolved in an isolated setting like an island or island chain, where the plants bearing them were able to develop a highly specialized relationship with some specific animal (a wasp, for example). Such a relationship, with a hypothetical wasp carrying pollen from one plant to another much the way fig wasps do today, could result in both the plant(s) and their partners developing a high degree of specialization. Note that the wasp example is not incidental; bees, which apparently evolved specifically due to mutualistic plant relationships, are descended from wasps.

Animals are also involved in the distribution of seeds. Fruit, which is formed by the enlargement of flower parts, is frequently a seed-dispersal tool that attracts animals to eat or otherwise disturb it, incidentally scattering the seeds it contains. While many such mutualistic relationships remain too fragile to survive competition and to spread widely, flowering proved to be an unusually effective means of reproduction, spreading (whatever its origin) to become the dominant form of land plant life.

Flower ontogeny uses a combination of genes normally responsible for forming new shoots. The most primitive flowers are thought to have had a variable number of flower parts, often separate from (but in contact with) each other. The flowers would have tended to grow in a spiral pattern, to be bisexual (in plants, this means both male and female parts on the same flower), and to be dominated by the ovary (female part). As flowers grew more advanced, some variations developed parts fused together, with a much more specific number and design, and with either specific sexes per flower or plant, or at least "ovary inferior".

Flower evolution continues to the present day; modern flowers have been so profoundly influenced by humans that some of them cannot be pollinated in nature. Many modern, domesticated flowers used to be simple weeds, which only sprouted when the ground was disturbed. Some of them tended to grow with human crops, perhaps already having symbiotic companion plant relationships with them, and the prettiest did not get plucked because of their beauty, developing a dependence upon and special adaptation to human affection.

A few palaeontologists have also come up with a theory that flowering plants, or angiosperms, might possibly have evolved because of dinosaurs; in other words, they believe that dinosaurs "created" flowers. One of the theory's biggest proponents is Robert T. Bakker. He theorizes that herbivorous dinosaurs, with their eating habits, forced plants to find new ways to develop new adaptations, in order to avoid predation by herbivores.

Classification

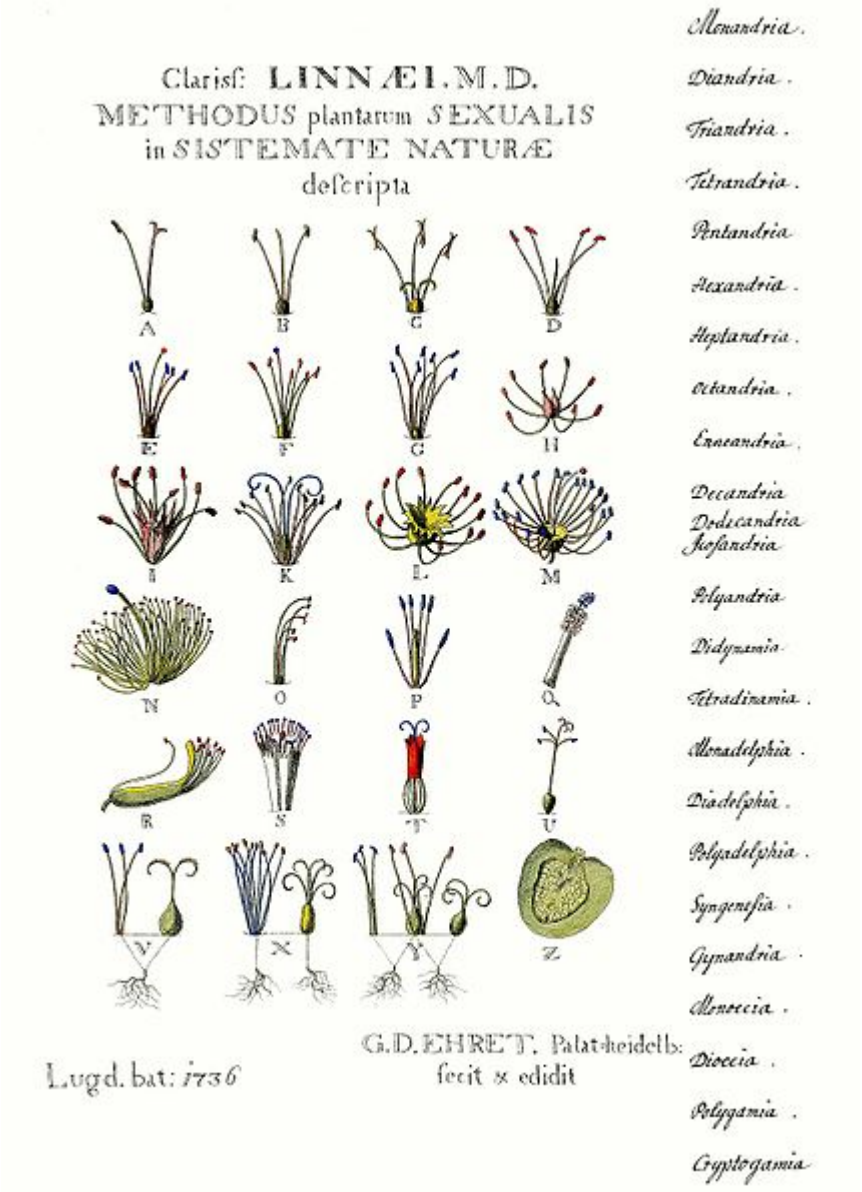
There are eight groups of living angiosperms:

- *Amborella* — a single species of shrub from New Caledonia
- Nymphaeales — about 80 species — water lilies and Hydatellaceae
- Austrobaileyales — about 100 species of woody plants from various parts of the world
- Chloranthales — several dozen species of aromatic plants with toothed leaves
- Magnoliidae — about 9,000 species, characterized by trimerous flowers, pollen with one pore, and usually branching-veined leaves — for example magnolias, bay laurel, and black pepper

- Monocotyledonae — about 70,000 species, characterized by trimerous flowers, a single cotyledon, pollen with one pore, and usually parallel-veined leaves — for example grasses, orchids, and palms
- *Ceratophyllum* — about 6 species of aquatic plants, perhaps most familiar as aquarium plants
- Eudicotyledonae — about 175,000 species, characterized by 4- or 5- merous flowers, pollen with three pores, and usually branching-veined leaves — for example sunflowers, petunia, buttercup, apples and oaks

The exact relationship between these eight groups is not yet clear, although there is agreement that the first three groups to diverge from the ancestral angiosperm were Amborellales, Nymphaeales, and Austrobaileyales. The term basal angiosperms refers to these three groups. The five other groups form the clade Mesangiospermae. The relationship between the three largest of these groups (magnoliids, monocots and eudicots) remains unclear. Some analyses make the magnoliids the first to diverge, others the monocots.. *Ceratophyllum* seems to group with the eudicots rather than with the monocots.

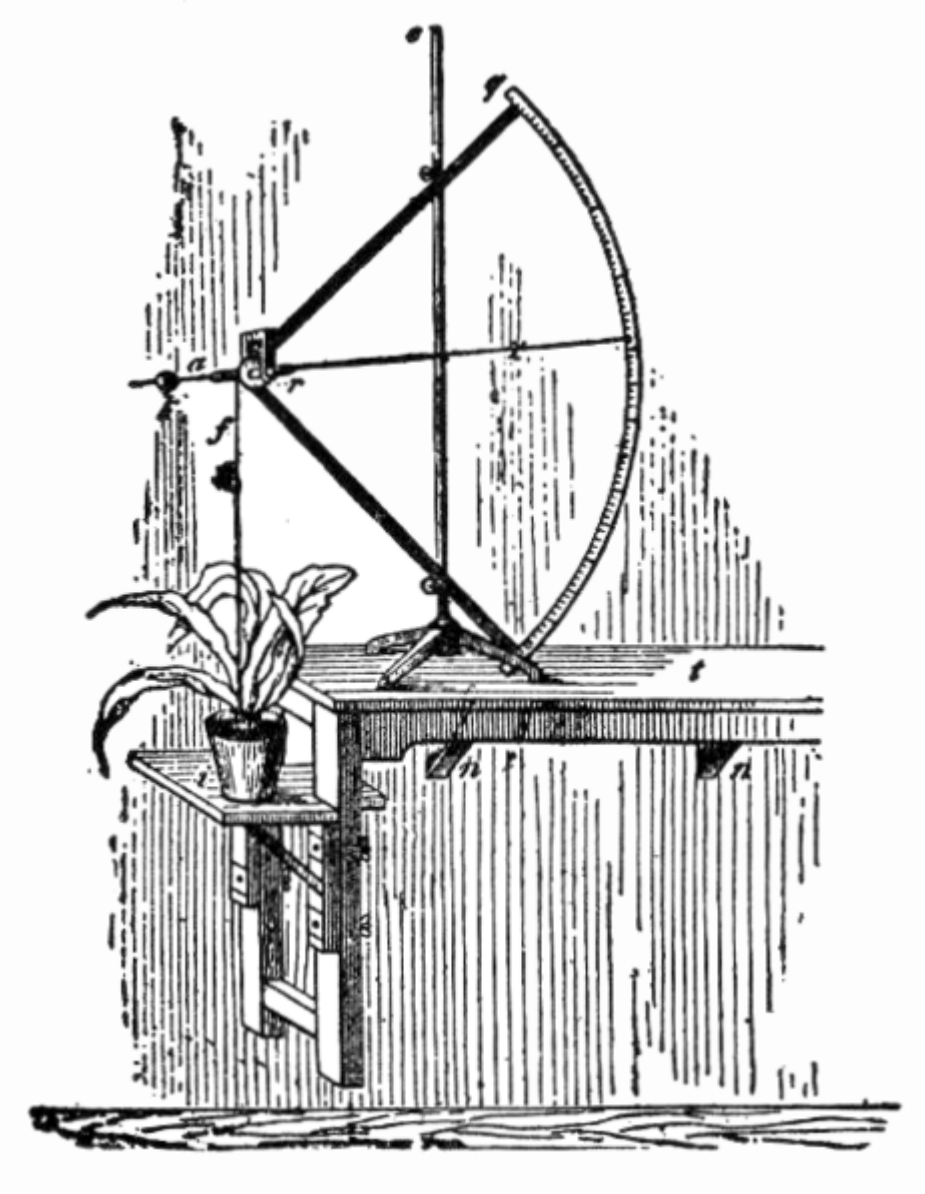
History of classification



From 1736, an illustration of Linnaean classification

The botanical term "Angiosperm", from the Ancient Greek αγγείον, *angeíon* (receptacle, vessel) and σπέρμα, (seed), was coined in the form Angiospermae by Paul Hermann in 1690, as the name of that one of his primary divisions of the plant kingdom. This included flowering plants possessing seeds enclosed in capsules, distinguished from his Gymnospermae, or flowering plants with achenial or schizo-carpic fruits, the whole fruit or each of its pieces being here regarded as a seed and naked. The term and its antonym were maintained by Carolus Linnaeus with the same sense, but with restricted application, in the names of the orders of his class Didynamia. Its use with any approach to its modern scope only became possible after 1827, when Robert Brown established the

existence of truly naked ovules in the Cycadeae and Coniferae, and applied to them the name Gymnosperms. From that time onwards, so long as these Gymnosperms were, as was usual, reckoned as dicotyledonous flowering plants, the term Angiosperm was used antithetically by botanical writers, with varying scope, as a group-name for other dicotyledonous plants.



Auxanometer: Device for measuring increase or rate of growth in plants

In 1851, Hofmeister discovered the changes occurring in the embryo-sac of flowering plants, and determined the correct relationships of these to the Cryptogamia. This fixed the position of Gymnosperms as a class distinct from Dicotyledons, and the term Angiosperm then gradually came to be accepted as the suitable designation for the whole

of the flowering plants other than Gymnosperms, including the classes of Dicotyledons and Monocotyledons. This is the sense in which the term is used today.

In most taxonomies, the flowering plants are treated as a coherent group. The most popular descriptive name has been Angiospermae (Angiosperms), with Anthophyta ("flowering plants") a second choice. These names are not linked to any rank. The Wettstein system and the Engler system use the name Angiospermae, at the assigned rank of subdivision. The Reveal system treated flowering plants as subdivision Magnoliophytina (Frohne & U. Jensen ex Reveal, Phytologia 79: 70 1996), but later split it to Magnoliopsida, Liliopsida and Rosopsida. The Takhtajan system and Cronquist system treat this group at the rank of division, leading to the name Magnoliophyta (from the family name Magnoliaceae). The Dahlgren system and Thorne system (1992) treat this group at the rank of class, leading to the name Magnoliopsida. The APG system of 1998, and the later 2003 and 2009 revisions, treat the flowering plants as a clade called angiosperms without a formal botanical name. However, a formal classification was published alongside the 2009 revision in which the flowering plants form the Subclass Magnoliidae.

The internal classification of this group has undergone considerable revision. The Cronquist system, proposed by Arthur Cronquist in 1968 and published in its full form in 1981, is still widely used but is no longer believed to accurately reflect phylogeny. A consensus about how the flowering plants should be arranged has recently begun to emerge through the work of the Angiosperm Phylogeny Group (APG), which published an influential reclassification of the angiosperms in 1998. Updates incorporating more recent research were published as APG II in 2003and as APG III in 2009.

Monocot (left) and dicot seedlings

Traditionally, the flowering plants are divided into two groups, which in the Cronquist system are called *Magnoliopsida* (at the rank of class, formed from the family name *Magnoliacae*) and *Liliopsida* (at the rank of class, formed from the family name *Liliaceae*). Other descriptive names allowed by Article 16 of the ICBN include *Dicotyledones* or *Dicotyledoneae*, and *Monocotyledones* or *Monocotyledoneae*, which have a long history of use. In English a member of either group may be called a *dicotyledon* (plural *dicotyledons*) and *monocotyledon* (plural *monocotyledons*), or abbreviated, as *dicot* (plural *dicots*) and *monocot* (plural *monocots*). These names derive from the observation that the dicots most often have two *cotyledons*, or embryonic leaves, within each seed. The monocots usually have only one, but the rule is not absolute either way. From a diagnostic point of view the number of cotyledons is neither a particularly handy nor reliable character.

Recent studies, as by the APG, show that the monocots form a monophyletic group (clade) but that the dicots do not (they are paraphyletic). Nevertheless, the majority of dicot species do form a monophyletic group, called the *eudicots* or *tricolpates*. Of the remaining dicot species, most belong to a third major clade known as the Magnoliidae, containing about 9,000 species. The rest include a paraphyletic grouping of primitive species known collectively as the basal angiosperms, plus the families Ceratophyllaceae and Chloranthaceae.

Flowering plant diversity

The number of species of flowering plants is estimated to be in the range of 250,000 to 400,000. The number of families in APG (1998) was 462. In APG II (2003) it is not settled; at maximum it is 457, but within this number there are 55 optional segregates, so that the minimum number of families in this system is 402. In APG III (2009) there are 415 families.

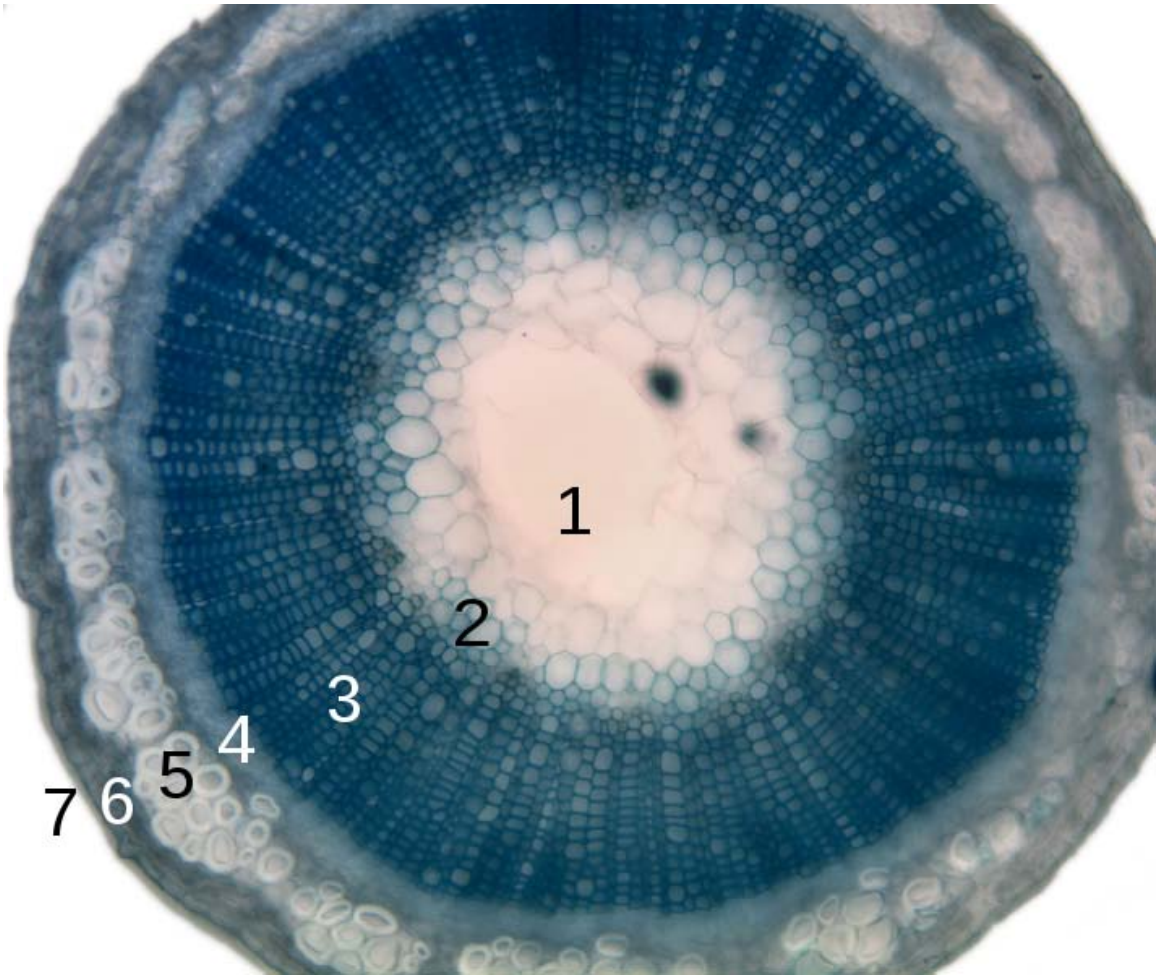
The diversity of flowering plants is not evenly distributed. Nearly all species belong to the eudicot (75%), monocot (23%) and magnoliid (2%) clades. The remaining 5 clades contain a little over 250 species in total, i.e., less than 0.1% of flowering plant diversity, divided among 9 families.

The most diverse families of flowering plants, in their APG circumscriptions, in order of number of species, are:

1. Asteraceae or Compositae (daisy family): 23,600 species
2. Orchidaceae (orchid family): 22,075 species
3. Fabaceae or Leguminosae (pea family): 19,400
4. Rubiaceae (madder family): 13,150
5. Poaceae or Gramineae (grass family): 10,035
6. Lamiaceae or Labiatae (mint family): 7,173
7. Euphorbiaceae (spurge family): 5,735
8. Melastomataceae (melastome family): 5,005
9. Myrtaceae (myrtle family): 4,620
10. Apocynaceae (dogbane family): 4,555

In the list above (showing only the 10 largest families), the Orchidaceae and Poaceae are monocot families; the others are eudicot families.

Vascular anatomy



Cross-section of a stem of the angiosperm flax:
1. Pith,
2. Protoxylem,
3. Xylem I,
4. Phloem I,
5. Sclerenchyma (bast fibre),
6. Cortex,
7. Epidermis

The amount and complexity of tissue-formation in flowering plants exceeds that of gymnosperms. The vascular bundles of the stem are arranged such that the xylem and phloem form concentric rings.

In the dicotyledons, the bundles in the very young stem are arranged in an open ring, separating a central pith from an outer cortex. In each bundle, separating the xylem and phloem, is a layer of meristem or active formative tissue known as cambium. By the formation of a layer of cambium between the bundles (interfascicular cambium) a

complete ring is formed, and a regular periodical increase in thickness results from the development of xylem on the inside and phloem on the outside. The soft phloem becomes crushed, but the hard wood persists and forms the bulk of the stem and branches of the woody perennial. Owing to differences in the character of the elements produced at the beginning and end of the season, the wood is marked out in transverse section into concentric rings, one for each season of growth, called annual rings.

Among the monocotyledons, the bundles are more numerous in the young stem and are scattered through the ground tissue. They contain no cambium and once formed the stem increases in diameter only in exceptional cases.

The flower, fruit, and seed

Flowers

A collection of flowers forming an inflorescence

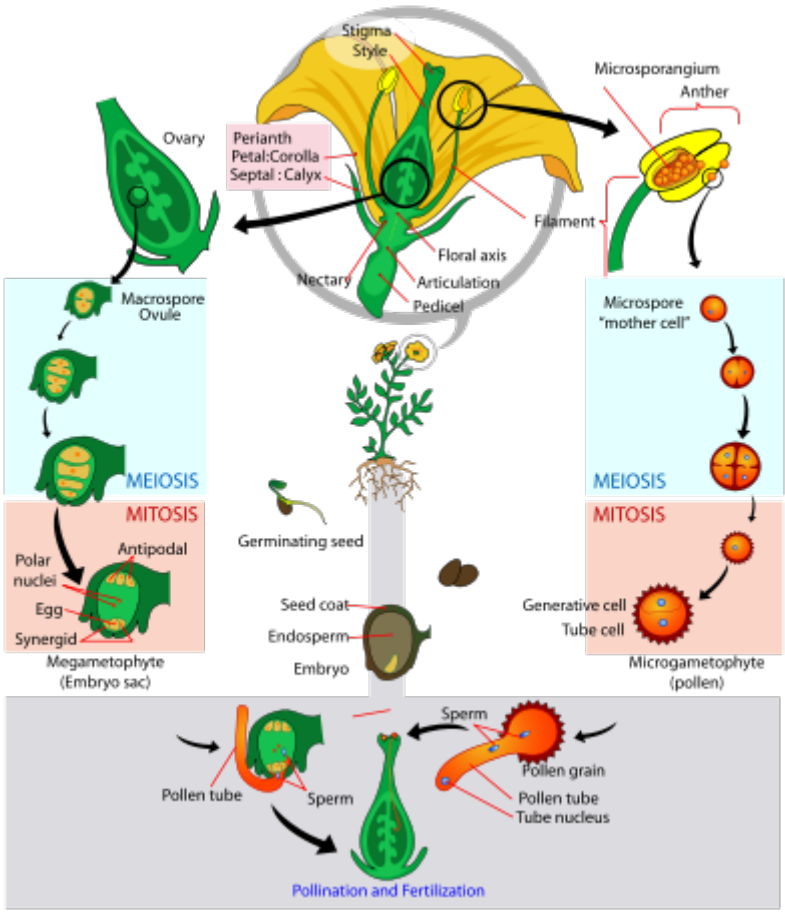
The characteristic feature of angiosperms is the flower. Flowers show remarkable variation in form and elaboration, and provide the most trustworthy external characteristics for establishing relationships among angiosperm species. The function of the flower is to ensure fertilization of the ovule and development of fruit containing seeds. The floral apparatus may arise terminally on a shoot or from the axil of a leaf (where the petiole attaches to the stem). Occasionally, as in violets, a flower arises singly in the axil of an ordinary foliage-leaf. More typically, the flower-bearing portion of the plant is sharply distinguished from the foliage-bearing or vegetative portion, and forms a more or less elaborate branch-system called an inflorescence.

The reproductive cells produced by flowers are of two kinds. Microspores, which will divide to become pollen grains, are the "male" cells and are borne in the stamens (or microsporophylls). The "female" cells called megaspores, which will divide to become the egg-cell (megagametogenesis), are contained in the ovule and enclosed in the carpel (or megasporophyll).

The flower may consist only of these parts, as in willow, where each flower comprises only a few stamens or two carpels. Usually other structures are present and serve to protect the sporophylls and to form an envelope attractive to 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. The inner series (corolla of petals) is generally white or brightly colored, and is more delicate in structure. It functions to attract insect or bird pollinators. Attraction is effected by color, scent, and nectar, which may be secreted in some part of the flower. The characteristics that attract pollinators account for the popularity of flowers and flowering plants among humans.

While the majority of flowers are perfect or hermaphrodite (having both male and female parts in the same flower structure), flowering plants have developed numerous morphological and physiological mechanisms to reduce or prevent self-fertilization. Heteromorphic flowers have short carpels and long stamens, or vice versa, so animal pollinators cannot easily transfer pollen to the pistil (receptive part of the carpel). Homomorphic flowers may employ a biochemical (physiological) mechanism called self-incompatibility to discriminate between self- and non-self pollen grains. In other species, the male and female parts are morphologically separated, developing on different flowers.

Fertilization and embryogenesis



Angiosperm life cycle

Double fertilization refers to a process in which two sperm cells fertilize cells in the ovary. This process begins when a pollen grain adheres to the stigma of the pistil (female reproductive structure), germinates, and grows a long pollen tube. While this pollen tube is growing, 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. As the pollen tube grows, it makes its way from the stigma, down the style and into the ovary. Here the pollen tube reaches the micropyle of the ovule and digests its way into one of the synergids, releasing its contents (which include the sperm cells). The synergid that the cells were released into degenerates and one sperm makes its way to fertilize the egg cell, producing a diploid ($2n$) zygote. The second sperm cell fuses with both central cell nuclei, producing a triploid ($3n$) cell. As the zygote develops into an embryo, the triploid cell develops into the endosperm, which serves as the embryo's food supply. The ovary now will develop into fruit and the ovule will develop into seed.

Fruit and seed

The fruit of the *Aesculus* or Horse Chestnut tree

As the development of embryo and endosperm proceeds within the embryo-sac, the sac wall enlarges and combines with the nucellus (which is likewise enlarging) and the integument to form the *seed-coat*. The ovary wall develops to form the fruit or pericarp, whose form is closely associated with the manner of distribution of the seed.

Frequently the influence of fertilization is felt beyond the ovary, and other parts of the flower take part in the formation of the fruit, *e.g.* the floral receptacle in the apple, strawberry and others.

The character of the seed-coat bears a definite relation to that of the fruit. They protect the embryo and aid in dissemination; they may also directly promote germination. Among plants with indehiscent fruits, the fruit generally provides protection for the embryo and secures dissemination. In this case, the seed-coat is only slightly developed. If the fruit is dehiscent and the seed is exposed, the seed-coat is generally well developed, and must discharge the functions otherwise executed by the fruit.

Economic importance

Agriculture is almost entirely dependent on angiosperms, either directly or indirectly through livestock feed. Of all the families plants, the Poaceae, or grass family, is by far the most important, providing the bulk of all feedstocks (rice, corn — maize, wheat, barley, rye, oats, pearl millet, sugar cane, sorghum). The Fabaceae, or legume family, comes in second place. Also of high importance are the Solanaceae, or nightshade family (potatoes, tomatoes, and peppers, among others), the Cucurbitaceae, or gourd family (also including pumpkins and melons), the Brassicaceae, or mustard plant family (including rapeseed and the innumerable varieties of the cabbage species *Brassica oleracea*), and the Apiaceae, or parsley family. Many of our fruits come from the Rutaceae, or rue family, and the Rosaceae, or rose family (including apples, pears, cherries, apricots, plums, etc.).

In some parts of the world, certain single species assume paramount importance because of their variety of uses, for example the coconut (*Cocos nucifera*) on Pacific atolls, and the olive (*Olea europaea*) in the Mediterranean region.

Flowering plants also provide economic resources in the form of wood, paper, fiber (cotton, flax, and hemp, among others), medicines (digitalis, camphor), decorative and landscaping plants, and many other uses. The main area in which they are surpassed by other plants is timber production.