

Chapter 29 - Plant Diversity I: How Plants Colonized Land

Overview: The Greening of Earth

- For the first 3 billion years of Earth's history, the land was lifeless.
- Thin coatings of cyanobacteria existed on land about 1.2 billion years ago.
- About 500 million years ago, plants, fungi, and animals joined the cyanobacteria.
- By about 370 million years ago, taller plants appeared, leading to the formation of the first forests.
- More than 290,000 species of plants inhabit Earth today.
- Most plants live in terrestrial environments, including mountaintops, deserts, and aquatic habitats.
 - Even aquatic plants are referred to as *land* plants, to distinguish them from algae.
- The presence of plants has enabled other organisms to survive on land.
 - Plant roots have created habitats for other organisms by stabilizing landscapes.
 - Plants are the source of oxygen and the ultimate provider of food for land animals.

Concept 29.1 Land plants evolved from green algae.

- Researchers have identified a lineage of green algae called charophytes as the closest relatives of land plants.
- Many key characteristics of land plants also appear in a variety of protists, primarily algae.
- Plants are multicellular, eukaryotic, photosynthetic autotrophs.
 - Red, brown, and some green algae also fit this description.
- Plants have cell walls made of cellulose.
 - So do green algae, dinoflagellates, and brown algae.
- Plants have chloroplasts with chlorophyll *a* and *b*.
 - So do green algae, euglenids, and a few dinoflagellates.
- The charophytes are the only algae that share the following four distinctive traits with land plants, which strongly suggests that they are the closest relatives of plants.

1. The plasma membranes of land plants and charophytes possess **rosette-shaped cellulose-synthesizing complexes** that synthesize the cellulose microfibrils of the cell wall.
 - ♣ These complexes contrast with the linear arrays of cellulose-producing proteins in noncharophyte algae.
 2. Both charophytes and land plants have **peroxisome enzymes** to help minimize the loss of organic products as a result of photorespiration.
 - ♣ Peroxisomes of other algae lack these enzymes.
 3. The **structure of flagellated sperm** of charophytes and land plants with sperm is very similar.
 4. Certain details of cell division are common to only land plants and the most complex charophyte algae.
 - ♣ These include the formation of a **phragmoplast**, an alignment of cytoskeletal elements and Golgi-derived vesicles during the synthesis of new cross-walls during cytokinesis.
- Comparisons of nuclear and chloroplast genes from a wide range of plants and algae support the hypothesis that the charophytes are the closest living relatives of land plants.
 - Many charophyte algae inhabit shallow waters at the edges of ponds and lakes, where they experience occasional drying.
 - In such environments, natural selection favors individuals that can survive periods when they are not submerged in water.
 - A layer of a durable polymer called **sporopollenin** prevents exposed charophyte zygotes from drying out until they are in water again.
 - This chemical adaptation may have been the precursor to the tough sporopollenin walls that encase plant spores.
 - The accumulation of such traits by at least one population of ancestral charophytes enabled their descendants—the first land plants—to live permanently above the waterline.
 - The evolutionary novelties of the first land plants opened up an expanse of terrestrial habitat previously occupied only by films of bacteria.
 - The new frontier was spacious.
 - The bright sunlight was unfiltered by water and plankton.
 - The atmosphere had an abundance of CO₂.
 - The soil was rich in mineral nutrients.
 - At least at first, there were relatively few herbivores or pathogens.
 - There were also challenges in the new environment: the risk of desiccation and a lack of structural support against gravity.

- A number of adaptations evolved in plants that allowed them to survive and reproduce on land.

Four key traits distinguish land plants from algae.

- What exactly is the line that divides land plants from algae?
 - We will adopt the traditional scheme, which equates the kingdom Plantae with embryophytes (plants with embryos).
 - Four key traits appear in nearly all land plants but are absent in charophyte algae.
 - We infer that these traits evolved as derived traits of land plants.
- The four traits are:
 1. Alternation of generations (along with multicellular, dependent embryos)
 2. Sporangia that produce walled spores
 3. Gametangia that produce gametes
 4. Apical meristems
- Some of these traits are not unique to plants; not every land plant exhibits all four traits.

Plant life cycles are characterized by alternation of generations, with multicellular, dependent embryos.

- All land plants show alternation of generations in which two multicellular body forms alternate.
 - This life cycle also occurs in various algae.
 - Alternation of generations does not occur in the charophytes, however, the algae most closely related to land plants.
- In alternation of generations, one of the multicellular bodies is called the **gametophyte** and has haploid cells.
- Gametophytes produce gametes, egg and sperm, by mitosis.
- The fusion of egg and sperm during fertilization forms a diploid zygote.
- Mitotic division of the diploid zygote produces the other multicellular body, the **sporophyte**.
- Meiosis in a mature sporophyte produces haploid reproductive cells called spores.
 - A spore is a reproductive cell that can develop into a new organism without fusing with another cell.
- Mitotic division of a plant spore produces a new multicellular gametophyte.
- Unlike the life cycles of other sexually producing organisms, alternation of generations in land plants (and some algae) results in both haploid and diploid stages that exist as

multicellular bodies.

- For example, humans do not have alternation of generations because the only haploid stage in the life cycle is the gamete, which is single-celled.
- Multicellular plant embryos develop from zygotes that are retained within tissues of the female parent.
- The multicellular, dependent embryo of land plants is such a significant derived trait that land plants are also known as **embryophytes**.
- The parent provides nutrients, such as sugars and amino acids, to the embryo.
 - The embryo has specialized placental transfer cells that enhance the transfer of nutrients from parent to embryo.
 - Transfer cells are sometimes present in the adjacent maternal tissues as well.
 - This interface is analogous to the nutrient-transferring embryo-mother interface of placental mammals.

In plants, walled spores are produced by sporangia.

- Plant spores are haploid reproductive cells that grow into gametophytes by mitosis.
- Sporopollenin makes the walls of spores very tough and resistant to harsh environments.
- Multicellular organs called **sporangia** are found on the sporophyte and produce spores.
 - Within sporangia, diploid cells called **sporocytes** undergo meiosis and generate haploid spores.
- The outer tissues of the sporangium protect the developing spores until they are ready to be released into the air.

Plant gametophytes produce gametes within multicellular organs called gametangia.

- A female gametangium, called an archegonium, produces a single egg cell in a vase-shaped organ.
 - The egg is retained within the base.
- Male gametangia, called **antheridia**, produce and release sperm into the environment.
- In many major groups of living plants, the sperm have flagella and swim to the eggs through a water film.
- Each egg is fertilized within an archegonium, where the zygote develops into the embryo.
- The gametophytes of seed plants are so reduced in size that archegonia and antheridia have been lost in some lineages.

Additional derived traits have evolved in many plant species.

- In addition to the four traits listed above, other derived traits have evolved in many plant species.
- The epidermis in many plant species has a **cuticle** consisting of polyester and wax polymers.
 - The cuticle acts as waterproofing, preventing water loss and protecting against microbial attack.
- Fossils dating from 420 million years ago show that early plants formed symbiotic associations with fungi.
 - Most modern plants are associated with mycorrhizal fungi, which form extensive networks of filaments through the soil, aiding in nutrient absorption.
 - The fungi transfer nutrients to their symbiotic plant partner.
 - This mutualism may have allowed plants to colonize land before the evolution of roots.
- Many land plants produce *secondary compounds*, products of secondary metabolic pathways.
 - Such pathways branch off the primary metabolic pathways that produce organic compounds common to all living things.
- Secondary compounds include alkaloids, terpenes, tannins, and phenolics such as flavonoids.
 - Alkaloids, terpenes, and tannins have a bitter taste, strong odor, or toxic effect that helps defend against herbivores and parasites.
 - Flavonoids absorb harmful ultraviolet radiation, while other phenolics deter attack by pathogens.
 - Many secondary compounds are used in spices and medicines.

Land plants have apical meristems.

- In terrestrial habitats, the resources that a photosynthetic organism requires are found in two different places.
 - Light and carbon dioxide are mainly above ground.
 - Water and mineral resources are found mainly in the soil.
- Therefore, plants show varying degrees of structural specialization for subterranean and aerial organs—roots and shoots in most plants.
- The elongation and branching of the shoots and roots maximize their exposure to

environmental resources.

- This growth is sustained by **apical meristems**, localized regions of cell division at the tips of shoots and roots.
- Cells produced by meristems differentiate into various tissues, including surface epidermis and internal tissues.

Land plants have diversified since their origin from algal ancestors.

- Fossils of plant spores have been extracted from 475-million-year-old rocks dating back to the Ordovician period.
- Although the fossil spores resemble those of living plants, they have some differences.
 - Unlike living plants, the fossil spores were fused together in groups of two and four.
 - Some scientists dispute the identification of these spores as plant material.
- In 2003, scientists extracted spores from 475-million-year-old rocks in Oman.
 - These spores were embedded in plant cuticle material similar to spore-bearing tissue in living plants.
- Land plants can be informally grouped based on the presence or absence of an extensive system of **vascular tissue**, cells joined into tubes that transport water and nutrients throughout the plant body.
 - Most plants have a complex vascular tissue system and are called **vascular plants**.
 - Plants that do not have an extensive transport system (liverworts, hornworts, and mosses) are described as “nonvascular plants,” although some mosses do have simple vascular tissue.

Nonvascular plants are informally called bryophytes.

- There is some uncertainty about whether *bryophytes* are monophyletic and represent a clade.
 - Some recent analyses of amino acid sequences in bryophytes indicate that bryophytes do form a monophyletic group or clade.
- Whether or not bryophytes represent a clade, they share some derived traits with vascular plants, such as multicellular embryos and apical meristems.
 - They lack roots and true leaves.
- Vascular plants form a clade consisting of 93% of all land plants.
- Three smaller clades are found within the vascular plants.
- **Lycophytes** include club mosses and their relatives.

- **Pterophytes** include the ferns and their relatives.
- These two clades are called the **seedless vascular plants**.
 - The seedless vascular plants are paraphyletic, not monophyletic.
 - A group such as the seedless vascular plants is called a **grade**, a collection of organisms that share a common level of biological organization or adaptation.
- A third clade of vascular plants is the seed plants, the vast majority of living plants.
- A **seed** is an embryo packaged with a supply of nutrients within a protective coat.
- Seed plants can be divided into two groups: gymnosperms and angiosperms.
- The two groups can be distinguished by the absence or presence of enclosed chambers in which seeds mature.
- **Gymnosperms** are called “naked seed” plants because their seeds are not enclosed in chambers.
 - Living gymnosperm species, including the conifers, probably form a clade.
- **Angiosperms** are a huge clade including all flowering plants.
 - Angiosperm seeds develop inside chambers called ovaries, which originate within flowers and mature into seeds.

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◇ **Concept 29.2 Mosses and other nonvascular plants have life cycles dominated by gametophytes.**

- The nonvascular plants (bryophytes) are represented by three phyla:
 1. Phylum Hepatophyta—**liverworts**
 2. Phylum Anthocerophyta—**hornworts**
 3. Phylum Bryophyta—**mosses**
- Note that the term *Bryophyta* refers to only one phylum, but the informal term *bryophyte* refers to *all* nonvascular plants.
- Systematists continue to debate the sequence in which the three phyla of bryophytes evolved.
- Bryophytes acquired many unique adaptations after their evolutionary split from the ancestors of modern vascular plants.
- Bryophytes also possess some ancestral traits characteristic of the earliest plants.

- In bryophytes, gametophytes are the largest and most conspicuous phase of the life cycle.
 - Sporophytes are smaller and are present only part of the time.
- Bryophyte spores germinate in favorable habitats and grow into gametophytes by mitosis.
- Germinating moss spores produce a mass of green, branched filaments that are one cell thick, called a **protonema**.
- A protonema has a large surface area that enhances absorption of water and minerals.
- In favorable conditions, a protonema produces one or more “buds.”
- Each bud-like growth has an apical meristem that generates a gamete-producing structure, the **gametophore**.
- A protonema and a gametophore make up the body of a moss gametophyte.
- Bryophyte gametophytes form ground-hugging carpets because their body parts are too thin to support a tall plant.
 - Lacking vascular tissue, most bryophytes are only a few centimeters tall.
 - The thin structure of bryophytes makes it possible to distribute materials without specialized vascular tissue.
- Some mosses, such as *Polytrichum*, have conducting tissue in the center of their “stems.”
 - These tissues are analogous to the conducting tissue of vascular plants.
 - As a result, some mosses can grow to 2 m in height.
- Gametophytes are anchored by delicate **rhizoids**, which are long, tubular single cells (in liverworts and hornworts) or filaments of cells (in mosses).
 - Unlike roots, rhizoids are not composed of tissues, lack specialized conducting cells, and do not play a primary role in water and mineral absorption.
- The mature gametophores of bryophytes form gametangia that produce gametes and are covered by protective tissue.
 - Each vase-shaped archegonium produces a single egg.
 - Elongated antheridia produce many flagellated sperm.
- Some bryophyte gametophytes are bisexual, but in mosses the archegonia and antheridia are carried on separate male and female gametophytes.
- Flagellated sperm swim through a thin film of water, drawn by chemical attractants to the archegonia.

- Sperm swim into the archegonia and fertilize the eggs.
- The zygotes and young sporophytes are retained and nourished by the parent gametophyte.
 - Layers of placental nutritive cells transport materials from parent to embryos.
- Bryophytes are best able to reproduce sexually in moist habitats with abundant gametophytes.
- Some mosses reproduce asexually by forming *brood bodies*, small plantlets that detach from the parent plant to grow into new, genetically identical copies of their parent.
- Although the bryophyte sporophyte does have photosynthetic plastids when young, it cannot live apart from the maternal gametophyte.
- A bryophyte sporophyte remains attached to its parental gametophyte throughout the sporophyte's lifetime.
 - It depends on the gametophyte for sugars, amino acids, minerals, and water.
- Bryophytes have the smallest and simplest sporophytes of all modern plant groups, consistent with the hypothesis that larger and more complex sporophytes evolved only later in vascular plants.
- Moss sporophytes consist of a foot, an elongated stalk (the seta), and a sporangium (the capsule).
 - Embedded in the archegonium, the **foot** absorbs nutrients from the parent gametophyte.
 - The **seta** or stalk conducts these materials to the sporangium or **capsule**, which uses them to produce spores by meiosis.
 - One capsule can generate up to 50 million spores.
- In most mosses, the seta becomes elongated, elevating the capsule to enhance spore dispersal.
- In most moss species, the upper part of the capsule features a ring of interlocking, tooth-like structures known as the **peristome**.
 - The teeth open under dry conditions and close when it is moist, releasing the spores gradually to be blown by wind.
- Liverworts have the simplest sporophytes among the bryophytes.
- Hornwort and moss sporophytes are larger and more complex.
- The sporophytes of hornworts and mosses have specialized pores called **stomata**, like those of vascular plants.
 - Stomata support photosynthesis by allowing the exchange of CO₂ and O₂ between

the outside air and the interior of the sporophyte.

- Stomata are the main avenues by which water evaporates from the sporophyte.
- In hot, dry conditions, the stomata can close to minimize water loss.
- The fact that stomata are present in mosses and hornworts but absent in liverworts has led to three hypotheses for their evolution.
 1. If liverworts are the deepest-branching lineage of land plants, then stomata evolved once in the ancestor of hornworts, mosses, and vascular plants.
 2. If hornworts or mosses are the deepest-branching lineage of land plants, or if bryophytes are monophyletic, then stomata evolved once and were lost in the liverwort lineage.
 3. If hornworts are the deepest-branching lineage and mosses are the closest relatives of vascular plants, then hornworts may have acquired stomata independently of mosses and vascular plants.
- Wind dispersal of lightweight spores has distributed bryophytes around the world.
- Bryophytes are common and diverse in moist forests and wetlands.
- Some bryophytes even inhabit extreme environments such as mountaintops, tundra, and deserts.
- Many mosses can exist in very cold or dry habitats because they are able to lose most of their body water and then rehydrate and reactivate their cells when moisture again becomes available.
 - Few vascular plants can survive the same degree of desiccation.
- *Sphagnum*, a wetland moss, is especially abundant and widespread.
- *Sphagnum* forms extensive deposits of undecayed organic material called **peat**.
 - Wet regions dominated by *Sphagnum* or “peat moss” are known as peatlands.
 - Peat’s organic materials do not decay readily because of resistant phenolic compounds and acidic secretions that inhibit bacterial activity.
- Peatlands play an important role as carbon reservoirs, stabilizing atmospheric carbon dioxide levels.
 - Worldwide, an estimated 400 billion tons of organic carbon are stored as peat.
- Today, peat is harvested for use as a soil conditioner and for packing plants’ roots because of the water-storage capacity of its large dead cells.

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Concept 29.3 Ferns and other seedless

vascular plants were the first plants to grow tall.

- Bryophytes were the prevalent vegetation for the first 100 million years that terrestrial communities existed.
 - Vascular plants still dominate most landscapes today.
- Fossils and living seedless vascular plants provide insights into plant evolution during the Devonian and Carboniferous periods, when vascular plants began to diversify but most groups of seed plants had not yet evolved.
 - Fossils show that lycophytes, ferns, and other seedless vascular plants had well-developed vascular systems by the Devonian period.
 - This innovation set the stage for vascular plants to grow taller than bryophytes.
- The sperm of ferns and all other seedless vascular plants are flagellated and must swim through a film of water to reach eggs.
 - Due to their swimming sperm and fragile gametophytes, modern seedless vascular plants are most common in damp environments.
- Fossils of the ancestors of today's vascular plants date back about 420 million years.
- Unlike bryophytes, these plants had branched sporophytes that did not remain dependent on gametophytes for growth.
 - Although vascular plant ancestors grew no taller than about 50 cm, their branching made possible more complex bodies with multiple sporangia.
- These plants had some derived traits characteristic of living vascular plants, but they lacked roots and other key adaptations that evolved later.
- Three main traits characterize modern vascular plants:
 1. Life cycles with dominant sporophytes
 2. Transport in vascular tissue called xylem and phloem
 3. Well-developed roots and leaves, including spore-bearing leaves called sporophylls

Vascular plants have life cycles with dominant sporophytes.

- Fossils suggest that the ancestors of vascular plants had life cycles characterized by gametophytes and sporophytes that were about equal in size.
- Among living vascular plants, the sporophyte (diploid) generation is the larger and more complex plant.
 - For example, the leafy fern plants that you are familiar with are sporophytes.
 - The gametophytes are tiny plants that grow on or just below the soil surface.
- The reduced size of the gametophytes is even more extreme in seed plants.

Vascular plants have two types of vascular tissue: xylem and phloem.

- **Xylem** conducts most of the water and minerals.
- The xylem of all vascular plants includes **tracheids**, tube-shaped cells that carry water and minerals up from roots.
 - Because nonvascular plants lack tracheids, vascular plants are sometimes referred to as *tracheophytes*.
- The water-conducting cells in vascular plants are *lignified*, strengthened by the phenolic polymer **lignin**.
- **Phloem** is a living tissue in which nutrient-conducting cells are arranged into tubes that distribute sugars, amino acids, and other organic products.
- Lignified vascular tissue permitted vascular plants to grow to greater heights than bryophytes.
 - The stems of vascular plants became strong enough to provide support against gravity, and they could transport water and mineral high above the ground.
- The ability to grow tall was a major evolutionary innovation.
 - Tall plants shaded other plants, reducing their access to sunlight
 - This height gave vascular plants a competitive edge over bryophytes, which rarely grow over 20 cm in height.

Lignified vascular tissue allowed the evolution of roots.

- **Roots** are organs that anchor vascular plants and enable them to absorb water and nutrients from the soil.
- Roots also allow the shoot system to grow taller.
- Roots may have evolved from the subterranean portions of stems in ancient vascular plants.
- It is not clear whether roots evolved once in the common ancestor of all vascular plants or independently in different lineages.
- Although the roots of living vascular plants from various lineages share many similarities, the fossil record suggests that roots evolved convergently in different lineages.
 - The oldest lycophyte fossils had simple roots 400 million years ago, when the ancestors of ferns and seed plants lacked roots.
- Studying genes that control root development may help resolve this controversy.

Leaves capture solar energy for photosynthesis.

- **Leaves** are organs that increase the surface area of vascular plants to capture light.
- In terms of size and complexity, leaves can be classified as microphylls and megaphylls.
 - All lycophytes have **microphylls**, small leaves with a single unbranched vein.
 - All other vascular plants have **megaphylls**, leaves with a highly branched vascular system.
- Megaphylls support more photosynthetic productivity than microphylls because of their larger surface area.
- Microphylls first appear in the fossil record 410 million years ago; megaphylls do not emerge until the end of the Devonian period, about 370 million years ago.
- According to one model of leaf evolution, microphylls originated from sporangia located on the side of the stem.
- Megaphylls may have evolved from a series of branches lying close together on a stem.
 - As one of these branches came to *overtop* the others, the lower branches became flattened and developed webbing, joining the branches.
 - The leaf was now attached to the overtopping branch.
- To better understand the origin of leaves, scientists are exploring genetic control of leaf development.

Vascular plants have sporophylls, modified plants that bear sporangia.

- Sporophylls vary greatly in structure.
- Ferns produce clusters of sporangia called **sori**, usually on the underside of sporophylls.
- In many lycophytes and most gymnosperms, groups of sporophylls form cones, or **strobili**.
- Most seedless vascular plants are **homosporous**, producing a single type of spore.
 - This spore develops into a bisexual gametophyte with both archegonia (female sex organs) and antheridia (male sex organs).
 - Most ferns are homosporous.
- A **heterosporous** species produces two kinds of spores.
 - Megasporangia on megasporophylls produce **megaspores**, which develop into female gametophytes.
 - Microsporangia on microsporophylls produce **microspores**, which develop into male gametophytes.

- All seed plants and a few seedless vascular plants are heterosporous.

Biologists recognize two clades of living seedless vascular plants.

- Living seedless vascular plants form two clades: the lycophytes (phylum Lycophyta) and the pterophytes (phylum Pterophyta).
 - Lycophytes include club mosses, spike mosses, and quillworts.
 - Pterophytes include ferns, horsetails, whisk ferns, and their relatives.
 - Recent molecular evidence has provided convincing evidence that all three pterophyte groups form a clade.

Phylum Lycophyta includes club mosses, spike mosses, and quillworts.

- Modern species of lycophytes are relicts of an eminent past.
- By the Carboniferous period, there were two evolutionary lineages of lycophytes: small, herbaceous plants and giant, woody trees standing 40 m tall.
 - The giant lycophytes became extinct as the climate cooled and dried at the end of the Carboniferous period.
 - The small lycophytes survived and are now represented by 1,200 species.
- The club and spike mosses are not true mosses, which are nonvascular plants.

Phylum Pterophyta includes ferns, horsetails, and whisk ferns.

- Ferns radiated extensively from their Devonian origins and grew with lycophytes and horsetails in the Carboniferous swamp forests.
- There are more than 12,000 species of living ferns.
- Ferns are most diverse in the tropics, they thrive in temperate forests, and some can even survive arid conditions.
- Ferns and other pterophytes are more closely related to seed plants than to lycophytes.
 - Both pterophytes and seed plants show overtopping growth, megaphyll leaves, and roots that branch along their length.
- Horsetails grew up to 15 m high during the Carboniferous period, the height of their diversity.
- Today, only 15 species of single-genus *Equisetum* survive in marshy places.
- *Pilotum*, the whisk fern, and a close relative form a clade of tropical epiphytes.
 - Whisk ferns are the only vascular plants lacking true roots.

- These plants had been considered “living fossils” because their dichotomous branching and lack of true roots seemed similar to early vascular plants.
- However, comparisons of DNA sequences and details of sperm ultrastructure indicate that they are closely related to ferns.
- The whisk fern’s ancestors lost true roots during evolution.

Seedless vascular plants played an important role in the history of life on land.

- The ancestors of modern lycophytes and ferns, along with their seedless vascular relatives, formed the first forests during the late Devonian and early Carboniferous periods.
- With the evolution of vascular tissue, roots, and leaves, these plants accelerated their rate of photosynthesis and dramatically increased the removal of CO₂ from the atmosphere.
 - Scientists estimate that CO₂ levels dropped by as much as a factor of 5 during the Carboniferous period, causing global cooling and widespread glacier formation.
- The first forests gave rise to modern-day coal.
 - In the stagnant waters of the Carboniferous period, dead plants did not fully decay.
 - The organic material turned to thick layers of peat. Marine sediments piled up on top, and over millions of years, heat and pressure converted the peat to coal.
- Humans still burn 6 billion tons of coal each year.
- Coal, formed from plants that contributed to global cooling, now contributes to global warming by returning carbon to the atmosphere.