Introduction

- More than 280,000 species of plants inhabit Earth today.
- Most plants live in terrestrial environments, including deserts, grasslands, and forests.
  - Some species, such as sea grasses, have returned to aquatic habitats.
- Land plants (including the sea grasses) evolved from a certain green algae, called charophyceans.

A. An Overview of Land Plant Evolution

1. **Evolutionary adaptations to terrestrial living characterize the four main groups of land plants**

   - There are four main groups of land plants: bryophytes, pteridophytes, gymnosperms, and angiosperms.
   - The most common bryophytes are mosses.
   - The pteridophytes include ferns.
   - The gymnosperms include pines and other conifers.
   - The angiosperms are the flowering plants.
   - Mosses and other **bryophytes** have evolved several adaptations, especially reproductive adaptations, for life on land.
     - For example, the offspring develop from multicellular embryos that remain attached to the “mother” plant which protects and nourishes the embryos.
   - The other major groups of land plants evolved vascular tissue and are known as the **vascular plants**.
• In **vascular tissues**, cells join into tubes that transport water and nutrients throughout the plant body.

• Most bryophytes lack water-conducting tubes and are sometimes referred to as “nonvascular plants.”

• Ferns and other **pteridiophytes** are sometimes called *seedless plants* because there is no seed stage in their life cycles.

• The evolution of the seed in an ancestor common to gymnosperms and angiosperms facilitated reproduction on land.

• A **seed** consists of a plant embryo packaged along with a food supply within a protective coat.

• The first *seed plants* evolved about 360 million years ago, near the end of the Devonian.

• The early seed plants gave rise to the diversity of present-day **gymnosperms**, including conifers.

• The great majority of modern-day plant species are flowering plants, or **angiosperms**.
  • Flowers evolved in the early Cretaceous period, about 130 million years ago.
  • A flower is a complex reproductive structure that bears seeds within protective chambers called ovaries.

• Bryophytes, pteridiophytes, gymnosperms, and angiosperms demonstrate four great episodes in the evolution of land plants:
  • The origin of bryophytes from algal ancestors.
  • The origin and diversification of vascular plants.
  • The origin of seeds.
  • The evolution of flowers.

**2. Charophyceans are the green algae most closely related to land plants**

• What features distinguish land plants from other organisms?

• Plants are multicellular, eukaryotic, photosynthetic autotrophs.
• But red and brown seaweeds also fit this description.

• Land plants have cell walls made of cellulose and chlorophyll a and b in chloroplasts.

• However, several algal groups have cellulose cell walls and others have both chlorophylls.

• Land plants share two key ultrastructural features with their closest relatives, the algal group called charophyceans.

• The plasma membranes of land plants and charophyceans possess rosette cellulose-synthesizing complexes that synthesize the cellulose microfibrils of the cell wall.

• These complexes contrast with the linear arrays of cellulose-producing proteins in noncharophycean algae.

• A second ultrastructural feature that unites charophyceans and land plants is the presence of peroxisomes.

• Peroxisomes are typically found in association with chloroplasts.

• Enzymes in peroxisomes help minimize the loss of organic products due to photorespiration.

• In those land plants that have flagellated sperm cells, the structure of the sperm resembles the sperm of charophyceans.

• Finally, certain details of cell division are common only to land plants and the most complex charophycean 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.

3. Several terrestrial adaptations distinguish land plants from charophycean algae

• Several characteristics separate the four land plant groups from their closest algal relatives, including:

• Apical meristems

• Multicellular embryos dependent on the parent plant

• Alternation of generations
• Sporangia that produce walled spores
• Gametangia that produce gametes

• In terrestrial habitats, the resources that a photosynthetic organism requires are found in two different places.
  • Light and carbon dioxide are mainly aboveground.
  • 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.
• Multicellular plant embryos develop from zygotes that are retained within tissues of the female parent.
• This distinction is the basis for a term for all land plants, **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.
  • These are sometimes present in the adjacent maternal tissues as well.
• All land plants show **alternation of generations** in which two multicellular body forms alternate.
  • This life cycle also occurs in various algae.
  • However, alternation of generation does not occur in the charophyceans, the algae most closely related to land plants.
• One of the multicellular bodies is called the **gametophyte** with haploid cells.
• Gametophytes produce gametes, egg and sperm.
• Fusion of egg and sperm during fertilization form 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.
• While the gametophyte and sporophyte stages of some algae appear identical macroscopically, these two stages are very different in their morphology in other algal groups and *all* land plants.
• The relative size and complexity of the sporophyte and gametophyte depend on the plant group.
  • In bryophytes, the gametophyte is the “dominant” generation, larger and more conspicuous than the sporophyte.
  • In pteridophytes, gymnosperms, and angiosperms, the sporophyte is the dominant generation.
    • For example, the fern plant that we typically see is the diploid sporophyte, while the gametophyte is a tiny plant on the forest floor.
• Plant spores are haploid reproductive cells that grow into a gametophyte by mitosis.
  • Spores are covered by a polymer called **sporopollenin**, the most durable organic material known.
  • This makes the walls of spores very tough and resistant to harsh environments.
• Multicellular organs, called **sporangia**, are found on the sporophyte and produce these spores.

• Within a sporangia, diploid **spore mother cells** 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.

• The gametophytes of bryophytes, pteridophytes, and gymnosperms produce their 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.

• Most land plants have additional terrestrial adaptations including:
  • Adaptations for acquiring, transporting, and conserving water.
  • Adaptations for reducing the harmful effect of UV radiation.
  • Adaptations for repelling terrestrial herbivores and resisting pathogens.

• Male gametangia, called **antheridia**, produce many sperm cells that are released to the environment.
  • The sperm cells of bryophytes, pteridophytes, and some gymnosperms have flagella and swim to eggs.

• A sperm fuses with an egg within an archegonium and the zygote then begins development into an embryo.

• In most land plants, the epidermis of leaves and other aerial parts is coated with a **cuticle** of polyesters and waxes.
  • The cuticle protects the plant from microbial attack.
  • The wax acts as waterproofing to prevent excessive water loss.

• Pores, called **stomata**, in the epidermis of leaves and other photosynthetic organs allow the exchange of carbon dioxide and oxygen between the outside air and the leaf interior.
  • Stomata are also the major sites for water to exit from leaves via evaporation.
• Changes in the shape of the cells bordering the stomata can close the pores to minimize water loss in hot, dry conditions.

• Except for bryophytes, land plants have true roots, stems, and leaves, which are defined by the presence of vascular tissues.
  • Vascular tissue transports materials among these organs.

• Tube-shaped cells, called **xylem**, carry water and minerals up from roots.
  • When functioning, these cells are dead, with only their walls providing a system of microscopic water pipes.

• **Phloem** is a living tissue in which nutrient-conducting cells arranged into tubes distribute sugars, amino acids, and other organic products.

• Land plants produce many unique molecules called secondary compounds.
  • These molecules are products of “secondary” metabolic pathways.
  • These pathways are side branches off the primary pathways that produce lipids, carbohydrates, and other compounds common to all organisms.

• Examples of secondary compounds in plants include alkaloids, terpenes, tannins, and phenolics such as Flavonoids.
  • Various secondary compounds have bitter tastes, strong odors, or toxic effects that help defend land plants against herbivorous animals or microbial attack.
  • Flavonoids absorb harmful UV radiation.
  • Other flavonoids are signals for symbiotic relationships with beneficial soil microbes.
  • Lignin, a phenolic polymer, hardens the cell walls of “woody” tissues in vascular plants, providing support for even the tallest of trees.

• Humans have found many applications, including medicinal applications, for secondary compounds extracted from plants.
  • For example, the alkaloid quinine helps prevent malaria.

**B. The Origin of Land Plants**
1. **Land plants evolved from charophycean algae over 500 million years ago**

- Several lines of evidence support the phylogenetic connection between land plants and green algae, especially the charophyceans, including:
  - Homologous chloroplasts
  - Homologous cell walls
  - Homologous peroxisomes
  - Phragmoplasts
  - Homologous sperm
  - Molecular systematics

- **Homologous chloroplasts**—The chloroplasts of land plants are most similar to the plastids of green algae and of eulgenoids which acquired green algae as secondary endosymbionts.
  - Similarities include the presence of chlorophyll $b$ and beta-carotene and thylakoids stacked as grana.
  - Comparisons of chloroplast DNA with that of algal plastids place the charophyceans as most closely related to land plants.

- **Homologous cellulose walls**—In both land plants and charophycean algae, cellulose comprises 20-26% of the cell wall.
  - Also, both share cellulose-manufacturing rosettes.

- **Homologous peroxisomes**—Both land plants and charophycean algae package enzymes that minimize the costs of photorespiration in peroxisomes.

- **Phragmoplasts**—These plate-like structures occur during cell division only in land plants and charopyceans.

- Many plants have flagellated sperm, which match charophycean sperm closely in ultrastructure.

- **Molecular systematics**—In addition to similarities derived from comparisons of chloroplast genes, analyses of several nuclear genes also provide evidence of a charophycean ancestry of plants.
  - In fact, the most complex charophyceans appear to be the algae most closely related to land plants.
• All available evidence upholds the hypothesis that modern charophyceans and land plants evolved from a common ancestor.

• The oldest known traces of land plants are found in mid-Cambrian rocks from about 550 million years ago.
  • Fossilized plant spores are plentiful in the mid-Ordovician (460 million years ago) deposits from around the world.
  • Some of these fossils show spores in aggregates of four, as is found in modern bryophytes, and the remains of the sporophytes that produce the spores.

2. Alternation of generations in plants may have originated by delayed meiosis
• The advanced charophyceans *Chara* and *Coleochaeta* are haploid organisms.
  • They lack a multicellular sporophyte, but the zygotes are retained and nourished on the parent.
• The zygote of a charophycean undergoes *meiosis* to produce haploid spores, while the zygote of a land plant undergoes *mitosis* to produce a multicellular sporophyte.
  • The sporophyte then produces haploid spores by meiosis.
• A reasonable hypothesis for the origin of sporophytes is a mutation that delayed meiosis until one or more mitotic divisions of the zygote had occurred.
  • This multicellular, diploid sporophyte would have more cells available for meiosis, increasing the number of spores produced per zygote.

3. Adaptations to shallow water preadapted plants for living on land
• Many charophycean algae inhabit shallow waters at the edges of ponds and lakes where they experience occasional drying.
A layer of sporopollenin prevents exposed charophycean zygotes from drying out until they are in water again.

This chemical adaptation may have been the precursor to the tough spore walls that are so important to the survival of terrestrial plants.

The evolutionary novelties of the first land plants opened an expanse of terrestrial habitat previously occupied by only films of bacteria.

The new frontier was spacious.

The bright sunlight was unfiltered by water and algae.

The atmosphere had an abundance of carbon dioxide.

The soil was rich in mineral nutrients.

At least at first, there were relatively few herbivores or pathogens.

4. Plant taxonomists are reevaluating the boundaries of the plant kingdom

The taxonomy of plants is experiencing the same turmoil as other organisms as phylogenetic analyses revolutionize plant relationships.

The classification of plants is being reevaluated based on cladistic analysis of molecular data, morphology, life cycles, and cell ultrastructure.

One international initiative, called “deep green,” is focusing on the deepest phylogenetic branching within the plant kingdom to identify and name the major plant clades.

Even “deeper” down the phylogenetic tree of plants is the branching of the whole land plant clade from its algal relatives.

Because a phylogenetic tree consists of clades nested within clades, a debate about where to draw boundaries in a hierarchical taxonomy is inevitable.

The traditional scheme includes only the bryophytes, pteridophytes, gymnosperms, and angiosperms in the kingdom Plantae.

Others expand the boundaries to include charophyceans and some relatives in the kingdom Streptophyta.

Still others include all chlorophytes in the kingdom Viridiplantae.
5. **The plant kingdom is monophyletic**

- The diversity of modern plants demonstrates the problems and opportunities facing organisms that began living on land.
- Because the plant kingdom is monophyletic, the differences in life cycles among land plants can be interpreted as special reproductive adaptations as the various plant phyla diversified from the first plants.

C. **Bryophytes**

1. **The three phyla of bryophytes are mosses, liverworts, and hornworts**

- Bryophytes are represented by three phyla:
  - Phylum Hepatophyta—liverworts
  - Phylum Anthocerophyta—hornworts
  - Phylum Bryophyta—mosses

- Note, the name Bryophyta refers only to one phylum, but the informal term bryophyte refers to all nonvascular plants.
- The diverse bryophytes are not a monophyletic group.
  - Several lines of evidence indicate that these three phyla diverged independently early in plant evolution, before the origin of vascular plants.
  - Liverworts and hornworts may be the most reasonable models of what early plants were like.
  - Mosses are the bryophytes most closely related to vascular plants.

2. **The gametophyte is the dominant generation in the life cycles of bryophytes**

- In bryophytes, gametophytes are the most conspicuous, dominant 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.

• The gametophyte is a mass of green, branched, one-cell-thick filaments, called a **protonema**.

• When sufficient resources are available, a protonema produces meristems.

• These meristems generate gamete-producing structures, the **gametophores**.

• Bryophytes are anchored by tubular cells or filaments of cells, called **rhizoids**.
  
  • Rhizoids are not composed of tissues.
  
  • They lack specialized conducting cells.
  
  • They do not play a primary role in water and mineral absorption.

• Bryophyte gametophytes are generally only one or a few cells thick, placing all cells close to water and dissolved minerals.

• Most bryophytes lack conducting tissues to distribute water and organic compounds within the gametophyte.
  
  • Those with specialized conducting tissues lack the lignin coating found in the xylem of vascular plants.

• Lacking support tissues, most bryophytes are only a few centimeters tall.

• The gametophytes of hornworts and some liverworts are flattened and grow close to the ground.

• The gametophytes of mosses and some liverworts are more “leafy” because they have stem-like structures that bear leaf-like appendages.
  
  • They are not true stems or leaves because they lack lignin-coated vascular cells.

• The “leaves” of most mosses lack a cuticle and are only once cell thick, features that enhance water and mineral absorption from the moist environment.

• Some mosses have more complex “leaves” with ridges to enhance absorption of sunlight.
  
  • These ridges are coated with cuticle.
• Some mosses have conducting tissues in their stems and can grow as tall as 2m.
  • It is not clear if these conducting tissues in mosses are analogous or homologous to the xylem and phloem of vascular plants.
• The mature gametophores of bryophytes produce gametes in gametangia.
  • Each vase-shaped archegonium produces a single egg.
  • Elongate antheridia produce many flagellated sperm.
• When plants are coated with a thin film of water, sperm swim toward the archegonia, drawn by chemical attractants.
  • They 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.

3. **Bryophyte sporophytes disperse enormous numbers of spores**
• While the bryophyte sporophyte does have photosynthetic plastids, 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.
• Liverworts have the simplest sporophytes among the bryophytes.
  • They consist of a short stalk bearing a round sporangia which contains the developing spores, and a nutritive foot embedded in gametophyte tissues.
• Hornwort and moss sporophytes are larger and more complex.
  • Hornwort sporophytes resemble grass blades and have a cuticle.
• The sporophytes of hornworts and mosses have epidermal stomata, like vascular plants.
• The sporophytes of mosses start out green and photosynthetic, but turn tan or brownish red when ready to release their spores.
• Moss sporophytes consist of a foot, an elongated stalk (the seta), and a sporangium (the capsule).
• The foot gathers nutrients and water from the parent gametophyte via transfer cells.
• The stalk conducts these materials to the capsule.
• In most mosses, the seta becomes elongated, elevating the capsule and enhancing spore dispersal.
• The moss capsule (sporangium) is the site of meiosis and spore production.
  • One capsule can generate over 50 million spores.
• When immature, it is covered by a protective cap of gametophyte tissue, the calyptra.
  • This is lost when the capsule is ready to release spores.
• The upper part of the capsule, the peristome, is often specialized for gradual spore release.

4. Bryophytes provide many ecological and economic benefits
• Wind dispersal of lightweight spores has distributed bryophytes around the world.
• They are common and diverse in moist forests and wetlands.
• Some even inhabit extreme environments like mountaintops, tundra, and deserts.
  • Mosses can lose most of their body water and then rehydrate and reactivate their cells when moisture again becomes available.
• Sphagnum, a wetland moss, is especially abundant and widespread.
• It forms extensive deposits of undecayed organic material, called **peat**.

• Wet regions dominated by *Sphagnum* or peat moss are known as peat bogs.

• Its organic materials do not decay readily because of resistant phenolic compounds and acidic secretions that inhibit bacterial activity.

• Peatlands, extensive high-latitude boreal wetlands occupied by *Sphagnum*, play an important role as carbon reservoirs, stabilizing atmospheric carbon dioxide levels.

• *Sphagnum* has been used in the past as diapers and as a natural antiseptic material for wounds.

• Today, it is harvested for use as a soil conditioner and for packing plants roots because of the water storage capacity of its large, dead cells.

• Bryophytes were probably Earth’s only plants for the first 100 million years that terrestrial communities existed.
  • Then vegetation began to take on a taller profile with the evolution of vascular plants.

**D. The Origin of Vascular Plants**

• Modern vascular plants (pteridophytes, gymnosperms, and angiosperms) have food transport tissues (phloem) and water conducting tissues (xylem) with lignified cells.

• In vascular plants the **branched sporophyte** is dominant and is independent of the parent gametophyte.

• The first vascular plants, pteridophytes, were seedless.

1. **Additional terrestrial adaptations evolved as vascular plants descended from mosslike ancestors**
Vascular plants built on the tissue-producing meristems, gametangia, embryos and sporophytes, stomata, cuticles, and sporopollenin-walled spores that they inherited from mosslike ancestors.

The **protracheophyte polysporangiophytes** demonstrate the first steps in the evolution of sporophytes.

- These terms mean “before vascular plants” and “plants producing many sporangia,” respectively.
- Like bryophytes, they lacked lignified vascular tissues, but the branched sporophytes were independent of the gametophyte.
  - The branches provide more complex bodies and enable plants to produce many more spores.
  - Sporophytes and gametophytes were about equal in size.

**2. A diversity of vascular plants evolved over 400 million years ago**

- *Cooksonia*, an extinct plant over 400 million years old, is the earliest known vascular plant.
  - Its fossils are found in Europe and North America.
  - The branched sporophytes were up to 50cm tall with small lignified cells, much like the xylem cells of modern pteridophytes.

**E. Pteridophytes: Seedless Vascular Plants**

- The seedless vascular plants, the pteridophytes consist of two modern phyla:
  - Phylum Lycophyta—lycophytes.
  - Phylum Pterophyta—ferns, whisk ferns, and horsetails.
- These phyla probably evolved from different ancestors among the early vascular plants.

**1. Pteridophytes provide clues to the evolution of roots and leaves**
Most pteridophytes have true roots with lignified vascular tissue.  
These roots appear to have evolved from the lowermost, subterranean portions of stems of ancient vascular plants.  
- It is still uncertain if the roots of seed plants arose independently or are homologous to pteridophyte roots.

**Lycophytes** have small leaves with only a single unbranched vein.  
- These leaves, called *microphylls*, probably evolved from tissue flaps on the surface of stems.  
- Vascular tissue then grew into the flaps.  
In contrast, the leaves of other vascular plants, *megaphylls*, are much larger and have a highly-branched vascular system.  
- A branched vascular system can deliver water and minerals to the expanded leaf.  
- It can also export larger quantities of sugars from the leaf.  
- This supports more photosynthetic activity.

The fossil evidence suggests that megaphylls evolved from a series of branches lying close together on a stem.  
- One hypothesis proposes that megaphylls evolved when the branch system flattened and a tissue webbing developed joining the branches.  
- Under this hypothesis, true, branched stems preceded the origin of large leaves and roots.

**2. A sporophyte-dominant life cycle evolved in seedless vascular plants**  
- From the early vascular plants to the modern vascular plants, the sporophyte 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.

• This reduction in the size of the gametophytes is even more extreme in seed plants.

• Ferns also demonstrate a key variation among vascular plants: the distinction between homosporous and heterosporous plants.

• A **homosporous** sporophyte produces a single type of spore.
  
  • This spore develops into a bisexual gametophyte with both archegonia (female sex organs) and antheridia (male sex organs).

• A **heterosporous** sporophyte produces two kinds of spores.
  
  • **Megaspores** develop into females gametophytes.
  
  • **Microspores** develop into male gametophytes.

• Regardless of origin, the flagellated sperm cells of ferns, other seedless vascular plants, and even some seed plants must swim in a film of water to reach eggs.

• Because of this, seedless vascular plants are most common in relatively damp habitats.

3. **Lycophyta and Pterophyta are the two phyla of modern seedless vascular plants**

• *Phylum Lycophyta*—Modern lycophytes are relicts of a far more eminent past.
  
  • By the Carboniferous period, lycophytes existed as either small, herbaceous plants or as giant woody trees with diameters of over 2m and heights over 40m.
  
  • The giant lycophytes thrived in warm, moist swamps, but became extinct when the climate became cooler and drier.

• The smaller lycophytes survived and are represented by about 1,000 species today.

• Modern lycophytes include tropical species that grow on trees as epiphytes, using the trees as substrates, not as hosts.

• Others grow on the forest floor in temperate regions.
The lycophyte sporophytes are characterized by upright stems with many microphylls and horizontal stems along the ground surface.

Roots extend down from the horizontal stems.

Specialized leaves (sporophylls) bear sporangia clustered to form club-shaped cones.

Spores are released in clouds from the sporophylls.

They develop into tiny, inconspicuous haploid gametophytes.

- These may be either green above-ground plants or nonphotosynthetic underground plants that are nurtured by symbiotic fungi.

The phylum Pterophyta consists of ferns and their relatives.

Psilophytes, the whisk ferns, used to be considered a “living fossil”.

Their dichotomous branching and lack of true leaves and roots seemed similar to early vascular plants.

However, comparisons of DNA sequences and ultrastructural details indicate that the lack of true roots and leaves evolved secondarily.

Sphenophytes are commonly called horsetails because of their often brushy appearance.

During the Carboniferous, sphenophytes grew to 15m, but today they survive as about 15 species in a single wide-spread genus, *Equisetum*.

Horsetails are often found in marshy habitats and along streams and sandy roadways.

Roots develop from horizontal rhizomes that extend along the ground.

Upright green stems, the major site of photosynthesis, also produce tiny leaves or branches at joints.

- Horsetail stems have a large air canal to allow movement of oxygen into the rhizomes and roots, which are often in low-oxygen soils.

Reproductive stems produce cones at their tips.

- These cones consist of clusters of sporophylls.
  - Sporophylls produce sporangia with haploid spores.

Ferns first appeared in the Devonian and have radiated extensively until there are over 12,000 species today.
• Ferns are most diverse in the tropics but are also found in temperate forests and even arid habitats.
• Ferns often have horizontal rhizomes from which grow large megaphyllous leaves with an extensively branched vascular system.
• Fern leaves or fronds may be divided into many leaflets.
• Ferns produce clusters of sporangia, called sori, on the back of green leaves (sporophylls) or on special, non-green leaves.
• Sori can be arranged in various patterns that are useful in fern identification.
• Most fern sporangia have springlike devices that catapult spores several meters from the parent plant.
• Spores can be carried great distances by the wind.

4. Seedless vascular plants formed vast “coal forests” during the Carboniferous period
• The phyla Lycophyta and Pterophyta formed forests during the Carboniferous period about 290-360 million years ago.
• These plants left not only living representatives and fossils, but also fossil fuel in the form of coal.
• While coal formed during several geologic periods, the most extensive beds of coal were deposited during the Carboniferous period, when most of the continents were flooded by shallow swamps.
• Dead plants did not completely decay in the stagnant waters, but accumulated as peat.
• The swamps and their organic matter were later covered by marine sediments.
• Heat and pressure gradually converted peat to coal, a “fossil fuel.”
• Coal powered the Industrial Revolution but has been partially replaced by oil and gas in more recent times.
• Today, as nonrenewable oil and gas supplies are depleted, some politicians have advocated a resurgence in coal use.
• However, burning more coal will contribute to the buildup of carbon dioxide and other “greenhouse gases” that contribute to global warming.

• Energy conservation and the development of alternative energy sources seem more prudent.