

CHAPTER 29

PLANT DIVERSITY I: THE COLONIZATION OF LAND

OUTLINE

- I. An Overview of Plant Evolution
 - A. Structural, chemical, and reproductive adaptations enabled plants to colonize land
 - B. The history of terrestrial adaptation is the key to modern plant diversity
- II. The Origins of Plants
 - A. Plants probably evolved from green algae called charophytes
 - B. Alternation of generations in plants may have originated by delayed meiosis
 - C. Adaptations to shallow water as preadapted plants for living on land
- III. Bryophytes
 - A. The embryophyte adaptation evolved in bryophytes
 - B. The gametophyte is the dominant generation in the life cycles of bryophytes
 - C. The three divisions of bryophytes are mosses, liverworts, and hornworts
- IV. The Origin of Vascular Plants
 - A. Additional terrestrial adaptations evolved as vascular plants descended from bryophyte-like ancestors
 - B. The branched sporophytes of vascular plants amplified the production of spores and made complex bodies possible
- V. Seedless Vascular Plants
 - A. A sporophyte-dominant life cycle evolved in seedless vascular plants
 - B. The three divisions of seedless vascular plants are lycophytes, horsetails, and ferns
 - C. Seedless vascular plants formed vast “coal forests” during the carboniferous period

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List characteristics that distinguish plants from organisms in the other kingdoms.
2. Diagram a generalized plant life cycle indicating which generation is the sporophyte/gametophyte, which individuals are haploid/diploid, where meiosis occurs and where mitosis occurs.
3. Describe four major periods of plant evolution that opened new adaptive zones on land.
4. Distinguish between the categories division and phylum.
5. Using the classification scheme presented in the text, list the plant divisions; give the common name for each; and categorize them into nonvascular, vascular seedless and vascular seed plants.
6. Provide evidence to defend the position that plants evolved from green algae.
7. Describe two adaptations that made the bryophytes' move onto land possible.

8. Explain how bryophytes are still tied to water.
9. List and distinguish among three division of Bryophyta.
10. Diagram the life cycle of a moss including gamete production, fertilization, and spore production.
11. Compare environmental conditions faced by algae in an aquatic environment and plants in a terrestrial environment.
12. Provide evidence that suggests the division Bryophyta is a phylogenetic branch separate from vascular plants.
13. Describe adaptations of vascular plants, including modifications of the life cycle and modifications of the sporophyte, that have contributed to their success on land.
14. List and distinguish among the four extant divisions of seedless vascular plants.
15. Distinguish between homosporous and heterosporous.
16. Distinguish among spore, sporophyte, sporophyll and sporangium.
17. Diagram the life cycle of a fern including spore production, gamete production and fertilization.
18. Point out the major life cycle differences between mosses and ferns.
19. Describe how coal is formed and during which geological period the most extensive coal beds were produced.

KEY TERMS

stomata	sporophyte	sporangium	megaspores
cuticle	vascular tissue	mosses	microspores
secondary products	gymnosperm	liverworts	lycophytes
lignin	angiosperm	hornworts	epiphytes
sporopollenin	division	xylem	sporophylls
gametangia	charophyte	phloem	horsetails
embryophyte	antheridium	homosporous	ferns
gametophyte	archegonium	heterosporous	

LECTURE NOTES

Plants appeared on land about 475 million years ago, and the evolutionary history of the plant kingdom reflects increasing adaptation to the terrestrial environment. The colonization of land by plants transformed the biosphere. This transformation created new adaptive zones and paved the way for other organisms.

I. An Overview of Plant Evolution

A. Structural, chemical, and reproductive adaptations enabled plants to colonize land

1. Some characteristics of plants

Plants are multicellular eukaryotes that are photosynthetic autotrophs; however, not all organisms with these characteristics are plants. Plants share the following characteristics with their green algal ancestors:

- Chloroplasts with the photosynthetic pigments: chlorophyll *a*, chlorophyll *b*, and carotenoids
- Cell walls containing cellulose
- Food reserve that is starch stored in plastids

It is the set of structural, chemical, and reproductive adaptations associated with terrestrial life that distinguishes plants from algae. Plants have evolved complex bodies with cell specialization for different functions.

- Plants have developed structural specializations in order to extract the resources needed for photosynthesis (water, minerals, carbon dioxide, light) from the terrestrial environment (above and below ground).
- In most plants, gas exchange occurs via *stomata*, special pores on the surfaces of leaves
- Chemical adaptation includes the secretion of a waxy *cuticle*, a coating on the surface of plants that helps prevent desiccation.
 - Cuticle waxes are *secondary products*, so named because they arise through metabolic pathways not common to all plants. (Cellulose is an example of a primary product).
 - Other secondary products include *lignin* (cell wall component of “woody” plants) and *sporopollenin* (a resilient polymer in the walls of spores and pollen grains).

2. Plants as embryophytes

With the move from an aquatic to terrestrial environment, a new mode of reproduction was necessary to solve two problems:

1. Gametes must be dispersed in a nonaquatic environment. Plants produce gametes within *gametangia*, organs with protective jackets of sterile (nonreproductive) cells that prevent gametes from drying out (see Campbell, Figure 29.1a). The egg is fertilized within the female organ.
2. Embryos must be protected against desiccation. The zygote develops into an embryo that is retained for awhile within the female gametangia's jacket of protective cells (see Campbell, Figure 29.1b). Emphasizing this terrestrial adaptation, plants are often referred to as *embryophytes*.

3. Alternation of generations: a review

Most plants reproduce sexually, and most are also capable of asexual propagation. All plants have life cycles with an *alternation of generations* (also occurs in some groups of algae).

- A haploid *gametophyte* generation produces and alternates with a diploid *sporophyte* generation. The sporophyte, in turn, produces gametophytes (see Campbell, Figure 29.2).
- The life cycles are heteromorphic; that is, sporophytes and gametophytes differ in morphology.
- The sporophyte is larger and more noticeable than the gametophyte in all plants but mosses and their relatives.

A comparison of life cycles among plant divisions is instructive because:

- It points to an important trend in plant evolution: reduction of the haploid gametophyte generation and dominance of the diploid sporophyte.
- Certain life cycle features are adaptations to a terrestrial environment; for example the replacement of flagellated sperm by pollen.

4. Some highlights of plant phylogeny

There are four major periods of plant evolution that opened new adaptive zones on land (see Campbell, Figure 29.3):

1. Origin of plants from aquatic ancestors (probably green algae) in the Ordovician about 475 million years ago (mya).
 - Cuticle and jacketed gametangia evolved which protected gametes and embryos.

- *Vascular tissue* evolved with conducting cells that transport water and nutrients throughout the plant.
2. Diversification of seedless vascular plants, such as ferns, during the early Devonian about 400 mya.
 3. Origin of the seed near the end of the Devonian about 360 mya.
 - *Seed* = Plant embryo packaged with a store of food within a resistant coat
 - Early seed plants bore seeds as naked structures and evolved into *gymnosperms*, including conifers.
 - Conifers and ferns coexisted in the landscape for more than 200 million years.
 4. Emergence of flowering plants during the early Cretaceous, about 130 mya.
 - Unlike gymnosperms, flowering plants bear seeds within the flower's protective ovaries.
 - Most contemporary plants are flowering plants or *angiosperms*.
5. **Classification of plants**
- The major taxonomic category of plants is the *division*; it is comparable to phylum, the highest category in the animal kingdom.
- Divisions are subdivided into lower taxa (class, order, family, genus).
 - Currently, eleven divisions of plants are recognized (see also Campbell, Table 29.1).

A CLASSIFICATION OF PLANTS

	Common Name	Approximate Number of Extant Species
Nonvascular Plants (byrrophytes)		
Division Bryophyta	Mosses	12,000
Division Hepatophyta	Liverworts	6,500
Division Anthocerophyta	Hornworts	100
Vascular Plants		
<i>Seedless Vascular Plants</i>		
Division Lycophyta	Lycophytes	1,000
Division Sphenophyta	Horsetails	15
Division Pterophyta	Ferns	12,000
<i>Seed Plants</i>		
Gymnosperms		
Division Coniferophyta	Conifers	550
Division Cycadophyta	Cycads	100
Division Ginkgophyta	Ginkgo	1
Division Gnetophyta	Gnetae	70
Angiosperms		
Division Anthophyta	Flowering plants	250,000

II. The Origin of Plants

A. Plants probably evolved from green algae called charophytes

The green algae are likely the photosynthetic protists most closely related to plants. This conclusion is based on homologies in:

- Cell wall composition
- Structure and pigmentation of chloroplasts

Available evidence supports the hypothesis that plants and green algae called *charophytes* both evolved from a common ancestor (see Campbell, Figure 29.4).

Researchers have found the following homologies between charophytes and plants:

1. Homologous chloroplasts
 - Green algae and plants both have the accessory pigments, chlorophyll *b* and beta-carotene.
 - Green algae and plants both have chloroplasts with thylakoid membranes stacked as grana.
 - Compared to chloroplast DNA of various green algae, plant chloroplast DNA most closely matches that of charophytes.
2. Biochemical similarity
 - Most green algae and plants contain cellulose in their cell walls. Charophytes are the most plantlike in wall composition with cellulose making up 20% - 26% to 26% of the wall material.
 - Charophyte peroxisomes are the only algal peroxisomes with the same enzyme composition as plant peroxisomes.
3. Similarity in mitosis and cytokinesis. During cell division in charophytes and plants:
 - The nuclear envelope completely disperses during late prophase.
 - The mitotic spindle persists until cytokinesis begins.
 - Cell plate formation during cytokinesis involves cooperation of microtubules, actin microfilaments, and vesicles.
4. Similarity in sperm ultrastructure. Charophyte sperm ultrastructure is more similar to certain plants than to other green algae.
5. Genetic relationship. DNA and rRNA similarities in charophytes and plants provides additional evidence for the hypothesis that charophytes are the closest relatives of plants.

B. Alternation of generations in plants may have originated by delayed meiosis

The alternation of haploid and diploid generations apparently evolved independently among various groups of algae.

- Since alternation of generations does not occur among modern charophytes, it is presumed that alternation of generations in plants has had a separate origin from alternation of generations in other algal groups.
- Its appearance in plants is thus *analogous*, not homologous, to the alternation of generations observed in various groups of algae.

How did alternation of generations evolve in plant ancestors?

Coleochaete, a modern charophyte, holds some clues:

- The *Coleochaete* thallus is haploid.
 - ⇒ In contrast to most algae, the parental thallus of *Coleochaete* retains the eggs, and after fertilization, the zygotes remain attached to the parent.

- ⇒ Nonreproductive cells of the thallus grow around each zygote, which enlarges, undergoes meiosis, and releases haploid swimming spores.
- ⇒ Haploid spores develop into new individuals.
- ⇒ The only diploid stage is the zygote; there is no alternation of multicellular diploid and haploid generations.
- If an ancestral charophyte delayed meiosis until after the zygote divided mitotically, there would be a multicellular diploid generation (sporophyte) still attached to the haploid parent (gametophyte). Such a life cycle would be an alternation of generations.
- If specialized gametophyte cells formed protective layers around a tiny sporophyte, this hypothetical ancestor would also be a primitive embryophyte (see Campbell, Figure 29.5).

What would be the adaptive advantage of delaying meiosis and forming a mass of diploid cells?

It may maximize the production of haploid spores.

- If the zygote undergoes meiosis directly, each fertilization event results in only a few haploid spores.
- Mitotic division of the zygote to form a multicellular sporophyte amplifies the sexual product. Many diploid cells can undergo meiosis producing a large number of haploid spores, enhancing the chances of survival in unfavorable environments.

C. Adaptations to shallow water preadapted plants for living on land

Some adaptations for life in shallow water could also have been adaptive for life on land.

- Many modern charophytes live in shallow water, and some ancient charophytes may have also lived in shallow-water habitats subject to occasional drying.
- About 440 million years ago, during the transition from Ordovician to Silurian, repeated glaciation and climatic changes caused fluctuations in the water levels of lakes and ponds.
- Natural selection may have favored shallow-water plants tolerant to periodic drying. Adaptations to shallow water may also have been preadaptive for terrestrial life.

Examples:

- | |
|--|
| <ul style="list-style-type: none"> • Waxy cuticles • Protection of gametes • Protection of developing embryos |
|--|
- Eventually, accumulated adaptations made it possible for ancestral plants to live permanently above the water line, opening a new adaptive zone with:
 - ⇒ Sunlight unfiltered by water and algae
 - ⇒ Soil rich in minerals
 - ⇒ Absence of terrestrial herbivores

III. Bryophytes

A. The embryophyte adaptation evolved in bryophytes

The *bryophytes* include plants found in three divisions:

- Bryophyta (mosses)
- Hepatophyta (liverworts)

- Anthocerophyta (hornworts)

Bryophytes display a pivotal adaptation that made the move onto land possible: the embryophyte condition.

- Gametangia protect developing gametes.
 - a. *Antheridium*, or male gametangium, produces flagellated sperm cells.
 - b. *Archegonium*, or female gametangium, produces a single egg; fertilization occurs within the archegonium, and the zygote develops into an embryo within the protective jacket of the female organ (embryophyte condition).

Bryophytes are not totally free from their ancestral aquatic habitat.

- They need water to reproduce. Their flagellated sperm cells must swim from the antheridium to the archegonium to fertilize the egg.
- Most have no vascular tissue to carry water from the soil to aerial plant parts; they imbibe water and distribute it throughout the plant by the relatively slow processes of diffusion, capillary action, and cytoplasmic streaming.

Bryophytes lack woody tissue and cannot support tall plants on land; they may sprawl horizontally as mats, but always have a low profile (see Campbell, Figure 29.6).

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

The life cycle of a bryophyte alternates between haploid and diploid generations (see Campbell, Figure 29.7)

- The sporophyte (2n) produces haploid spores by meiosis in a *sporangium*; the spores divide by mitosis to form new gametophytes.
- Contrary to the life cycles of vascular plants, the haploid gametophyte is the dominant generation in mosses and other bryophytes. Sporophytes are generally smaller and depend on the gametophyte for water and nutrients.

C. The three divisions of bryophytes are mosses, liverworts, and hornworts

1. Mosses (Division Bryophyta)

A tight pack of many moss plants forms a spongy mat that can absorb and retain water.

Each plant grips the substratum with *rhizoids*, elongate cells or cellular filaments.

Photosynthesis occurs mostly in the small stemlike and leaflike structures found in upper parts of the plant; these structures are not homologous with stems and leaves in vascular plants.

Mosses cover about 3% of the land surface, and they contain vast amounts of organic carbon (see Campbell, Figure 29.6).

2. Liverworts (Division Hepatophyta)

Liverworts are less conspicuous than mosses.

They sometimes have bodies divided into lobes.

They have a life cycle similar to mosses. Their sporangia have elaters, coil-shaped cells, that spring out of the capsule and disperse spores.

They can also reproduce asexually from gemmae (small bundles of cells that can bounce out of cups on the surface of the gametophyte when hit by rainwater) (see Campbell, Figure 29.8).

They display their greatest diversity in tropical forests.

3. Hornworts (Division Anthocerophyta)

Hornworts resemble liverworts, but sporophytes are horn-shaped, elongated capsules that grow from the matlike gametophyte (see Campbell, Figure 29.9).

Their photosynthetic cells have only one large chloroplast, unlike the many smaller ones of other plants.

Recent molecular evidence suggest that they are most closely related to vascular plants.

IV. The Origin of Vascular Plants

A. Additional terrestrial adaptations evolved as vascular plants descended from bryophyte-like ancestors

In addition to cuticles and jacketed sex organs, other adaptations for terrestrial life evolved in vascular plants as they colonized land:

1. *Regional specialization of the plant body.* Unlike aquatic environments, terrestrial environments spatially segregate the resources of water and light. This problem was solved as plants evolved subterranean roots that absorb water and minerals from the soil and an aerial shoot system of stems and leaves to make food.
2. *Structural support.* In aquatic environments, the denser medium of water buoys plants up toward the light, but in terrestrial environments plants must have structural support to stand upright in air. Such support was provided as the hard material lignin was embedded into the cellulose matrix of cell walls.
3. *Vascular system.* Regional specialization of the plant body presented the problem of transporting substances between the root and shoot systems. This problem was solved as a vascular system evolved with two types of conducting tissues:

Xylem = Complex, plant vascular tissue that conducts water and minerals from the roots to the rest of the plant

- Composed of dead, tube-shaped cells that form a microscopic water-pipe system
- Cell walls are usually lignified, giving the plant structural support

Phloem = Plant vascular tissue that conducts food throughout the plant

- Composed of living cells arranged into tubules
- Distributes sugars, amino acids, and other organic nutrients

4. *Pollen.* Pollination eliminated the need for water to transport gametes.
5. *Seeds*
6. *Increased dominance of the diploid sporophyte*

B. The branched sporophytes of vascular plants amplified the production of spores and made more complex bodies possible

Oldest fossilized vascular plant is *Cooksonia* (late Silurian):

- Discovered in both European and North American Silurian rocks; North America and Europe were probably connected during the late Silurian, about 400 million years ago
- Simple plant that displayed dichotomous branching and bulbous terminal sporangia on sporophyte (see Campbell, Figure 29.10)
- True roots and leaves were absent; the largest species was about 50 cm tall
- Grew in dense stands around marshes
- As vascular plants became more widespread, new species appeared

V. Seedless Vascular Plants

The earliest vascular plants were seedless and they dominated the Carboniferous forests. Modern flora includes three divisions of seedless vascular plants.

A. A sporophyte-dominant life cycle evolved in seedless vascular plants

The sporophyte (diploid) generation emerged as the larger and more complex plant from the time of *Cooksonia* and other early vascular plants. It is the dominant stage in the life cycle in all extant vascular plants.

The sporophyte-dominant life cycle is exemplified by ferns, one group of the seedless vascular plants (see Campbell, Figure 29.11).

- The familiar leafy plant is the sporophyte.
- Gametophytes are quite small and grow on or below the surface of the soil.

Vascular plants display two distinct reproductive strategies:

- The sporophyte of a *homosporous* plant produces a single type of spore (e.g., ferns); each spore develops into a bisexual gametophyte with both male (antheridia) and female (archegonia) sex organs.
- The sporophyte of a *heterosporous* plant produces two kinds of spores:
 1. *Megaspores* develop into female gametophytes possessing archegonia.
 2. *Microspores* develop into male gametophytes possessing antheridia.

B. The three divisions of seedless vascular plants are lycophytes, horsetails, and ferns**1. Lycophytes (division Lycophyta)**

The division Lycophyta includes the club mosses and ground pines.

Lycophytes survived through the Devonian period and dominated land during the Carboniferous Period (340–280 million years ago).

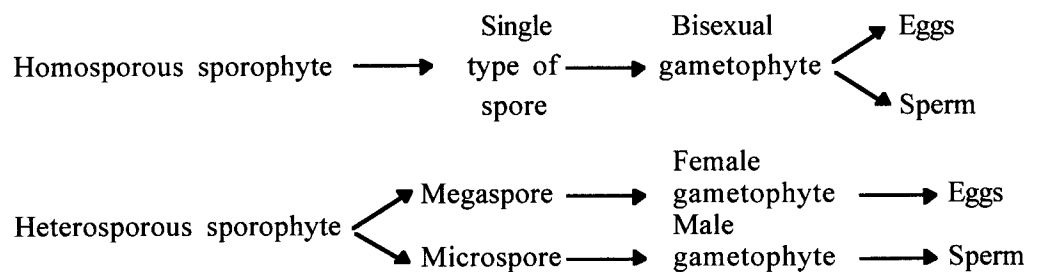
Some are temperate, low-growing plants with rhizomes and true leaves.

Some species of *Lycopodium* are *epiphytes*, plants that use another organism as a substratum, but are not parasites.

- The sporangia of *Lycopodium* are borne on *sporophylls*, leaves specialized for reproduction. In some, sporophylls are clustered at branch tips into club-shaped strobili—hence the name club moss.
- Spores develop into inconspicuous gametophytes. The non-photosynthetic gametophytes are nurtured by symbiotic fungi.

Most are homosporous.

Genus *Selaginella* is heterosporous.

**2. Horsetails (division Sphenophyta)**

The division Sphenophyta includes the horsetails; it survived through the Devonian and reached its zenith during the Carboniferous period.

The only existing genus is *Equisetum*, which (see Campbell, Figure 29.13):

- Lives in damp locations and has flagellated sperm
- Is homosporous
- Has a conspicuous sporophyte generation

- Has photosynthetic, free-living gametophytes (not dependent on the sporophyte for food)

3. Ferns (division Pterophyta)

Appearing in the Devonian, ferns radiated into diverse species that coexisted with tree lycopods and horsetails in the great Carboniferous forests.

- Ferns are the most well represented seedless plants in modern floras. There are more than 12,000 existing species of ferns; most diverse in the tropics.
- Fern leaves are generally much larger than those of lycopods and probably evolved in a different way.
 - ⇒ Lycopods have microphylls, small leaves that probably evolved as emergences from the stem that contained a single strand of vascular tissue.
 - ⇒ Ferns have megaphylls, leaves with a branched system of veins. Megaphylls probably evolved from webbing formed between separate branches growing close together.

Most ferns have fronds, compound leaves that are divided into several leaflets (see Campbell, Figure 29.11).

- The emerging frond is coiled into a fiddlehead that unfurls as it grows.
- Leaves may sprout directly from a prostrate stem (bracken and sword ferns) or from upright stems many meters tall (tropical tree ferns).

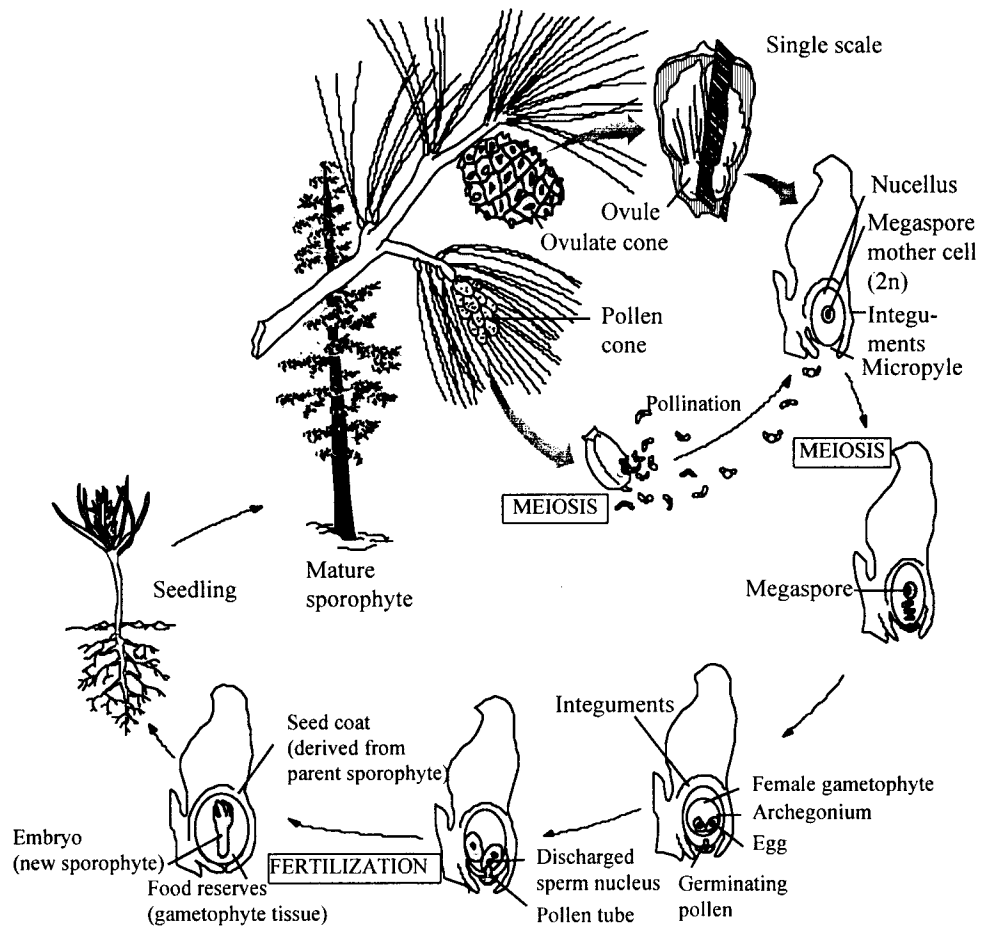
Ferns are *homosporous* and the conspicuous leafy fern plant is the sporophyte.

- Specialized sporophylls bear sporangia on their undersides; many ferns have sporangia arranged in clusters called sori and are equipped with springlike devices that catapult spores into the air, where they can be blown by the wind far from their origin.
- The spore is the dispersal stage.
- The free-living gametophyte is small and fragile, requiring a moist habitat.
- Water is necessary for fertilization, since flagellated sperm cells must swim from the antheridium to the archegonium, where fertilization takes place.
- The sporophyte embryo develops protected within the archegonium.

C. Seedless vascular plants formed vast “coal forests” during the Carboniferous period

During the Carboniferous period, the landscape was dominated by extensive swamp forests

- Organic rubble of the seedless plants mentioned above accumulated as peat.
- When later covered by the sea and sediments, heat and pressure transformed the peat into coal.



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- Raven, P.H., R.F. Evert and S.E. Eichhorn. *Biology of Plants*. 6th ed. New York: Worth Publishers, Inc., 1998.