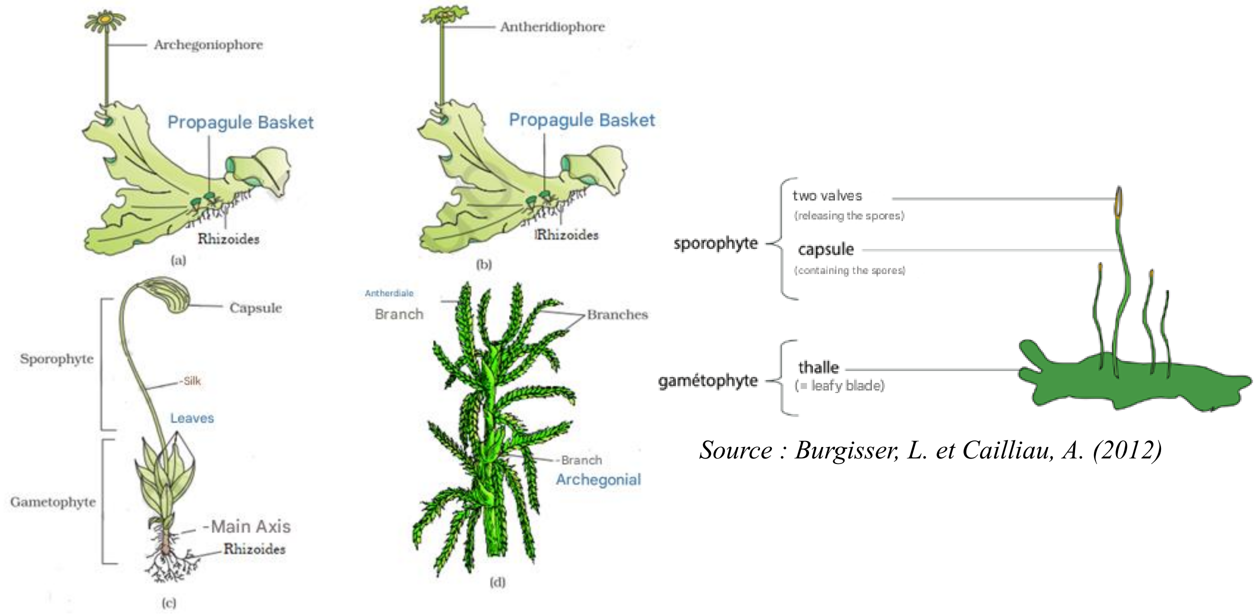
4. *Bryophytes*

Bryophytes are non-vascular terrestrial plants that can be either thalloid or leafy. Among modern plants, terrestrial and aquatic bryophytes have retained many characteristics of the first plants to colonize land. The ancestors of all land plants, including bryophytes, are green algae from the group *Charophyceae*. Although some anatomical features allow them to resist desiccation, bryophytes remain highly dependent on water or moist environments—at the very least, on a minimum level of humidity during reproduction.



Source : Burgisser, L. et Cailliau, A. (2012)

Figure 5.9: Bryophytes *sensu lato*
Marchantiophyta : *Marchantia* (a) Thall female (b) Thall male
Mosses: (c) *Funaria*, gametophyte and sporophyte (d) Gametophyte sphagnum.
Anthocerotophyta: Left.

Despite this dependency, they exhibit significant ecological plasticity, allowing them to grow in diverse environments across the globe, from the equator to the poles.

In the broad, traditional sense, the term *bryophyte* includes the three phyla of land plants that lack a true vascular system: **Marchantiophyta** (liverworts), **Bryophyta** in the strict sense (mosses and sphagnum mosses), and **Anthocerotophyta** (hornworts). These groups are sometimes classified within the subkingdom *Bryobiotina* of the kingdom *Chlorobiota*. However, in strict botanical usage, the phylum *Bryophyta* includes only mosses and sphagnum mosses, excluding liverworts and hornworts.

Bryophytes represent the second-largest group of land plants after angiosperms. There are approximately **13,000 to 14,000 species of mosses**, **7,500 to 9,000 species of liverworts**, and about **200 to 250 species of hornworts** currently recognized.

4.1 Bryophytes biology

a. Cell Structure in Bryophytes

- Made of **cellulose**, **pectins**, and **hemicelluloses**, similar to vascular plants.
- Some species (e.g., *Sphagnum*) produce **phenolic compounds** in the walls, which contribute to antimicrobial properties and peat formation.

b. Water-Conducting Cells 💧

- **No true xylem/phloem**, but:
  - **Hydroids**: Water-conducting cells (analogous to tracheids) in some mosses.
  - **Leptoids**: Sugar-conducting cells (similar to phloem).
- These are **non-lignified**, limiting mechanical support and water transport efficiency.

c. Plastids 🧪

- **Chloroplasts** are present in all green tissues and are typically **large and few per cell**.
- Hornworts have a **single large chloroplast per cell** with a pyrenoid—this is rare in land plants and resembles algae.

4.2 Developmental Biology

a. Apical Growth

- Gametophytes grow via **apical cells** (single or multiple), which divide in a specific pattern.
- This leads to **thalloid** (e.g., in liverworts and hornworts) or **leafy forms** (e.g., mosses).

b. Cell Division

- Cell walls form by **phragmoplast**-mediated cytokinesis, like in vascular plants.
- Cell differentiation is minimal, but some tissues (e.g., epidermis, storage parenchyma) are present.

c. Tissue Organization

- **Liverworts and hornworts** have **simple tissue organization**, often only a few cell layers thick.
- **Mosses** can develop more complex tissues, including:
  - **Midribs (costae)** with hydroids and leptoids
  - **Photosynthetic cells** (lamellae in *Polytrichum*)

d. Leaf Development in Mosses

- Moss "leaves" (phyllids) are typically **one cell layer thick**, without stomata (except in sporophytes).
- No cuticle in gametophytes (except some desert species); thus, prone to water loss.

e. Sporophyte Development

- Dependent on the gametophyte for nutrition.
- Development begins after **zygote formation** in the archegonium.
- Produces:
  - **Foot** (anchors to gametophyte)
  - **Seta** (stalk)
  - **Capsule** (spore-producing organ)
- Capsule may have **stomata** (in mosses and hornworts) and **peristome teeth** for spore dispersal control.

🧬 **Recent Developmental & Genetic Insights**

- Bryophytes like *Physcomitrium patens* are model organisms in evo-devo studies.
- Genes involved in **apical growth, cell polarity, and hormone signaling (auxin, cytokinin, ABA)** are conserved with vascular plants.
- Development of bryophytes sheds light on the **evolution of land plant traits**, including **embryogenesis**, **multicellularity**, and **tissue specialization**.

4.3 ***Ecology*** 🌍

- Found in **nearly all ecosystems**, from rainforests to deserts to polar regions.
- Often pioneers in **primary succession** (e.g., colonizing bare rocks).
- Important in **soil formation**, **water retention**, and **carbon cycling**.
- Sphagnum mosses are key in **peat bogs**, storing significant global carbon.

🧬 **Adaptations**

- Some can survive **extreme desiccation** (poikilohydric species).
- **Simple morphology** but with complex cellular structures adapted to retain moisture.
- **No roots**, but **rhizoids** anchor the plant and absorb water.

🧪 **Phylogeny & Evolution**

- Bryophytes are a **paraphyletic group**, representing early diverging lineages of land plants.
- Molecular studies place them close to the base of the **embryophyte tree**, possibly as a **monophyletic group** or in a **stepwise divergence** before vascular plants.

4.4 Bryophytes reproduction

☞ ***Vegetative Reproduction***

Bryophytes exhibit vegetative reproduction, particularly through fragmentation, whereby detached plant parts develop into new individuals. In some liverworts, specialized reproductive structures known as **propagules** have evolved to facilitate dispersal. Similarly, certain mosses produce **gemmae** or **bulbils**, which serve as asexual propagules. These units are primarily dispersed by **wind**, although **zoochory**—dispersal by animals such as bats, ants, and slugs—may also occur. The **allocation of resources**, or the distribution of nutrients within the plant, reflects evolutionary trade-offs between **sexual reproduction**, which is typically favored during phases of habitat colonization, and **asexual reproduction**, which is often predominant in well-established colonies.

☞ ***Sexual reproduction***

As in green algae and other land plants, the life cycle of mosses involves an **alternation of generations** between **sporophytes and gametophytes**. The **sperm cells (antherozoids)** and **egg cells (oospheres)** are produced and protected within **antheridia** and **archegonia**, respectively—structures also characteristic of vascular plants. **Sexual organs**, such as **antheridiophores** and **archegoniophores**, bear the **fertile structures** (antheridia and archegonia) that house the gametangia. The **motile, flagellated sperm** are released from the antheridia and transported by **water** to reach the egg for **fertilization**.

The resulting **embryo** is **nourished and protected by the gametophyte**, on which the **sporophyte remains physically attached and nutritionally dependent**, never becoming fully autonomous. **Spores** produced by the sporophyte are protected by a **sporopollenin-rich wall**, which prevents desiccation during dispersal. The **life cycle is haplodiplontic**, with a **dominant gametophyte phase** and a reduced sporophyte phase. Fertilization can lead to the development of one or more sporophytes from one or more archegonia.

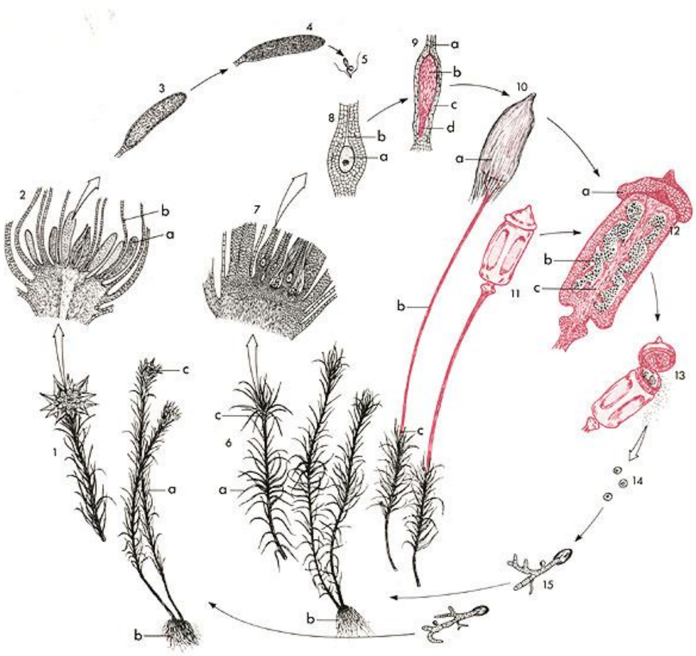


Figure 5.10: Life cycle of a moss from the genus *Polytrichum*. The diploid structures are shown in red.

1. Male leafy gametophyte
2. Antheridiophore
a. Leaves
b. Rhizoids
c. Antheridiophore
a. Antheridium
b. Paraphysis
3–4. Antheridium
5. Antherozoid
6. Female leafy gametophyte
a. Leaves
b. Rhizoids
c. Archegoniophore
7. Archegoniophore
8. Archegonium
a. Oosphere (egg cell)
b. Neck of the archegonium
9. Archegonium
a. Oosphere (egg cell)
b. Embryo (sporophyte)
c. Venter of the archegonium
d. Foot
10. Sporophyte carried on the gametophyte
a. Calyptra
b. Seta
c. Foot
11. Capsule (with calyptra removed)
12. Capsule
a. Operculum
b. Spores
c. Spore mother cells
13. Dehiscent sporophyte
14. Spore
15. Protonema

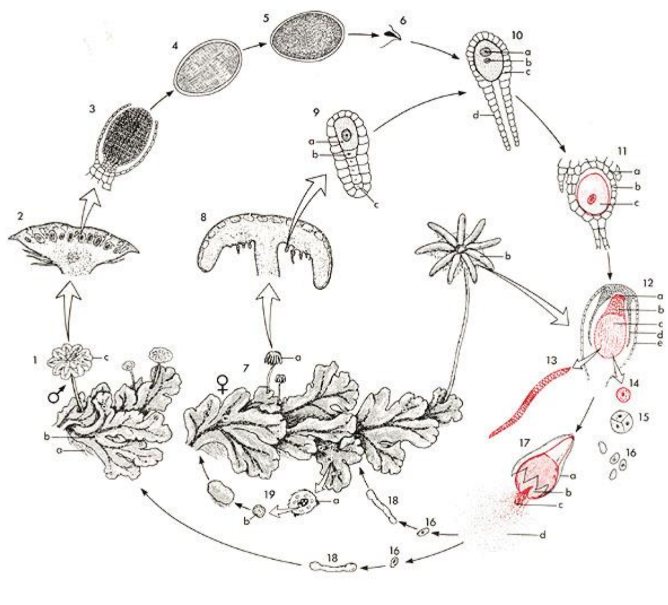


Figure 5.11: Life cycle of the liverwort *Marchantia polymorpha*. The diploid structures are shown in red.

1. Thallus (gametophyte)
a. Rhizoids
b. Gemma cup
c. Antheridiophore
2. Antheridiophore
3–5. Antheridium
6. Antherozoid
7. Thallus (gametophyte)
a. Young archegoniophore
b. Mature archegoniophore
8. Archegoniophore
9. Archegonium
a. Oosphere (egg cell)
b. Ventral canal cell
c. Apical canal cell
10. Archegonium
a. Nucleus of the oosphere
b. Nucleus of the antherozoid
c. Venter of the archegonium
d. Neck of the archegonium
11. Archegonium
a. Calyptra (involucre)
b. Venter
c. Zygote
12. Developed archegonium
a. Foot
b. Seta
c. Capsule
d. Venter
e. Calyptra (involucre)
13. Elater
14. Spore mother cell
15. Tetrad
16. Spores
17. Dehiscent sporophyte
a. Calyptra (involucre)
b. Capsule
c. Elaters
d. Spores
18. Germinating spore
19. Asexual reproduction cycle
a. Gemma cup
b. Gemma (propagule)

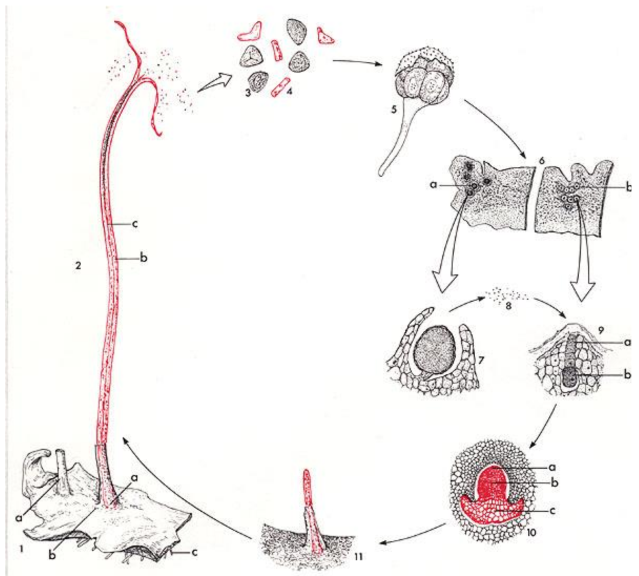


Figure 5.12: Life cycle of a hornwort from the genus *Anthoceros*. The diploid structures are shown in red.

1 Gametophyte
a Tubular Involucre
b Thall
c Rhizoids
2 Sporophyte
a Stipe
b Epidermis
c Centrale Columella
3 Spores
4 Elaters
5 Spore germination
6 Gametophyte: dorsal surface
a Antheridium
b Archegonia
7 Antheridia
8 Antherozoids
9 Archegonia
a Neck canal cells
b O(v)sphere
10 Young sporophyte in the thallus
a Amphithecia
b Endothecium
c Stipe
11 Young sporophyte emergent from the involucre

4.5 Bryophytes and their environment

Bryophytes are ubiquitous organisms found in a wide range of terrestrial habitats, though they are absent from **marine environments** and **extremely arid regions**. Thanks to various adaptations, they have colonized nearly all types of terrestrial ecosystems, extending even into **subpolar zones**. They grow on **soil**, **humus**, **peatlands**, **rocks**, **dead wood**, and even as **epiphytes** on trees. Their ability to **retain water**, particularly in **sphagnum mosses**, is remarkable, making them essential components of ecosystems by contributing to **water retention and regulation**.

Bryophytes are primarily **autotrophic through photosynthesis**, but a few species, such as *Cryptothallus mirabilis*, lack chlorophyll and rely on **symbiotic relationships with fungi** for nutrition. Despite their ecological importance, they are **rarely grazed by herbivores** due to the production of **poorly digestible defensive compounds**. Nevertheless, they play **critical ecological roles** by providing **microhabitats** for a wide range of organisms, offering food for certain species, and participating in the **decomposition of organic matter**.

In addition, bryophytes deliver numerous **ecosystem services** to humans. They are used in **industry**, **agriculture**, **medicine**, and **construction**. Their sensitivity to atmospheric conditions makes them effective **bioindicators of air quality and heavy metal contamination**, making them valuable tools in **environmental biomonitoring**. Their ability to **accumulate pollutants** also highlights their role in **detoxifying contaminated environments**.

1. Pteridophytes

Pteridophytes include **horsetails, ferns, lycophytes**, and **whisk ferns**. They represent the first land plants to possess **vascular tissues—xylem** and **phloem**. Pteridophytes are commonly found in **cool, humid, and shaded environments**, although certain species can thrive in **sandy or xeric soils** (e.g., *Selaginella lepidophylla*).

Modern classification, based on molecular phylogenetics, divides pteridophytes into **two main lineages**:

- **Lycophytes** (*Selaginella*, *Lycopodium*)
- **Monilophytes** (*Equisetum*, *Psilotum*, and true ferns like *Pteris*, *Adiantum*, *Dryopteris*)

Whereas **bryophytes** (e.g., mosses, liverworts) have a **dominant gametophyte phase**, pteridophytes have a dominant **sporophyte phase** that is differentiated into **true roots, stems, and leaves**. These organs are equipped with **well-developed vascular tissues**. The leaves can be either **microphylls** (small, with a single vein, as in *Selaginella*) or **megaphylls** (large, with branched venation, as in ferns).

Pteridophytes have several uses: they are valued for their **medicinal properties**, **soil-binding capacity**, and are frequently cultivated as **ornamental plants**.

Importantly, the group historically referred to as **"Pteridophyta"** is **paraphyletic**: although it included both **Lycophytes** and **Ferns**, modern phylogenetic studies show that **ferns**

(Monilophytes) are more closely related to **seed plants (Spermatophyta)** than to **lycophytes**. Therefore, the term "pteridophytes" is useful descriptively but not phylogenetically precise.

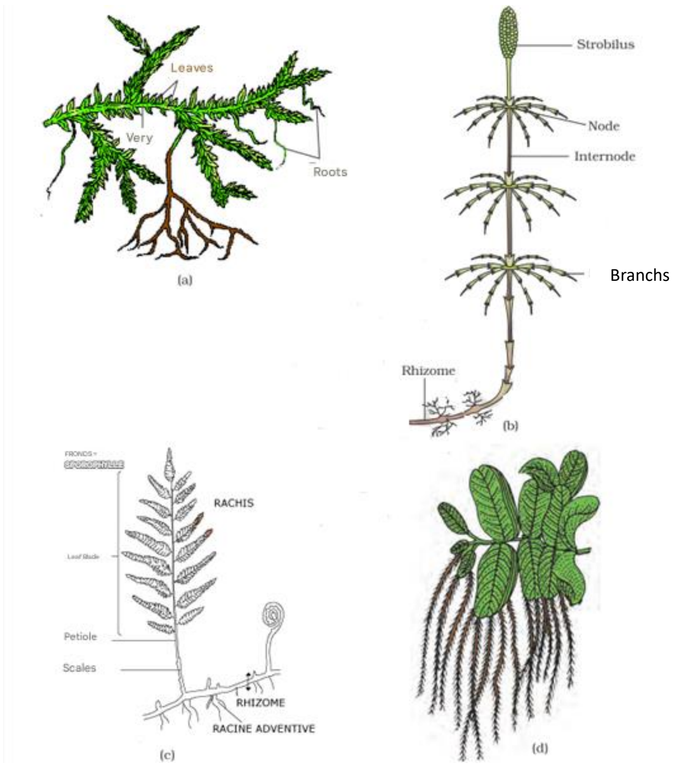


Figure 5.13: Pteridophytes

(a) *Selaginella*

(b) *Equisetum*

(c) Frens

(d) *Salvinia*

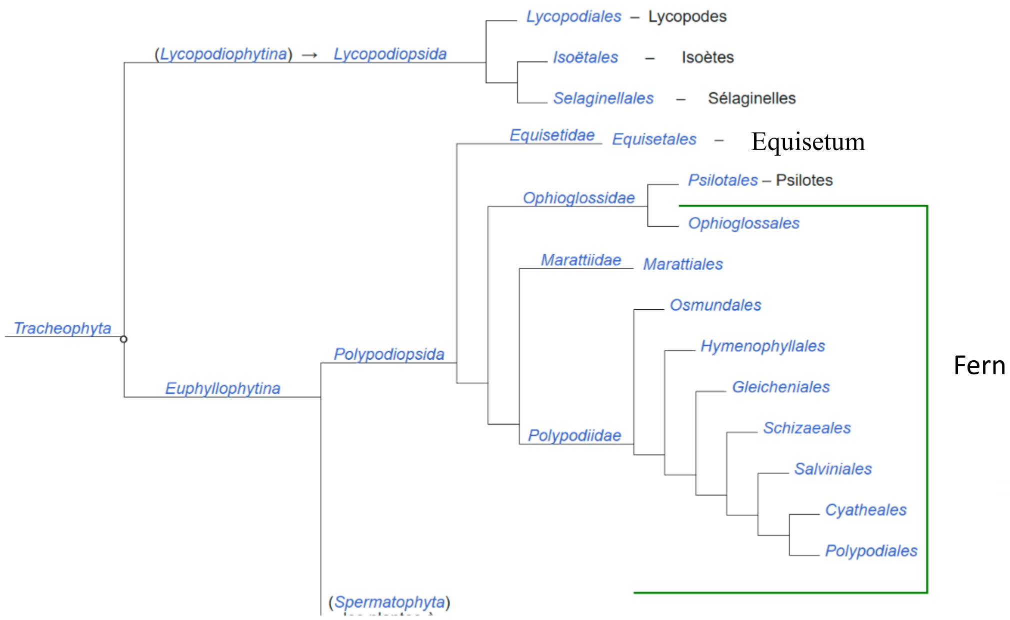


Fig 5.13 a: Phylogeny of Pteridophytes after the *Pteridophyte Phylogeny Group* (2016)

5.1 Biology of Pteridophytes

Pteridophytes are vascular plants that reproduce via spores, rather than seeds. They are part of the **Tracheophytes** group, meaning they possess vascular tissues—**xylem** for water and nutrient transport, and **phloem** for transporting sugars and other organic molecules.

5.1.1 Structure and Organs

Pteridophytes have highly specialized structures adapted to their terrestrial environments.

a. **Roots**
   - **True roots** develop from the embryo and anchor the plant to the soil. They have vascular tissues (xylem and phloem), which allow for the efficient transport of water and nutrients.
   - In lycophytes, roots are simple, with one vascular strand. In ferns, roots are more complex, with multiple vascular strands.

b. **Stem (Caulome)**
   - The **stem** serves as the central axis for photosynthesis and nutrient transport. In ferns, the stem is often **rhizomatous** (underground) or **erect**.
   - In horsetails (*Equisetum*), the stem is **jointed**, with silica deposits in the cells, making the plant stiff and resilient.

c. **Leaves (Microphylls and Macrophylls)**
   - **Microphylls** (small leaves with a single vein) are found in lycophytes like *Selaginella* and *Lycopodium*.
   - **Macrophylls** (larger leaves with branched venation) are characteristic of **ferns**. These leaves, often referred to as **fronds**, are typically divided into smaller leaflets called **pinnae**.
   - **Ferns** have specialized structures for reproduction on the underside of their fronds called **sori**, which contain **sporangia** that release spores.

d. **Sporangia and Spores**
   - **Sporangia** are the reproductive organs where spores are produced. In ferns, they are typically found on the underside of the fronds, clustered in structures called **sori**. In lycophytes, sporangia may be found on specialized leaves or cones.
   - Pteridophytes produce **haploid spores**, which germinate into the **haploid gametophyte**, which is often a small, heart-shaped structure in ferns.

e. **Gametophyte**
   - The **gametophyte** is a small, often **photosynthetic** structure that develops from a spore. In ferns, it is a **prothallus**, which is usually **bisexual**, containing both **antheridia** (sperm-producing organs) and **archegonia** (egg-producing organs).

5.1.2 Ecology of Pteridophytes

Pteridophytes are found in a wide range of environments, but most species thrive in **moist, shaded habitats** due to their reliance on water for reproduction (the sperm must swim to the egg in aquatic conditions). They can be found in:

a. **Forest Floors and Wetlands**
   - Many ferns and horsetails thrive in **temperate** and **tropical** forest environments, where they often form dense undergrowth.
   - They can survive in shaded, humid areas of the forest, where they help in **soil stabilization** and act as **ground cover**.

b. **Tropical Rainforests**
   - Ferns are particularly abundant in **tropical rainforests**, where they occupy the forest understory. They play an important role in the **carbon cycle** by contributing to **carbon fixation** through photosynthesis.

c. **Disturbed Habitats**
   - Pteridophytes are among the first plants to colonize **disturbed or cleared areas**. For example, horsetails and certain ferns are common in areas that have been impacted by logging, deforestation, or natural disturbances like landslides and volcanic eruptions.

d. **Epiphytic Environments**

- Some ferns, such as those in the genus *Asplenium*, are **epiphytic**, meaning they grow on the surface of other plants, typically trees. They do not harm the host plant but rely on rain and air moisture for survival.

e. Tolerance to Harsh Conditions

- Certain species, especially in the genus Selaginella, are adapted to xeric (dry) conditions and can survive droughts by entering a dormant state. These species are typically found in arid regions with seasonal rainfall.

5.2 Ecological Roles

- **Soil Stabilization:** Pteridophytes, especially ferns, help stabilize the soil, prevent erosion, and retain moisture. This is particularly important in forest ecosystems, where the roots of pteridophytes help hold the soil in place.
- **Carbon Sequestration:** By performing photosynthesis, pteridophytes contribute to the sequestration of carbon dioxide in the environment.
- **Pioneer Species:** Many pteridophytes are pioneers in disturbed habitats, aiding in the recovery of ecosystems after disturbances (e.g., forest fires, volcanic eruptions, and landslides).
- Due to their **toxicity or other defense mechanisms**, they are **not consumed by herbivores**.
- They also appear capable of **accumulating large amounts of toxic metals without dying**.

5.3 Economic Importance

- **Medicinal Uses:** Many pteridophytes have traditional medicinal uses. For example, **Dryopteris filix-mas** (male fern) has been used to treat parasitic infections like tapeworms.
- **Ornamental Use:** Ferns and some lycophytes are widely cultivated as ornamental plants due to their attractive fronds and adaptability to low-light conditions.
- **Soil Binding:** Pteridophytes, particularly horsetails and ferns, are used in soil erosion control and landscape restoration projects.

5.4 Life cycle

The **life cycle** of pteridophytes involves an alternation of generations, with a dominant **sporophyte** generation (diploid), which produces spores through **meiosis**. The **gametophyte** generation (haploid), which is smaller and more ephemeral, develops from the spores and produces gametes (sperm and eggs). Fertilization occurs in water, where sperm swim to the egg, resulting in the formation of a **zygote** that grows into the sporophyte.

5.5 Reproduction

The sporophytes bear sporangia, which are subtended by leaf-like appendages called sporophylls. In some pteridophytes such as *Selaginella* and *Equisetum*, the sporophylls are arranged into **compact cone-like structures called strobili**. Inside each sporangium, **spores are produced by meiosis** from diploid spore mother cells.

These spores germinate into **small, multicellular, mostly photosynthetic, free-living thalloid gametophytes**, known as **prothalli**. These gametophytes thrive only in **cool, moist, and shaded environments**, as they are delicate and need water for fertilization. Because of this **ecological dependence on moisture** and the requirement for **water-mediated sperm transfer**, the **geographic distribution** of living pteridophytes is often **restricted to humid areas**.

The **gametophytes bear both male and female sex organs**—called **antheridia** and **archegonia**, respectively. **Motile male gametes (antherozoids)** released from antheridia swim through a film of water to reach the archegonia. The **fusion of the antherozoid and the egg** results in a **zygote**, which develops into a **multicellular, well-differentiated sporophyte**. This sporophyte becomes the **dominant phase in the life cycle**, unlike in bryophytes where the gametophyte dominates.

Most pteridophytes are **homosporous**, meaning they produce only one type of spore that develops into a **bisexual gametophyte**. However, some genera—such as *Selaginella* and *Salvinia*—are **heterosporous**, producing two types of spores: **megaspores (large)** and **microspores (small)**. These develop into **female and male gametophytes**, respectively. In heterosporous species, the **female gametophyte is retained on the parent sporophyte**, and **fertilization and embryo development occur internally**, resembling an **evolutionary precursor to the seed habit** seen in higher plants.

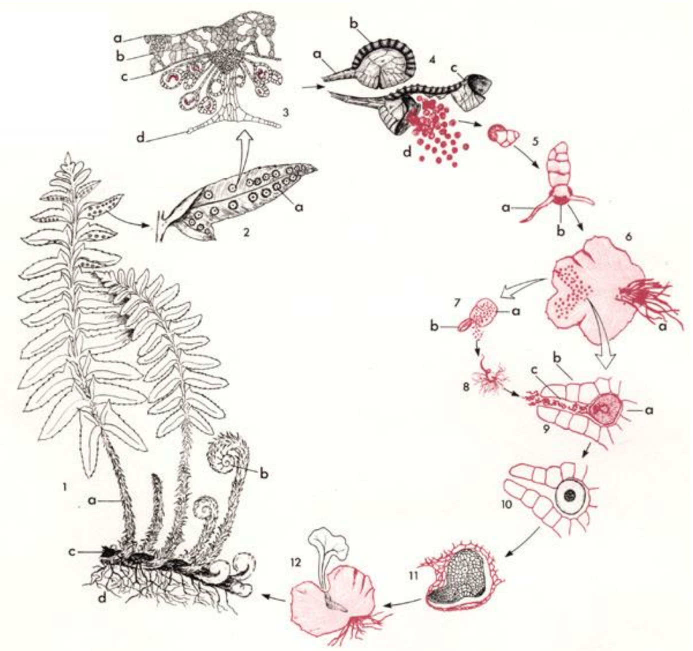


Figure 5.14: Life cycle of a fern. The haploid structures are shown in red.

1. Mature sporophyte
a. Petiole
b. Circinate frond (= coiled)
c. Rhizome
d. Adventitious roots
2. Underside of a leaflet (pinna)
a. Sorus
3. Cross-section of a sorus
a. Upper epidermis
b. Spongy tissue
c. Lower epidermis
d. Indusium
4. Sporangium
a. Stalk
b. Annulus (mechanical ring)
c. Lip cell
d. Spores
5. Young prothallus (= gametophyte)
a. Rhizoids
b. Spore wall
6. Mature prothallus (= gametophyte)
a. Rhizoids
7. Antheridium
a. Annular cell
b. Opercular cell
8. Antherozoids
9. Archegonium with oosphere
a. Venter
b. Neck
c. Neck cell
10. Zygote in the archegonium
11. Embryonic sporophyte
12. Sporophyte on the gametophyte

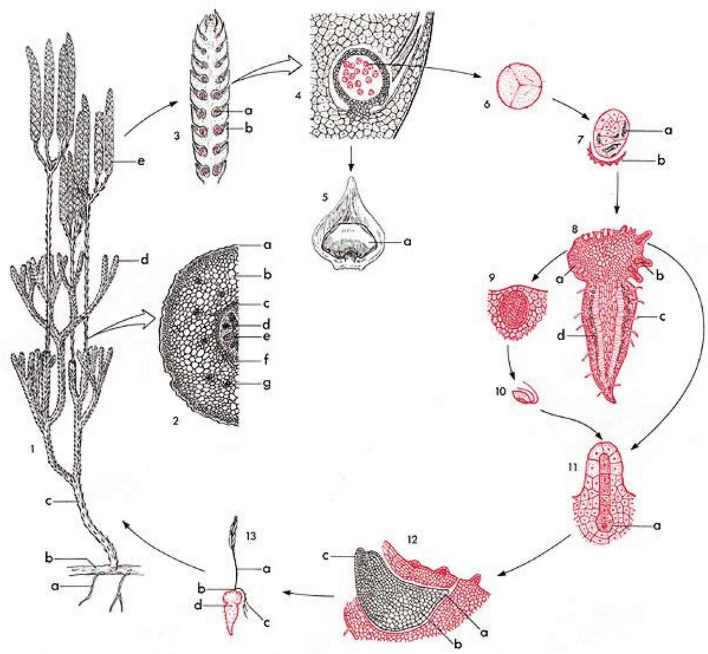


Figure 5.14: Life cycle of a clubmoss of the genus *Lycopodium*. The haploid structures are shown in red.

1. Sporophyte
a. Root
b. Rhizome
c. Stem
d. Leaves
e. Strobilus
2. Sporophyte stem
a. Epidermis
b. Cortex
c. Pericycle
d. Phloem
e. Xylem
f. Endodermis
g. Leaf trace
3. Strobilus
a. Sporangium
b. Sporophyll
4. Sporangium
5. Sporophyll
a. Sporangium
6. Spore tetrad
7. Germinated spore
a. Endophytic fungus
b. Spore coat
8. Gametophyte
a. Antheridium
b. Archegonium
c. Rhizoid
d. Endophytic fungus
9. Antheridium
10. Antherozoid
11. Archegonium
a. Oosphere
12. Embryo

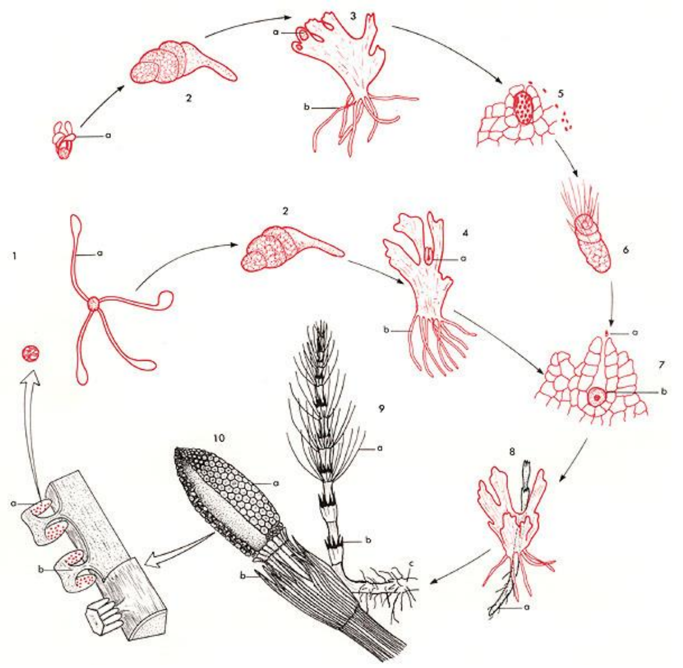


Figure 5.15: Life cycle of a horsetail of the genus *Equisetum*. The haploid structures are shown in red.

Gametophyte:

1. Spores
a. Elaters
2. Germinating spores
3. Prothallus
a. Antheridium
b. Rhizoids
4. Prothallus
a. Archegonium
b. Rhizoids
5. Antheridium
6. Antherozoid
7. Archegonium
a. Antherozoid
b. Oosphere

Sporophyte:

8. Young sporophyte on gametophyte
a. Primary root
9. Vegetative shoot
a. Whorls
b. Leaf scale
c. Rhizome
10. Fertile shoot
a. Strobilus
b. Leaf scale
11. Portion of strobilus with 3 sporophylls
a. Sporangium
b. Sporangiophore

2. Spermatophytes

The Spermatophytes, also known as **Spermaphytes** (superdivision *Spermatophyta*, or clade *Spermatophytina*, or sometimes class *Spermatopsida*), formerly referred to as **phanerogams**, constitute a major group of **vascular plants that produce seeds**—hence their common name "seed plants."
They include two major lineages:

- **Gymnosperms** (non-flowering seed plants such as conifers, cycads, and Ginkgo)
- **Angiosperms** (flowering plants, the most diverse and widespread group)

Modern phylogenetic systems (e.g., APG IV) recognize *Spermatophytina* as a monophyletic clade within the vascular plants (*Tracheophyta*), distinct from spore-producing plants like ferns and lycophytes.

Seed plants are characterized by:

- The production of **seeds** from **ovules** following fertilization.
- **Heterospory** (production of microspores and megaspores).
- A **dominant sporophyte phase**, with **highly reduced gametophytes**.
- In angiosperms, **flowers** and **fruits** as key reproductive adaptations.

6.1 Gymnosperms

Gymnosperms (from Greek *gymnos* = naked, *sperma* = seed) are seed-producing vascular plants whose ovules are not enclosed within an ovary. Instead, the ovules—and subsequently the seeds—are exposed on the surface of cone scales or similar structures, both before and after fertilization. This contrasts with angiosperms, where seeds are enclosed within fruits.

Classification: Modern phylogenetic studies classify gymnosperms into four major extant divisions: