Chapter 4. **The evolutionary classification of land plants**

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Land plants evolved from a group of green algae, possibly as early as 500–600 million years ago. Their closest living relatives in the algal realm are a group of freshwater algae known as stoneworts or Charophyta. According to the fossil record, the charophytes' growth form has changed little since the divergence of lineages, so we know that early land plants evolved from a branched, filamentous alga dwelling in shallow fresh water, perhaps at the edge of seasonally-desiccating pools.

The biggest challenge that early land plants had to face ca. 500 million years ago was surviving in dry, non-submerged environments. Algae extract nutrients and light from the water that surrounds them. Those few algae that anchor themselves to the bottom of the waterbody do so to prevent being carried away by currents, but do not extract resources from the underlying substrate. Nutrients such as nitrogen and phosphorus, together with CO_2 and sunlight, are all taken by the algae from the surrounding waters. Land plants, in contrast, must extract nutrients from the ground and capture CO_2 and sunlight from the atmosphere. The first terrestrial plants were very similar to modern mosses and liverworts, in a group called **Bryophytes** (from Greek *bryos*=moss, and *phyton*=plants; hence "moss-like plants"). They possessed little root-like hairs called **rhizoids**, which collected nutrients from the ground. Like their algal ancestors, they could not withstand prolonged desiccation and restricted their life cycle to shaded, damp habitats, or, in some cases, evolved the ability to completely dry-out, putting their metabolism on hold and reviving when more water arrived, as in the modern "resurrection plants" (*Selaginella*). Additionally, these early bryophytes developed special structures to protect their embryos from drying-out, the **archegonium**, where the male sperm would swim to fertilize the ovule, much like in animals.

Because early land plants lacked organs able to move large quantities of water and nutrients from the ground to the photosynthetic fronds, they relied on cell-to-cell diffusion for transport and could only grow near ground-level, only a few inches high at the most. The next morphological revolution in terrestrial plants occurred some 350 million years ago, when some plants started to develop specialized vascular tissue that could transport substances between the roots and the fronds. Vascular tissue allowed these plants to spatially separate the root functions (nutrient and water assimilation) from the canopy functions (capturing light and carbon dioxide). With the advent of vascular tissue land plants could, for the first time, elevate their canopies and start competing for light while still maintaining their roots safely anchored to the ground. Tree-like growth forms started to develop, and by the middle of the Jurassic Period, some 160 million years ago, this new group of plants, the **Pteridophytes** (*pteridos*=fern), composed by ferns and allies such as horsetail ferns (*Equisetum*) and tree-ferns, dominated a large part of the vegetation of the earth.

Ferns and fern-allies, however, reproduce by spores, like mosses or green algae. But as the vegetation of the earth prospered and became denser, competition for light, water, and nutrients became more intense. Under such conditions, the chances of successful establishment for a small spore can be dim. Some plants started retaining the cross-fertilized spores within specialized structures in the form of embryos, attached to the plant by a connective tissue called a placenta. They also endowed these embryos with a surrounding reserve tissue, called the **endosperm**, rich in nutrients and starch. The structures containing the embryos, which we call **seeds**, were eventually detached from the plant to germinate with the sustenance of the maternal endosperm, which greatly enhanced the chances of offspring survival. This first group of plants with seeds, called the **gymnosperms** (*gymnos*: naked, *sperma*: seed) appeared in the earth some 270 million years ago.

Despite the obvious advantage of producing seeds, the diversification of plants on earth started making the process of sexual reproduction more and more competitive. In gymnosperms, the fertilization of the ovule is done by a wind-driven process: the male pollen is carried by the wind and the microscopic pollen grains —the male gamete— have to land in a receptive ovule in order to fertilize it. But the chances of a flying pollen grain reaching a minutely small ovule are very small, and the plants needed to flood the air with pollen grains in order to attain successful reproduction. As more and more species of gymnosperms appeared, occupying different niches, the chances of a pollen grain finding its way on to a receptive ovule of its same species became diminishing low in many environments. At this point, some plants started to attract the service of small animals (mostly insects) to carry their pollen to other plants by offering the pollinators some reward in terms of nutritional secretions. Competition started to attract the service of these little sex helpers of the animal world by developing increasingly showy reproductive structures: The evolution of flowers, and the beginning of the angiosperms had begun.

Angiosperms (*angios*: vessel, *sperma*: seed) evolved ca 100 million years ago in the Cretaceous period, as a diverse group of plants with showy flowers that protect their seeds within a closed ovary. The big novelty of the angiosperm growth form is the protection of embryos inside a closed receptacle —the ovary— and nectar-producing flowers that attract pollinators. Angiosperm flowers evolved rapidly at the end of the Cretaceous (100–60 million years ago) and radiated into a prodigious array of colors, shapes, and fragrances. Plant flowers co-evolved with modern insects: as myriad groups of insects appeared and diversified, so did the complexity and diversity of floral forms competing to attract the best and most effective pollinating services.

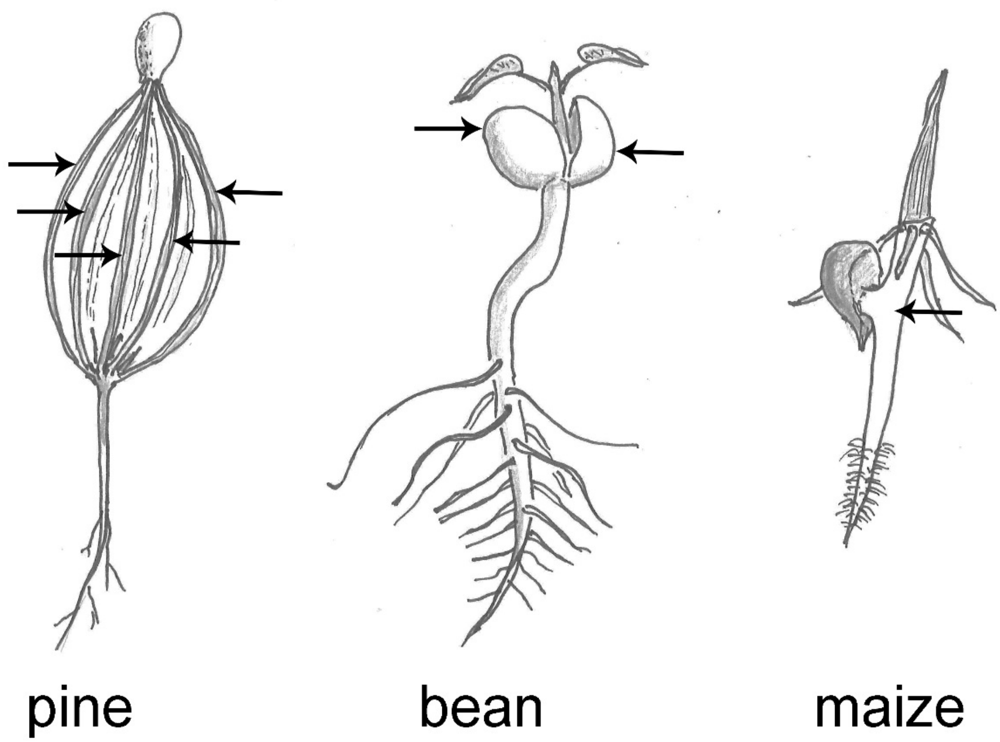

Figure 4.1. Reduction in the number of cotyledons from gymnosperms to angiosperms: (a) The Monterey pine (*Pinus radiata*) has multiple cotyledons (5 shown in the forefront of the illustration) that form a green cage-like structure connecting the embryo to the endosperm in the seed. (b) The common bean (*Phaseolus vulgaris*, a dicot) has two cotyledons that contain the maternal endosperm inside the cotyledon itself. (c) The maize seedling (*Zea mays*, a monocot) has only one cotyledon that links the germinating embryo with the seed endosperm. In all three illustrations the cotyledons are marked by an arrow.

From early times flowering plants radiated into two contrasting classes: Monocotyledons and Dicotyledons (known for short as "monocots" and "dicots"). The cotyledons are the first leaves of the embryos in seed plants. They play an important role in feeding the embryo from the maternal seed reserves, the endosperm. Gymnosperms, such as pines, have many cotyledons. In flowering plants, the number of cotyledons is reduced to two, or simply one (Figure 4.1). Linnaeus, who was an excellent plant morphologist, realized that many other traits were correlated with the number of cotyledons: Monocots have floral parts (sepals and petals) in multiples of three, their leaves have always a simple parallel venation pattern, and they are mostly herbaceous, as they lack the ability to form true wood. Dicots, in contrast, have floral parts in multiples of four or five, their leaves have a more complex, reticular pattern of venation, and, if they live for more than one year, they form woody trunks.

Thus, the kingdom of terrestrial plants —also known as **embryophytes**— is divided into three dividisions: (a) mosses (or bryophytes), (b) ferns (or pteridophytes), and (c) seed plants (or spermatophytes). Seed plants, in turn, are divided into two subdivisions: (i) gymnosperms and (b) angiosperms. Finally, the angiosperms, or flowering plants, are divided into two classes: (1) monocots and (2) dicots (Figure 4.2).

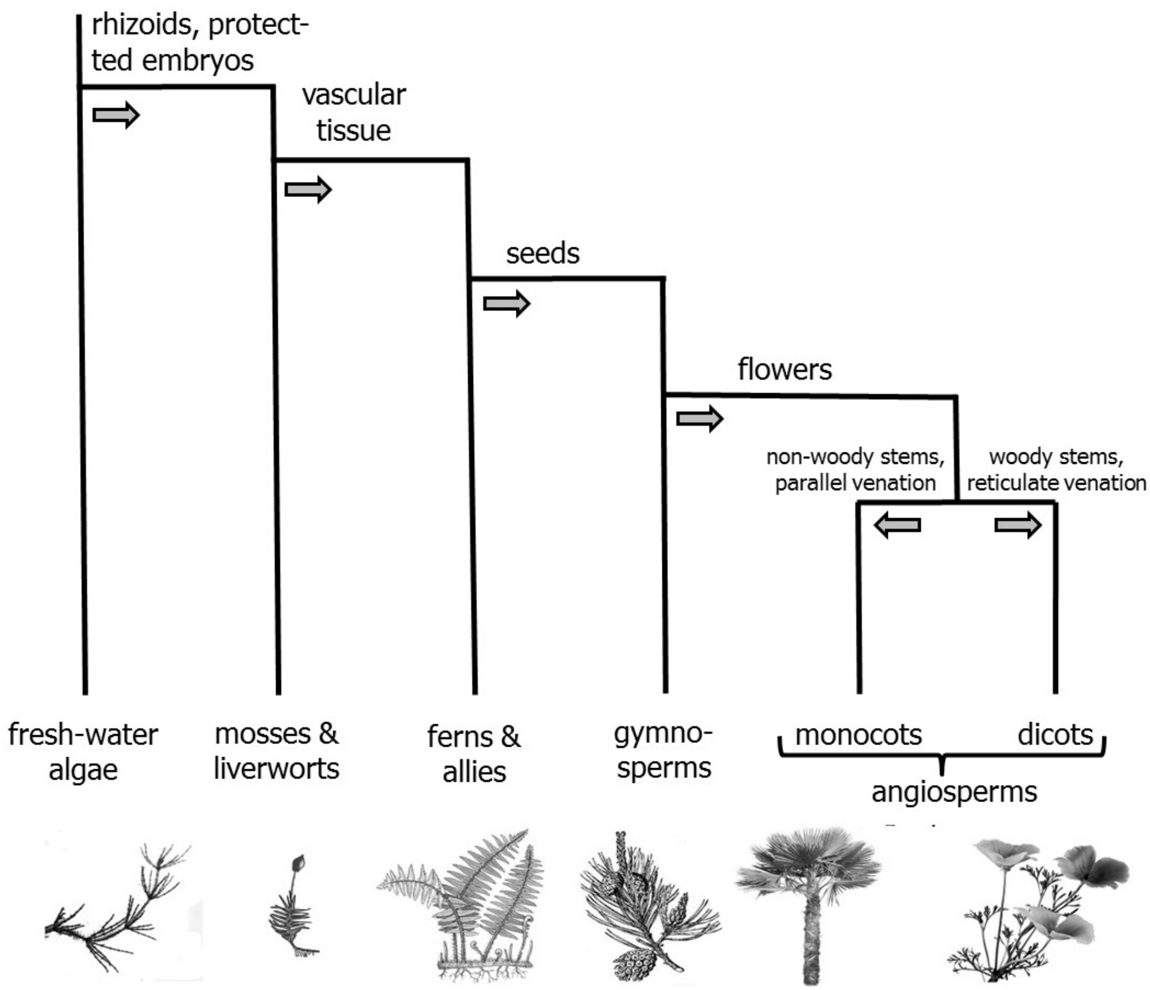

Figure 4.2. The evolution of land plants.

The main traits of land plant evolution can be summarized as follows: All land plants, including mosses, ferns, gymnosperms, and angiosperms, belong in the Kingdom **Plantae**, also known as **Embryophytes**. Land plants, in turn, are often divided into those that reproduce by spores, or **Cryptogams**, and those that reproduce by seed, or **Phanerogams**. The set of all land plants that have vascular tissue (ferns+gymnosperms+angiosperms) is often referred to **Tracheophytes** or vascular plants.

<table>
<tr><th>Algae</th><th>mosses & allies (Bryophytes)</th><th>ferns & allies (Pteridophytes)</th><th>gymnosperms</th><th>Angiosperms</th></tr>
<tr><td></td><td colspan="4">land plants (also called Embryophytes)</td></tr>
<tr><td></td><td colspan="2">hidden reproduction (Crytogams)</td><td colspan="2">exposed reproduction (Phanerogams)</td></tr>
<tr><td></td><td></td><td colspan="3">vascular plants (also called Tracheophytes)</td></tr>
<tr><td></td><td></td><td></td><td colspan="2">seed plants (Spermatophytes)</td></tr>
<tr><td></td><td></td><td></td><td></td><td>flowering plants</td></tr>
<tr><td></td><td></td><td></td><td></td><td>Monocots | Dicots</td></tr>
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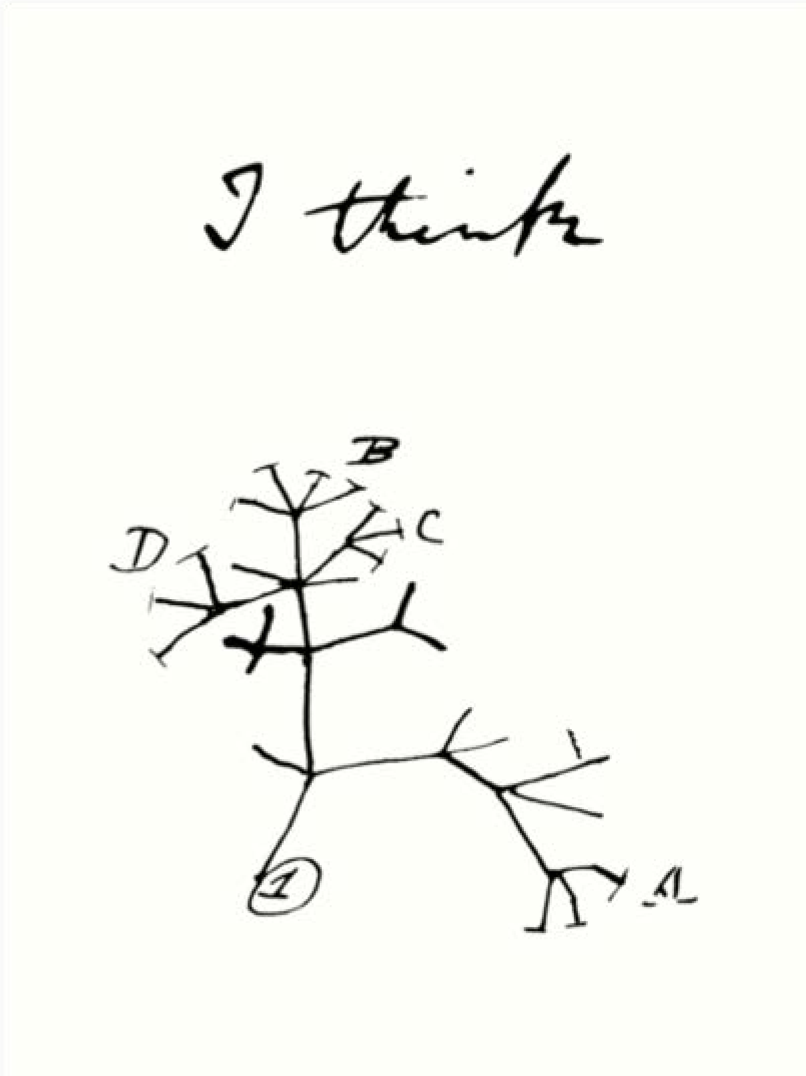
Table 4.1. The main taxonomic subdivisions of land plants.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