Plant evolution

Contributed by: James A. Doyle
Publication year: 2014

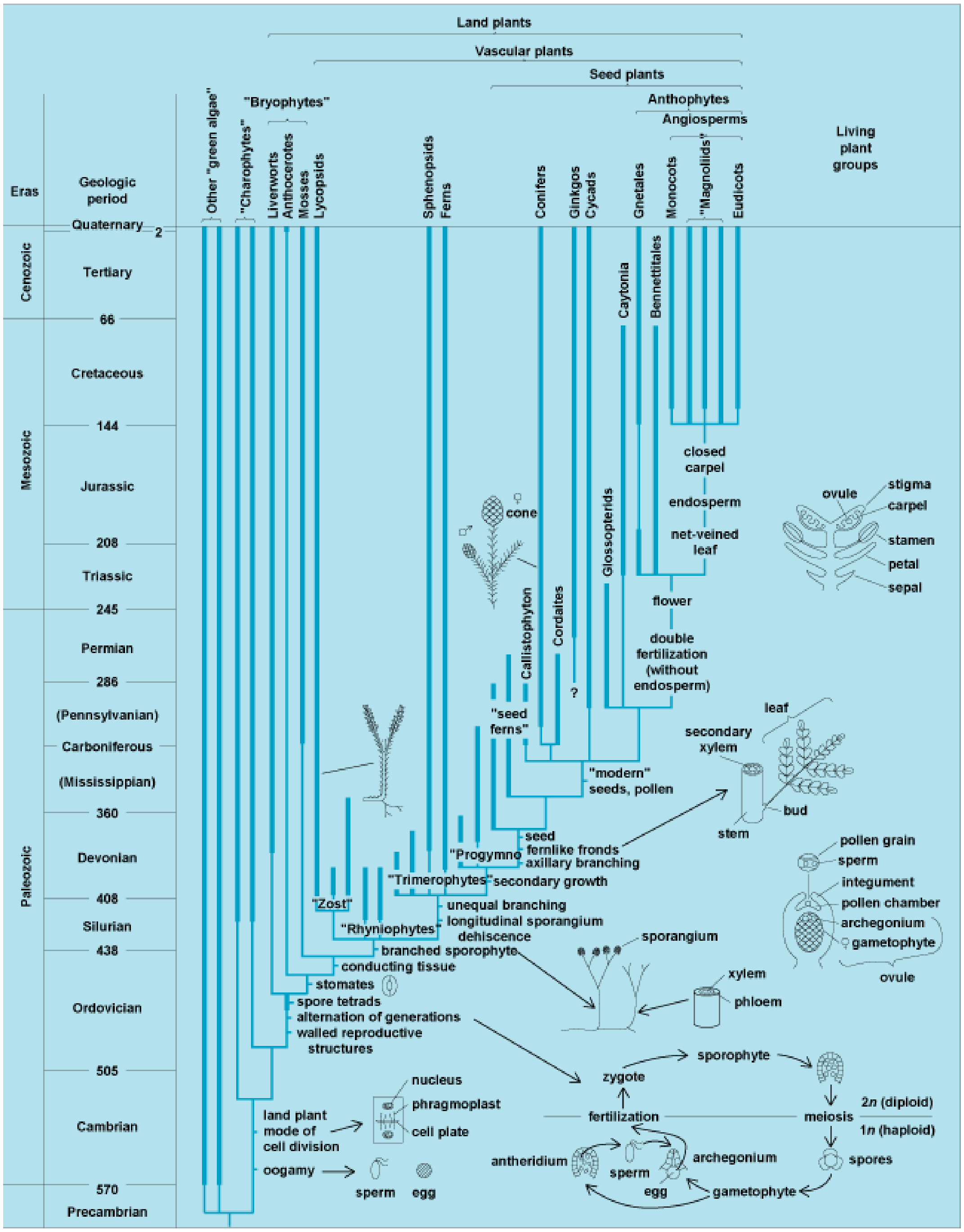
The process of biological and organic change within the plant kingdom by which the characteristics of plants differ from generation to generation. Understanding of the course of plant evolution is based on several lines of evidence. The main levels (grades) of evolution have long been clear from comparisons among living plants, but the fossil record has been critical in dating evolutionary events and revealing extinct intermediates between modern groups, which are separated from each other by great morphological gaps (evolutionary changes in many characters). Plant evolution has been clarified by cladistic methods for estimating relationships among both living and fossil groups. These methods attempt to reconstruct the branching of evolutionary lines (phylogeny) by using shared evolutionary innovations (for example, presence of a structure not found in other groups) as evidence that particular organisms are descendants of the same ancestral lineage (a monophyletic group, or clade).

Many traditional groups are actually grades rather than clades; these are indicated below by names in quotes. Convergence, where the same new feature evolves in different lines, and reversal, where an older condition reappears, confuse the picture by producing conflicts among characters. These are resolved by using as many characters as possible and applying the principle of parsimony, that is, seeking the tree that requires the fewest total character changes, aided by a computer. Progress has also come from studies of molecular data [deoxyribonucleic acid (DNA) sequences of the same gene in different groups]; bases at any point along the DNA can change like any other kind of character and can be analyzed in the same way.

Most botanists restrict the term plants to land plants, which invaded the land after 90% of Earth history (see **illustration**). There is abundant evidence of photosynthetic life extending back 3.5 billion years to the early Precambrian, in the form of microfossils resembling cyanobacteria (prokaryotic blue-green algae) and limestone reefs (stromatolites) made by these organisms. Larger cells representing eukaryotic "algae" appear in the late Precambrian, followed by macroscopic "algae" and animals just before the Cambrian. *See See also:* ALGAE; EUKARYOTAE; FOSSIL; PROKARYOTAE.

Origin of land plants

Cellular, biochemical, and molecular data place the land plants among the "green algae," specifically the "charophytes," which resemble land plants in their mode of cell division and differentiated male and female gametes (oogamy). Land plants themselves are united by a series of innovations not seen in "charophytes," many



Inferred evolutionary relationships of major groups of plants, including some of their most important evolutionary innovations, and their distribution in geologic time (thick lines: known geologic range). Groups in quotes represent grades (levels of evolution).

of them key adaptations required for life on land. “Charophytes” have a haploid life cycle, in which the zygote undergoes meiosis, and single-celled reproductive structures; but land plants have an alternation of generations, with a haploid, gamete-forming (gametophyte) and diploid, spore-forming (sporophyte) phase. Their reproductive organs (egg-producing archegonia, sperm-producing antheridia, and spore-producing sporangia) have a protective layer of sterile cells. The sporophyte, which develops from the zygote, begins its life inside the archegonium. The spores, produced in fours by meiosis, are air-dispersed, with a resistant outer wall that prevents desiccation. *See See also:* CHAROPHYCEAE; PLANT REPRODUCTION.

Land plants have been traditionally divided into “bryophytes” and vascular plants (tracheophytes). These differ in the relative role of the sporophyte, which is subordinate and permanently attached to the gametophyte in “bryophytes” but dominant and independent in vascular plants. In vascular plants, tissues are differentiated into an epidermis with a waxy cuticle that retards water loss and stomates for gas exchange, parenchyma for photosynthesis and storage, and water- and nutrient-conducting cells (xylem, phloem). However, cladistic analyses imply that some “bryophytes,” namely anthocerotes (hornworts) and mosses, are closer to vascular plants than others (liverworts, or hepatics). Both groups resemble vascular plants in having stomates, and mosses also have conducting cells, although of a more primitive type. This implies that the land-plant life cycle originated before the full suite of vegetative adaptations to land life, and that the sporophyte began small and underwent a trend toward elaboration and tissue specialization. *See See also:* EPIDERMIS (PLANT); PHOTOSYNTHESIS; PRIMARY VASCULAR SYSTEM (PLANT).

In the fossil record, the first recognizable macroscopic remains of land plants are Middle Silurian vascular forms with a branched sporophyte, known as “rhyniophytes.” These differed from modern plants in having no leaves or roots, only dichotomously branching stems with terminal sporangia. However, spore tetrads formed by meiosis are known from older beds (Middle Ordovician); these may represent more primitive, bryophytic plants. *See See also:* BRYOPHYTA *See*; RHYNIOPHYTA.

In one of the most spectacular adaptive radiations in the history of life, vascular plants diversified through the Devonian. At the beginning of this period, vegetation was low [perhaps at most 1 ft (30 cm) tall] and probably confined to wet areas, but by the Late Devonian, size had increased in many lines, resulting in large trees and forests with shaded understory habitats. Of the living groups of primitive vascular plants, the lycopsids (club mosses), with pointed, one-veined leaves (microphylls), branched off first, along with the extinct “zosterophyllopsids,” which were leafless but resembled lycopsids in having lateral sporangia. A second line, the “trimerophytes,” which showed incipient differentiation of a main trunk and side branches, and terminal sporangia with longitudinal dehiscence, gave rise to sphenopsids (horsetails), with simple leaves in a whorled arrangement, and ferns (filicopsids), with pinnately compound leaves (fronds) derived from whole branch systems. This radiation culminated in the coal swamp forests of the Late Carboniferous, with tree lycopsids (Lepidodendrales), sphenopsids (*Calamites*), and ferns (Marattiales). Remains of these plants make up much of the coal of Europe and eastern North America, which were then located on the Equator; these plants had many peculiar anatomical features apparently requiring wet and constant conditions. *See See also:* LYCOPODIALES; MARATTIALES; SPHENOPHYTA.

Seed plants

Perhaps the most significant event after the origin of land plants was evolution of the seed. Primitive seed plants ("gymnosperms") differ from earlier groups in their reproduction, which is heterosporous (producing two sizes of spores), with separate male and female gametophytes packaged inside the pollen grain (microspore), and the ovule (a sporangium with one functional megaspore, surrounded by an integument, which develops into the seed). The transfer of sperm (two per pollen grain) from one sporophyte to another through the air, rather than by swimming between gametophytes living on or in the soil, represents a step toward independence from water for reproduction. This step is comparable to the evolution of the amniote egg in vertebrates, and it must have helped plants invade drier areas than they had previously occupied. In addition, seed plants have new vegetative features, particularly secondary growth, which allows production of a thick trunk made up of secondary xylem (wood) surrounded by secondary phloem and periderm (bark). Together, these innovations have made seed plants the dominant organisms in most terrestrial ecosystems ever since the disappearance of the Carboniferous coal swamps. *See See also:* ECOSYSTEM; PTERIDOSPERMS; SEED.

A major breakthrough in understanding the origin of seed plants was recognition of the "progymnosperms" (for example, *Archaeopteris*) in the Middle and Late Devonian. These plants, which were the first forest-forming trees, had secondary xylem, phloem, and periderm, but they still reproduced by spores, implying that the anatomical advances of seed plants arose before the seed. Like sphenopsids and ferns, they were apparently derived from "trimerophytes." The earliest seed plants of the Late Devonian and Carboniferous, called "seed ferns" because of their frondlike leaves (a convergence with true ferns), show steps in origin of the seed, by fusion of branchlets surrounding the megasporangium into the integument. Origin of the typical mode of branching in seed plants, from buds in the axils of the leaves, occurred at about the same time. *See See also:* PTERIDOSPERMS.

Among seed plants, coniferopsids (fossil cordaites, living conifers, and possibly ginkgos), with fan-shaped to needlelike leaves, have often been considered an independent line of evolution from "progymnosperms." However, cladistic analyses indicate that coniferopsids were derived from "seed ferns" with coniferlike pollen and seeds, similar to the Late Carboniferous genus *Callistophyton*. This event may have involved the elimination of fronds and their replacement by scale leaves, which occur around the buds in all seed plants. Cordaites and conifers both appear in the Late Carboniferous; comparisons of their early members indicate that the seed-bearing cone of conifers is a complex structure, in which the cone scales are actually modified branches. *See See also:* CORDAITALES; PINALES.

Seed plants became dominant in the Permian during a shift to drier climate and extinction of the coal swamp flora in the European-American tropical belt, and glaciation in the Southern Hemisphere Gondwana continents. Early conifers, with small, needlelike leaves, predominated in the tropics; extinct glossopterids, with simple, deciduous, net-veined leaves, inhabited Gondwana. Moderation of climate in the Triassic coincided with the appearance of new seed plant groups, including the living cycads and ginkgos (today reduced to one species, *Ginkgo biloba*) and the extinct Bennettitales (cycadeoids), with cycadlike pinnate leaves but flowerlike reproductive structures, as well as more modern ferns. Many Mesozoic groups show adaptations for protection of seeds against animal predation, while flowers of the Bennettitales constitute the first evidence for attraction of insects for cross-pollination, rather than transport of pollen by wind.

Angiosperms

The last major event in plant evolution was the origin of angiosperms (flowering plants), the seed plant group that dominates the modern flora. Angiosperms show numerous innovations that allow more rapid and efficient reproduction. The flower, typically made up of protective sepals, attractive petals, pollen-producing stamens, and ovule-producing carpels (all considered modified leaves), favors more efficient pollen transfer by insects. The ovules are enclosed in the carpel, so that pollen germinates on the sticky stigma of the carpel rather than in the pollen chamber of the ovule. The carpels (separate or fused) develop into fruits, which often show special adaptations for seed dispersal. Other advances include an extreme reduction of the gametophytes, and double fertilization whereby one sperm fuses with the egg, and the second sperm with two other gametophyte nuclei to produce a triploid, nourishing tissue called the endosperm. Angiosperms also developed improved vegetative features, such as more efficient water-conducting vessels in the wood and leaves with several orders of reticulate venation. These features may have contributed to their present dominance in tropical forests, previously occupied by conifers with scale leaves. *See See also:* RAINFOREST.

The origin of angiosperms has been considered a great mystery of plant evolution, since angiosperms were thought to appear in diverse, modern forms during the Early Cretaceous, with no obvious links to other groups. However, most botanists believed that the most primitive living angiosperms are "magnoliid dicots," based on their "gymnosperm"-like pollen (with one aperture for germination), wood anatomy, and flower structure. Studies of Cretaceous fossil pollen, leaves, and flowers confirm this view by showing a rapid but orderly radiation beginning with "magnoliid"-like and monocotlike types, followed by primitive eudicots (with three pollen apertures), some related to sycamores and lotuses. *See See also:* MAGNOLIOPHYTA.

There is still a gap between angiosperms and other groups, but both morphological and molecular data imply that angiosperms are monophyletic and most closely related to Bennettitales and Gnetales, a seed plant group that also radiated in the Early Cretaceous but later declined to three living genera. Gnetales also experience a type of double fertilization, but without formation of endosperm, an exclusively angiospermous innovation. Since all three groups have flowerlike structures, suggesting that the flower and insect pollination arose before the closed carpel, they have been called anthophytes. The closest relatives of anthophytes are controversial, whether advanced "seed ferns" (*Caytonia*, glossopterids) or coniferopsids. These relationships, plus problematical Triassic pollen grains and macrofossils with a mixture of angiospermlike and more primitive features, suggest that the angiosperm line goes back to the Triassic, although perhaps not as fully developed angiosperms. Within angiosperms, it is believed that "magnoliids" are relatively primitive, monocots and eudicots are derived clades, and wind-pollinated temperate trees such as oaks, birches, and walnuts (amentiferae) are advanced eudicots. However, "magnoliids" include both woody plants (for example, magnolias and laurels) and herbs (for example, waterlilies and peppers), and their flowers range from large, complex, and insect-pollinated to minute, simple, and wind-pollinated. These extremes are present among the earliest Cretaceous angiosperms, and cladistic analyses disagree on which is most primitive.

Although plant extinctions at the end of the Cretaceous have been linked with radiation of deciduous trees and proliferation of fruits dispersed by mammals and birds, they were less dramatic than extinctions in the animal kingdom. During the Early Tertiary, climates were still much milder than today, but mid-Tertiary cooling led to contraction of the tropical belt and expansion of seasonal temperate and arid zones. These changes led to the diversification of herbaceous angiosperms, such as composites and grasses, and the origin of open grassland vegetation, which stimulated the radiation of hoofed mammals, and ultimately the invention of human agriculture. *See See also:* AGRICULTURE; FLOWER; PALEOBOTANY; PLANT KINGDOM.

James A. Doyle

Bibliography

C. B. Beck, *Origin and Evolution of Gymnosperms*, 1988

E. M. Friis, W. G. Chaloner, and P. R. Crane, *The Origins of Angiosperms and Their Biological Consequences*, 1987

L. E. Graham, *Origin of Land Plants*, 1993

P. M. Richardson, Origin and relationships of the major plant groups, *Ann. Missouri Bot. Grad.*, 81:403–567, 1994

W. N. Stewart and G. W. Rothwell, *Paleobotany and the Evolution of Plants*, 1993

Additional Readings

Y. Jiao et al., Ancestral polyploidy in seed plants and angiosperms, *Nature*, 473(7345):97–100, 2011
DOI: http://doi.org/10.1038/nature09916

R. Jones et al., *The Molecular Life of Plants*, Wiley-Blackwell, Chichester, West Sussex, UK, 2013

C. Starr, C. A. Evers, and L. Starr, *Biology: Today and Tomorrow without Physiology*, Brooks/Cole, Belmont, CA, 2010

S. Wodniok et al., Origin of land plants: Do conjugating green algae hold the key?, *BMC Evol. Biol.*, 11(1):104, 2011 DOI: http://doi.org/10.1186/1471-2148-11-104