

j9

Late Devonian vegetated hillslopes < seeds, planate leaves >

They [plants] don't evolve in a straightforward way. —Ellen L. Simms.¹

Hillslopes today, in areas that are not too arid (parched or frozen) are typically clothed with vegetation. This is so because of the existence of seed-shedding plants (deciduous trees and shrubs, perennial and annual herbs, and grasses). Hillslope vegetated scenery, dates back to before the appearance of the flowering plants (angiosperms), which in the Late Carboniferous stemmed (possibly) from cycads and conifers,² to the appearance in the Early Carboniferous of those gymnosperms along with ginkgos and seed ferns. Gymnosperm means “naked seed.” Gymnosperms do not have flowers—their male (small) cones shed pollen and their female (large) cones, when pollinated, produce seeds. Progression in the appearance of plants was first noted by Adolphe Brongniart (1801-1876) in *Forerunner of a history of fossil plants* (1828).

Seeds

A distinction can be made between a pollen-shedding plant and a spore-shedding plant (**Figure j9.1**). The difference can be illustrated by explaining how the living ginkgo propagates itself in comparison to a fern. Both, in their sporophyte generation, are sap circulating higher plants. However, the ginkgo does not shed its spores, whereas a fern does (*see* Topic *j10*).

The spore that is shed, if it travels airborne, will, upon arrival in a suitable environment (wet ground with the necessary, soluble, inorganic, nutrients, and light), undergo, if viable, cell division without delay. The persistence of the sporophyte generation in the evolution of the plants is presumably because this generation reproduces sexually (which allows for genetic variability, through mutations, to mix into the species' gene pool). The growing gametophyte has no store of organic food to aid its growth and, because evolution has not provided it with vascular tissue, it cannot reach maturity if the ground, on which it lies, dries out. This problem is solved, in the evolutionary sense, by the pollen-shedding plants. Not shed is female the gametophyte generation which lives parasitically on the parent sporophyte. What is shed is pollen (a dormant male gametophyte) and, ultimately, to propagate the species, a seed (an already growing, but dormant, sporophyte).

The ginkgo, the most primitive of extant seed plants, does not shed its spores. The Maidenhair tree (*Ginkgo bilboa*), by the caprices of fortune, is the only surviving member. This living fossil is a familiar street-tree grown (the male that is, for the female tree produces smelly fruit that drops and messes) for its hardiness.³ Pollen grows parasitically on the male plant to maturity and produces motile sperm that must swim to reach an ovule produced by the mature female megasporophyll that grows parasitically on female plant. This is a feature not advanced over the once seed ferns' presumed means of sexual propagation. Seed ferns cannot be recognized as such since the Jurassic. What happened to them? The answer can be discerned from the following: Ginkgos evolved in the Triassic. Cycads evolved in the Carboniferous. Neither of these seed plants are derivable from the other and each is assumed to have evolved independently from a seed fern stock. By such evolutionary transformations, the seed ferns became extinct taxonomically (i.e. they no longer exists as a taxon).

In reviewing the evolutionary strategy of the higher plants, which enable these to propagate on land, what is found is that virtually every strategy that one cares to consider as possible has been tried by nature.⁴ For example, of the lycopsids at the height of their evolutionary success in the Carboniferous *Lepidocarpon* produced a fructification with a large mass of gametophyte tissue. Significantly, as to their purpose, these have never been found attached to the parent. In their shed state they would have had the function of seeds having sufficient mass and moisture to continue growth and the establishment of a new sporophyte removed from the sporophyte parent. According to Chester A. Arnold (1947), “the best reason for regarding the *Lepidocarpon* fructification as a seed is that it functioned as such.”⁵

The retention of the nonvascular gametophyte generation on the parent plant and the continued growth of the male gametophyte (pollen) on the fruiting part of the species, is a strategy that evolution has repeatedly been guided to by natural selection. It appeared first in the Early Devonian in the seed ferns (class Pteridospermae)—then, the only seed-bearing plants. Other plants at the time, and from when the first land plants appeared, were all spore shedding. Direct evidence of the first bona fide land plants are spores in large numbers within sporangia in Ordovician plant-fragment fossils in Oman, described by Charles H. Wellman in 2003.⁶

Phylogenetic analyses, reported by Kathleen M. Pryer in 2001 of the morphology and four genes from 35 representatives of extant vascular plants, found three monophyletic groups (clades):

I) lycophytes

II) seed plants

III) true ferns, psilotophytes (“whisk ferns”), and equisetophytes (jointed-stem plants called “horsetails” when whorls of very slender branches radiating from each joint impart a bushy-look, and “scouring rushes” when stems are plain—American pioneers used bound-together bunches of these silica-accumulator plants to scour pots and pans).

Maximum-likelihood analysis reveals clades (II) and (III) evolved contemporaneously and are closest relatives in their ancient lineage, and (I) evolved separately since the three clades diverged in the Devonian. This refutes the evolutionary grade concept that seed plants (and extinct seed ferns) evolved via true ferns and equisetophytes, from bryophytes.⁷

Leaves

Leaves with broad lamina evolve via leaves with dissected lamina from leafless branching stems.

Planate (flat blade) leaves are the base of the food chain for tetrapods and insects. Planate leaves (megaphylls) were abundant in the Early Carboniferous and have been common to most vascular land plants since the Late Devonian.

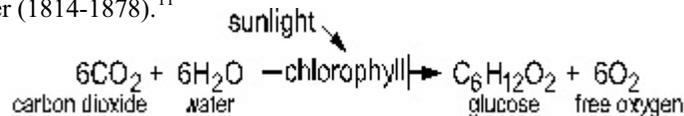
The fully “webbed” (that is, laminate) planate leaves with dichotomous venation developed from much-branched determinate lateral systems (“proto-leaves”) in the Early Devonian. Already evolved then in *Eophyllophyton bellum* were the leaf meristem, vasculature, cuticle, and epidermis.⁸

Silurian plants had short, cylindrical, aerial stems which had minute enation leaves (microphylls) or were leafless.

The change of the typical land-plant leaf to megaphyll from microphyll was slow (taking 40 million years). The structurally far more complex evolution of the seed habit from homospority occurred during that same time.

Planate leaves have high stomatal densities in comparison to the low stomatal densities of pinate leaves. In 2001, David J. Beerling made the case that this was a necessary (if at first glance paradoxical) preadaptation for cooling the leaf that kept ahead of a decrease of the world’s atmospheric CO₂ (**Footnote j9.1**) by 90 % (and so, with less hothouse evaporation, a concomitant decrease in cloudiness shading). That environmental change was brought about by the spread of plants onto the hills and the development of soil (which the plant ground cover makes possible) by the deep weathering of silicate rocks that plant roots promote, and by organic carbon burial.⁹ □

Footnote j9.1¹⁰ “The plants take in one form of power, light: and produce another power, chemical difference.”—Julius Robert von Mayer (1814-1878).¹¹



The plant uses glucose directly for energy of metabolism or polymerizes it to starch that is stored for future energy needs.