Preamble In 1826, botanists began to regard plants as collections of cells, each a unit of vegetable morphology, as elucidated by Matthias Jacob Schleiden's cell theory that was extended in 1839 by Theodor Schwann's (pronounced *taodor shvän*) *Microcsopic Investigations on the Accordance in the Structure and Growth of Plants and Animals* [1] and furthered by Rudolf Virchow who in 1858 demonstrated that pathological tissues are collections of proliferating cells: *omnis cellula a cellula* (all cells come from cells) which is the cell theory principle that: "Where a cell exists, there must have been a preexisting cell." [2]

j11 The first land plants < tracheid cell, riparian>

> Legend has it that Aphrodite discovered oregano in the ocean and took it to the top of Mount Ida to be closer to the sun. The Greeks called it 'joy of the mountain' (*oros* is mountain, *ganos* is joy or brightness) —Molly O'Neill.[3]

> Chlorophyll, the green pigment common to all photosynthetic cells, absorbs all wavelengths of visible light except green, which it reflects to be detected by our eyes. —Michael J. Farabee.[4]

In their transition to land, the first land plants had to solve a range of problems related to keeping moist whatever plant part is not immersed in water (see ***Footnote j11.1***).[5]

Similar to living psilopsids (class Psilopsidae), the oldest fossil plants in which sap could circulate are extinct psilopsid (class Rhyniaceae) vascular plant genera: bushy *Rhynia*, creeping *Aglaophyton,* and bulbous-rhizomed *Horneophyton*, fossilized in detail by silica replacement in the Early Devonian (Pragian age) Rhynie Chert (a fossil bog), Aberdeenshire, Scotland.[6] Individual *Rhynia* plants were small and little more than a horizontal "stalk" from which grew vertical (<20 cm high) "stems" (diameter <3mm). The stalk lay in swampy ground and, without true roots, it was a rhizome. The stems bore short branches and spore sacs. True leaves were absent. Significantly, the stalk, stems, and branches, had simple vascular tissue and even delicate strands of wood cells. Rhynie animals are mites, extinct trigonotarbid arachnids, springtails, myriapods, and harvestmen.[7]

The evolutionary step of the development of vascular tissue, in which plant cells (which are typically box-shaped) have a mutated elongate-form, was a small one genetically but a giant one for all life as it allowed plants, and hence animal life, to move onto the land. This elongated cell is called a *tracheid cell*. Upon reaching maturity, it dies and after the interior matter and its ends have decomposed, the cell-wall remains as a cellulose tube for the circulation of sap. H. H. Dixon's cohesion–tension theory proposed in 1896, and discussed by Melvin T. Tyree and M. H. Zimmermann in *Xylem Structure and the Ascent of Sap,* 2002,[8] is that evaporation maintains in leaf pores a concave air-water interface meniscus and so a negative pressure in cohesive water below. This tensional force, to –15 MPa, is transmitted downward through cohesive water that fills a xylem conduit. So water is caused to flow to leaf pores from the roots. Cavitations that break the water cohesion (critical height is ~10 m) are frequent but at any time are few compared to the number of water-filled flowing conduits. For this to be so, evolution keeps optimized conduit diameters to between 5 and 10 µm in the tallest slow-growing trees (Coast Redwoods reach 379 feet and sap takes 2 weeks to ascend—but water is also absorbed by their crown needles directly from mist)[9] and about 500 µm in fast-growing low plants.[10] A question to be considered (*see* Topic *j27*) is, why did so many billions of years pass before this (surely, easy to evolve) structure became advantageous?

Originally, the most ancient fossil vascular plants known were those described by William Dawson in 1859 from fragmentary fossils in the Lower Devonian of Gaspé sandstone, Newfoundland, Canada. In 1917, R. Kidston and W. H. Lang formally described the Rhynie psilopsids[11] discovered in 1912 by William Mackie.[12] Spores associated with these are comparable to spores discovered in Lower Silurian rocks from Libya.[13]

Comparisons of the psilopsids and ferns are limited in that no gametophytes of the extinct primitive psilopsids of the Paleozoic (class Rhyniaceae) have yet been found. Living plants most closely comparable to them, belong to an order comprised of two genera: tropical *Psilotum* and subtropical *Tmesipteris*. However, these have no fossil record and their likeness to the Rhyniaceae could be the result of convergent evolution. Speculating about these matters becomes like delving into the structure of Klingon grammar.[14] One can take it much further than there can be any sense in going.

A plant with vascular tissue can live: part of it without sunlight underground where it takes in oxygen and inorganic salts dissolved in groundwater, and part of it exposed to air and light above ground where it transpires and manufactures organic nutrients by photosynthesis as Jean Senebier (1742-1809) first showed in 1782. The vascular tissue that transports the inorganic salts is the *xylem*, and that which transports the organic products of photosynthesis is the *phloem*.[15] A vascular system for the circulation of sap exists in some aquatic plants. Such could have been a preadaptation in forbears that made possible a terrestrial life style for descendant plants. Recently Dianne Edwards described a Devonian plant that resembles a liverwort but with spores like those associated with earlier Ordovician plant fragments. Different from continuing liverworts, it had specialized structural cells like those of higher plants and so likely had simple root hairs. Possibly vascular tissue appeared independently in several stocks of plants. If so, the higher plants have polyphylenogic origins. However, monophyly of the embryophytes (the first land plants) is not at odds with the total available evidence of land plant morphology, male gamete ultrastructure, and molecular sequences reviewed by Paul Kenrick and Peter Crane in *The origin and Early Diversification of Land Plants: A Cladistic Study*, 1998.[16] Gametangiophores of three taxa from the Rhynie Chert were described in 1993.[17]

Bare hillslopes before the Middle Devonian

As plants cannot walk, the sporophyte generation, which comes to be from, and on, the gymnosperm generation, is confined to that plant's habitat. For about 20 million years, land vegetation was only in sloughs (pronounced *slows*), boggy riparian, and terrain-shaded wet areas. The hills during that time were bare of vegetation as the existing higher plants (psilopsids, lycopsids, sphenopsids, and ferns) were spore shedding and aquatic in their gymnosperm generation. Even so, as long ago as the Early Devonian experimentation for an alternative to shedding spores, but yet not evolved to the level of shedding seeds, is hinted at by *Rhynia Gwynne-Vaughani.*[18] Its aerial stems were stubbed with small hemispherical outgrowths that sometimes developed into adventitious branches with vascular strands. However, the vascular interior of these side branches did not connect to the vascular tissue of the parent stem. Also, these branches were narrowly constricted at their point of attachment so that they could easily break off. This could have been the plant's means of vegetative reproduction. *Cooksonia* (grab-bag name, honoring Isabel Cookson) is a paraphyletic grade of centimeter-sized first "land-plants." Their fossils are of stems that bifurcated several times and end in small sporangia with rounded, spherical, elongated, or reniform shapes, which distinguish the 4 "species." Early Devonian specimens, first described by W. H. Lang in 1937, have tracheid-resembling internal conducting cells. Earliest specimens are from Middle Silurian Wenlock strata, Tipperary, Ireland. ❑

Footnote j11.1 Evolutionary prerogatives for land plants

Free to those who can afford it. —A line from the *Withnail & I* movie. [19]

Embryophytes are "land plants" in that their members posses at least some features that are clearly adaptations to part of the plant living out of water in the gaseous realm. Unequal in their success in this regard are the two embryophyte groups: tracheophytes (which include higher plants of lycopsid, *Equisetum,* seed fern, and fern lineages) and bryophytes (which include liverworts, hornworts and mosses).

Higher plants have the ability to circulate sap, which transports water and dissolved substances throughout the plant. Aqueous plants with this preadaptation can have descendants that make the transition to living fully out of water on the land, by evolving solutions to:

1. Preventing excessive loss of water by evaporation.
2. Maintaining a sufficiently extensive moist surface for gas exchange when the surrounding medium is air instead of water.
3. Carrying out reproduction when there is little water through which flagellated sperm may swim and when the zygote and early embryo are exposed to desiccation.
4. Withstanding the extreme fluctuations in temperature, humidity, wind, light, and other environmental conditions to which terrestrial organisms are often subjected.
5. Supporting a heavy and tall (sunlight reaching) plant body against the pull of gravity when the floatation buoyancy of an aqueous medium is absent.