

EMBRYOPHYTA

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Summary

This chapter summarizes our knowledge on embryophytes phylogeny, diversity and evolution based on morphological, anatomical, paleontological and molecular approaches.

The Embryophytes, commonly named “land plants” contain a very diverse group of “photosynthetic” organisms, namely: Bryophytes (hornworts, liverworts, mosses), Seedless vascular plants (lycophytes, ferns) and Spermatophytes (seed plants) which include Gymnosperms and Angiosperms (flowering plants).

The term “Embryophyta” refers to plants producing a diploid (2n chromosomes) embryo resulting from the fertilization of the female gamete “oosphere” by a spermatozoid (male gamete), giving rise to a single-celled diploid zygote. The life history of the embryophytes differs strongly from that of animals. It is characterized by the alternation of two morphologically different generations: a haploid *gametophyte* and a diploid *sporophyte*.

The emergence of embryophytes on Land was indeed one of the most important “macroevolutionary” events in the history of life on Earth, being the starting point of irreversible changes of climate and biogeochemical cycles driven by the extension of an increasingly dense and diversified vegetal cover. This taxon may have originated around the middle Ordovician (c. 473–471 Ma) as attested by the discovery of the oldest known microspores produced by land plants, the earliest embryophytic megafossil being, at the

moment, dated Late Ordovician. Today, thanks to the support of new molecular data, the main taxonomic units of Embryophyta became much better resolved than ever before.

The phylogenetic relationships between most of the lineages of Embryophytes are analyzed through comparative developments on the biological, morphological and anatomical characteristics of the different taxa and supported by drawings of the relevant phylogenetic trees. Together with examining the phylogenetic processes of the Embryophyte emergence based on the fossil records, the main steps of the evolutionary transitions at the origin of the diversification of the vegetal cover, leading to the main extant taxa distributed into various biomes on the earth, are analyzed at the geological time scale.

1. Short Introduction to Green Plants

The term “Green plants” refers to autotrophic eukaryotic organisms that convert light energy into chemical energy using oxygenic photosynthesis. This process allows them to produce carbohydrates from carbon dioxide and water, thanks to chlorophyll inside of a plastid element: the “chloroplast”.

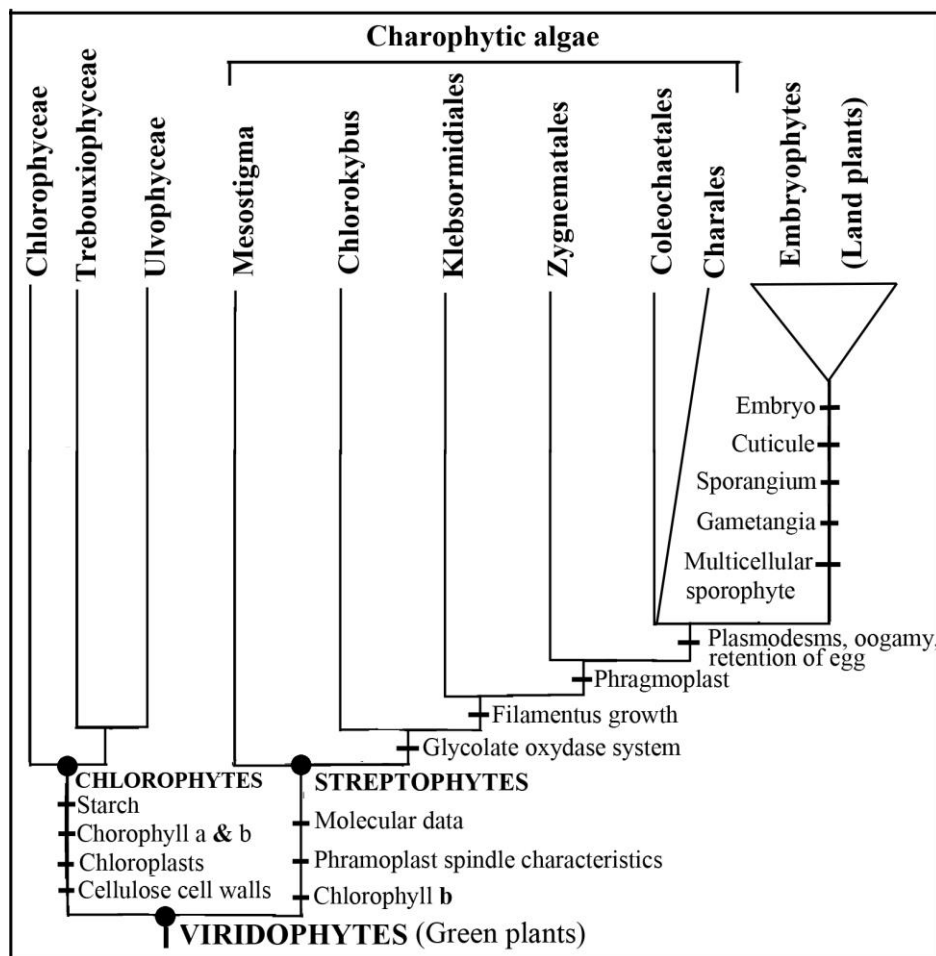


Figure 1. Phylogenetic relationships within the green plants (Modified and redrawn, adapted from data after Judd et al., 2008 and M. G. Simpson, 2006).

Green plants represent a clade called “*Viridiplantae*” (Viridophytes) encompassing all the “green algae” and the “embryophytes” (land plants) (Figures 1, 2, 3). It includes some 300,000 described species *i.e.*, one-sixth of all known extant species. Viridiplantae monophyly is supported by chemical, morphological and structural features as well as by molecular evidence including DNA sequence data from the nucleus and organelles (Leliaert et.al., 2011).

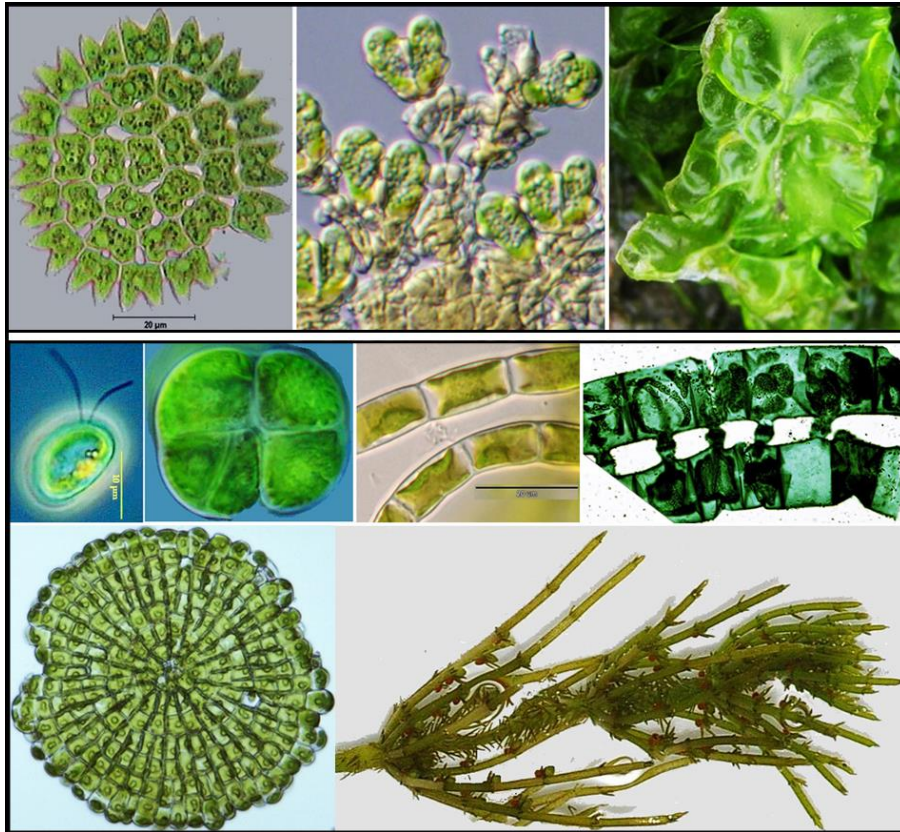


Figure 2. From left to right and up to down,
I) Elements of the Diversity of the Chlorophytes: 1 *Pediastrum* (Chlorophycée);
2- *Botryococcus* (Trebouxiophycées); 3- *Ulva* (Ulvophycées);
II) Elements of the Diversity of the charophytic algae: 4 – *Mesostigma*; 5- *Chlorokybus*;
6- *Klebsormidium* (Klebsormidiales); 7- *Spirogira* (Zygnematales); 8- *Coleochaete*
(Coleochaetales); 9- *Chara* (Charales).

Pediastrum: By Dr. Ralf Wagner,
<https://commons.wikimedia.org/w/index.php?curid=7853731>;
Botryococcus braunii: <https://commons.wikimedia.org/w/index.php?curid=12703054>;
Ulva: By Fleliaer –Ownwork
<https://commons.wikimedia.org/w/index.php?curid=25870268>;
Klebsormidium bilatum <https://commons.wikimedia.org/w/index.php?curid=39971728>.

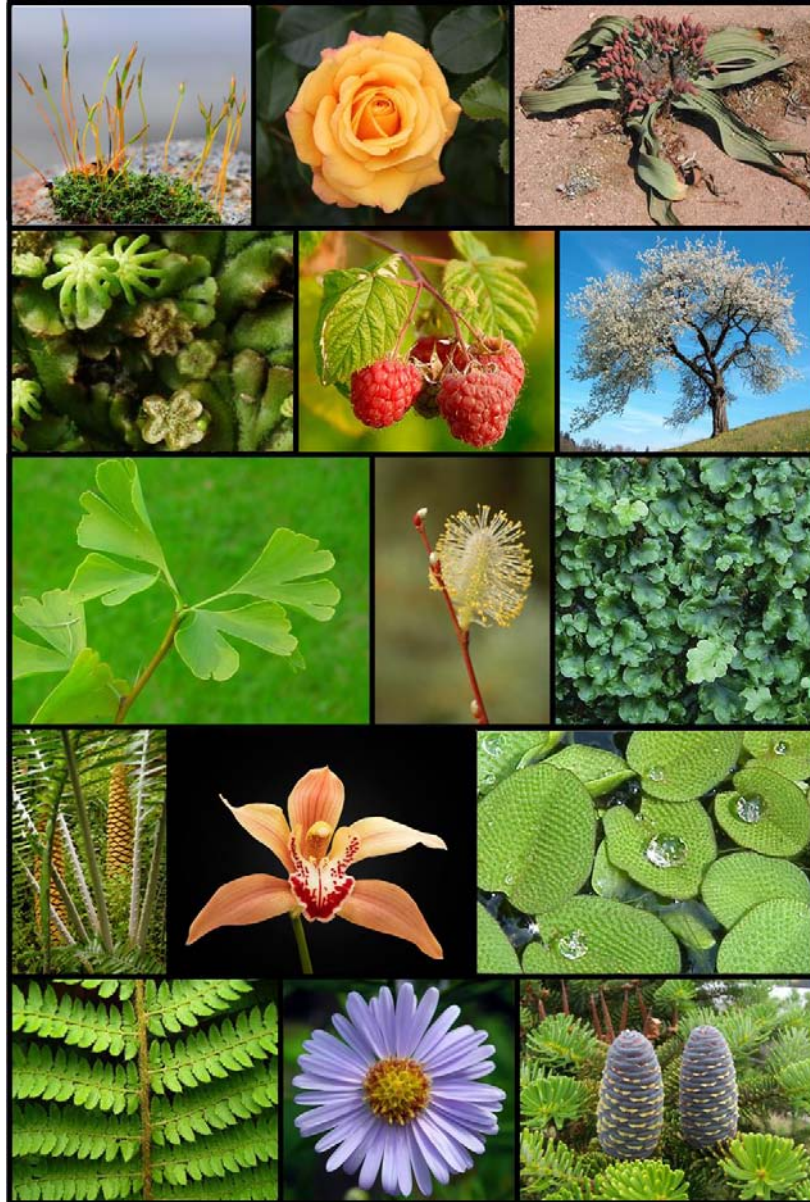


Figure 3. Elements of the diversity the Embryophytes. From left to right and up to down: 1) Moss with mature sporogones (Bryophytes); 2- *Rosa amber* (Angiosperms); 3- *Welwitschia mirabilis* (Gnetophytes); 4 *Marchantia polymorpha* (Marchantiophytes, liverwort); 5 *Rubus ideaus* (Raspberry - Angiosperms); 6 - *Prunus cerasus* tree (Angiosperms); 7- *Ginkgo biloba* (Ginkgophyte); 8 - Male catkin of *Salix* sp. (Angiosperms); 9 - *Pellia epiphylla* (Marchantiophytes); 10 - *Encephalartos villosus* (Cycadophytes); 11 - *Cymbidium* sp. (Orchidacées); *Salvinia natans* (aquatic water fern, Hymenophyllales); 12 – Fern foliage; 13 *Aster tartaricus* composite “flower” (Angiosperms); *Abies coreana* (Conifers).

By Rkitko

https://commons.wikimedia.org/wiki/File%3ADiversity_of_plants_image_version_5.png (slightly modified)

2. Embryophytes: Characteristics and Diversity

Familiarly the embryophytes are often named “land plants” which is not strictly true as rare algal lineages have also independently become terrestrial such as the Chaetophoraceous alga *Fritschiella*. Therefore “embryophyte” is a preferable term. This term, by itself, means “plant with an embryo” *i.e.*, a diploid pluricellular structure issued from the female phase of the lifecycle, which results from the fertilization of the female gamete “oosphere” by a spermatozoid (male gamete), giving rise to a single-celled, diploid zygote. The zygote becomes an embryo once cell divisions begin. In addition to this embryo, the embryophytes share: a pluricellular sporophyte; multicellular reproductive organs: male and female gamete-producing organs (gametangia: male antheridium and female archegonium); sporangia (the site of meiosis); and a cuticle (a waxy or fatty protective layer on the external wall of epidermal cells). The life history of all embryophytes differs strongly from that of animals. It is characterized by the alternation of two morphologically different pluricellular generations: a haploid gametophyte and a diploid sporophyte. (Figure 4)

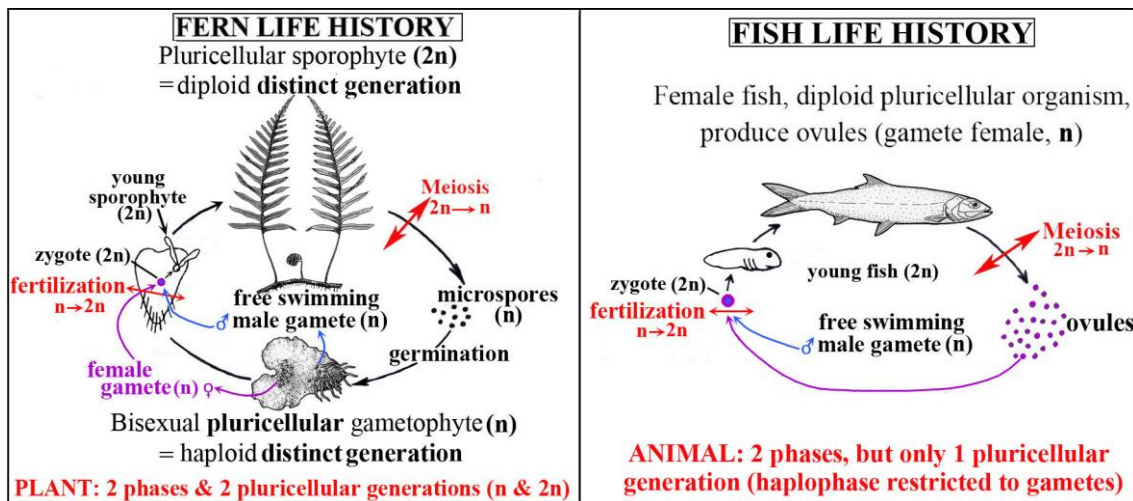


Figure 4. The life histories of plants and animals compared (inspired from Hallé, 1999).

2.1. Human Use of Embryophytes

Plants are the source of food (seeds, fruits, vegetables...) and, thereby, metabolic energy for nearly all other organisms. Vital products to human beings derived from trees include: wood, cork, fibers, latex, drugs, oils, pigments, gum, resins...; other non-arborescent forms include medicinal and ornamental plants. Last but not least, coal and petroleum are fossil substances derived from plants.

In this framework it is necessary to draw attention to the flowering plants (“angiosperms”, see Section 5.2). They are by far the dominant living plants including some 258.000 species in 400-500 families, representing at least 95% of the living vascular plants (Table 1). They are for sure the vegetal organisms (perhaps even living organisms!) that most directly affect human beings on Earth. As examples, they include all crop plants like wheat, rice, corn... that constitute, worldwide, the basic food supply. The nutritive tissue of the seed, the so-called endosperm, is produced in conjunction

with fertilization and has a triploid chromosome count. It provides nutrition for the maturation of the embryo, including starch and, in some flowering plants, oils and proteins. These contents are what make endosperm such an important source of nutrition for human beings. To wit, wheat endosperm is an important component of flour for bread, and barley endosperm being the main source of sugar for beer production! Flowering plants are also essential to human survival in many respects such as: wood for building, medicinal derivatives, and various fibers for paper and textiles.

2.2. Importance of the Embryophytes in the History of Life

We can state, undoubtedly, that without embryophytes there would be no animals on land. It is now well established that land plants occurred and evolved prior to animals in terrestrial environments (see chapters “Chordata and Hexapoda” in the book “Evolution of Phylogenetic Tree of Life”, EOLSS Ed.. As the vegetal cover expanded and diversified, plants provided animals with progressively more and more food, shelter and convenient environments in which to grow, reproduce and... compete!

Today, there are around 280,000 identified species of embryophytes (Table 1). For 400 Ma they have been playing and still play a key role in the evolutionary history of life on land. They introduced photosynthesis to terrestrial environments, injecting additional oxygen into the atmosphere as they proliferated and diversified. Since their origin, land plants have been at the base of the terrestrial food chain as “primary producers”. Almost all the other living organisms on earth feed on organic matter produced by photosynthetic plants often through mycorrhizal symbioses with fungi, the oldest known dating back more than 400 millions years see chapter “Kingdom Fungi” in the book “Evolution of Phylogenetic Tree of Life”, EOLSS Ed

INFORMAL GROUP	DIVISION NAME	COMMON NAMES	Estimated no. of living species
BRYOPHYTES	Marchantiophyta	Liverworts	5200
	Bryophyta	Mosses	12,000
	Anthocerotophyta	Hornworts	300
PTERIDOPHYTES	Lycopodiophyta	Club mosses	1,200
	Monilophyta	Ferns, Whiskferns, Horsetails	11,000
	Cycadophyta	Cycads	160
SEED PLANTS	Ginkgophyta	Ginkgo biloba	1
	Coniferophyta	Conifers	630
	Gnetophyta	Gnetophytes	70
	Anthophyta	Flowering plants	258,000

Table 1. Estimated numbers living embyophyte species.

Moreover embryophytes are often the structural components of their natural habitats. The names of most of the Earth's “biomes”, such as “Tundra”, “Savanna” or “Forests (Figure 5) have been based on the type of vegetation of these regions. This reflects the

fact that plants are the dominant organisms in those biomes, structuring the spaces and the ecological interactions inside the living world, and in feedback interactions with the climate and soil.

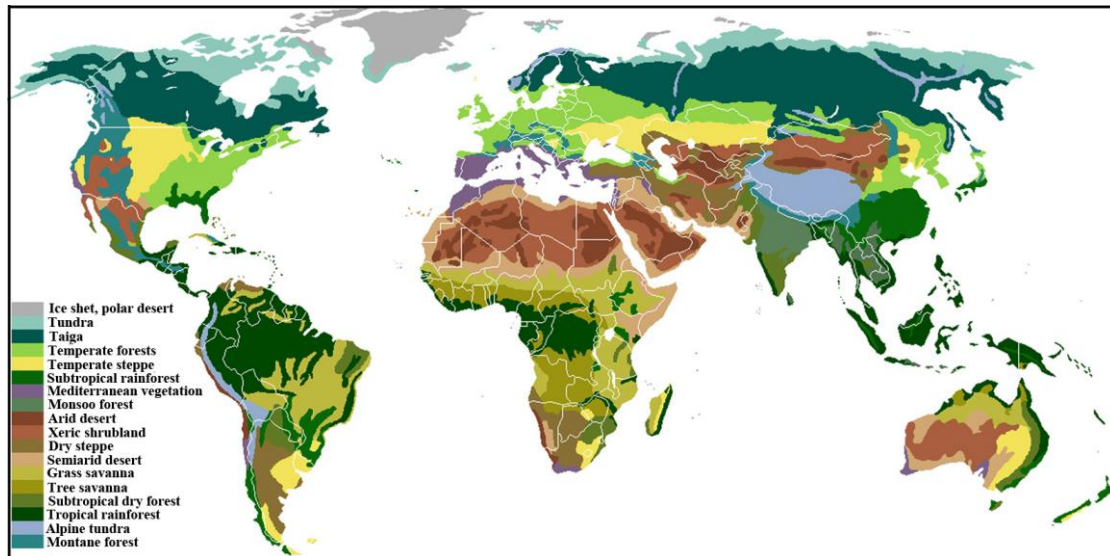


Figure 5. Map showing the distribution of the main biomes in the modern world (By Sten Porse -CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=3344457>).

2.3. Phylogenetic Emergence of the Embryophytes: The “Streptophytes” Concept

The most recent synthetic analyses indicate a basal split of green plants into a chlorophyte clade (Figure 2-I), encompassing most of the traditional “green algae,” and a streptophyte clade (Figure 1) associating some peculiar green algae lineages, transferred into a distinct unit of “charophytic taxa”, and the embryophytes (Figures 2-II, 6). The recognition of a “streptophyte lineage” began, when ultrastructural studies of cell division evidenced a major difference in the orientation of the spindle microtubules among species previously all classified within the “green algae” (McCourt 1995). More precisely, they were found to have a phragmoplast spindle perpendicular to the formation of the cell wall, formerly believed to be restricted to the embryophytes. Therefore, it appeared that this “phragmoplastic condition” occurred in the so-called “charophyte algae”, particularly Coleochaetales and Charales. Then the idea emerged that these aquatic plants were actually more closely related to land plants than to the other green algae. Later on, it became evident that some additional former “green algae”, such as Zygnematales, belong in this streptophyte clade. Furthermore, based on chloroplast-genome data, it appeared that despite the few similarities in cellular organization among the Zygnematales, Coleochaetales and embryophytes, a clade combining Zygnematales and Coleochaetales is in a sister group relationship with land plants. As a matter of fact, the comparative analysis of structural cpDNA features shows that the chloroplast genome has remained almost unchanged during the transition from charophycean green algae to land plants. Moreover, Coleochaetales and Charales share with land plants a fundamental trait of life history: they retain the diploid zygote on the haploid thallus following an oogamous fertilization of the oosphere by a swimming

sperm. In at least one species of *Coleochaete* this attached zygote stimulates the growth of a layer of parental cells, which form a covering entirely enclosing the zygote. The internal walls of these cells develop ingrowths like those occurring at the gametophyte-sporophyte junction of bryophytes and many vascular plants. These “transfer cells” likely act in nutrient transport from the haploid gametophyte to the diploid zygote which grows bigger on this “mother” gametophyte.

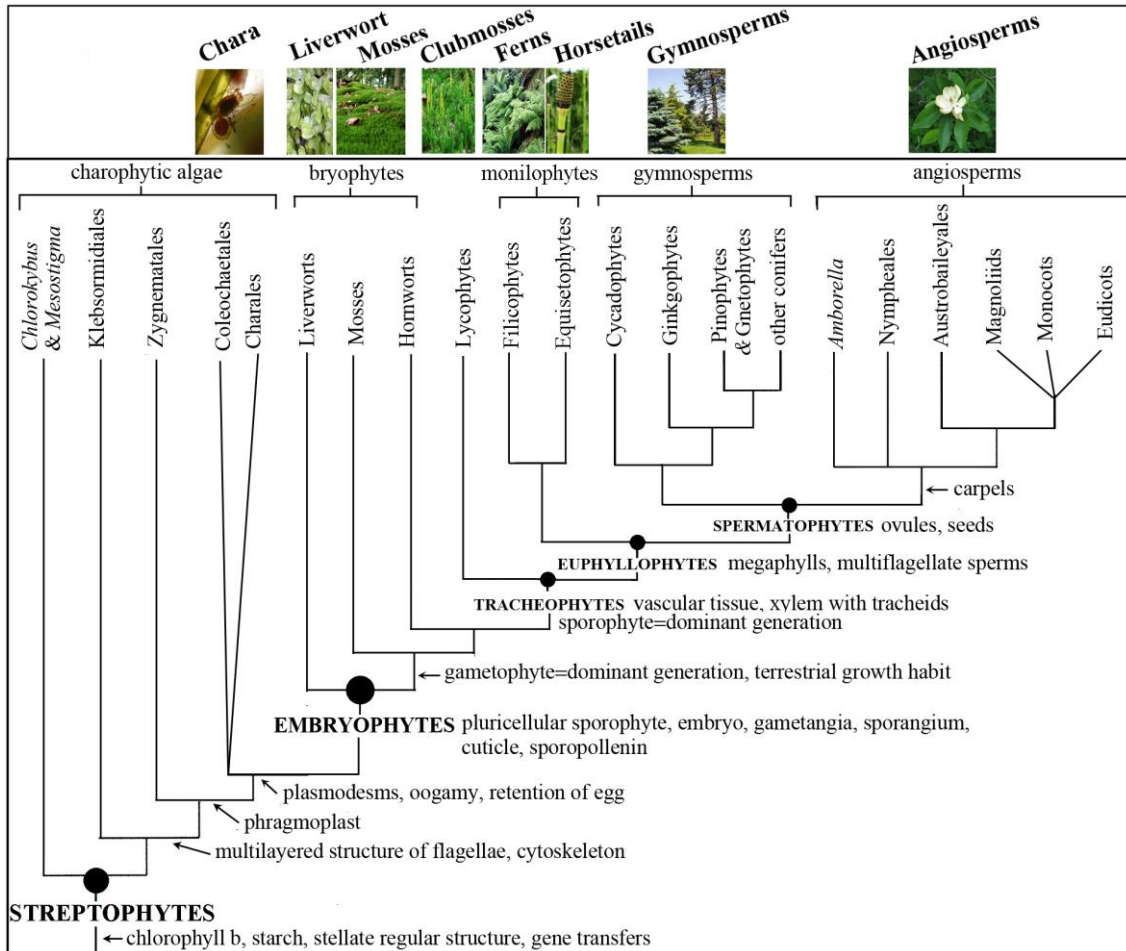


Figure 6. Embryophytes relationships among the streptophyte clade, (topology modified and completed after Qiu Yin-Long 2008).

2.4. Evolutionary Origin of the Embryophytes: The Phyletic Lineages within the Embryophytes

Numerous lines of morphological and molecular evidence now strongly indicate that the embryophytes represent a monophyletic group stemming from a single common ancestor (Figure 6). Based on other DNA evidence and morphology, vascular plants are now universally supported as monophyletic. Conversely, bryophytes remain a grade of three monophyletic lineages: mosses, liverworts and hornworts, the relationships to each other and to vascular plants remaining unclear. In such a phylogeny, the base of vascular plants appears as a “tetrachotomy” (Figure 8). Either liverworts or hornworts, long have been considered as candidate to be sister of land plants. Extensive

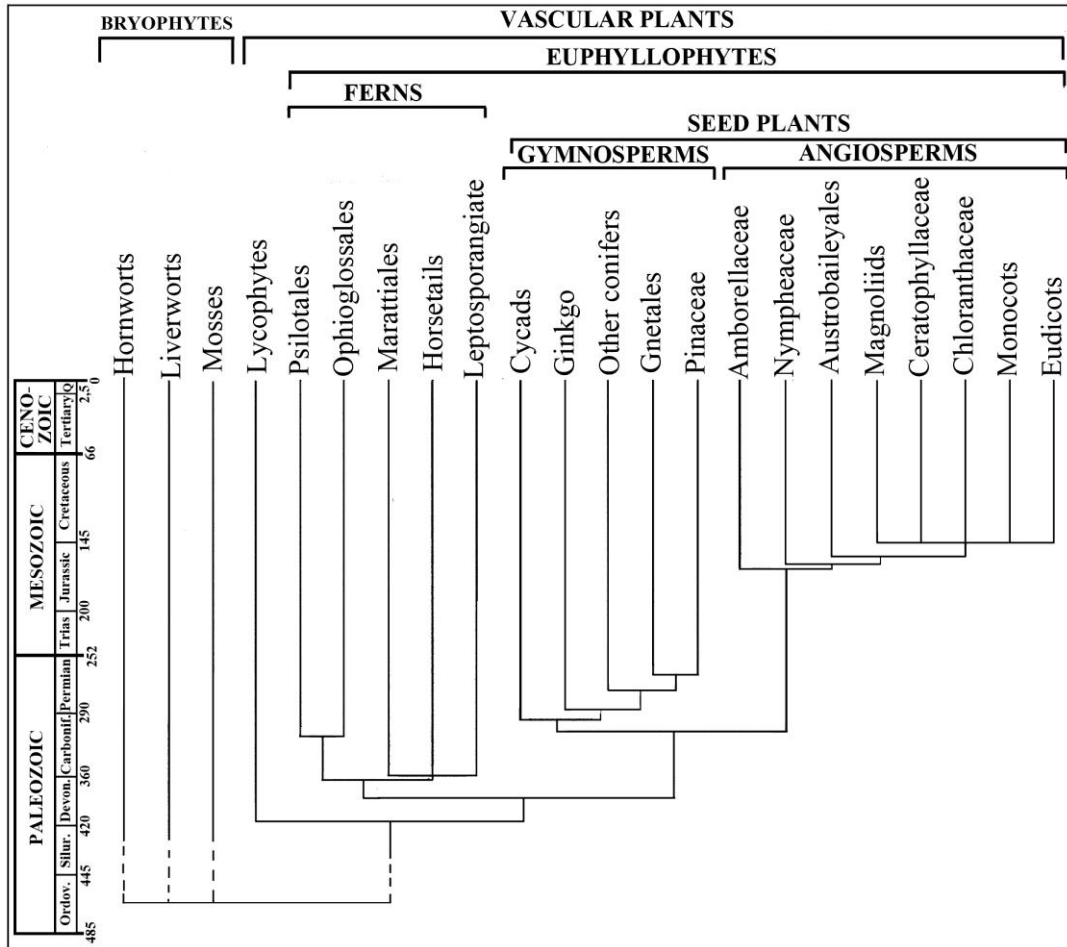


Figure 8. Chronogram indicating the divergence times phylogenetic relationships among major groups of living land plants (Topology follows Palmer et al., 2004).

2.5. Invasion of Land and Air by the Embryophytes: A Complex Evolutionary Success

The evolutionary success of the monophyletic group “Embryophytes” in almost all the terrestrial environments resulted from a complex “step by step” adaptive evolution from some freshwater plants that migrated from the aquatic to the terrestrial habitat (Figure 9, 10)

The settlement of plants in terrestrial environments is more an invasion of “air” than of the terrestrial substratum (Niklas, 1997). Plants became able to survive, grow and reproduce in the terrestrial environment thanks to a set of adaptive innovations. The main adaptation mediating this step from ancestral aquatic to air habitat, was the ability to resist or tolerate desiccation by sun and wind. The acquisition of this ability implies numerous morphological, anatomical and physiological transformations. These include the following. 1) Morphological features that protect against desiccation. Among these are a protective epidermis made of a single layer of cells covered by a “waterproof” cuticle, microscopic holes (stomata) in that epidermal surface allowing for gaseous exchange with the atmosphere, and specialized cells (guard cells) to regulate the loss of

internal water and the direct communication between the external atmosphere and the plant's internal moisture (Figure 9). 2) Similarly, the spores important for reproduction, which are disseminated through the air by wind, became desiccation-resistant by the addition of a "sporopollenin-coated" external wall (see Section 2.6). 3) In terrestrial environments, maintenance of the water supply necessary for the internal physiology of a plant also becomes a "limiting factor", something not faced by plants living in an aquatic environment. As a matter of fact, except for bryophytes, such as mosses, living prostrate on the moist substrate, erect vascular plants need to extract the water from the soil and diffuse it into and throughout the whole plant. This implies the evolution of a complex morphological and physiological system to acquire water, including water absorbing organs (roots), and specialized cells to conduct that water actively from the root system to the aerial parts of the plant.

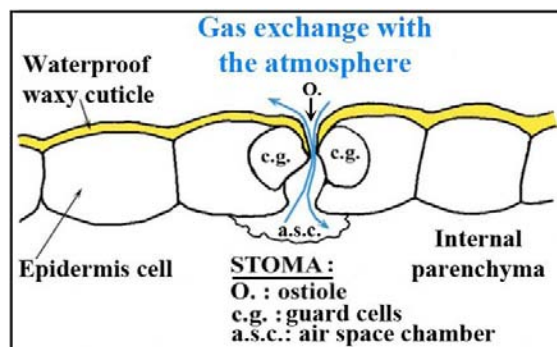


Figure 9. Organization of a stomatiferous epidermis.

These first adaptive innovations concerned exclusively the vegetative plant body. But vegetative acclimatization is not enough to secure long-term persistence of plants on land. It must be combined with adaptations that ensure also a genetic continuity of each species through time. As stated by Niklas (1997), an appropriate ecological definition of "land plants" would be: "*any photosynthetic eukaryote that can survive and sexually reproduce on land*".

The reproductive modalities of the bryophyte-like first land plants remained the same as their aquatic algae "ancestors" *i.e.*: "external zoidogamy". The fertilization process implies that the spermatozoid (male gamete) was disseminated on the soil by the germination of the microspore, and then had to swim in the water of the external environment to reach the oosphere (female gamete) in the bottom of an archegonium on the female gametophyte (!). This kind of fertilization persists in all the non-vascular (bryophytes *s.l.*) and vascular (lycophytes and ferns) "seed-less" plants (Figures 10, 16). But such a chancy process explains why vegetative cloning (asexual multiplication) is widespread in these lineages of seed-less plants.

Then, as early as Late Devonian, the emergence of the first "ovuliferous" vascular plants, like *Elkinsia* (Figure 38 C), one of the first known "seed-ferns" (so-called because they combine the characters of fern-like foliage and reproduction by seeds) appeared. Male microspores then, by definition, became pollen grains, and were wind transported, directly to the ovule (megasporangium with a single functional large spore containing the female gametophyte) (Figure 38 A).

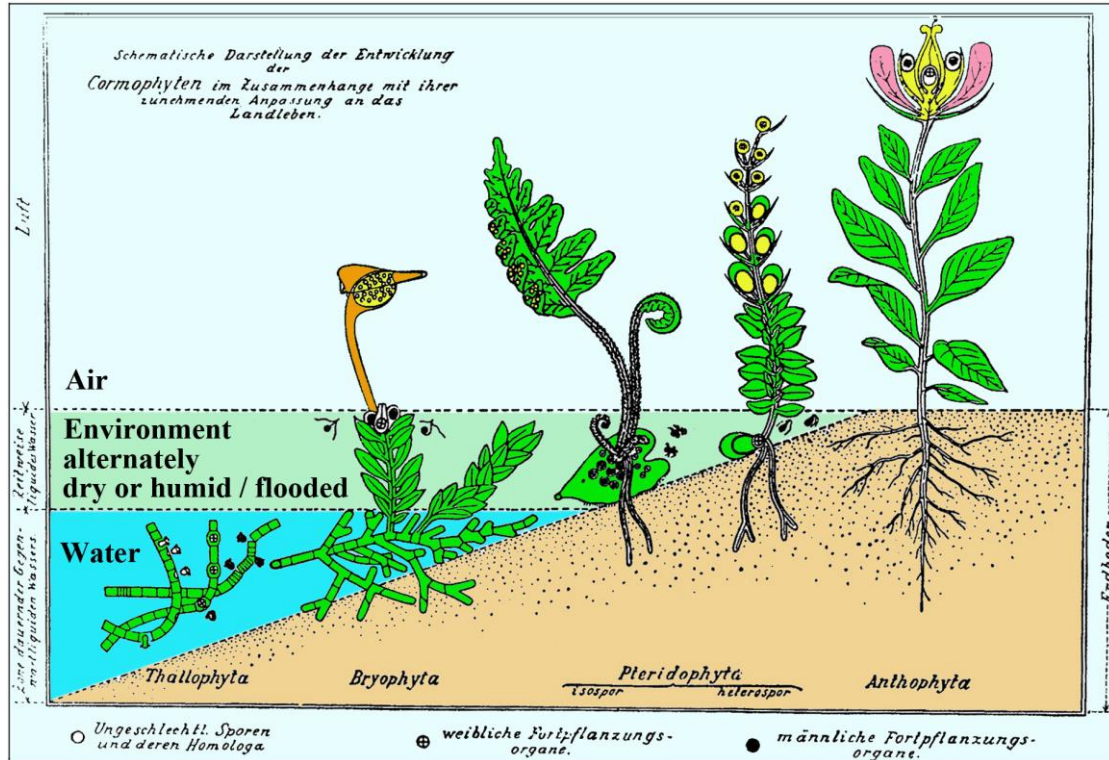


Figure 10. The evolutionary pathway by which plants invaded the land (from Richard Wettstein, 1901).

After this new evolutionary step, two main processes of fertilization appeared in seed plants.

1) Fertilization that still results from swimming sperm, but in a liquid produced by the ovule, filling up a tiny internal cavity: the “pollen chamber”. This process, which implies a “haustorial pollen grain” (one that attaches to the enclosed female tissues and releases sperm), is referred to as “internal zoidogamy”. It was widespread among Carboniferous-Mesozoic pteridosperms and gymnosperms. This strange modality was discovered in 1896 in two extant plant groups, *Ginkgo biloba* and Cycadales, by the Japanese botanists Hirase and Ikeno, and in Carboniferous fossil pteridosperms by the French paleobotanist Bernard Renault (see Sections 6.1.1 and 6.1.2).

2) The final step of this evolutionary trend led to overcoming totally the necessity for any liquid (external or internal) for fertilization. This is accomplished through a process known as “siphonogamy”. In this system of fertilization, the male gametes have lost their flagellae and can no longer swim. They are carried into the ovule up to the female egg by a narrow tubular structure that grows from the pollen grain, known as the “pollen tube”. This modality characterizes all seed plants today, other than the ginkgophytes and cycads, thus the two most conspicuous groups, the Conifers (Figure 49 A) and Angiosperms (Figures 59, 60).

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Biographical sketch

Jean Broutin: after getting a PhD of “Natural Sciences” of the Paris Faculty of Sciences (1973), received his State Doctorate of “Natural Science” at the University Paris 6 France (1981) and was appointed Professor as head of a research team “Palaeobiodiversity, Systematics and Evolution of the Embryophytes” in the same University (1993). He has been then appointed as Head of the Master degree of “Biology of the Populations and Ecosystems” (1995-2004) and for the creation of a New Master degree courses of “Systematics, Evolution and Palaeontology”(2004-2008). He supervised 10 Doctoral

Dissertations and numerous Master Diplomas of Botany, Palaeobotany and Palaeoenvironment. He has published several dozens of scientific papers dealing mainly with Paleobotany, Paleophytogeography and environments, mostly in international journals. He was involved, as leader or collaborator, in various national and international collaborative research-programs and projects promoted by the Paris 6 University, the CNRS and the National Science Foundation of China. He was therefore able to participate in numerous fieldtrips researches and collected fossil plants in various countries to be studied in his Paris laboratory in collaboration with the concerned foreign scientists.

Since 2012 he is Professor Emeritus at the University “Pierre and Marie Curie” Paris 6 and still active as co-director of PhD students in the framework of the research project “*Recovery of fossil plants after the Permian-Triassic Boundary mass extinction in Western Guizhou and Eastern Yunnan, South China*” - NSFC n° 415/2005 (01/01/2016-30/12/2019: 10 papers published in international scientific journals).