5

COLONISATION AND RISE OF EARLY LAND PLANTS

The colonization of land by plants was one of the most significant evolutionary events.

By early Silurian (~430Ma) plants that were permenantly adapted to a terrestrial or water deficient habitat (land plants) had evolved.

However, before such colonization could occur, major changes were necessary to enable growth of plants outside the aquatic environment. Such changes included :-

a. Environmental changes.
b. Biological changes – such changes enabled successful colonization of land by plants.

[A] ENVIRONMENTAL CHANGES.

(During Cambrian & Ordovician)

Land surfaces were available for colonization for plants, however during Cambrian & Ordovician (543 - 443 Ma), other essential environmental prerequisites including :-

(a) Formation of sizeable & stable near shore environments.
(b) Development of soils.
(c) Development of atmospheric & climatic conditions suitable for land plant survival.

I. Formation of new sizable & Stable near-shore environment.

i) During the Cambrian & Ordovician (543 to 443 Ma) a combination of climatic changes & changing continental configurations resulted in widespread flooding of the continental plates.

ii) This was followed by a period of glaciation at the end of Ordovician (440Ma) which led to a dramatic reduction in sea level & exposure of large areas of continental shelf.

– This led to formation of land masses with near shore environment convinient for establishment of land plants.

II. Formation of soils

Processes important for the early development of soils included :-

(a) Input of atmospheric element in the form of N, P, Fe – either by environmental effect or by microorganisms.

(b) Weathering of surface by acid rain and organic acids produced by early microbial organisms & lichens.

Geological evidences suggest that by the end of Ordovician (~440 Ma) well ~~developed~~ established soil profiles were developed.

III. Development of Suitable climatic & Atmospheric conditions :–

1. Global climates became much more variable & certain regions became cool & moist by late Ordovician (458 ~ 443 Ma).

2. These climatic changes are attributed to two main factors :-

a) Reduction in atmospheric CO_2 leading to reduced greenhouse effect &

b) The formation of glaciers at the South Pole.

– These conditions led to formation of suitable climatic and atmospheric conditions for origin of land plants.

BIOLOGICAL CHANGES FOR PLANT TERRESTRIALISATION

The transmigration of plants to land occured probably from Middle Ordovician to early Silurian (470 – 430 Ma).

From the middle Ordovician to early Silurian evidence started to emerge in the plant fossil record for the following changes that enabled the transmigration to land.

(a) Development of specialized cells for water & nutrient transport.

(b) Various measures to protect plant against dessication.

(c) Development of structures for mechanical support.

(d) Development of reproductive mode that did not depend predominatly upon external water sources

– All these morphological & anatomical changes were prerequistes for the establishment of plants in terrestrial habit.

I. Reduction of Dependence on water for reproduction :-

(a) Elaboration of sporophyte with simultaneous reduction of gametophyte

Gametophytic stage is dependent on availability of water since water is essential for the survival of the gametophyte, and transfer of sperm to egg & initial growth of the sporophytic embryo. – thus in constant moist environment, with little dessication stress – the gametophytic phase was selected.

Elaboration of the gametophytic phase is thus seen in predominantly aquatic plants (algae) & members who ~~need~~ are amphibians and need water to complete their lifecycle (bryophytes).

Establishment and elaboration of the sporophytic phase would have decreased the necessity for water, since neither the production nor the dissimenation of spores is dependent on water.

Thus, land habit ie dessicating environments would have imposed intense selection pressure in favour of amplification of the sporophytic generation in place of gametophytic generation.

Hence, the sporophytic generation is elaborated in tracheophytes which transmigrated to land – in contrast to predominant gametophytic phase as in algae (aquatic) & bryophytes (amphibian – with predominant gametophyte, hence restricted to damp, moist areas.

(b) <u>Production of spores instead of gametes</u> :-

Production of spores (by sporophyte) instead of gametes (gametophyte) ensured that reproduction becomes less water dependent.

Fossil evidence in the form of tetrahedral arrangement of spores has been reported in Late Ordovician (~450 Ma) and fossils of single spores have been reported in Early Silurian (~430 Ma) – the two form are indicative of elaboration of the sporophytic phase and that of meiotic division.

(c) <u>Elaboration of reproductive system which is not dependent on water.</u>

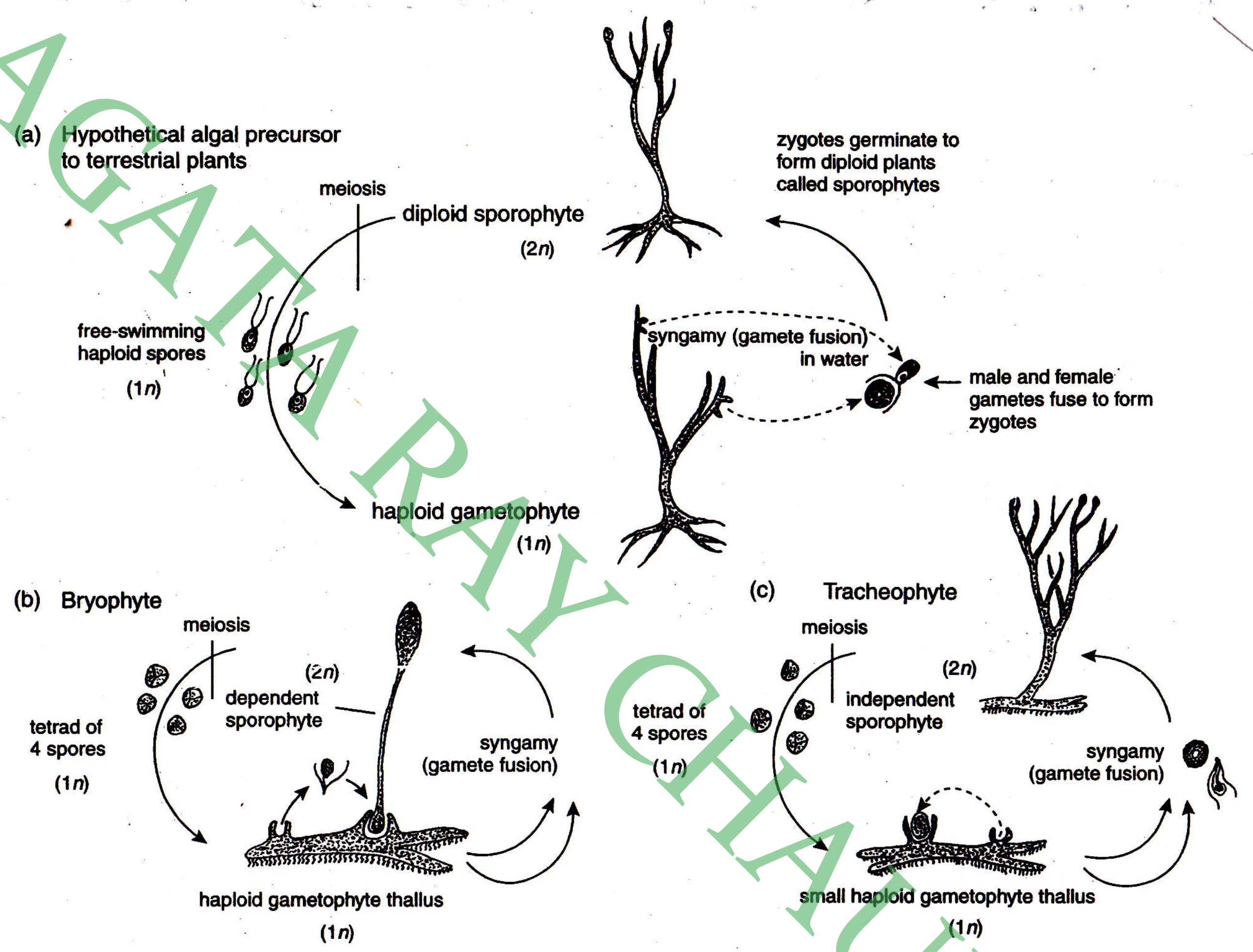


Figure 3.6 Diagram of simplified plant life cycle, showing alteration of generation phases. (a) Simplified diagram to indicate the alteration of two phases of generation in algal reproduction; (b) the cycle with an amplified gametophyte generation—most bryophytes follow this mode of reproduction; and (c) the cycle w an amplified sporophyte generation—all vascular plants follow this mode of reproduction (redrawn from Price, 1996).

II. Protection against dessication:-

Migration of plants to land habit resulted in their exposure to air & sunlight - which needed the plants to develop a mechanism to avoid dessication.

The following changes occured to ensure this protection:-

(a) Development of cuticle that covers & impregnates the walls of epidermal cells. Cuticle is a layer of wax & insoluble lipid polymers that covers & impregnates the walls of the epidermal cells to reduce water loss, & is present on the aerial part of every living land plant.

Fossil evidence for sheets of cuticle appear in early Silurian (~430 Ma).

(b) Development of sporopollenin: Development of spores with sporopollenin ensured protection against dessication & long distance dispersal by wind.

Sporopollenin is found on the walls of most extant pollen & spores in both vascular & nonvascular plants - is a complex polymer that provides dessication resistance, robustness & protection from UV radiation. This evolution of dessication resistance spores were extremely important to the terrestrialization process. It enabled long distance spore dispersal by wind & a means of establishment of isolated communities far into continental interiors.

(c) Origin of Stomata:- Formation of cuticle, would have protected against dessication, it also would have prevented the flow of gases (CO_2 & O_2) into & out of the plant. Origin of stomata, approximately 408 million years ago (Late Silurian & early Devonian) ensured a regulated entry & exit of gases & water.

Development of Specialized cells for water & nutrient uptake

Aquatic plants has little requirement for specialized system to distribute water, solutes, photosynthetic products – since all cells are a short distance from source of water & nutrients.

However with terrestrialization – early land plants needed specialized conducting tissue to transport food & water – specially if vertical growth was involved.

Long distance source of water and nutrients required specialized conducting tissue.

The origin & evolution of water conducting tissue system i.e vascular tissues originated & evolved as follows :-

(a) Kenrick & Crane hypothesized that elongated cells which are organized into tissue along the length of the plant – were part of the water conducting tissue – water was transferred from base to erect portion through this water conducting cells.

(b) Some of the water conducting cells in early fossils had cell walls with thickened rings containing lignin.

(c) From ~430 Ma (early Silurian) various tubes appear in fossil records. Some were narrow (8-20 μm diameter & 50 μm long) & smooth while others were longer (~200 μm) with thickening.

(d) Thickening occurs differentially to avoid cell wall being collapsed. Thickening were helical thickening, annular reticulate thickening & scalariform pittings.

(e) In 380 Ma old rocks – advanced water conducting cells – tracheids were observed. Tracheids are long, thin, tapering cells that have :-

1) A thickened, lignin containing secondary cell wall in addition in a cellulose based primary cell wall &

ii) Pits in the sides and ends of the cell where the secondary cell wall is absent, where water can flow efficiently from one tracheid to the next.

. The secondary cell wall gave tracheids the ability to provide better structural support, but water could still move through the cells easily because of the pits.

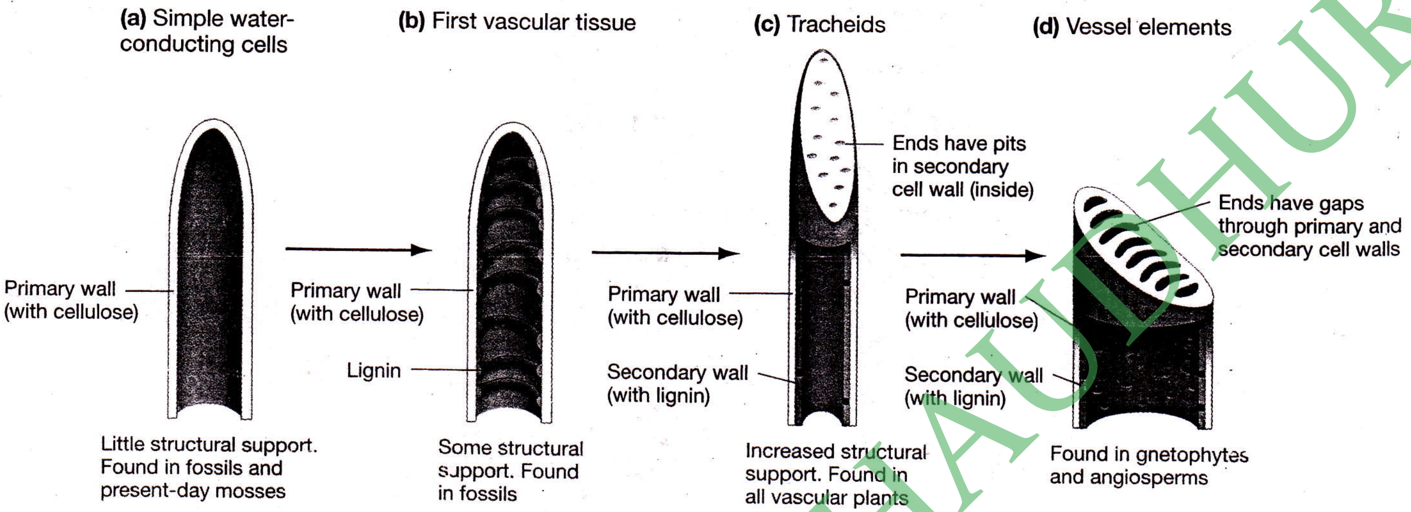


FIGURE 30.9 Evolutionary Sequence Observed in Water-Conducting Cells. According to the fossil record and the phylogeny of green plants, water-conducting cells became stronger over time due to the evolution of lignin and secondary cell walls. Efficient water transport was maintained through pits where the secondary cell wall is missing, or gaps where both the secondary and primary cell wall are absent.

✔**QUESTION** Biologists claim that vessels are more efficient than tracheids at transporting water, in part because vessels are shorter and wider than tracheids. Why does this claim make sense?

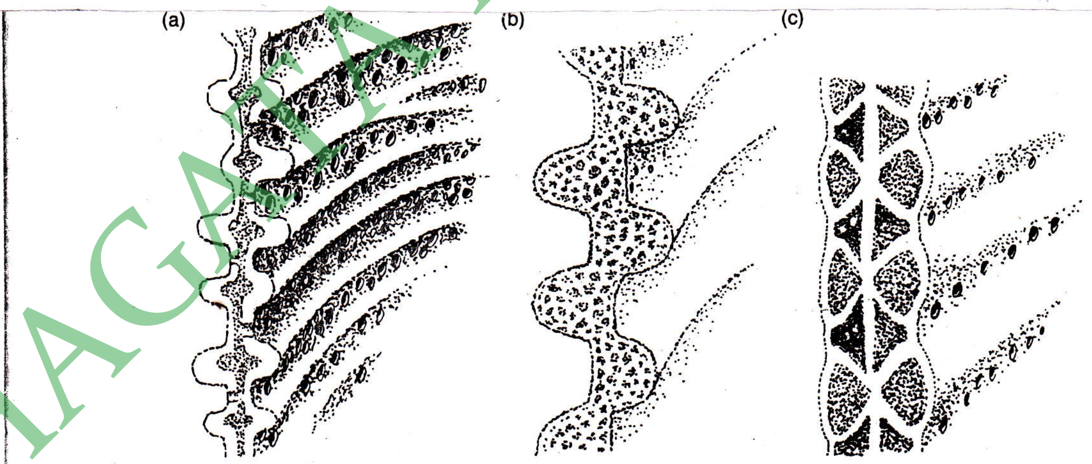


Figure 3.9 Cell wall structure of early tubes and tracheids in the fossil record (redrawn from Kenrick and Crane, 1997a). Three types of tracheid have been distinguished according to their cell wall construction, as follows: (a) G-type cell wall with annular–reticulate thickenings; (b) S-type cell wall with helical thickenings that appear to combine certain features of tracheids (e.g. lignified thickenings) and moss hydroids; and (c) P-type cell wall with scalariform pittings (pits in the secondary cell wall that are elongated transversely and parallel to each other).

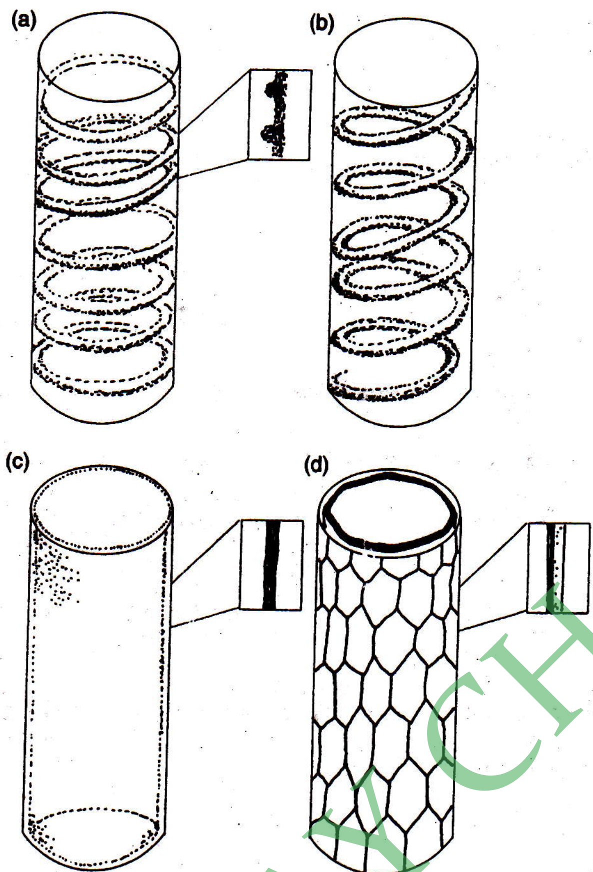


Figure 3.8 Structure of early fossil records of tubes and tracheids and comparison to extant plants (redrawn from Taylor and Taylor, 1993). (a) Tracheid of extant vascular plant. (b) Silurian tubes (*c.* 440 Ma) with helical thickenings on the inner surface. These tubes have measured up to 200 μm in length. (c) Extant moss hydroid with smooth inner surface. (d) Tube from fossil *Aglayphton major* (up to 50 μm in length).

Mechanical Support :-

Adaptation necessary in the process of terrestrialization was a means of staying upright and providing mechanical support to the plant.

The following adaptations occurred during terrestrialization :-

1. Biomechanics of staying upright for attaining maximum surface area of light reception & gaseous exchange resulted in vertical growth.

2. The best biomechanical solution was to allow a plant to grow longitudinally with only minor reduction to volume to surface area ratio - resulted in a large, wide, flat top and a small stem - best shape for such a stem would be a cylinder.

3. Calculations suggest that if flexural rigidity is to be maintained/maximized, stems must be solid &/or thick walled & as broad as possible.

4. Evidence from fossil records indicates that the earliest land plants had short wide stems with a photosynthetic 'rind' just below the surface & hydrostatic tissue (parenchyma) in centre - which was hydrostatic.

5. However, to attain greater height - than a few centimeters - it would have been necessary to have some specialized mechanical tissue - (cortical tissue, collenchyma) between the photosynthetic rind & hydrostatic core.

6. Greater heights were attained by compartmentalization of functions of plant body into those for photosynthesis & those for mechanical support.

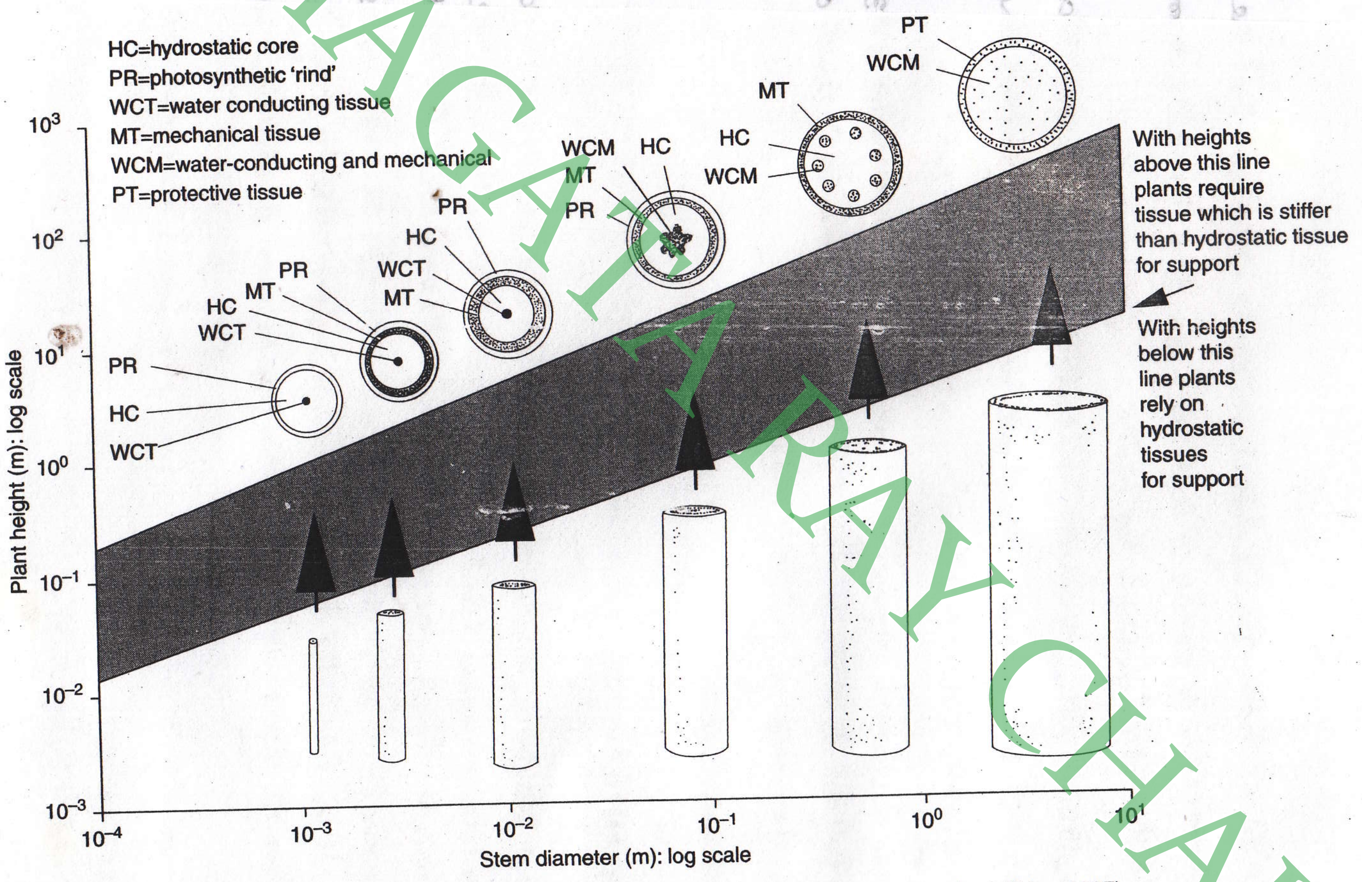


Figure 3.10 Relationship between stem diameter and stelar construction (after Niklas, 1997).

Anchoring Mechanism :-

Early land plants also needed to aquire a system to anchor them to the ground and enable them to obtain the mineral elements necessary for nutrition and water from soil.

1. Root system developed around 408 million years ago (early Devonian) from the Lower plant parts covered with mud.

2. This early rooting system were relatively undifferentiated from aerial parts of the plant.

In summary - evidence from plant fossil records suggest that the period between late ordovician & early silurian was the time of a major innovation - the transmigration to land.

The terrestrialization process included the evolution of a reproductive system that was not primarily dependent on water & various mechanisms to enable plant growth outside of an aquatic environment.

All these features appeared between 470 Million years & 430 million years ago - followed closely by evidences of ~~plan~~ land plant organs from early devonian (~408 MYa).

EARLIEST LAND PLANTS :-

Early land plants ie vascular plants started to appear in early devonian. Evidence for entire vascular land plant organs - like stem & reproductive structures appear in fossil records in early Devonian (~408 Ma).

Such macrofossils (rather than microfossils of single tubes, tracheids spores etc) have been identified from enough localities to suggest a vegetation of small structured vascular plants was established in many continents.

Six common early land plants found in fossil records are :-

a) *Cooksonia*

b) *Aglaophyton major*

c) *Rhynia gwynne-vaughanii*

d) *Zosterophyllum divericatum*

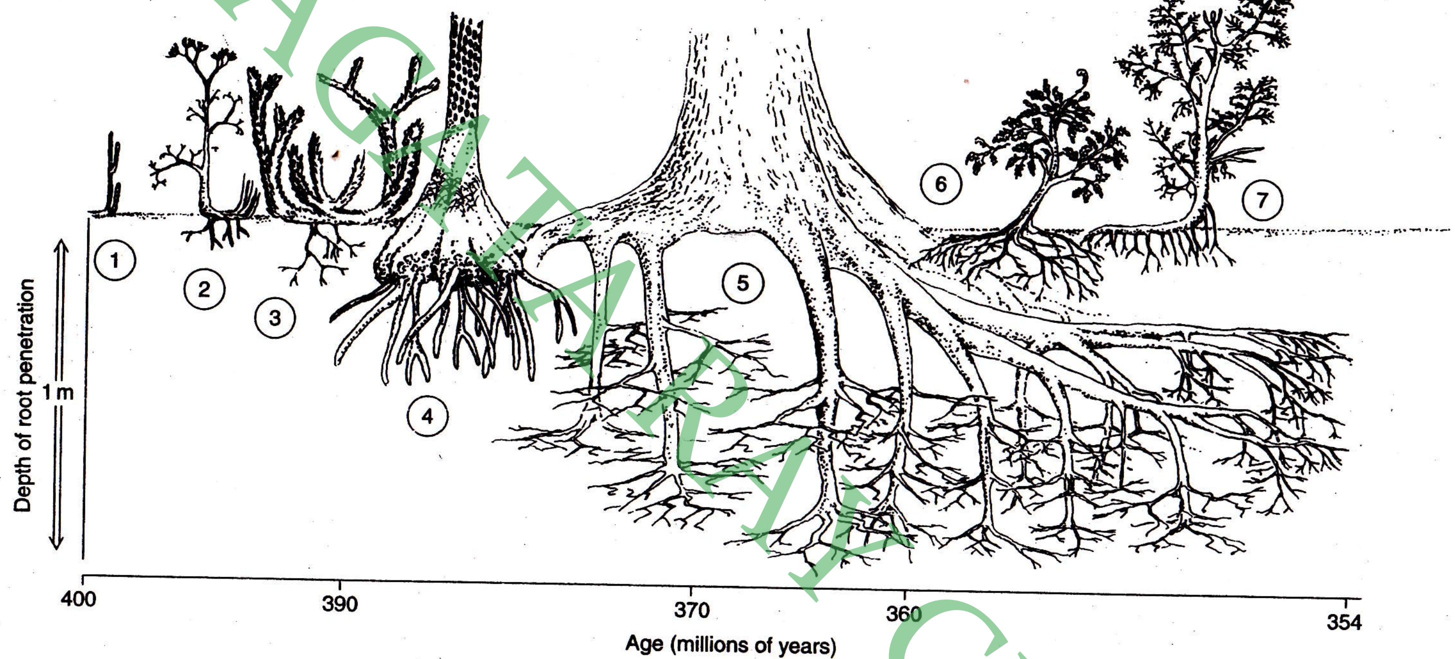


Figure 4.6 Relative sizes, shapes, and penetration depths of root systems during the early, middle, and late Devonian (~400–354 Ma; age axis is not drawn to scale) (redrawn from Algeo and Scheckler, 1999). Representative plant types are as follows: 1, Rhyniopsida, e.g. *Aglaophyton*; 2, trimerophytes, e.g. *Psilophyton*; 3, early herbaceous lycopsids, e.g. *Asteroxylon*; 4, early tree lycopsids, e.g. *Lepidodendron*; 5, progymnosperm, e.g. *Archaeopteris*; 6, early gymnosperm, e.g. *Elkinsia*; and 7, filicopsid, e.g. *Rhacophyton*.

e) *Baragwanathia longifolia*

f) *Psilophyton dawsonii*.

Recent cladistic studies indicate that the early plants can be divided into ~~three~~ the following groups.

a) Polysporangiophytes: Basal clade incorporating features of both nonvascular & vascular plants — branching sporophyte & independent gametophyte (*Aglaophyton*)

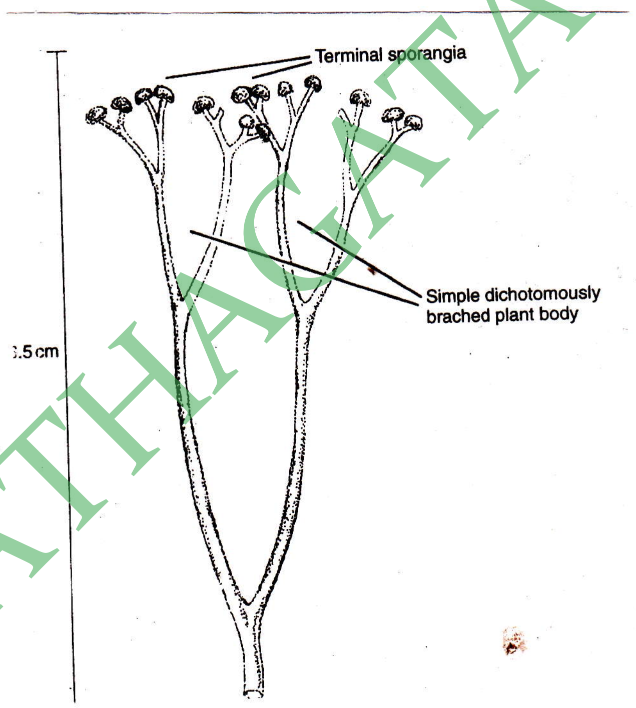
b) Tracheophytes: Early & extant plants which had well defined tracheids. — the tracheophytes can be divided into two clades:-

b1) Rhyniopsida :- S-type tracheid present. eg. *Rhynia*, &

b2) Eutracheophytes.

c) Eutracheophytes :- A nested group within tracheophytes - includes all vascular land plants with characteristic ~~flora~~ of present day flora. (*Zosterophyllum*, *Baragwanathia*)

This group again split into two clades.



Cooksonia

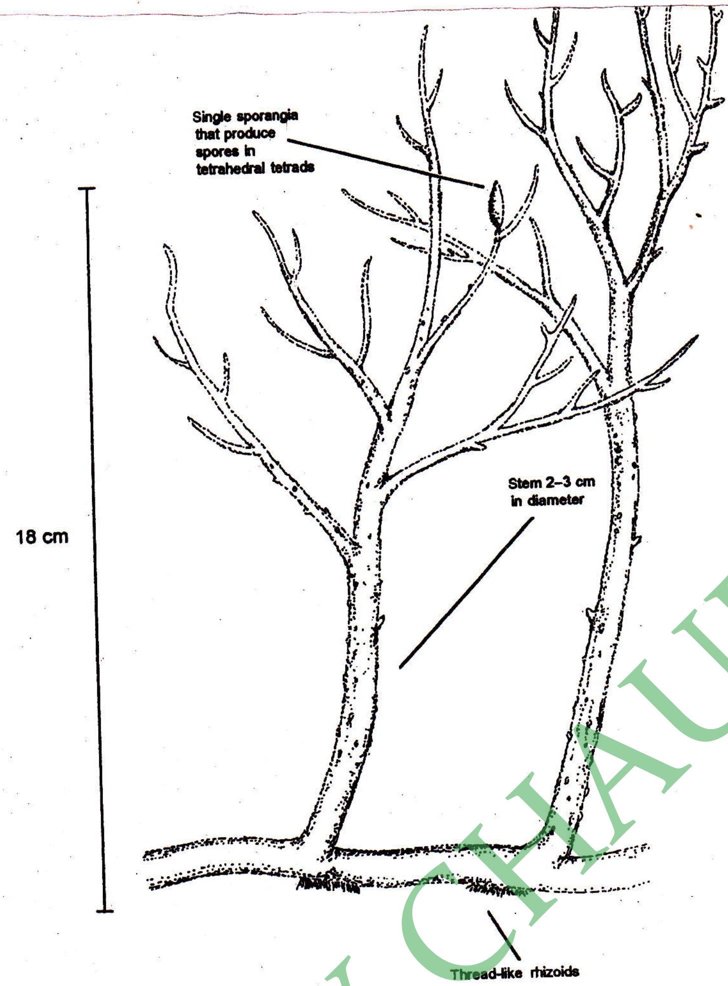
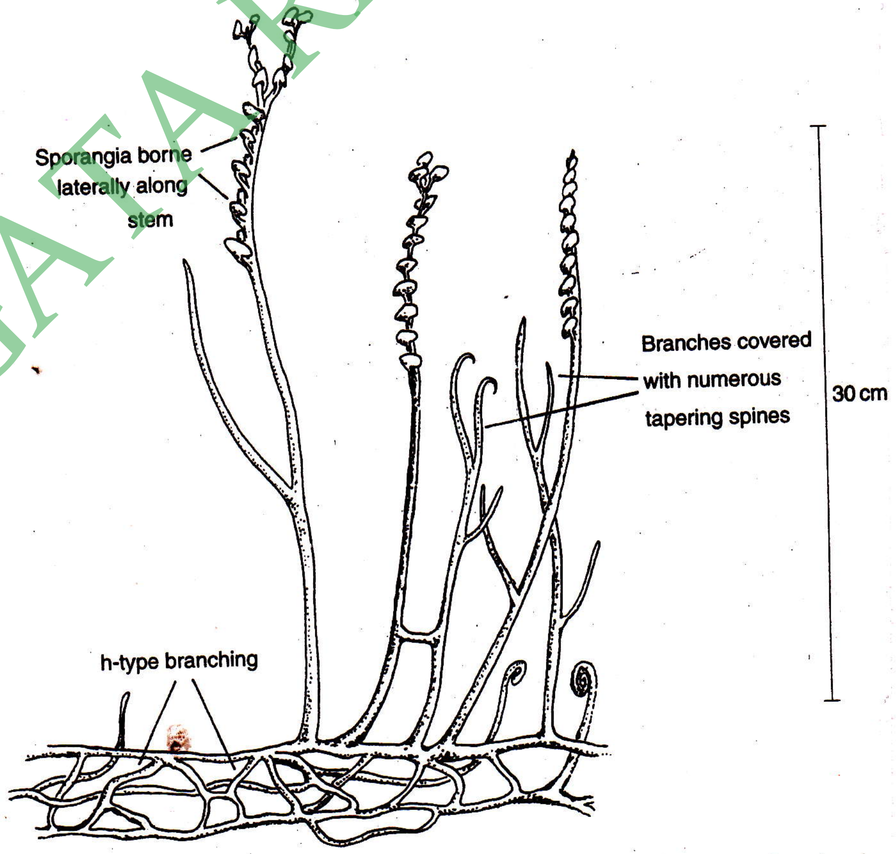


Figure 3.14 Reconstruction of fossil *Rhynia gwynne-vaughanii* (redrawn from Kenrick and Crane, 1997a).



igure 3.15 Reconstruction of fossil *Zosterophyllum divaricatum* (redrawn from Gensel and ndrews, 1987; Bell, 1992; White, 1990).

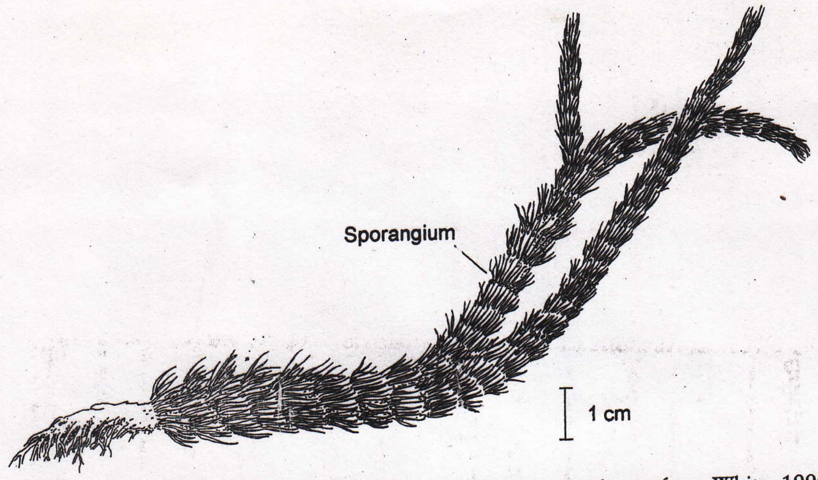
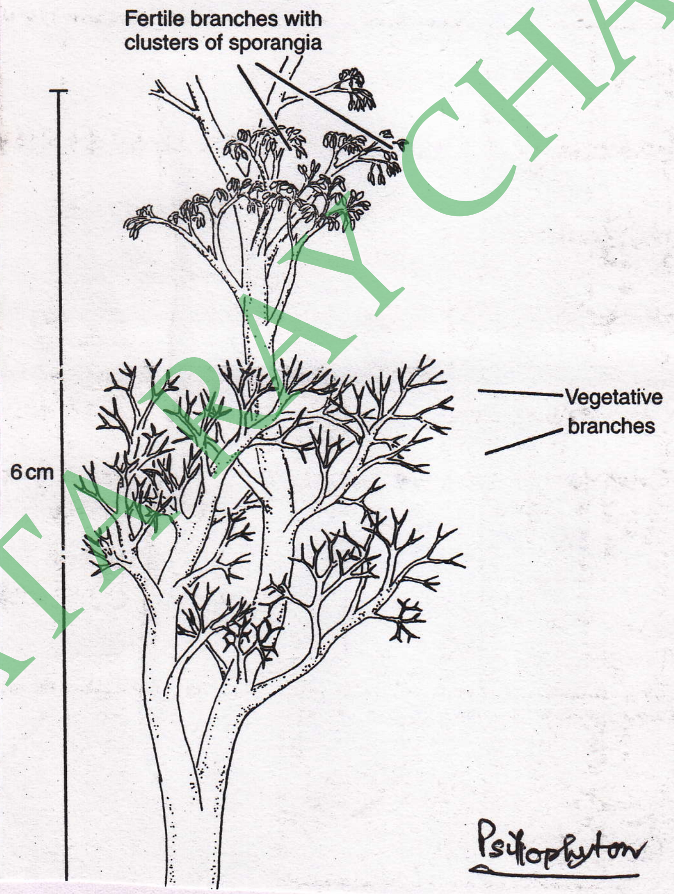
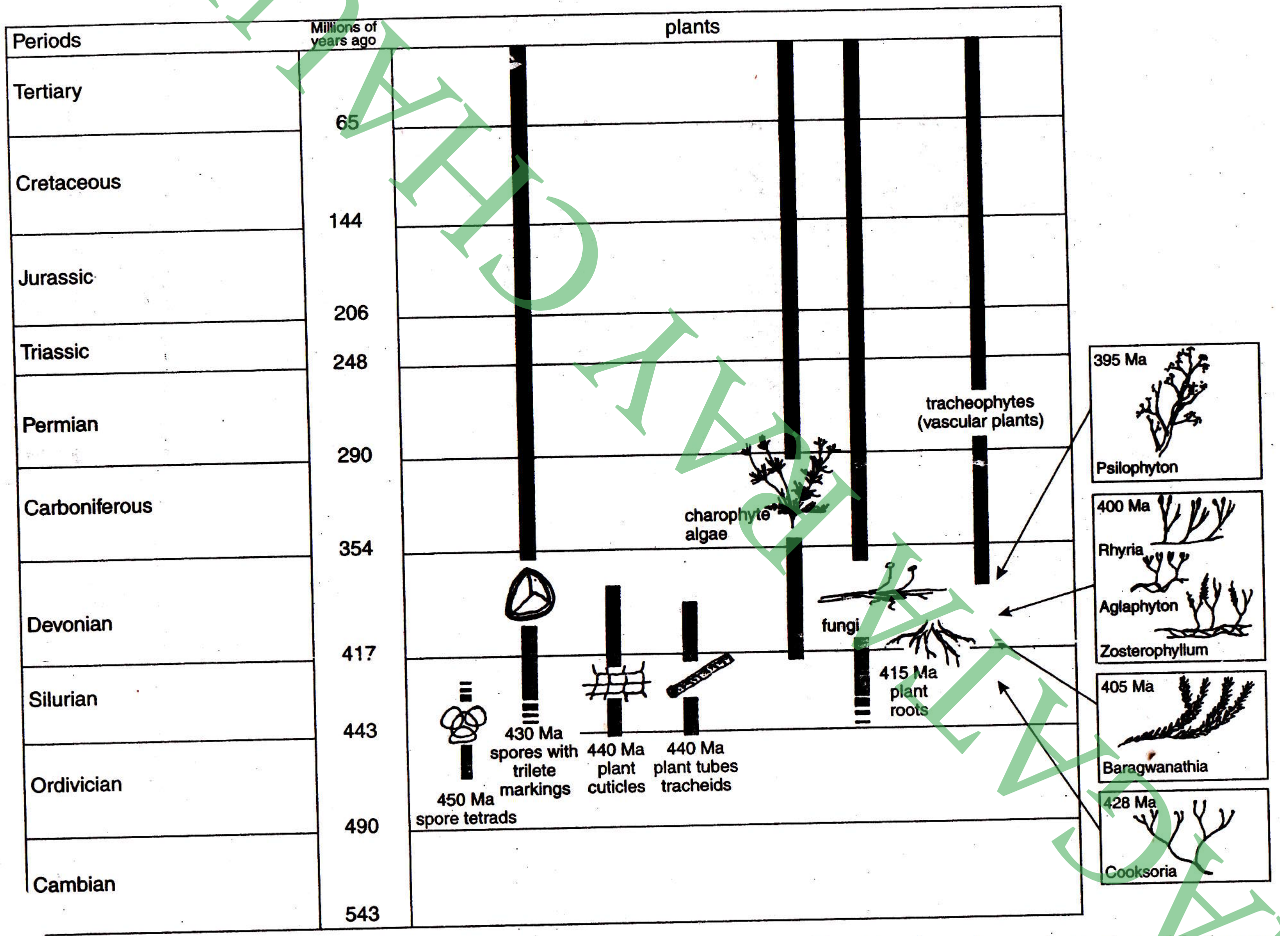


Figure 3.16 Reconstruction of fossil *Baragwanathia longifolia* (redrawn from White, 1990).





t appearance in the plant fossil record of innovatio.ıs leading to the colonization of land by plants. Approximate time of first appearance of spore ith trilete markings, plant cuticles, plant tubes and tracheids, and plant roots (redrawn from Gray and Shear, 1992).

EVOLUTIONARY TRENDS

Various lines of evidence, including biochemical, morphological & molecular analysis of extant groups, in combination with evidence from fossil record, indicate that :-

a) Green algae to Land Plants

All land plants evolved from green algae (Chlorophyta) and in particular the Charophyceae.

b) Nonvascular to Vascular plants

i) Tracing the evolutionary links between vascular & nonvascular plants through geological, morphological & molecular evidence suggest that all land plants (vascular & nonvascular) evolved from a common ancestor - probably the green algal group

ii) The land plant lineage then split between the liverworts & the other land plants.

iii) ~~Finally a split~~. A second split occurred between the hornwort ~~liverworts~~ & all other land plants.

iv) Finally a split occurs between the mosses & the two vascular clades Lycophytes & Euphyllophytes.

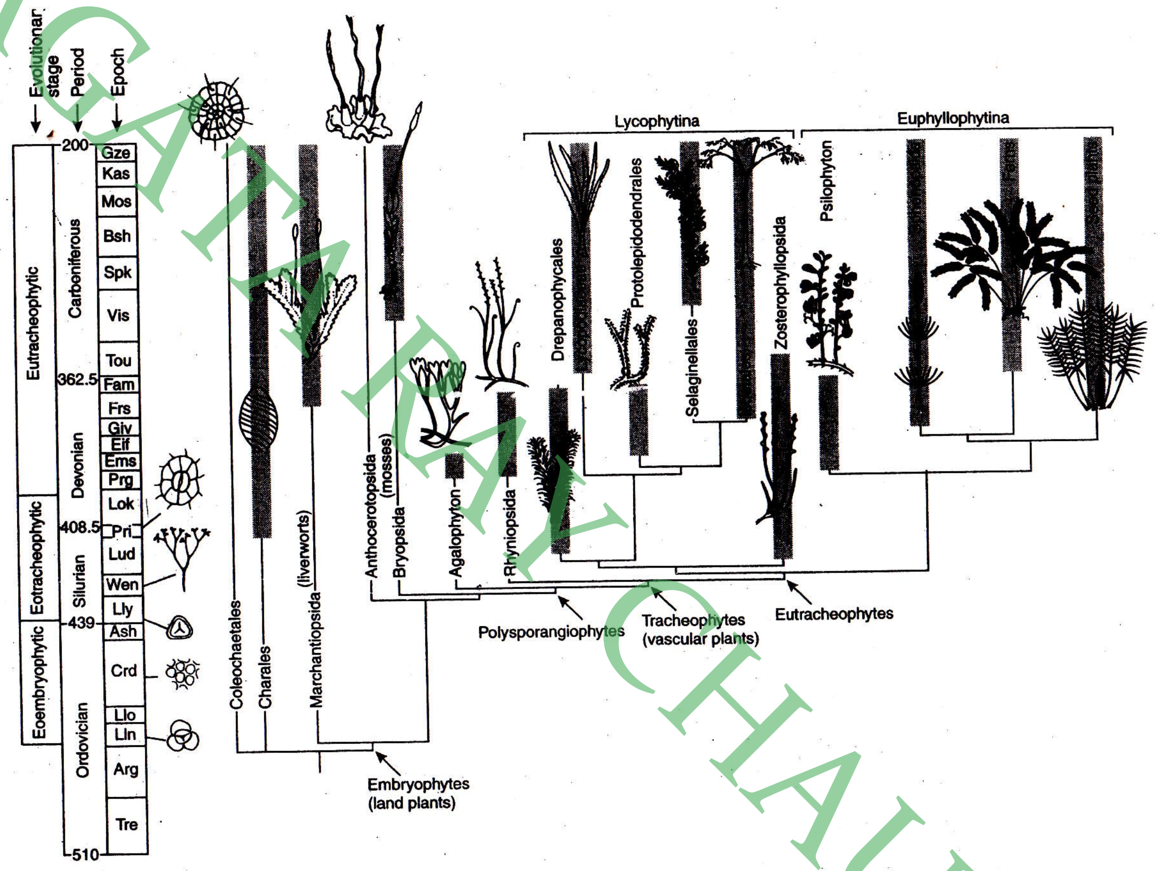


Figure 3.18 Phylogenetic relationship between extinct and extant early plants (based on cladistic analyses of morphological traits) (redrawn from Kenrick Crane, 1997b)