CHAPTER 2

Early Land Plants and the Salient Features of Vascular Plants

ONE of the most significant events in the long evolutionary development of the plant kingdom was the origin of the first land plants. These organisms, which in all probability arose from some ancient group of green algae, were extremely simple in organography. For example, the ancient plant *Rhynia gwynne-vaughanii* was a rootless, leafless plant that was low in stature, with a simple and primitive vascular system and simple reproductive structures located at the tips of the aerial branches.

A land flora was possible only after the detrimental effects of solar radiation, the ultraviolet (UV) radiation, became shielded by an ozone layer in the atmosphere. During the exceedingly long Precambrian and Cambrian Eras (Chapter 1, Table 1-1) little oxygen was evolved from photosynthesis, and hence little ozone was produced. Aquatic algae would have been shielded from the UV effects by immersion. With an increasing density of algae, more oxygen would have been formed and an ozone layer created.

In addition to formation of the protective ozone layer, there was the evolution of biochemical conversion, by plants living in the littoral zone, of certain primary metabolites (amino acids and sugars) to secondary products (alkaloids, anthocyanins, tannin, lignin, and other phenolic substances) which could provide some protection from UV, parasitic fungi, protozoa, and other predators.

For vascular plant evolution the formation of the polymer lignin is of paramount importance. This substance provides the strength to keep a plant upright so that it can present a maximum photosynthetic surface. It made possible the dominance of vascular plants on earth, thereby permitting the evolution of animals. Lignin is a tough, hard substance that fills the microcapillaries between cellulose microfibrils in the cell walls of water-conducting cells (tracheary elements) and fibers; it is not present in bryophytes (Niklas and Pratt, 1980).

Whether the bryophytes (liverworts and mosses) and vascular plants were derived from an aquatic multicellular ancestral algal group(s) which then migrated to land, or originated from algae already present in terrestrial habitats, may never be resolved. This subject will be discussed more fully later in this chapter in the section on Alternation of Generations. However, there are certain features that land plants developed during millions of years for successful existence on land. Some of these modifications are shared by bryophytes and vascular plants, whereas others are exclusive to vascular plants and have made possible their eminent success. The following features pertain mainly to vascular plants:

1 Development of an anchorage and water- (and dissolved minerals) absorbing system, such as underground stems (rhizomes) with rhizoids (extensions of epidermal cells), performing the function of roots. True roots apparently developed later.
2 Development of a water-and-mineral–conducting system (xylem), and a system (phloem) for the conduction of photosynthates. The xylem would also provide support by the incorporation of lignin in walls of cells.
3 Prevention of desiccation by the formation of a waxy layer (cuticle) on aerial branch systems.
4 Development of structures for aerial gas exchange (stomata).
5 Development of specialized photosynthetic tissue in aerial stems; leaves, as we know them, were undoubtedly formed later in evolution.
6 Production of spores with the cell wall impregnated with sporopollenin, a substance that prevents desiccation and is virtually indestructible by microorganisms.

Except for the previously existent photosynthetic system in algae, all of the above adaptive modifications developed over an exceedingly long time. (For expanded discussions of this subject, the reader is referred to Niklas, 1976, 1981; Lowry, Lee, and Hébant, 1980; Stebbins and Hill, 1980; Niklas and Pratt, 1980.)

In this chapter an effort will be made to select and to describe briefly the salient morphological features that are common to most living vascular plants. Such an orientation is necessary for the more detailed treatment of comparative morphology presented in subsequent chapters. For convenience in exposition, the definitive features of sporophyte and gametophyte generations will be described separately.

Sporophyte Generation

The normal origin of this generation is from the zygote, a diploid cell which results from the fertilization of the egg by a male gamete (a motile sperm in ferns, for example) (Fig. 2-1). There is considerable variation in vascular plants with respect to the length of the period of attachment and physiological dependency of the young multicellular sporophyte upon the gametophyte generation. Ultimately, the sporophyte gains physiological independence (except for certain parasitic plants) and develops into the dominant, typically photosynthetic, phase of the life cycle. *This physiological independence and dominance of the sporophyte constitutes one of the most definitive characters of vascular plants.*

From an organographic viewpoint, the sporophyte typically consists of a shoot system (usually aerial) made up of stems, various types of foliar organs, and roots. The latter may vary widely in their origin during embryogeny and later phases of growth. Shoots and roots are theoretically capable of unlimited apical growth, branching, and organ formation because of the maintenance at their tips of apical meristems. This capacity for continued indefinite apical growth is not found in the small dependent sporophytes of mosses and liverworts and hence represents a fundamentally important distinction between these organisms and vascular plants.

From an anatomical viewpoint, one of the most definitive features of the sporophyte is the presence of a vascular system. The form and arrangement of the vascular system vary not only among different groups of vascular plants but among different organs of the same plant as well. Because of its remarkably well-preserved condition in fossils, the vascular system often provides important clues to relationships and to trends of phylogenetic development. Except for the vein endings, which in leaves or floral organs consist largely of tracheary

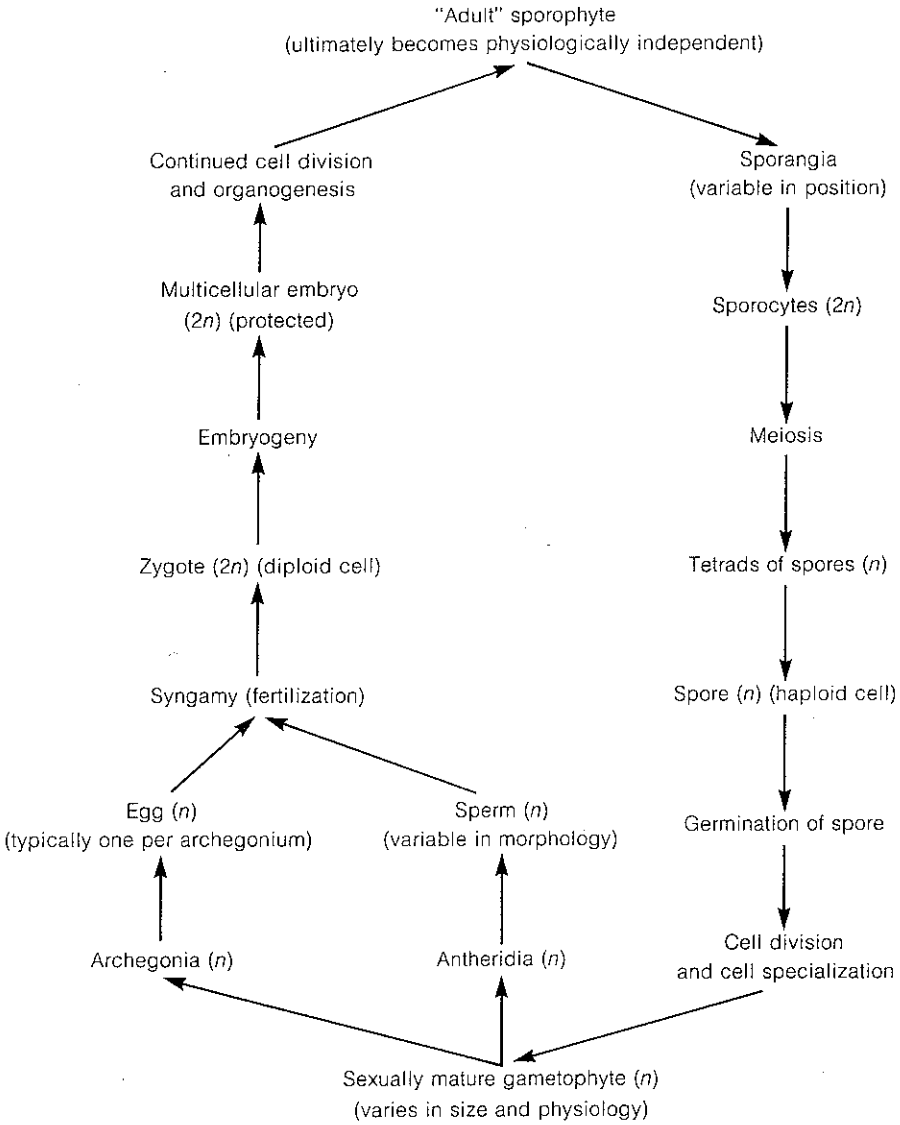


FIGURE 2-1 Alternation of sporophyte and gametophyte generations in the complete life cycle of lower vascular plants. The processes and structures represented are discussed in detail in the text.

cells, the vascular system consists typically of two distinctive tissues: ***phloem***, with conducting sieve elements, and *xylem*, with tracheary elements. Vascular tissues are essential to the conduction of water, mineral solutes, and soluble organic compounds—upon their coordinated functioning depends the normal physiology and growth of the sporophyte. Evidently, in the early occupation of the land by plants, the rapid evolution of an effective vascular system must have been of primary importance.

The characteristic reproductive structure of the sporophyte is the sporangium. As will be shown in detail in Chapter 4, sporangia differ significantly in their position, methods of origin and development, and mature structure including sporangium wall and spore type. These differences provide reliable criteria, in many instances, for classifying vascular plants.

Gametophyte Generation

The normal origin of the gametophyte generation is from a spore, which, in turn, is a product of the meiotic divisions of sporocytes in the sporangium (see Fig. 2-1). The gametophyte may be a free-living photosynthetic plant or subterranean and apparently dependent upon the presence of an endophytic fungus for its existence. In marked contrast, the gametophytes of angiosperms are much smaller and are physiologically dependent upon the sporophyte generation. Aside from these morphological and physiological variations, the chief importance of the gametophyte is the production of male gametes (or sperms) and female gametes (or eggs). These gametes are developed in distinctive multicellular gametangia in all lower vascular plants, the sperms arising in antheridia and the solitary egg developing within the archegonium. In angiosperms, the male and female gametes are produced directly by the greatly reduced and modified gametophytes, and morphologically definable sex organs are not developed. The position, ontogeny, and structure of gametangia and gametes furnish important characters used in the comparison and classification of the groups of lower vascular plants. A full discussion of the comparative morphology of gametangia is presented in Chapter 5.

Although typical vascular tissue is usually restricted to the sporophyte generation, tracheary tissue has been observed in the gametophytes of certain plants. The best known example is the subterranean gametophyte of *Psilotum,* a vascular plant of uncertain phylogenetic origin and systematic relationships (see Chapter 8). Gametophytes, 1 millimeter or more in diameter, may have a central conducting strand, demarcated by an endodermis. A well-developed strand consists (in transection) of one to three tracheids with annular or scalariform thickenings, surrounded by elongated cells appearing to be the exact counterparts of the sporophytic sieve elements (Hébant, 1976). The vascular strand arises at the apical meristem of the gametophyte but commonly is discontinuous, fading out and reappearing usually several times in the length of a few millimeters.

Several "explanations" for the occurrence of a vascular strand in *Psilotum* gametophytes were made by Holloway (1939) and deserve brief examination especially in the light of additional studies made since the publication of his paper.

First of all, it might be argued that the vascularized gametophytes of *Psilotum* are "abnormal" in chromosome number which "conditions" the development of a conducting strand. Manton (1950) discovered that *all sizes* of gametophytes were diploid (2*n*) and that the sporophytes, to which they were related, were tetraploid (4*n*), and Bierhorst (1968) only found vascular tissue in the larger diploid gametophytes of *P. nudum.* Haploid gametophytes of the same species were entirely devoid of a vascular system.

A second possible interpretation of vascularized gametophytes in *Psilotum* is that some type of physiological change occurs after a given gametophyte has reached a certain size in its growth. Holloway (1939) correlated "the presence of the conducting strand in *Psilotum* . . . with special robustness of growth." Bierhorst (1953) reached a similar conclusion and stated that "all the gametophytes are potential producers of vascular strands, and that a given gametophyte apex can, if the bulk of it meristem reaches a given threshhold, produce a strand."

A third interpretation of the vascular strand in the gametophytes is that it represents the persistence of a type of vasculature that was characteristic of the gametophytes of at least *some* of the ancient and primitive vascular plants of the Devonian, such as *Rhynia.* (For a more complete description of the morphology of rhyniophytes, see Chapter 7, p. 76. During the past 20 years suggestions have been made that the axes of *Rhynia gwynne-vaughanii,*which had previously been interpreted by Kidston and Lang (1921) as portions of the sporophyte, might actually represent vascularized gametophytes, comparable with those of *Psilotum.* The axes of *R. gwynne-vaughanii* have hemispherical projections on their surfaces, and Pant (1962) suggested that these might be young attached sporophytes. Lemoigne (1968, 1969, 1970) described what appear to be archegonia on certain vascularized axes of *R. gwynne-vaughanii,* although no antheridia were observed as is characteristic of *Psi-*

lotum. However, Pant (1962) cautiously suggested that the presumptive gametophytes of *Rhynia gwynne-vaughanii* might eventually prove to be the sexual generation of *Rhynia major.* Recently this idea has been questioned by Edwards (1980, 1986) who was able to establish that sporangia were attached to some axes of *R. gwynne-vaughanii*—thereby identifying it as a sporophyte. Also, Edwards (1986) believes that *R. major* is not a vascular plant because the conducting strand in the stems resembles that of certain nonvascular plants such as mosses. It was renamed *Aglaophyton major.* (See Chapter 7 for a more complete discussion of the basis for this change in name.)

There is, however, evidence of gametophytic plants from the Devonian Rhynie Chert in Scotland (Remy and Remy, 1980; Remy, 1982). These gametophytes consist of radially symmetrical axes that terminate in concave, disklike pads (gametophores) that bear either antheridia or archegonia, or both, that resemble those of certain bryophytes. The internal anatomy of the axes and the presence of stomata, however, resemble that of *Rhynia.* The investigators are careful to point out that it is difficult to decide where the taxonomic affinities of these fossils lie. For the present, they suggest that one should perhaps regard them as gametophytes of plants "representing an evolutionary stage previous to the separation of land plants into bryophytes and higher land plants." However, the results of their investigations offer the hope that future paleobotanical discoveries may reveal whether there is a relationship between these gametophytic plants and the well-known sporophytes (such as *Rhynia* and *Horneophyton*) of the Rhynie Chert (Chapter 7).

Alternation of Generations

Alternation of generations, or phases in the life cycle is a consistent feature of all groups of vascular plants and hence represents the basic pattern of reproduction in these dominant plants of the modern world. Figure 2-1 represents schematically the structures and processes common to the complete life cycle of *lower vascular plants.* The reader must understand this generalized life cycle clearly before becoming involved in the infinite variations of detail which occur in the cycle of reproduction of specific genera or groups of plants.

Because the sporophyte generation is the obvious and dominant phase of the life cycle, we may properly begin our analysis of Fig. 2-1 with the zygote. This diploid cell results from the union of a male gamete with the egg. The next event is the process of embryogeny, which involves the production from the zygote of a multicellular embryo, the early development, form, and organography of which are often specific in a given group. By means of further growth and differentiation from the shoot and root apices of the embryo, the adult and independent sporophyte is developed. Ultimately the sporophyte plant forms sporangia in which spore-mother cells, or sporocytes, are produced. These cells, like all normal cells of the vegetative sporophyte, are diploid. However, each sporocyte can by meiotic division give rise to a tetrad or group of four haploid spores. When circumstances are favorable a spore germinates and by cell division and cell specialization produces the gametophyte generation. The salient function of this phase is the production of male gametes and eggs. The union—called fertilization or syngamy—of a male gamete and an egg restores the diploid chromosome number and produces a zygote from which a new sporophytic plant may develop.

It should be clear from this description that the alternation of sporophyte and gametophyte phases in the life cycle is normally coordinated with a periodic doubling followed by a halving of the chromosome number. The diploid zygote ($2n$), from which the sporophyte arises contains twice the number of chromosomes typical of the spore (n) that produces the gametophyte. Is this difference in chromosome number of spore and zygote a clue to the remarkable morphological and functional differences between the generations which arise from these cells? Or, to ask the question in another way: Are syngamy and meiosis *always essential processes* in the production, respectively, of sporophyte and gametophyte? These questions apparently deserve an answer in the negative because of certain deviations from a "normal" reproductive cycle, namely, *parthenogenesis, apospory,* and *apogamy.*

In certain angiosperms and a few ferns, the embryo arises from an unfertilized egg, a phenomenon designated as parthenogenesis (i.e., "virgin birth").

The phenomenon termed *apospory* is the development of gametophytes, without a haploid spore stage, from vegetative cells of the sporophyte. Very commonly, aposporous gametophytes bear functional antheridia and archegonia, and chromosome studies have shown that their gametes are diploid and that a sporophyte resulting from their union is tetraploid (see Steil, 1939, 1951 for further information on apospory).

A third deviation from the usual reproductive cycle of a vascular plant is the phenomenon of *apogamy*, which is the formation of a sporophyte, without the act of fertilization, from vegetative cells of the gametophyte. Depending upon the chromosome number of the gametophyte (i.e., whether normal n or aposporous $2n$), the apogamous sporophyte may be either haploid or diploid in chromosome number.

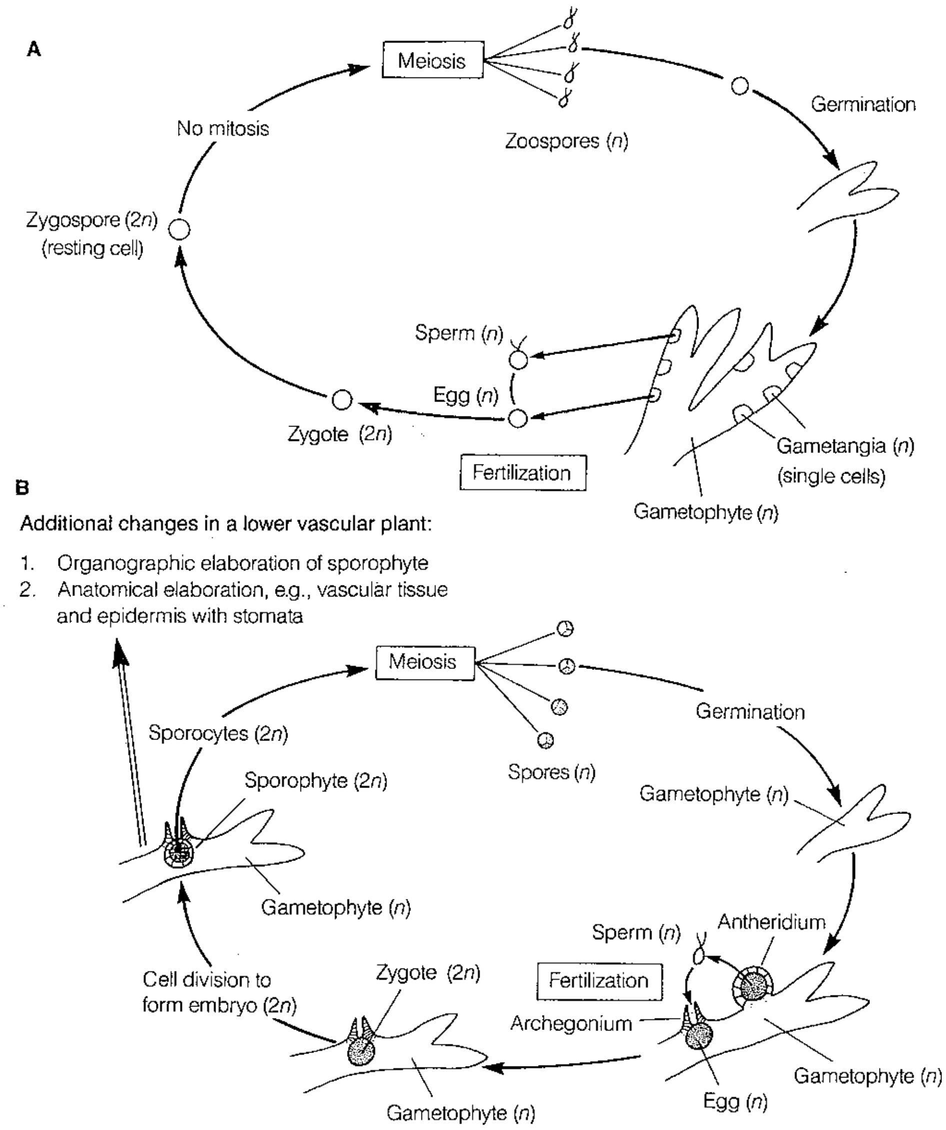
Quite apart from the interesting questions raised by the phenomena of parthenogenesis, apospory, and apogamy, there remains the broader and still unsolved problem of the phylogenetic origin of the type of alternation of generations which is "normal" and prevalent throughout all living vascular plants. If, as is commonly believed, the remote ancestors of terrestrial plants were green algae, the central question at issue is the evolutionary origin of the diploid, vascularized, independent sporophyte typical of the vast majority of vascular plants.

A century ago, Celakovsky (1874) recognized two principal forms of alternation which he distinguished by the terms "antithetic" and "homologous." In his opinion, antithetic alternation, which is characteristic of archegoniate plants (i.e., bryophytes and vascular plants with archegonia), arose during evolution by the interpolation of a new phase, i.e., the sporophyte, between successive gametophytes. In contrast, he limited his concept of homologous alternation to the succession of morphologically similar phases which occurs in the reproductive cycles of certain fungi and algae.

Today the terms "antithetic" and "homologous" are usually applied to two divergent theories which both seek to explain phylogenetically the characteristic type of life cycle in vascular plants. Bower (1935) has urged that in place of "antithetic" and "homologous" theories it would be more appropriate to speak, respectively, of the "interpolation theory" and the "transformation theory." In his view, these substitute terms are explicit in that they convey the alternative methods of phylogenetic origin of the sporophyte generation. This point may be clarified by the following brief contrast between the two theories. For a more detailed analysis, the reader is referred to Bower (1935), Fritsch (1945), and Wardlaw (1952).

According to the *interpolation theory*, which was strongly championed by Bower, the origin of the sporophyte generation was fundamentally the result of the postponement of meiosis and the development from the zygote of a "new" diploid vegetative phase. During subsequent evolution, this vegetative phase or sporophyte became increasingly complex, both organographically and anatomically but "meiosis and spore formation, though delayed, would still be the final result" (Fig. 2-2). Bower also maintained that the gradual specialization of an independent spore-producing diploid phase was closely connected, in a biological sense, with the transition from aquatic to terrestrial life by the algal-like "progenitors" of the first land plants.

The *transformation theory* of alternation, in contrast, postulates that the spore-producing and gamete-producing *individuals* of the *original* parental green algae were morphologically similar and hence that the life cycle was *isomorphic* in type (Fig. 2-3). This idea was developed in great detail by Fritsch (1945) and some of his interesting ideas deserve brief attention at this point. According to Fritsch, the first step in the long evolutionary development of archegoniate plants from aquatic green algae was the attainment of a morphological distinction between *erect* branches and a creeping prostrate system. This resulted in what is termed a *heterotrichous habit* of growth. Further elaboration of the upright system by means of longitudinal divisions in some of the cells then produced a more-or-less "parenchymatous" type of organization. Fritsch regarded this second step a "most significant evolutionary advance, since in it lay the germ for the development of a plant body of almost unlimited size." Evolutionary modifications then occurred that would have led to morphological divergence between sporophytic and gametophytic individuals and the adoption of a heteromorphic type of life cycle (Fig. 2-3). In Fritsch's view, the gametophyte, at this stage in evolution, corresponded in form and dichotomous branching to the



Additional changes in a lower vascular plant:

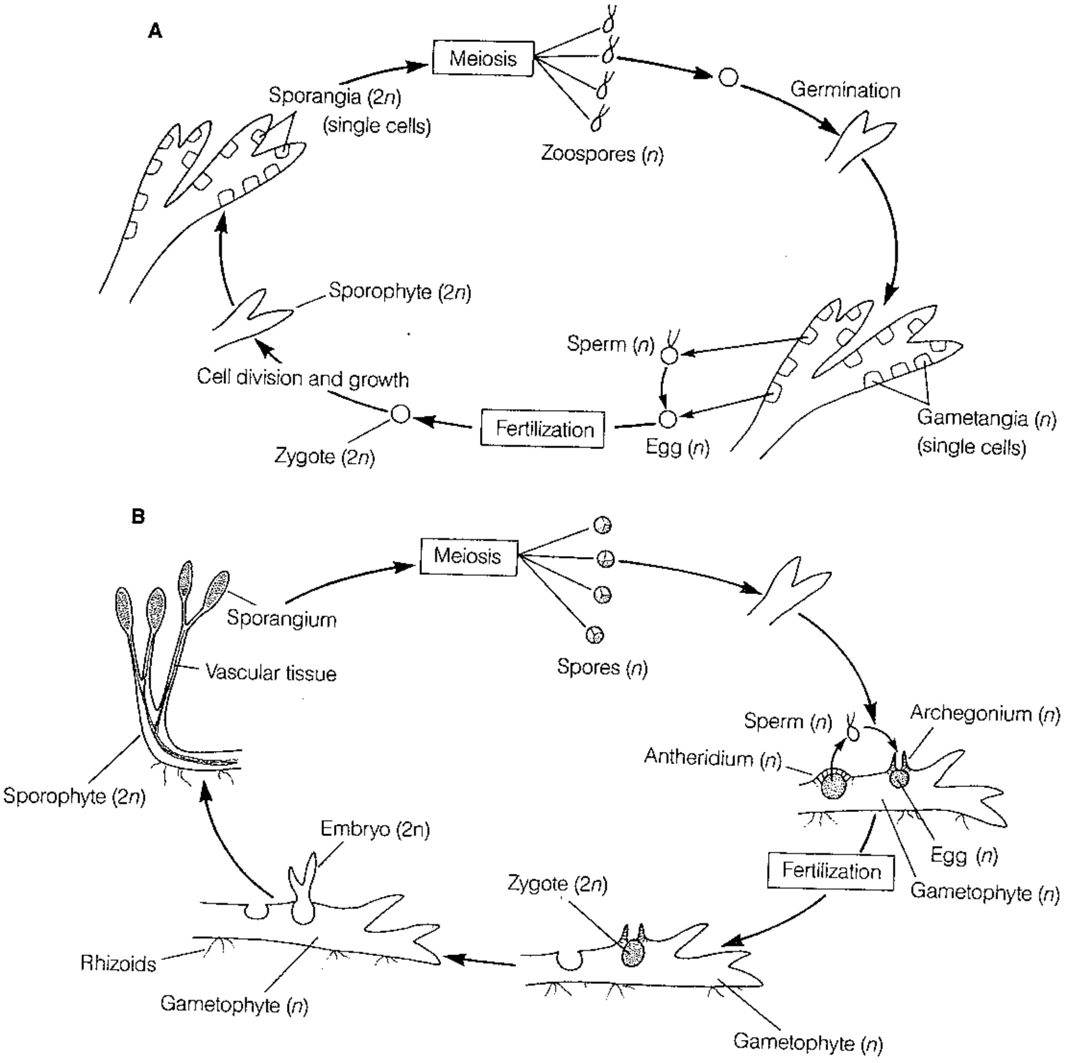
1. Organographic elaboration of sporophyte
2. Anatomical elaboration, e.g., vascular tissue and epidermis with stomata

Evolutionary changes:

* 1. Postponement of meiosis
* 2. Development of a "new" 2n phase
3. Cutinized spore wall
4. Multicellular gametangia
5. Retention of egg
6. Embryo development within archegonium

*Changes unique to this theory

FIGURE 2-2 Schematic representation of the origin of alternation of generations or phases in the life cycle according to the interpolation (or antithetic) theory. A, Hypothetical haploid green alga with oogamy. B, Development of a simple multicellular sporophyte; note additional features required for the evolution of a simple vascular plant. [Modified from class handout by Dr. R. Schmid.]



Evolutionary changes:

1. Cutinized spore wall
2. Vascular tissue in sporophyte
3. Multicellular sporangia and gametangia
4. Cuticle on epidermis; stomata
5. Retention of egg
6. Embryo development within archegonium

FIGURE 2-3 Schematic representation of the origin of alternation of generations or phases in the life cycle according to the transformation (or homologous) theory. A, Hypothetical green alga with isomorphic alternation of generations and oogamy. B, Homosporous lower vascular plant (generalized). [Modified from class handout by Dr. R. Schmid.]

primary underground system of the sporophyte and had "lost the capacity for emergence over-ground."

This conclusion is particularly interesting in light of discoveries of possible "rhizomelike" gametophytes (Lemoigne, 1968, 1969; Remy,1982) from the Devonian.

For many years it has been assumed that some group in the class Chlorophyceae of the green algae (Chlorophyta) was the progenitor of land plants, from which bryophytes and vascular plants later evolved. Indeed, an argument in support of this assumption is that vascular plants, bryophytes, and the Chlorophyceae share certain basic features: chlorophylls *a* and *b*, a cellulose wall, and starch as a reserve product. Some of the living Chlorophyceae have an isomorphic alternation of generations, so essential to Fritsch's concept. While the idea of shared attributes is appealing, recent research has cast doubt on the concept that the Chlorophyceae is the ancestral group from which bryophytes and vascular plants originated. It is probably impossible to select a specific living algal progenitor, but recent studies have pointed toward the green-algal class Charophyceae (stoneworts), including *Coleochaete* (Stewart and Mattox, 1975; Pickett-Heaps, 1976), as being more likely candidates. These algae possess the attributes enumerated previously for the Chlorophyceae, but ultrastructural and biochemical studies have revealed basic differences between the two classes. Charophytes, bryophytes, and vascular plants display a persistent mitotic spindle, followed by formation of the new cell wall. In the Chlorophyceae, however, the spindle collapses at telophase, the daughter nuclei often approach each other, and microtubules are formed at right angles to the original spindle. The new cell wall is then formed parallel to the new microtubules by cell plate formation or cleavage. In addition, the Charophyceae possess glycolate oxidase similar to that in higher plants but which has not been identified in Chlorophyceae. Furthermore, planes of cell division and branching patterns in *Coleochaete* have been cited as examples of how land-plant meristems and parenchyma may have evolved from branched, filamentous charophycean green algae (Graham, 1982; Hagemann, 1978). Also, details of sexual reproduction in *Coleochaete* provide support for the interpolation theory of the origin of alternation of generations (Graham, 1985).

Classification of Vascular Plants

The dominant land plants of the earth, despite their extraordinary diversity in habit, organography, and method of reproduction, share one highly important character: the presence of a vascular system. This anatomical character has been widely accepted as the basis for designating all plants with *tracheary tissue,* i.e., xylem, as "tracheophytes" (Sinnott, 1935), or more technically, "Tracheophyta" (Eames, 1936).

Certainly from a broad evolutionary viewpoint, the origin of a vascular system must have been highly significant in the development of the sporophyte generation and in its continued adaptation to life on land. In the second edition of this book the term Tracheophyta (a division) was used to designate all vascular plants. Twelve classes were recognized as constituting the Tracheophyta. These classes consisted of groups of plants that are generally recognizable based on consistent morphological features. Acceptance of the Tracheophyta as a major taxon does imply a monophyletic origin of vascular plants (Stewart, 1983). In recent years there has been a tendency to recognize several divisions of vascular plants, instead of only one. In these systems, what were formerly classes, for example, have been raised to divisional status. Embodied in these systems is the concept of polyphyletic origin of vascular plants, whether stated or implied. Paleobotanical research in recent years has resulted in the recognition of what appear to be separate evolutionary lines of vascular plants as far back as the Lower Devonian and even into the mid-Silurian period. Thus far no megafossils of vascular plants from earlier periods have been discovered, although microfossils (e.g., isolated tracheidlike cells, spores) that could be from vascular plants or bryophytes have been described. Thus there are many uncertainties as to whether all vascular plants can be traced back to one origin from an algal group, or whether the acquisition of vascular tissue is the expression of an adaptive tendency appearing in seemingly unrelated groups, as is the case with the development of leaves, vessels, and the seed habit. Only with additional paleobotanical evidence may we ultimately be able to answer this question.

All phylogenetic schemes of classification are, at best, tentative. No one scheme satisfies contemporary morphologists and paleobotanists with respect to the number of divisions, orders, and families. One of the difficulties, just mentioned, is the absence of convincing phyletic interconnections between the various groups of vascular plants that have been proposed. Moreover, there is considerable confusion at the level of formal schemes of classification because of the shifting of lower taxa (e.g., classes) to higher categories (e.g., divisions) or vice versa, merely by changing the suffix of certain names.

In view of these difficulties and nomenclature problems, no attempt will be made to contrast the various schemes of classifying vascular plants. However, instead of using "Tracheophyta" as the one division for vascular plants, in this edition we recognize fifteen divisions. Each of these formerly represented a class or even an order. This system is more in line with those of some contemporary botanists. The plants in each division have characters that are recognizable and can be used to differentiate them from those in other divisions, as well as to provide the bases for making comparisons and for establishing tentative phylogenetic relationships.

The conspectus shown in Table 2-1 lists the divisions of vascular plants recognized in the present text and relates them to the categories used in the previous edition. We introduce the conspectus at this point simply to orient the reader to the names and representative examples of the divisions of vascular plants. More detailed taxonomic treatment of each of the divisions will be found in subsequent chapters.

For additional reading on systems of classification and phylogeny, the reader is referred to Newman, 1947; Stewart, 1960, 1961, 1983; Banks, 1970; Bold et al., 1980; Taylor, 1981.

Table 2-1 Classification of vascular plants

Classification from *Comparative Morphology of Vascular Plants,* 2d edition	Classification used in present edition (Names in parentheses are used in some other systems for the same group)
Tracheophyta (division)	Divisions
Rhyniopsida*	1. Rhyniophyta (extinct plants, e.g., *Rhynia, Cooksonia*)
Zosterophyllopsida	2. Zosterophyllophyta (extinct plants, e.g., *Zosterophyllum*)
Trimerophytopsida	3. Trimerophytophyta (extinct plants, e.g., *Psilophyton, Trimerophyton*)
Psilopsida	4. Psilophyta (Psilotophyta) (two living genera, *Psilotum* and *Tmesipteris*)
Lycopsida	5. Lycophyta (Microphyllophyta) (extinct forms such as *Protolepidodendron* and *Lepidodendron,* and the living genera *Lycopodium, Selaginella, Phylloglossum, Isoetes,* and *Stylites*)
Sphenopsida	6. Sphenophyta (Arthrophyta) (mostly extinct plants, e.g., *Calamites, Sphenophyllum;* the one living genus is *Equisetum*)
Filicopsida	7. Filicophyta (Pteridophyta) (living and extinct ferns)
Progymnospermopsida	8. Progymnospermophyta (extinct plants, e.g., *Archaeopteris*)
Cycadopsida	
Pteridospermales (order)	9. Pteridospermophyta (extinct seed ferns, e.g., *Lyginopteris, Medullosa*)
Cycadales (order)	10. Cycadophyta (extinct and living cycads, e.g., *Cycas, Zamia*)
Cycadeoidales (order)	11. Cycadeoidophyta (extinct cycadeoids, e.g., *Cycadeoidea*)
Coniferopsida	
Ginkgoales (order)	12. Ginkgophyta (extinct members and living *Ginkgo biloba*)
Coniferales (order)	13. Coniferophyta (extinct and living conifers, e.g., pine, fir)
Gnetopsida	14. Gnetophyta (*Ephedra, Gnetum, Welwitschia*)
Angiospermopsida	15. Magnoliophyta (Anthophyta) (angiosperms or flowering plants)

* The taxonomic level in the left column is class unless otherwise indicated.

REFERENCES

Banks, H. P.
1970. *Evolution and Plants of the Past.* Wadsworth, Belmont, Calif.

Bierhorst, D. W.
1953. Structure and development of the gametophyte of *Psilotum nudum. Amer. Jour. Bot.* 40:649–658
1968. On the Stromatopteridaceae (Fam. Nov.) and on the Psilotaceae. *Phytomorphology* 18:232–268.

Bold, H. C., C. J. Alexopoulos, and T. Delevoryas
1980. *Morphology of Plants and Fungi,* 4th edition. Harper and Row, New York.

Bower, F. O.
1935. *Primitive Land Plants.* Macmillan, London.

Celakovsky, L.
1874. *Bedeutung des Generationswechsels der Pflanzen.* Prag.

Eames, A. J.
1936. *Morphology of Vascular Plants. Lower Groups.* McGraw-Hill, New York.

Edwards, D. S.
1980. Evidence for the sporophytic status of the Lower Devonian plant *Rhynia gwynne-vaughanii* Kidston and Lang. *Rev. Palaeobot. Palynol.* 29:177–188.
1986. *Aglaophyton major,* a non-vascular land-plant from the Devonian Rhynie Chert. *Bot. J. Linnean Soc.* 93:173–204.

Fritsch, F. E.
1945. Studies in the comparative morphology of the algae. IV. Algae and archegoniate plants. *Ann. Bot.* n. s. 9:1–29.

Graham, L. E.
1982. The occurrence, evolution, and phylogenetic significance of parenchyma in *Coleochaete* Bréb. (Chlorophyta). *Amer. Jour. Bot.* 69:447–454.
1985. The origin of the life cycle of land plants. *Am. Scientist* 73:178–186.

Hagemann, W.
1978. Zur Phylogenese der terminalen Sprossmeristeme. *Ber. Deut. Bot. Ges.* 91:699–716.

Hébant, C.
1976. Evidence for the presence of sieve elements in the vascularised gametophytes of *Psilotum* from Holloway's collections. *New Zealand J. Bot.* 14:187–191.

Holloway, J. E.
1939. The gametophyte, embryo, and young rhizome of *Psilotum triquetrum* Swartz. *Ann. Bot.* n.s. 3:313–336.

Kidston, R., and W. H. Lang
1921. Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. IV. Restorations of the vascular cryptogams and discussion of their bearing on the general morphology of the Pteridophyta and the origin of the organization of land plants. *Trans. Roy. Soc. Edinb.* 52:831–854.

Lemoigne, Y.
1968. Observation d'archégones portés par des axes du type *Rhynia gwynne-vaughanii* Kidston et Lang. Existence de gamétophytes vascularisés au Dévonien. *Compt. Rend. Acad. Sci.* (Paris) 266:1655–1657.
1969. Contribution à la connaissance du gamétophyte *Rhynia gwynne-vaughanii* Kidston et Lang. Probléme des protuberances et processus de ramification. *Bull. Mens. Soc. Linn. Lyon* 38(4):94–102.
1970. Nouvelles diagnoses du genre *Rhynia* et de l'espèce *Rhynia gwynne-vaughanii. Bull. Soc. Bot. France* 117:307–320.

Lowry, B., D. Lee, and C. Hébant
1980. The origin of land plants: a new look at an old problem. *Taxon* 29:183–197.

Manton, I.
1950. *Problems of Cytology and Evolution in the Pteridophyta.* Cambridge University Press, London.

Newman, I. V.
1947. The place of ferns and seed plants in classification. *Trans. Roy. Soc. New Zealand* 77:154–160.

Niklas, K. J.
1976. The role of morphological biochemical reciprocity in early plant evolution. *Ann. Bot.* 40:1239–1254.
1981. The chemistry of fossil plants. *BioScience* 31:820–825.

Niklas, K. J., and L. M. Pratt
1980. Evidence for lignin-like constituents in Early Silurian (Llandoverian) plant fossils. *Science* 209:396–397.

Pant, D. D.
1962. The gametophyte of the Psilophytales. *Proc. Summer School Bot. Darjeeling, India* (Held June 2–15, 1960) Pp. 276–301.

Pickett-Heaps, J.
1976. Cell division in eucaryotic algae. *BioScience* 26:445–450.

Remy, W.
1982. Lower Devonian gametophytes: relation to the phylogeny of land plants. *Science* 215:1625–1627.

Remy, W., and R. Remy
1980. Devonian gametophytes with anatomically preserved gametangia. *Science* 208:295–308.

Sinnott, E. W.
1935. *Botany. Principles and Problems,* 3d edition. McGraw-Hill, New York.

Stebbins, G. L., and G. J. C. Hill
1980. Did multicellular plants invade the land? *Am. Nat.* 115:342–353.

Steil, W. N.
1939. Apogamy, apospory, and parthenogenesis in the pteridophytes. *Bot. Rev.* 5:433–453.
1951. Apogamy, apospory, and parthenogenesis, II. *Bot. Rev.* 17:90–104.

Stewart, K. D., and K. R. Mattox
1975. Comparative cytology, evolution and classification of the green algae with some consideration of the origin of other organisms with chlorophylls *a* and *b*. *Bot. Rev.* 41:104–135.

Stewart, W. N.
1960. More about the origin of vascular plants. *Plant Sci. Bull.* 6:1–5.
1961. The origin of vascular plants: monophyletic or polyphyletic? *Rec. Adv. Bot.* 2:960–963.
1983. *Paleobotany and the Evolution of Plants.* Cambridge University Press, Cambridge.

Taylor, T. N.
1981. *Paleobotany: An Introduction to Fossil Plant Biology.* McGraw-Hill, New York.

Wardlaw, C. W.
1952. *Phylogeny and Morphogenesis.* Macmillan, London.