CHAPTER 3

The Vegetative Sporophyte

THIS chapter reviews those features of the vegetative sporophyte of vascular plants that figure most commonly in morphological comparisons and interpretations. For the convenience of the reader, the material is presented in five categories: (1) the contrasts between shoot and root, (2) the methods of branching or ramification of shoots, (3) the concept of microphylls and megaphylls, (4) the comparative anatomy of the sporophyte, and (5) the stelar theory.

Shoots and Roots

In the great majority of living vascular plants the developing embryo gives rise to a leafy stem, or shoot, and a primary root. Further development of the young sporophyte results, through the activity of apical meristems, in the formation of additions to the original shoot and root components.

From the standpoints of organography, function, and anatomy, shoots and roots are very different types of systems. Roots develop no superficial extensions other than the absorbing root hairs and are to be regarded as naked axes; their chief functions are anchorage and the absorption of water and solutes. In contrast, shoots have a jointed or segmental organography because the axis or stem bears conspicuous lateral appendages, or leaves. The chief functions of shoots are photosynthesis, storage, and reproduction.

In regard to apical growth and branching, roots and shoots differ in several important respects. The root apex consists of a root cap that functions as a protective buffer to the delicate meristem, which lies beneath it. This subterminal meristem of roots is the point of origin of two different patterns of cell formation. One adds new cells outwardly to the root cap, the other contributes the cells which become a part of the root body (Fig. 3-1, A). Except for hairs, the only lateral extensions that may occur are lateral roots, and these structures, unlike the usually superficially developed branches of the shoot, originate deep within the tissue of the parent root. In marked contrast to the root apex, the apex of the shoot consists of the terminal meristem itself, and no cap of tissue comparable to a root cap is developed. Aside from giving rise to the primary stem tissues, a very important function of the shoot apex is the formation of new leaves (Fig. 3-1, B).

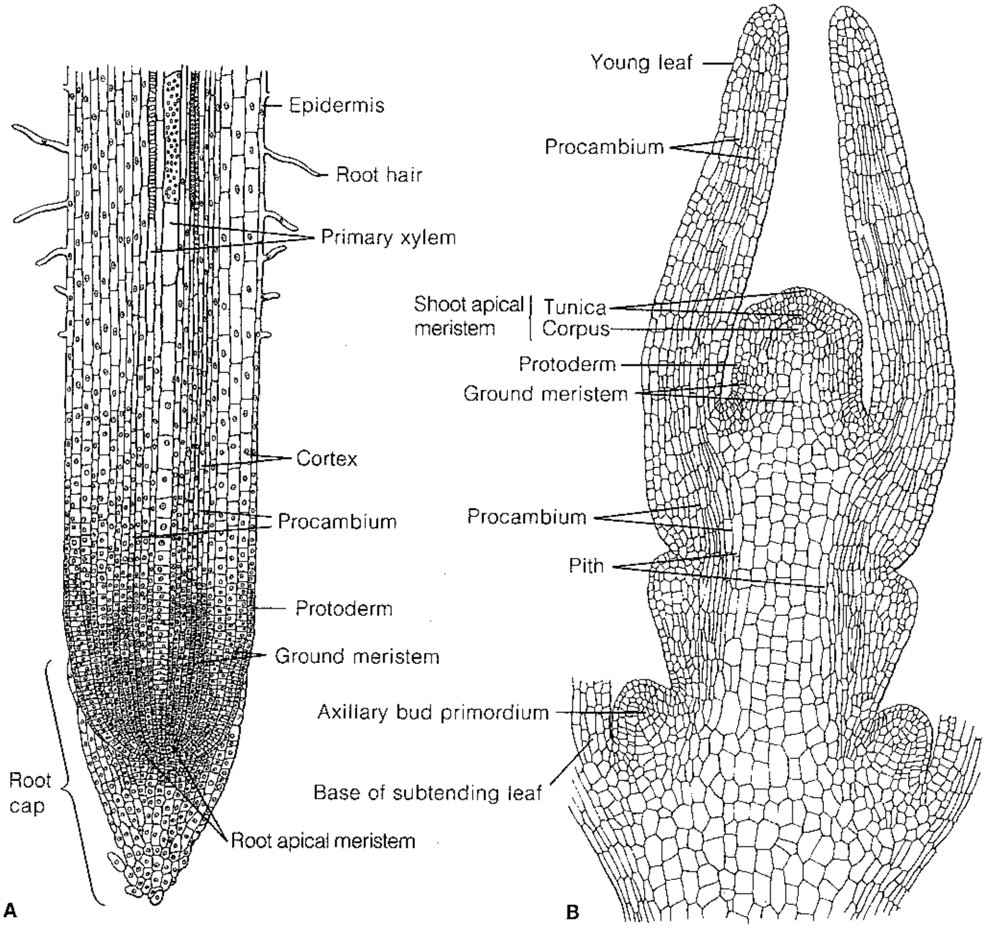


FIGURE 3-1 Longisections showing the apical meristems and the origin of the primary meristematic tissues in the root and shoot of angiosperms. **A,** root tip of *Hordeum sativum;* **B,** shoot tip of *Hypericum uralum.* [A redrawn from *A Textbook of General Botany,* 4th edition, by R. M. Holman and W. W. Robbins. Wiley, New York. 1951; B redrawn from Zimmermann, *Jahrb. Wiss. Bot.* 68:289, 1928.]

Leaves originate as primordia (singular, primordium) by means of localized cell division and cell extension at discrete loci or nodes on the flanks of the shoot apex. Leaf primordia typically arise in acropetal sequence; that is, the youngest stages in leaf development are found nearest the summit of the meristem. In addition to their acropetal order of development, the primordia of leaves are laid down usually in an orderly and often distinctive arrangement or *phyllotaxis* with reference to the stem. In the most common type of phyllotaxis (or phyllotaxy) a single leaf is initiated at each node, and the leaves form a spiral (or helix) around the stem—an arrangement designated *alternate spiral* or *alternate helical* (Fig. 3-2, A). In other plants the leaves are formed in pairs (*opposite phyllotaxis,* Fig. 3-2, B). If the successive pairs are at right angles to one another, the arrangement is termed *decussate phyllotaxis.* Leaves may also occur in groups of three or more *(whorled phyllotaxis).* The term *distichous* refers to a phyllotactic pattern in which leaves are in two rows. The causal factors responsible for phyllotactic patterns are poorly understood. (See Wardlaw, 1952, 1965, and Cutter, 1965, for résumés of experimental studies, and Young, 1978, for computer models.)

The differentiation between distinct root and shoot systems in most living vascular plants is of

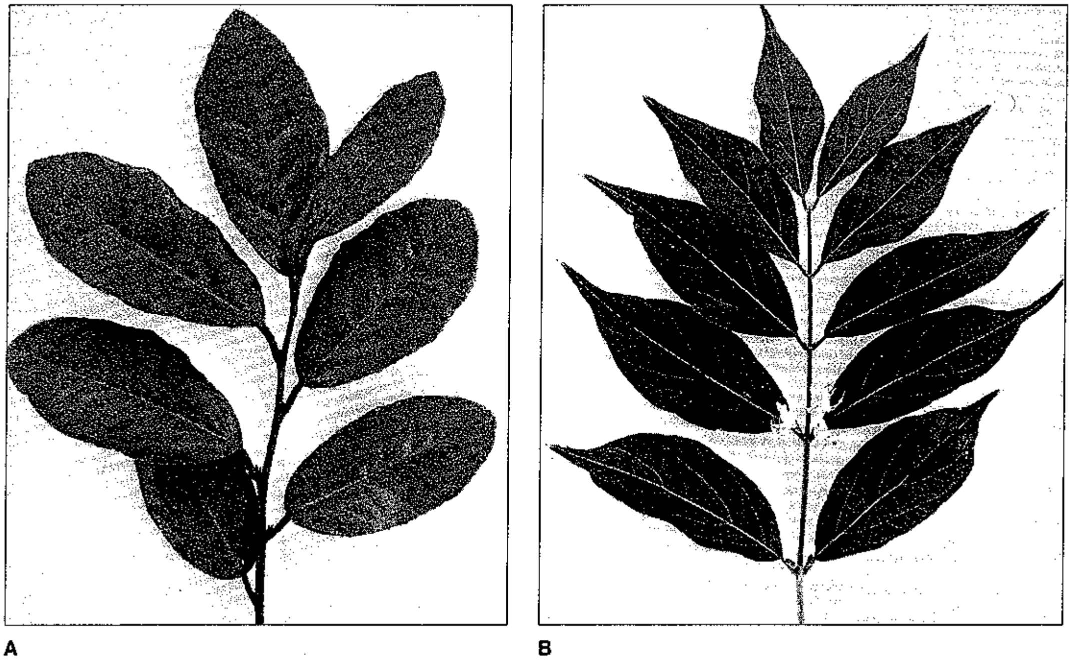


FIGURE 3-2 Two types of leaf arrangement (phyllotaxis). **A**, alternate spiral or alternate helical *(Elaeagnus)*. **B**, opposite *(Lonicera)*. Note buds in the axils of leaves (flowers and floral buds associated with the lower two leaf pairs in **B**).

considerable interest from an evolutionary viewpoint. It is now rather generally agreed that this differentiation did not exist in such Devonian land plants as *Horneophyton* and *Rhynia* (Chapter 7). In these archaic organisms portions of the underground system of stems apparently served physiologically as roots. It seems reasonable to postulate that roots were acquired later in the evolution of vascular plants. However, the steps in the evolutionary divergence of roots from primitive shoots, which led to the acquisition of a root cap, a prevalent internal or endogenous origin of roots, and the retention of a primitive type of vascular system, are unfortunately obscure today. (See Chapter 19 for a more detailed account of root morphology and anatomy.)

Types of Branching in Shoots

The types of branching of the shoot system, in both extinct and living vascular plants, are highly varied and often definitive for the larger taxa, i.e., divisions or classes. At this point in our discussion of the vegetative sporophyte, we will briefly consider the major patterns of branching in vascular plants. Additional details on the types of ramification in the various groups of vascular plants will be found in later chapters of this book.

From the broadest possible morphological viewpoint, two principal types of ramification may be distinguished: dichotomous and lateral.

Dichotomous Branching

Two of the widely accepted morphological characteristics of a dichotomously branched shoot system are (1) the absence of a dominant, or "major," axis and (2) the occurrence of a *sequence* of paired branches which are *not* associated with subtending leaves. These characteristics are the result of a particular type of apical ontogeny in which the terminal meristem itself divides into two more-or-less equal and divergent apices (Figs. 3-3, A–C;

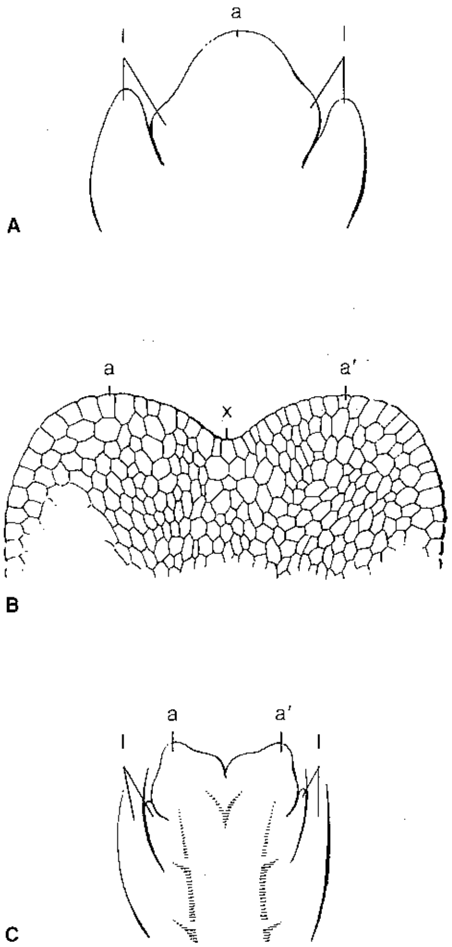


FIGURE 3-3 Dichotomous branching in *Lycopodium alpinum*. **A,** vegetative shoot apex (a) with leaf primordia (1); **B,** dichotomous division of a reproductive shoot apex (x) into two new apices, (a and a′); **C,** later stage in dichotomy of vegetative shoot apex. [From *Vergleichende Morphologie der höheren Pflanzen* by W. Troll. Gebrüder Borntraeger, Berlin. 1937.]

3-4, B). This process of apical forking, or dichotomy, may be repeated on an indefinite scheme, leading in many cases to a very regular and distinctive kind of shoot system (Fig. 3-4, A).

If the successive bifurcations occur in one plane, a flattened dorsiventral system is formed. Troll (1937) terms this type of branching "flabellate dichotomy." In other types of plants, each dichotomy of the axis is at approximately right angles to the preceding bifurcation and the resulting shrublike shoot system is termed "cruciate dichotomy" by Troll.

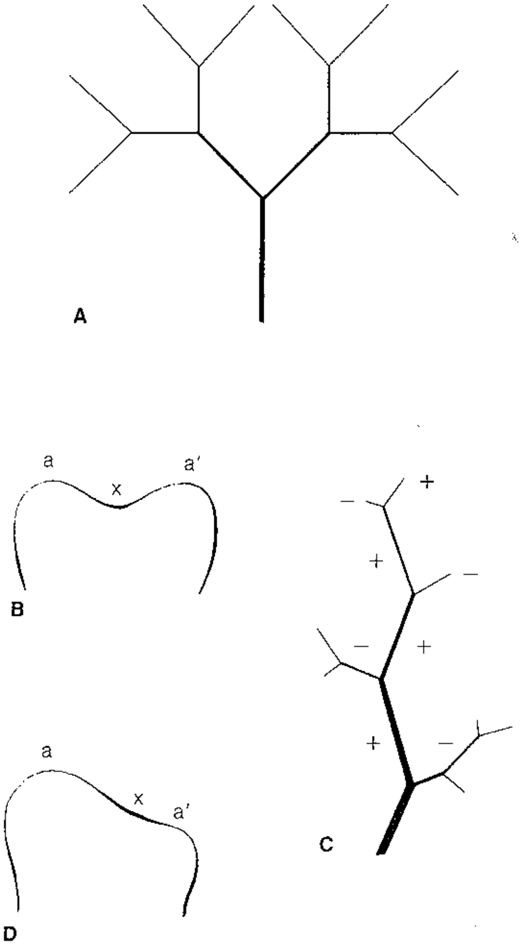


FIGURE 3-4 Isotomous and anisotomous types of dichotomous branching. **A,** isotomous branching, showing equal development following each dichotomy; **B,** origin of isotomous branch primordia (a, a′) by equal division of shoot apex (x); **C,** anisotomous branching, showing unequal development of stronger (+) and weaker (−) branches following each dichotomy; **D,** origin of anisotomous branch primordia (a, a′) by unequal division of shoot apex (x). [From *Vergleichende Morphologie der höheren Pflanzen* by W. Troll. Gebrüder Borntraeger, Berlin. 1937.]

Many of the nineteenth century botanists limited their concept of dichotomy to those plants in which the initiation of branching resulted from the longitudinal division of the apical cell in the shoot apex. Each of the two daughter cells produced by such a division was then observed to function as the new apical cell of a branch primordium.

However, if "dichotomy" is defined in the above restrictive sense, this type of branching would have to be regarded as extremely rare because the shoot apex of the majority of vascular plants lacks a definable apical cell.

The dichotomy of the shoot apex may produce successive pairs of branches approximately equal in size and degree of development. Troll (1937) terms this kind of symmetrical branching *isotomous dichotomy* (Fig. 3-4, A, B). The two members of a bifurcation also may develop unequally. One member—or "shank"—of each pair develops more strongly and soon overtops its weaker sister branch (Fig. 3-4, C, D). This derivative form of dichotomy is termed *dichopodial branching* by Bock (1962) who characterizes it, in its simplest expression, as the alternate promotion of the right and left shanks of successive dichotomies. The repetition of this *anisotomous dichotomy,* as Troll designates it, results in the formation of a zig-zag "axis" and shorter, more-or-less determinate "lateral branches." Bock regards the origin of dichopodial branching as a highly significant event in evolution that led to lateral branching, pinnate leaves, and the gradual formation of a midvein in the early phylogeny of venation patterns in leaves. (For further details, consult Bock, 1962, 1969).

Lateral Branching

In contrast to dichotomy, lateral branching of a shoot system originates by the expansion of buds more-or-less distal to the shoot apex of the main or dominant axis (Fig. 3-1, B). This kind of ramification is commonly termed "monopodial branching" to distinguish it from typical dichotomous or dichopodial branching.

Lateral buds, as shown by Troll (1937), most frequently arise in some type of relationship to the leaves of a shoot. In some fern species that have dorsiventral rhizomes buds arise without reference to leaves ("acrogenous branching," according to Troll's terminology), but it is more common in ferns for buds to originate near or from the abaxial side of the leaf bases or from the petiole (Troop and Mickel, 1968). *Equisetum* appears unique among vascular plants with monopodial branching in that the buds *alternate in position* with the fused leaves at each node (Chapter 10). In seed plants, however, the dominant type of branching is *axillary* (Fig. 3-1, B).

One of the most remarkable details of axillary bud formation in the angiosperms is the development, in a single leaf axil, of a series of *accessory buds* in addition to the main bud. Accessory buds, arranged in one or two vertical rows in the leaf axil, are known as "serial buds." If the accessory buds are arranged in a crescentic pattern in the leaf axil, they are termed "collateral buds." (Detailed treatments of accessory buds are given by Sandt, 1925, and Troll, 1937).

In many dicotyledons with normal axillary branching, it is common for the development of a terminal inflorescence or the abortion and subsequent abscission of the entire tip of a vegetative shoot to result in the continuation of the growth of such shoots from one or more of the uppermost axillary buds (Garrison and Wetmore, 1961; Millington, 1963). If shoot-tip abortion occurs in a plant with decussate phyllotaxy, the uppermost pair of axillary buds may subsequently expand into shoots and give the false impression that branching is dichotomous. Troll (1935) designates this type of pseudodichotomy as a *dichasial sympodium,* in contrast to the *monochasial sympodium,* which is produced when only a single axillary bud continues the development of the shoot.

Microphylls and Megaphylls

The problem of interpretation of the morphology and evolutionary history of the leaves of vascular plants has attracted much attention. Leaves, regardless of their size, form, or structure, arise as lateral protuberances from a shoot apex and at maturity represent the typical lateral appendages of the axis or stem. From an ontogenetic viewpoint, a leaf is a determinate organ. In contrast to the theoretically unlimited or open type of apical growth characteristic of the stem, the apical growth of the leaf primordium in most plants ceases early in ontogeny and is followed by a phase of tissue specialization and enlargement which culminates in the production of the final shape and structure of the adult foliar organ. The question is: How did the distinction between an indeterminate axis and its lateral foliar appendages arise during the evolutionary history of vascular plants? The answer to this question is particularly important in the light of paleobotanical studies on certain Devonian and Silurian plants, some of which represent the simplest vascular plants known to science. The sporophytes of *Rhynia* and *Horneophyton* are of exceptional interest because their aerial dichotomously branched axes were entirely devoid of foliar appendages (see Chapter 7).

Morphological Contrasts

MICROPHYLLS. Unfortunately the term "microphyll"—literally "small leaf"—which botanists generally apply to a certain leaf type unduly, and often inaccurately, emphasizes the small dimension of an appendage rather than its distinctive vascular anatomy and phylogenetic mode of origin. From a more precise morphological standpoint, one of the salient characters of a microphyll is its extremely simple and presumably primitive vascular system. As is shown in Fig. 3-5, D, the vascular supply of a typical microphyll consists of a single strand—the leaf trace—which diverges from the periphery of the *stele* (i.e., the vascular cylinder) of the stem and extends as an unbranched midvein through the leaf. It must be emphasized that the divergence of the single trace at the node of a microphyll is *not* associated with a corresponding break, or *leaf gap,* in the stele. This is also true for certain taxa that have microphylls and are siphonostelic (their stem has a central pith).

There are two exceptions to the presence of an unbranched vein in the leaves generally considered to be microphylls. For example, in some extinct arborescent lycopods there were two veins in the leaf blade which presumably arose from a dichotomy of the leaf trace. Also, there is a *Selaginella* species with a branched venation system (Chapter 9).

MEGAPHYLLS. The megaphyll (called "macrophyll" by some authors) is illustrated by the comparatively large pinnate leaves of ferns, although here too the salient feature is not size but rather morphological and anatomical organization. In contrast to a microphyll, the divergence of the leaf trace (or traces) in most of the living ferns is associated with the formation of parenchymatous areas, or *leaf gaps,* in the vascular cylinder of the stem (Figs. 3-6, 3-19, B). There are, however, notable exceptions to this anatomical correlation between

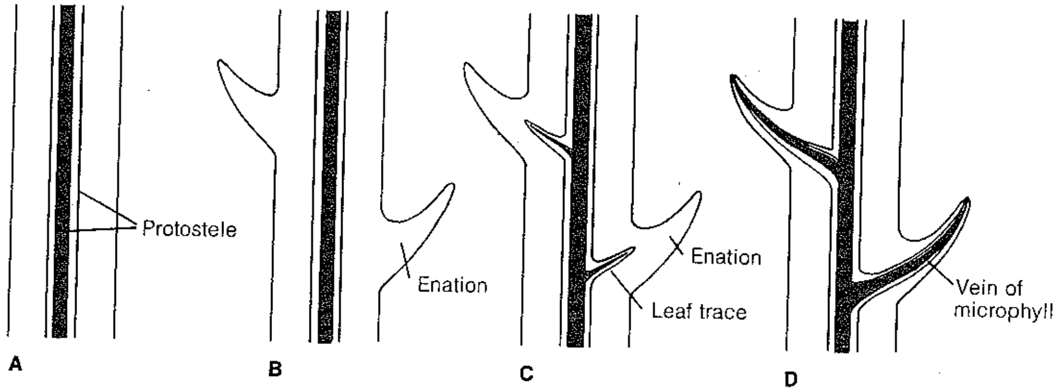


FIGURE 3-5 Longisectional diagrams showing the origin and evolutionary development of microphylls according to the enation theory. **A**, the leafless, protostelic axis of *Rhynia;* **B**, primitive enations, devoid of leaf traces, as illustrated by the shoot of *Psilotum;* **C**, portion of the "shoot" of the extinct lycopod *Asteroxylon,* showing the termination of leaf traces at the bases of the veinless enations; **D**, typical microphylls, in which a leaf trace extends as an unbranched midvein into each of the foliar appendages. The condition in D is the prevailing pattern in *Lycopodium, Selaginella,* and other members of the Lycophyta. [Redrawn from Lemoigne, *Bull. Mens. Soc. Linn. Lyon,* 37(9):367, 1968.]

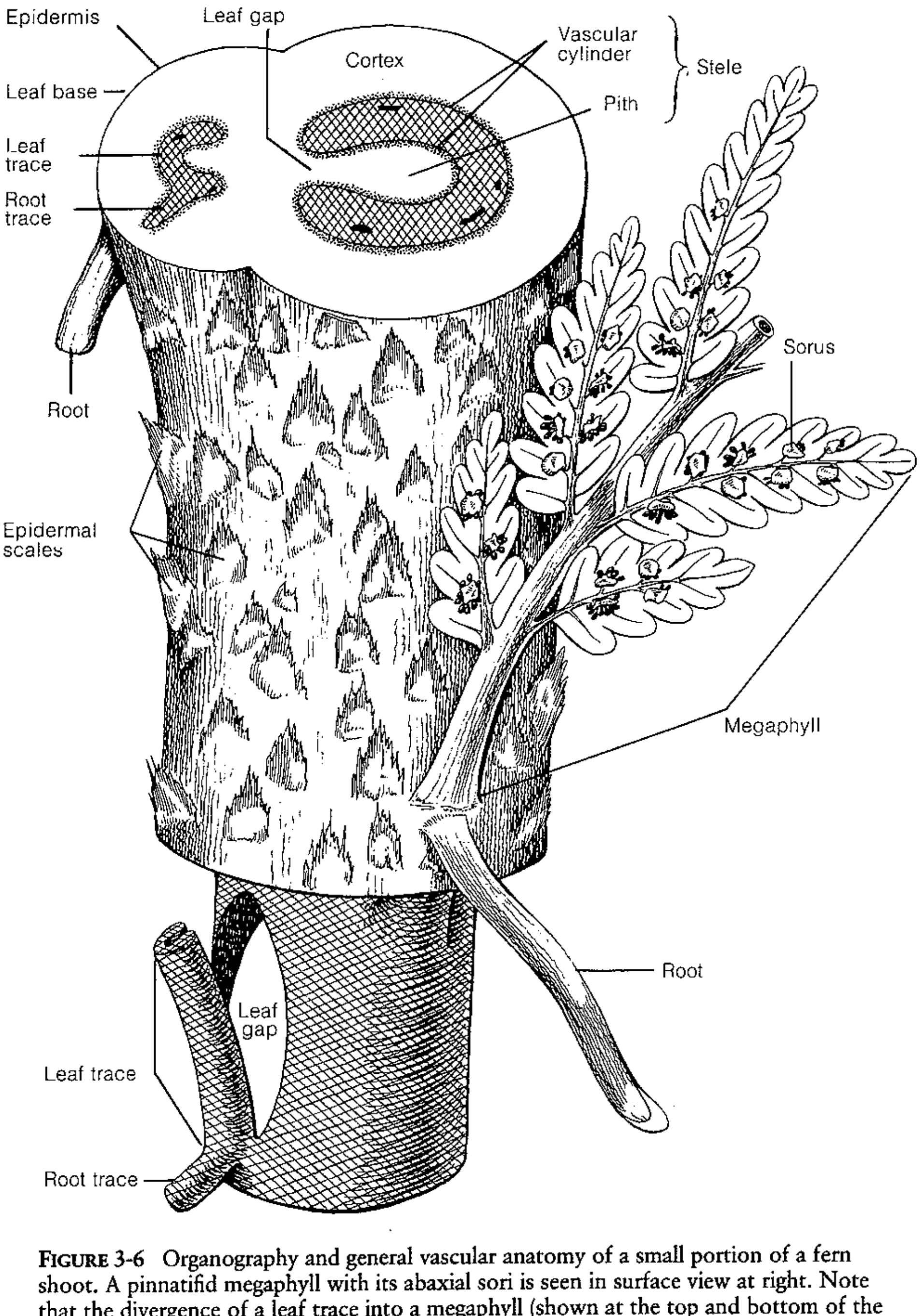


FIGURE 3-6 Organography and general vascular anatomy of a small portion of a fern shoot. A pinnatifid megaphyll with its abaxial sori is seen in surface view at right. Note that the divergence of a leaf trace into a megaphyll (shown at the top and bottom of the figure) is associated with a leaf gap in the stele of the stem. [From *The Anatomy of Woody Plants* by E. C. Jeffrey. University of Chicago Press, Chicago. 1917.]

leaf traces and leaf gaps where the vascular cylinder of the axis is a protostele and devoid of leaf gaps. Fern megaphylls differ from microphylls by their more complex patterns of venation. In contrast to the univeined microphyll, the lamina of a fern leaf, whether simple or pinnate in organization, develops a relatively complex system of branched vascular strands.

Phylogenetic Origin

As Bower (1935) has clearly pointed out, the evolutionary significance of the morphological differences between microphylls and megaphylls "can only be solved by comparison between various types living and fossil, aided where possible by reference to individual development." From this broad outlook, Bower postulated that the microphylls and megaphylls of lower vascular plants are the results of separate paths of foliar evolution, i.e., the two leaf types are not homologous from a phyletic point of view.

Figure 3-5 shows diagrammatically the theoretical steps in the evolution of the microphyll. Beginning with the leafless type of axis found in an ancient plant such as *Rhynia,* the earliest stage in microphyll evolution may have been a simple emergence or "enation" devoid of a leaf trace (Fig. 3-5, A). The further elaboration of primitive enations would be indicated by the initiation of "leaf traces" which diverged from the periphery of the protostele and terminated at the bases of the appendages. This theoretical stage in phylogeny is illustrated by the extinct lycopod *Asteroxylon* and possibly by the enation "leaves" of the living *Psilotum* (Fig. 3-5, B, C). In the final stage of mircophyll evolution, a vascular strand, or leaf trace, continued as a single midvein into the microphyll (Fig. 3-5, D). This type of univeined microphyll is typical of the living members of the Lycophyta. (For further details on the microphylls of the Lycophyta, see Chapter 9.)

According to another theory, microphylls may have evolved phylogenetically through progressive reduction of dichotomously branched, lateral, leaflike appendages. This concept will be discussed at the end of the next section (The Telome Theory).

In contrast to the progressive evolutionary specialization of microphylls from enations, megaphylls are considered by Bower to have evolved by the specialization of the distal regions of dichotomized branch systems. His theory, based on the earlier ideas of Lignier (1903), postulates that the fern megaphyll is a "cladode leaf," and that the first stage in its origin was a gradual change from equal dichotomous branching to a dichopodial type of growth. This consisted in the unequal development of the sister branches of dichotomizing axes, one continuing as the main axis or "stem," the other becoming laterally "overtopped" and representing the precursor of a megaphyll (Fig. 3-7, A, B). Subsequent flattening or "planation" occurred, and finally the ultimate divisions of each of the overtopped branch systems became united by development of laminar tissue, forming a simply di-

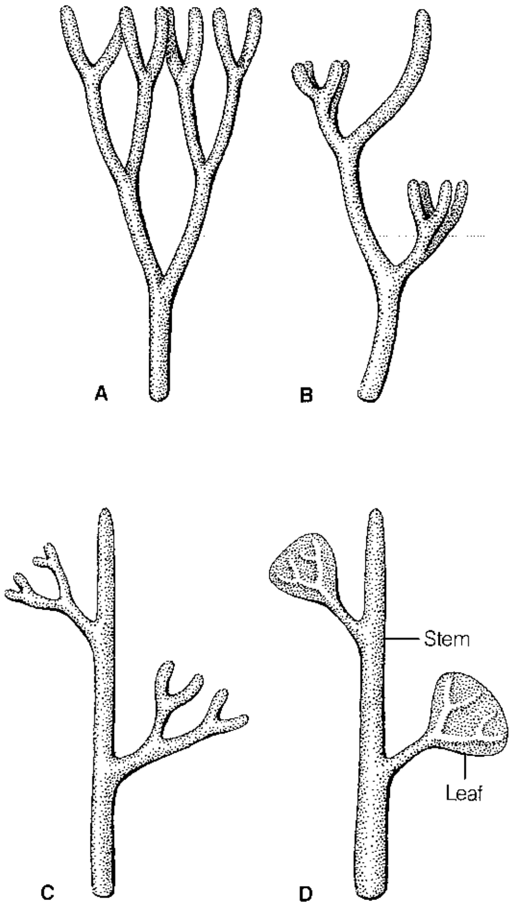


FIGURE 3-7 Schematic representation of the phylogenetic origin and development of the megaphyll according to the telome theory. **A,** isotomous branch system, without distinction between axis and megaphylls; **B,** unequal dichotomy or "overtopping," the weaker branches representing initial stages in megaphyll evolution; **C,** dichotomous branching of primitive megaphylls in a single plane ("planation"); **D,** union between forked divisions of megaphylls ("webbing") has produced a flat, dichotomously veined lamina. [Adapted from *Cryptogamic Botany, Vol. II. Bryophytes and Pteridophytes* by G. M. Smith. McGraw-Hill, New York. 1955.]

chotomously veined megaphyll (Fig. 3-7, C, D). Possible examples of overtopping can be found in the extinct division Trimerophytophyta from the Devonian (Chapter 7).

The Telome Theory

During the early development of plant morphology, the study of homologies was based on the belief that the organography of the sporophyte in vascular plants *as a whole* could be interpreted with reference to such angiospermic organs as leaf, stem, and root. Paleobotanical studies made during the early part of the present century suggested the need for a "new outlook" in phyletic morphology, especially a reappraisal of the evolutionary history of the sporophyte. The most comprehensive synthesis of the major steps in the evolution of vascular plants was made by Walter Zimmermann, who, in 1930, originated the telome theory (Zimmermann, 1953, 1959, 1965).

We will outline only the most salient features of the telome theory. Readers interested in the historical aspects of this theory and a more detailed analysis of it should consult Zimmermann (1965), Wilson (1953), and Stewart (1964).

Zimmermann selected *Rhynia* as a type of very ancient "primordial" land plant that provides a relatively simple example of the application of his telome theory. According to his interpretation, the dichotomously branched sporophyte of *Rhynia* was composed of morphological "units," which he designated as "telomes" and "mesomes." Reference to Fig. 3-8 will serve to explain his use of these terms. A telome, in the broadest sense of the term, is one of the distal branches of a dichotomized axis. Each telome ends at the point of forking of the axis whereas a mesome represents the "internodal" region between two successive dichotomies of an axis. In ontogeny, a given telome becomes "converted" to a mesome if dichotomous branching continues (see Fig. 3-8, upper right). From a functional standpoint, telomes are classified as "fertile" when they terminate in sporangia, and as "vegetative" when they constitute "phylloides." A system of united telomes and mesomes, as illustrated in Fig. 3-8, is termed a "primordial syntelome." Anatomically, the entire telome system is vascularized by a continuous protostele and is further morphologically differentiated into a creeping subterranean portion, composed of rhizoid-bearing telomes and an upright aerial portion terminating in sporangia and phylloides.

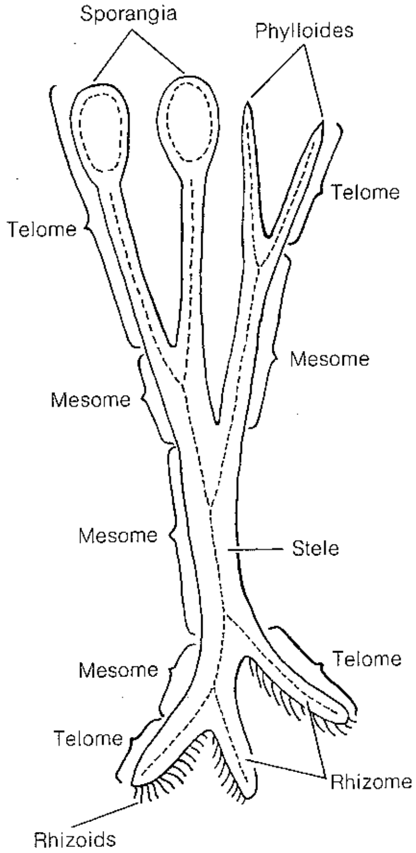
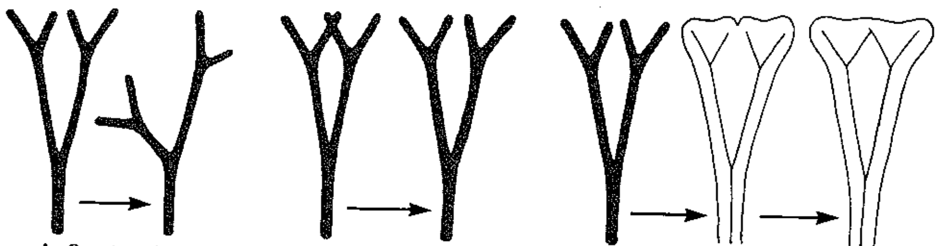
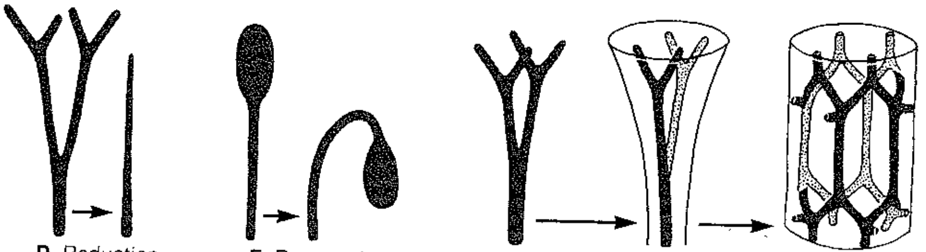


FIGURE 3-8 Simplified diagram showing the general organography of a primordial vascular land plant of the type of *Rhynia*. The morphological "units" of this elemental sporophyte (or "primordial syntelome"), according to Zimmermann's concept, are telomes (i.e., sporangia and vegetative phylloides) and mesomes. The telomes of the underground creeping rhizome bore rhizoids. See text for further explanation. [Adapted from *Die Telomtheorie* by W. Zimmermann. Gustav Fischer Verlag, Stuttgart. 1965.]

According to Zimmermann, the further phylogenetic development of the *Rhynia* type of telome system resulted from the operation of five "elementary processes" (Fig. 3-9). Independently — or more commonly in various combinations — these processes were responsible for the gradual evolution of the diverse types of leaves and sporophylls (sporan-



A. Overtopping **B.** Planation **C.** Fusion in leaf phylogeny



D. Reduction **E.** Recurvation **F.** Fusion in stem phylogeny

FIGURE 3-9 Diagrams illustrating the five elementary processes that, beginning with primordial system of telomes (see Fig. 3-8), were operative in the phylogenetic specialization of vascular plants. See text for further explanation. [Adapted from *Die Telomtheorie* by W. Zimmermann. Gustav Fischer Verlag, Stuttgart. 1965.]

gium-bearing structures) characteristic of the main taxa of vascular plants.

One of the most important of the elementary processes was "overtopping," i.e., the unequal development of certain parts of a dichotomously branched system, the subordinated overtopped lateral members representing the beginning of "leaves," and the overtopping portions, stemlike axes (Fig. 3-9, A). The additional processes of planation and "fusion" (syngenesis) are considered by Zimmermann to have been particularly significant with reference to leaf and sporophyll evolution. Planation resulted in the arrangement of groups of telomes and mesomes in a single plane (Fig. 3-9, B) while fusion, which at first only entailed parenchyma formation, connected these units into a flat dichotomously veined lamina. Subsequent fusion of the vascular strands in the leaf led to the formation of reticulate venation and fusion in the stem resulted in the anastomosis of the originally separate steles (Fig. 3-9, C, F).

According to the telome theory the elementary process of "reduction" accounts for the origin of the microphyllous type of leaf (Figs. 3-9, D; 3-10). This interpretation rejects the "enation theory" of microphyll evolution (see pp. 30–31) and holds that *both* microphylls and megaphylls originated from subordinated and dichotomously branched portions of a primordial syntelome (see Zimmermann, 1965). Following planation and webbing, a group of telomes became progressively reduced to a single univeined "needle-leaf" or microphyll (Figs. 3-9, D; 3-10). It is of interest to note that Zimmermann's phylogenetic concept of the origin of microphylls includes not only the foliar organs of the Lycophyta but also the univeined leaves of such members of the Sphenophyta as *Equisetum* and the needle-leaves of the Coniferales.

Some support for the reduction concept is derived from the study of certain Devonian lycopods (e.g., *Protolepidodendron, Leclercqia*) in which leaves were bifurcated or had more than two distal segments (Chapter 9). It is possible, of course, that microphylls may have originated phylogenetically in various groups either by the progressive method (enation concept) or by the processes of reduction. The final solution will depend upon future paleobotanical discoveries.

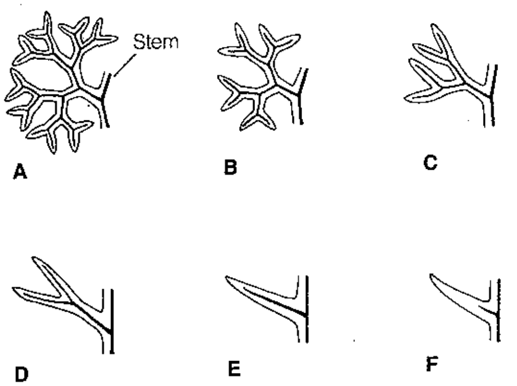


FIGURE 3-10 Origin of the microphyll by processes of reduction from a dichotomizing lateral branchlike system, according to the telome theory (**A–F**). [Redrawn from *Die Telomtheorie* by W. Zimmermann. Gustav Fischer Verlag, Stuttgart. 1965.]

The elementary process of "recurvation" was responsible for the phylogenetic origin of the sporangium-bearing organs of the Sphenophyta. Recurvation, as conceived by Zimmermann, is a process resulting in the bending or "anatropous curvature" of the stalks of a group of sporangia, and is illustrated by the single curved fertile telome represented in Fig. 3-9, E. Subsequent fusion of the bases of the curved sporangium stalks led to the distinctive peltate sporangiophores of the strobilus of the modern genus *Equisetum* (see Zimmermann, 1965; Chapter 10, Fig. 10-12, A).

It was, of course, inevitable that the telome theory, because of its comprehensiveness, would elicit decidedly mixed reactions from paleobotanists and morphologists. In his most recent monograph, Zimmermann (1965) vigorously defended his theory and rejected the numerous objections that have been raised against it. He concludes his book with the statement that the "universality" of his concept has dealt with all the "test cases" and that, so far, no alternative theory has been proposed that so satisfactorily accounts for the enormous diversity of vascular plants as the telome theory.

It should be strongly emphasized that Zimmermann's concept of phylogeny is "hologenetic"—i.e., he regards evolution as the result of the *progressive modification* of ontogenetic processes which have been in operation over a time span of many millions of years. In more explicit terms, an ontogenetically *mature* structure, such as a telome or a system of telomes, does not give rise to a more advanced type of mature organ, such as a microphyll or a megaphyll. On the contrary, from the standpoint of hologeny, new types of fertile and sterile organs are the result of *changes in the genotype* that in turn are expressed ontogenetically by the gradual modification in the organs and structures formed by the embryo and the apical meristems of the developing plant. (For a more detailed discussion of hologeny, see Zimmermann, 1966.)

Recent paleobotanical discoveries have detracted somewhat from the telome theory. Zimmermann selected *Rhynia* (see Chapter 7) from the Devonian as the prototype. One can also cite another genus, *Cooksonia* (mid-Silurian), unknown to Zimmermann when he formulated his concept, in support of his theory. *Cooksonia* was basically dichotomously branched and had terminal sporangia. However, several genera from the Lower Devonian had lateral sporangia on their stems, although the rhyniophyte *Renalia* (see Chapter 7) could be cited as showing how overtopping and reduction functioned to produce short lateral branches with terminal sporangia (see Chapter 7). Paleobotanists will continue to test the validity of the telome concept as they discover other plants of the Silurian and Lower Devonian.

Comparative Anatomy of the Sporophyte

The organographic evolution of the sporophyte has reached various levels in the different groups of living vascular plants. Paleobotanical evidence reveals that the evolution of cell types and tissues was similarly complex and variable. Indeed, one of the most important achievements in paleobotany has been the discovery and description of the well-preserved anatomy of several ancient groups of vascular plants. This has made possible at least the beginning of a true phylogenetic interpretation and classification of cell types and tissues (Foster, 1972). It seems reasonable to conclude this chapter with a brief review of the outstanding aspects of sporophyte anatomy. Of course, this resume should in no sense be regarded as a satisfactory condensation of the vast subject matter of plant anatomy (Esau, 1965), but we hope that it will provide the indispensable orientation needed by readers in an introductory approach to the comparative anatomy of stem, leaf, and root.

Sachs' Classification of Tissue Systems

One of the most useful schemes for understanding the general topographical anatomy of the adult sporophyte was devised by the celebrated German botanist, Julius von Sachs (1875). The great merit of his classification is its simplicity and its wide applicability to the primary structure of the stem, leaf, and root. According to Sachs, the early phylogenetic development of vascular plants resulted in the differentiation of three principal systems of tissues: the external epidermal and cork layers collectively termed the *dermal system;* the strands of conducting phloem and xylem tissue which compose the *fascicular system;* and the remaining internal tissue or tissues designated the *fundamental* or *ground tissue system.* Sachs emphasized that each of these tissue systems may comprise the most varied cell types and that his scheme of classification was concerned with the broadest possible contrast between systems of tissues.

Figure 3-11 shows diagrammatically the application of Sachs' classification and terminology to the gross anatomy of the stem, leaf, and root of flowering plants. This figure indicates plainly that the fascicular tissue system is the most variable of the three, from the standpoint of its pattern of development within plant organs. In stems the fascicular system appears either as a central cylinder of phloem and xylem or in the form of vascular bundles arranged in a cylinder or scattered throughout the ground tissue system (see Fig. 3-11, A; also Fig. 3-20). The form of the fascicular system of the leaf ranges from one to many bundles or a cylinder in the petiole, to a complex system of veins, usually arranged in a single plane, in the lamina (Fig. 3-11, B). In the root the pattern of the fascicular system is very distinctive, consisting of a radial and alternate series of phloem and xylem strands; commonly the latter are joined at their inner edge to form a solid core of xylem as shown in Fig. 3-11, C.

In contrast with these diverse patterns exhibited by the fascicular system, the form and arrangement of Sachs' other tissue systems are comparatively simple. The dermal system, in all foliar organs and in young stems and roots, is represented by the epidermis (Figs. 3-11, 3-12). Typically this is a single layer of superficial cells which are tightly joined except for the stomatal openings; in some groups of dicotyledons the leaf may develop on one or both surfaces a multiple epidermis consisting of two or

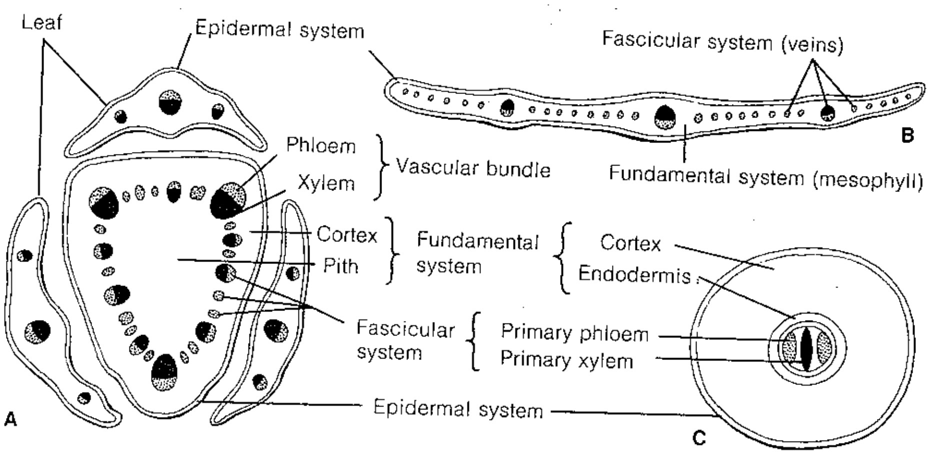


FIGURE 3-11 Diagrams (based on *Linum usitatissimum*) illustrating the positions and patterns of the epidermal, fascicular, and fundamental tissue systems in the vegetative organs of a dicotyledon. A, transection of stem and three leaf bases; B, transection of lamina of leaf; C, transection of root. [Redrawn from *Plant Anatomy* by K. Esau. Wiley, New York. 1953.]

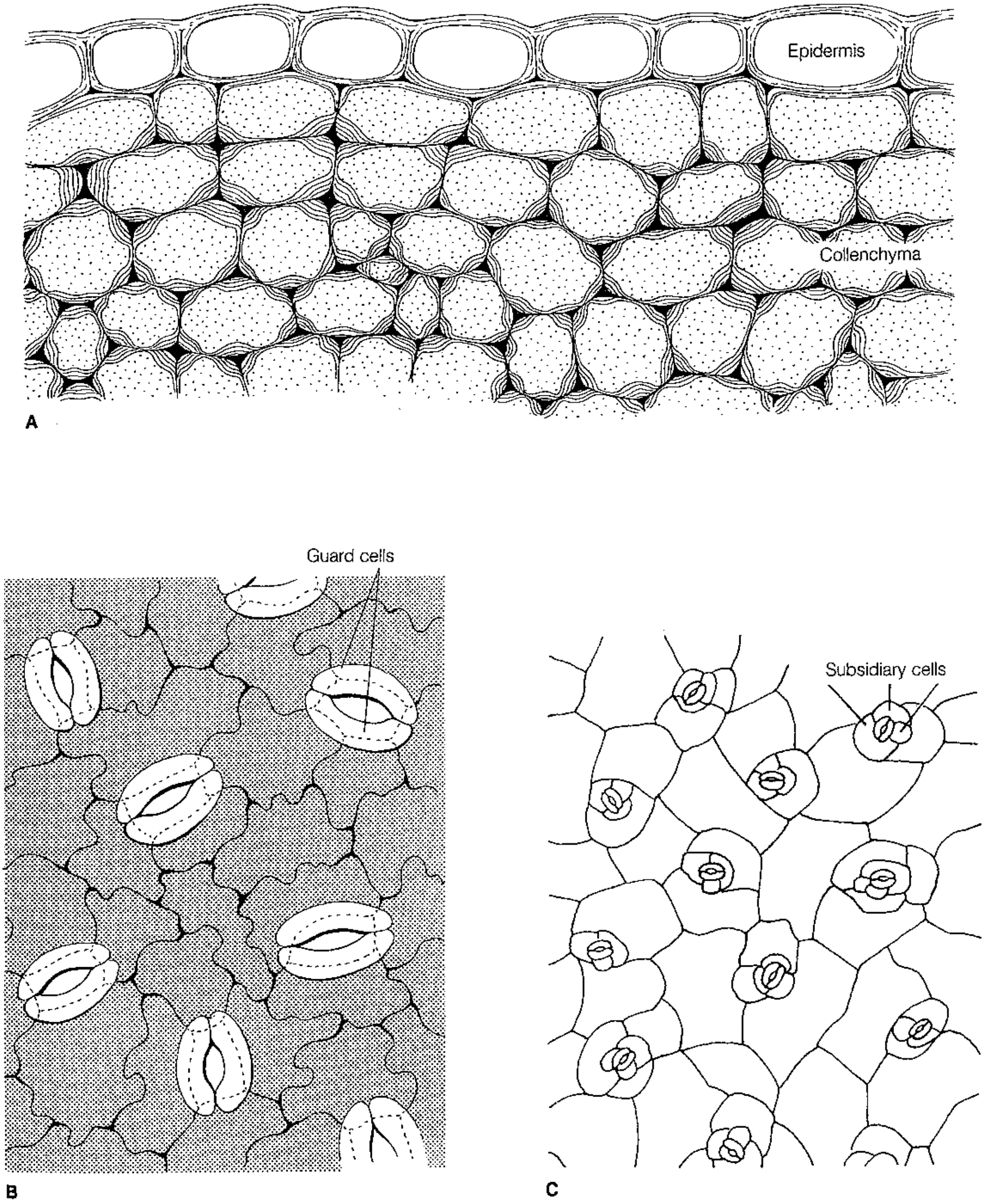


FIGURE 3-12 A, transection of epidermis and collenchyma tissue in stem of *Cucurbita;* **B,** surface view of stomata in lower epidermis of leaf of *Capsicum;* C, surface view of stomata with subsidiary cells in lower epidermis of leaf of *Sedum.* [A, redrawn from *Plant Anatomy* by K. Esau. Wiley, New York. 1953; **B,** courtesy of E. F. Artschwager; C redrawn from *Anatomy of Seed Plants,* 2d edition, by K. Esau. Wiley, New York. 1977.]

many layers of cells, all of which have originated from the subdivision of the original surface layer of cells (Fig. 3-13, C). In the stems and roots of many vascular plants the epidermis is eventually sloughed away by the development beneath it of *cork*. Like the cells of the epidermis, cork cells are compactly arranged, and it is only at certain areas known as lenticels that well-developed intercellular air-space systems are found. Situated below the dermal system and external to or surrounding the fascicular system is the fundamental tissue system (Fig. 3-11). In dicotyledonous stems, for example, this tissue system is represented by the cortex—a cylinder of tissues between epidermis and phloem, and the pith—a central column of parenchyma (see Fig. 3-11, A). The stems of the majority of the Lycophyta and the roots of most plants develop the cortical portion of the fundamental system but lack a pith (Fig. 3-11, C). In the lamina of leaves the photosynthetic mesophyll represents the fundamental tissue system (Fig. 3-11, B).

Structure and Development of Tissue Systems

In addition to its value in the topographical description and comparison of primary tissue systems, Sachs' scheme is very helpful in the morphological interpretation of *tissue development* at the apices of shoots and roots. Apical meristems, as shown by numerous studies, are extraordinarily variable in their histology. (See Esau, 1965; Gifford, 1954; Gifford and Corson, 1971, for literature on the subject.) In some plants, for example, *Equisetum* and the leptosporangiate ferns, a single well-defined apical cell occupies the tip of the axis and represents the ultimate point of origin of all the meristematic tissue of the apex of root and shoot (see Fig. 19-28). However, the shoot apices of *Lycopodium*, of certain eusporangiate ferns, and of a great many gymnosperms possess several superficial apical initials. And finally, the shoot apices of the angiosperms have a typical stratified arrangement of cells, the outer layer or layers being the *tunica*, which surrounds a central mass of meristem designated the *corpus*; in this type of apex, the number and position of individualized apical initials is very uncertain in most instances (Figs. 3-1, B; 19-18). Despite the histological differences among the types of apices in vascular plants, an essentially similar pattern of early histogenesis or tissue formation is common to all of them. This consists in the ultimate segregation, behind the apex of shoot and root, of three primary meristematic tissues: the *protoderm*, the *procambium*, and the *ground meristem* (Fig. 3-1). These tissues are the precursors of the epidermal, fascicular, and fundamental tissue systems, respectively; we will now briefly examine their salient features.

THE EPIDERMIS. The protoderm, derived from the cells of the shoot or root apex, is a uniseriate layer of dividing cells that ultimately forms the epidermis of mature organs (Figs. 3-1, 3-12, 3-13). Certain protoderm cells enlarge, acquire cutinized outer walls, and differentiate as the typical epidermal cells of leaves and stems. In many plants large numbers of protoderm cells develop into the various types of epidermal appendages or trichomes. The stomata are characteristic of the epidermal system of foliage leaves, and many types of stems, floral organs, and fruits (Fig. 3-12, B, C). Paleobotanical evidence shows clearly that stomata were present in such ancient and simple vascular plants as the Rhyniophyta. Stomata develop by the division and differentiation of certain protoderm cells into pairs of guard cells between which a stomatal opening or pore is formed. In many plants two or more of the cells bordering upon the stoma are distinctive in form and are termed subsidiary cells (Fig. 3-12, C). The epidermis of fossil plants, particularly the arrangement and structure of its stomata, provides very important clues about the phylogeny and relationships of extinct vascular plants.

THE FUNDAMENTAL TISSUE SYSTEM. This system of tissues originates from the ground meristem and is represented by the tissues found in the cortex of stems and roots, the pith of stems, and the mesophyll of foliar organs (Figs. 3-1; 3-11). In contrast to the elongated and often spindle-shaped procambial cells, ground meristem cells, prior to differentiation, are polyhedral cells which closely approximate tetrakaidecahedra (fourteen-sided bodies) in form. Cells of this type very commonly enlarge,

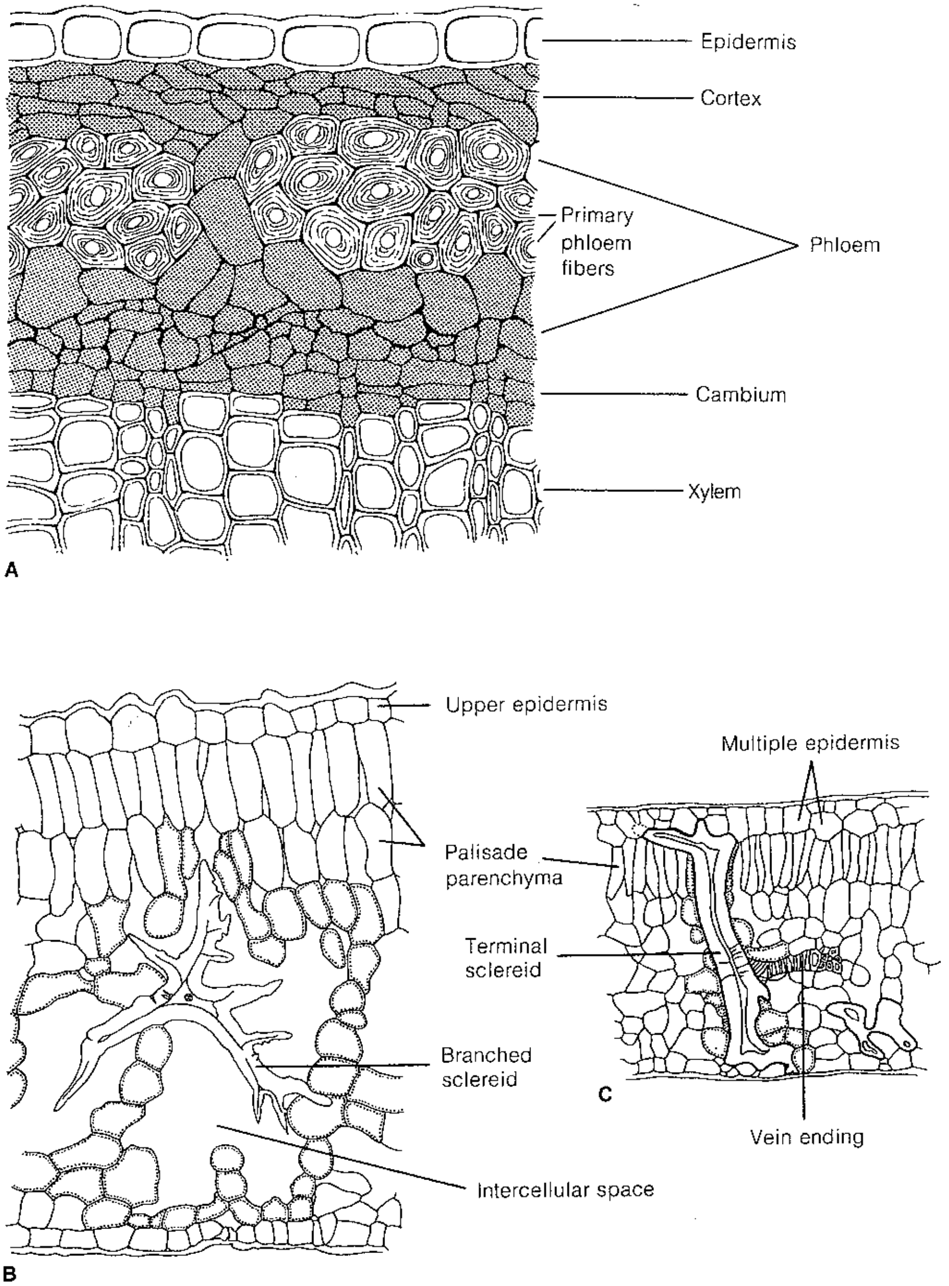


FIGURE 3-13 **A,** transection, stem of *Linum usitatissimum* illustrating position of strands of primary phloem fibers; **B,** transection, portion of lamina of *Trochodendron aralioides* showing a branched sclereid; **C,** transection, portion of lamina of *Mouriria huberi,* showing a columnar, ramified terminal sclereid. [**A,** redrawn from *Plant Anatomy* Ed. 2, by K. Esau, Wiley, New York, 1965; **B,** redrawn from A. S. Foster, *Amer. J. Bot.* 32:456, 1945; **C,** redrawn from A. S. Foster, *Amer. J. Bot.* 34:501, 1947.]

become separated by intercellular spaces, and mature into the parenchyma tissue, which often is the principal component of the fundamental tissue system. But additional cell types and tissues may originate from unspecialized ground meristem and become part of the fundamental tissue system of plant organs. A common example of this is *collenchyma,* which is very commonly developed in the outer region of the cortex of stems and in the subepidermal region of petioles (Fig. 3-12, A). In the ontogeny of collenchyma the ground meristem cells divide and elongate, ultimately producing compact strands or a cylinder of living cells with unevenly thickened primary walls; very commonly the thickest portions of the wall are laid down at the angles or corners where several collenchyma cells meet. Regarded functionally, collenchyma tissue provides support and flexibility for growing organs and at maturity is characterized by considerable tensile strength.

Another extremely common type of tissue in the fundamental tissue system is *sclerenchyma,* which is composed of cells with thick, lignified secondary walls. Two fairly well-demarcated cell types are included under sclerenchyma: *fibers,* which typically are conspicuously elongated cells with pointed ends, and *sclereids,* which are polygonal (the so-called stone cells), columnar, or profusely branched in form. At maturity fibers very commonly are dead cells, devoid of cytoplasm, and occur as strands or cylinders of tightly joined cells which evidently provide mechanical strength to plant organs (Fig. 3-13, A). Sclereids may occur in compact masses in various parts of the fundamental tissue system, but they also occur as isolated cells or *idioblasts.* In the leaves of many dicotyledons, branched idioblastic sclereids are frequently diffuse in their distribution in the mesophyll (Fig. 3-13, B), but in certain genera the sclereids are terminal, or restricted to the vein endings (Fig. 3-13, C).

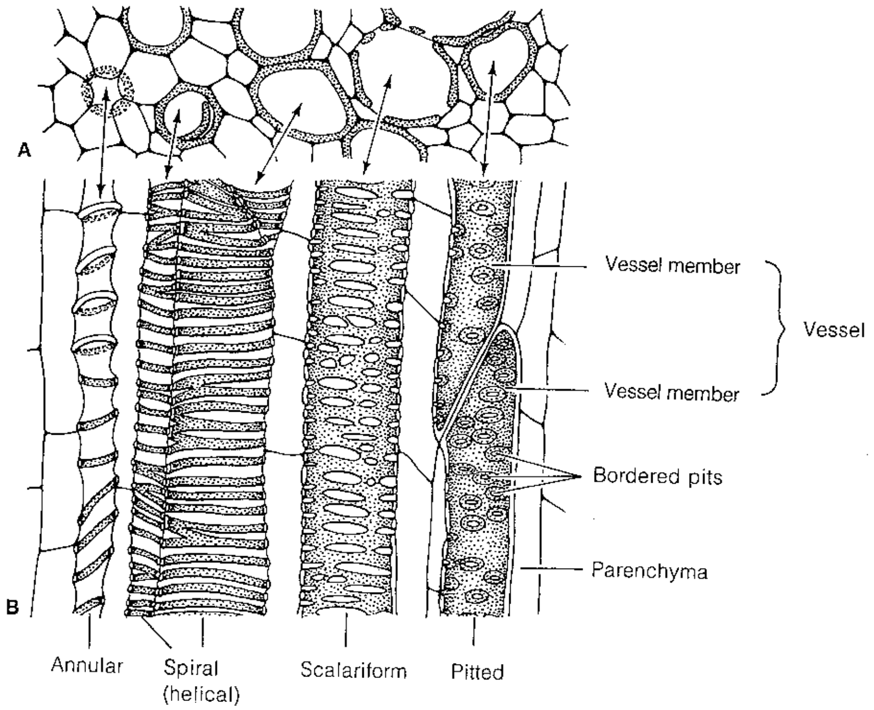


FIGURE 3-14 A portion of the primary xylem of the stem of *Aristolochia* in transverse (A) and longisectional (B) view. Note diversity in types of secondary wall patterns of tracheary elements in progressing from protoxylem at left to metaxylem at right. [From *Plant Anatomy* by K. Esau. Wiley, New York. 1953.]

THE FASCICULAR TISSUE SYSTEM. From what we have said regarding the variable patterns of the fascicular system, a corresponding variability is to be expected in the patterns of procambium formation in young organs. In the young, terminal regions of many stems (particularly the stems of gymnosperms and angiosperms) and in differentiating leaves the procambium consists of discrete cellular strands composed of elongated cells (Fig. 3-1, B); each strand matures as a vascular bundle composed of primary phloem and primary xylem tissue. In the stems of certain lower vascular plants (*Lycopodium,* and certain ferns) and in many roots, the procambium is a central core or column of tissue from which the vascular cylinder, devoid of pith, originates.

It is important first to understand the general structure and organization of primary xylem and the meaning of the terms *protoxylem* and *metaxylem.* Protoxylem designates the pole of earliest developed primary xylem and includes all tracheary tissue that differentiates (i.e., completes its growth and secondary wall development) during the period of organ elongation. Tracheary elements of the protoxylem, as shown in Fig. 3-14, often develop their secondary walls as a series of rings (annular elements) or as one or more spiral bands (spiral elements). The metaxylem is the remaining portion of the primary xylem, which completes its differentiation after the organ in which it occurs has ceased to elongate. Metaxylem cells, also shown in Fig. 3-14, usually have more extensively developed secondary walls which commonly appear as a series of connected bars (scalariform elements) or a network (reticulate elements), or else the wall is pitted.

The common and basic type of tracheary element in the xylem of vascular plants is the *tracheid.* A tracheid is a water-conducting cell, dead at maturity, generally elongate, with a lignified secondary wall. The dimensions of tracheids vary considerably among different vascular plant groups. In ferns, cycads, and conifers the length varies from about 1 millimeter to 5 to 7 millimeters, whereas in most flowering plants (angiosperms) a tracheid may be 1 to 2 millimeters or less in length. A conspicuous morphological feature of tracheids with extensive secondary walls is the occurrence of pits (Fig. 3-15). Pits are not complete holes, but are small areas lacking secondary wall deposition. The pits occur opposite each other (pit pairs) in adjacent cells. This alignment more readily permits the movement of water through the xylem.

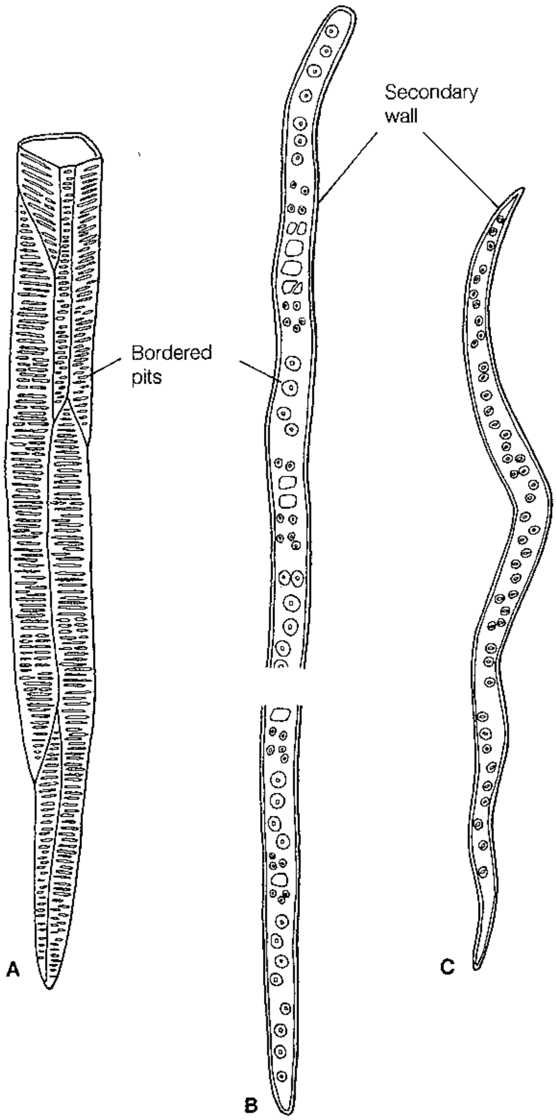


FIGURE 3-15 Representative tracheids from three major groups of vascular plants. **A,** *Woodwardia,* a fern (one-sixth of cell shown). **B,** *Pinus,* a conifer (one-third of cell shown). **C,** *Quercus,* oak. [Redrawn from *An Introduction to Plant Anatomy* by A. J. Eames and L. H. MacDaniels, McGraw-Hill, New York. 1947.]

The second type of tracheary element is the *vessel member,* which may resemble a tracheid but has at maturity several actual holes (perforations) or

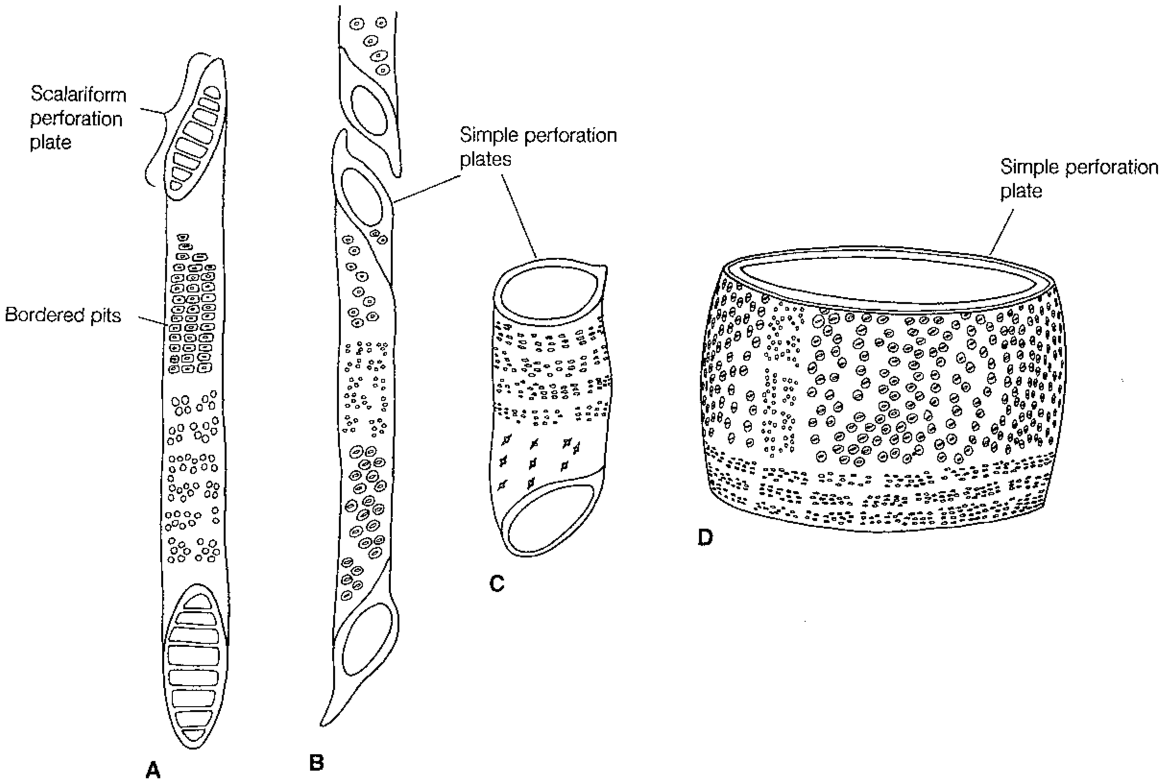


Figure 3-16 Representive angiosperm vessel members. **A**, *Liriodendron* (tulip tree); **B**, *Quercus* (oak); **C**, *Acer* (maple); **D**, *Quercus*. [Redrawn from *An Introduction to Plant Anatomy* by A. J. Eames and L. H. MacDaniels. McGraw-Hill, New York. 1947.]

one large hole at each end of the cell (Fig. 3-16). Several to many vessel members, joined end to end, constitute a *vessel*. The possession of vessels is the prevailing condition in angiosperms (Magnoliophyta), and they also occur in some other groups of vascular plants. Pits occur in the lateral walls where each vessel member is in contact with the other tracheary elements and parenchyma (Fig. 3-16). Perforations permit the conduction of a larger volume of water per unit of time by reducing the impedance to water.

It must be emphatically stated that the primary xylem may consist wholly of tracheids or of both tracheids and vessel members. The type of secondary wall pattern is therefore not necessarily correlated with the presence or absence of vessel members.

Because the xylem of extinct plants is often well preserved in fossils, the recognition of the position of protoxylem in relation to metaxylem is a matter of considerable significance in phylogenetic interpretations. In the roots of all vascular plants, in the stem of *Psilotum*, and in the majority of all investigated Lycophyta, the first protoxylem cells to acquire secondary walls occur at the outermost edge (in the direction of the surface of stem and root) of the procambial cylinder; these cells establish the future pattern of xylem differentiation which

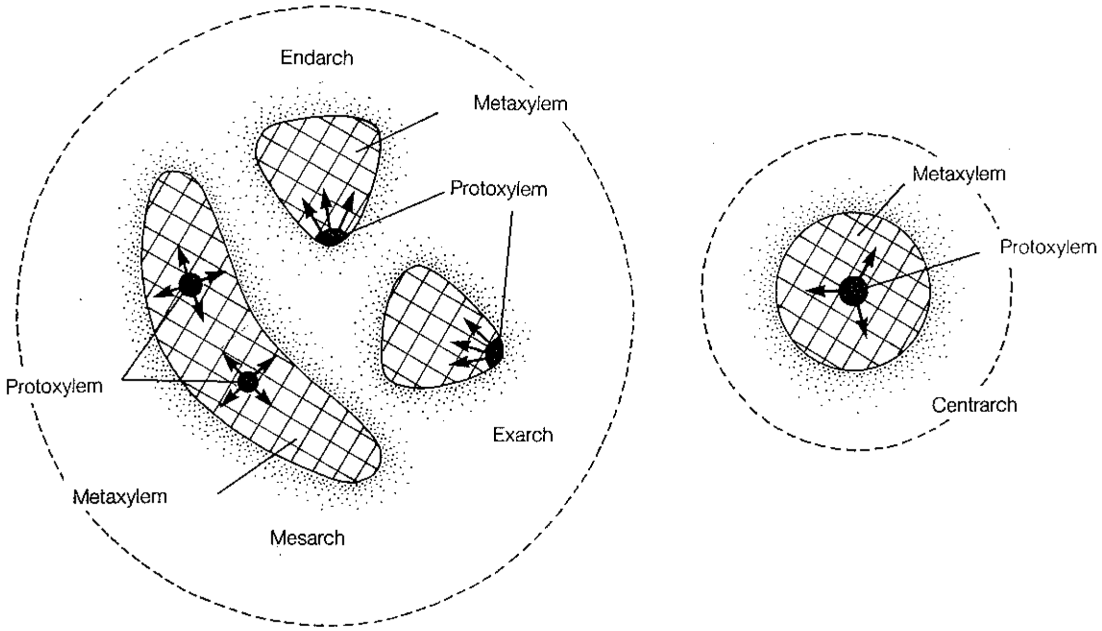


FIGURE 3-17 Schematic representation of the directions of radial maturation of tracheary elements in the primary xylem of vascular plants. Broken lines indicate the periphery of the stems.

occurs *centripetally*—toward the center of the axis. Primary xylem of this type is termed *exarch* and is regarded as a primitive condition in vascular plants (Fig. 3-17). In the stems of modern seed plants, however, the protoxylem begins its development from the innermost procambial cells—those situated next to the pith—and the remainder of the process of primary xylem differentiation occurs *centrifugally* or toward the periphery of the stem (Fig. 3-17). This type of primary xylem is termed *endarch xylem* and is believed to be the most highly advanced type. In the leaf and stem bundles of many ferns the primary xylem is *mesarch*. This means that the protoxylem begins development within a procambial strand and that further xylem formation occurs centripetally as well as centrifugally; consequently, at maturity the protoxylem cells are surrounded by the metaxylem, as can be seen in Fig. 3-17. Another type, *centrarch* xylem, is now recognized in certain extinct plants of the Devonian. In these plants (e.g., *Rhynia*) there is but one vascular strand in the stem and the protoxylem is in the center (hence, centrarch) surrounded by metaxylem (Fig. 3-17; see also Chapter 7). The distinction between these types of xylem maturation is of considerable importance, not only among different groups of vascular plants but even between root and stem of the same plant.

The specialized types of cells involved in translocation of photosynthetic products are termed *sieve elements*. A definitive feature, at least in angiosperms, is the absence at maturity of a nucleus and the presence of more or less specialized *sieve areas* and *sieve plates* in the cell walls. A sieve area is a modified portion of the primary wall traversed by connecting strands of protoplasm. Each of these, at an early ontogenetic stage, is surrounded by a cylinder of *callose* (1 → 3(-β-d)-glucan), a carbohydrate differing from cellulose in the type of linkage between molecules. One type of sieve element is the *sieve cell* that occurs in lower vascular plants and gymnosperms. The sieve cells are elongate and often have numerous sieve areas (Fig. 3-18, A, B). Each sieve area is matched by another one in an adjacent sieve cell, thus providing an interconnected system throughout the phloem. In many angiosperms the sieve elements (termed *sieve-tube members*) occur in superposed series collectively termed *sieve tubes.* The end walls of sieve-tube members may have several large sieve areas (Fig. 3-18, C, D) or one large *sieve plate* in which the pores are larger than in sieve areas (Fig. 3-18, E–G). In addition to the specialized sieve elements (sieve cells and sieve-tube members), primary as well as secondary phloem may contain parenchyma, sclereids, and fibers. For detailed treatments of ontogeny and structure of both primary and secondary phloem consult Esau, Cheadle, and Gifford, 1953, and Esau, 1965, 1969, 1977.

Last we need to consider the concept of secondary vascular tissues and their demarcation from the primary vascular system. Secondary vascular tissues are produced from the *vascular cambium,* and since the cells of the secondary xylem are often arranged in radial rows this system of tissues often is clearly demarcated from the more irregular pattern of cells of the primary vascular system. But the criterion of orderly versus irregular cell arrangement is not always valid; in some angiosperms and gymnosperms the tracheary cells of the primary as well as the secondary xylem are in regular radial alignment. As a consequence, the boundary between the primary and secondary vascular systems can be only approximately determined even when the entire ontogenetic development has been studied. Secondary growth by means of a vascular cambium has repeatedly arisen during the evolution of vascular plants. Many extinct groups (for example, *Lepidodendron* and *Calamites;* see Figs. 10-27, B; 9-44) showed conspicuous secondary growth, and secondary growth is a prominent feature of all living gymnosperms and of a large number of the angiosperms. (See Chapters 17 and 19 for detailed descriptions of the secondary xylem of conifers and dicotyledons.) However, most of the lower vascular plants of today are devoid of cambial activity. In these organisms, as in most of the monocotyledons, the fascicular system is entirely primary and derived ontogenetically from the procambium.

The Stelar Theory

During the latter half of the nineteenth century the increasing emphasis placed on the importance of the vascular system in morphological interpretation led to the formulation of the stelar theory. This theory, which was developed by Van Tieghem and his students (Van Tieghem and Douliot, 1886) deserves our attention because of its far-reaching effects on modern concepts of the morphology and evolution of the primary vascular system. According to Van Tieghem, the primary structure of the stem and root are fundamentally similar in that each organ consists of a central *stele* enveloped by the cortex, the outer layer of which is the epidermis. The term stele was used in a collective sense by Van Tieghem to designate not only the primary vascular tissues but also the so-called conjunctive tissues associated with them: pericycle, vascular rays, and, when it occurs, the pith tissue.

One of the critical — and, in the light of modern studies, controversial — aspects of the stelar theory is the nature of the anatomical boundaries which separate the cortex from the stele. Van Tieghem considered that the inner boundary of the cortex is the endodermis, a cylinder of living cells which, from a strict histological viewpoint, are characterized by the presence of casparian strips. These strips or bands are chemically modified portions of the radial and end walls of the endodermal cells and are thought to contain both lignin and suberin.

In roots and in the stems of many of the lower vascular plants an endodermis is present and represents a tangible boundary between cortex and stele (Fig. 8-4, A). But an endodermis, in the sense just defined, is absent from the stems of a large proportion of the seed plants, especially woody types, and in plants lacking an endodermis the limits between cortex and stele are more difficult to establish. The pericycle likewise is not present in all vascular plants. Although the pericycle is a recognizable cylinder of cells at the outer edge of the stele of roots and the stems of lower vascular plants, ontogenetic

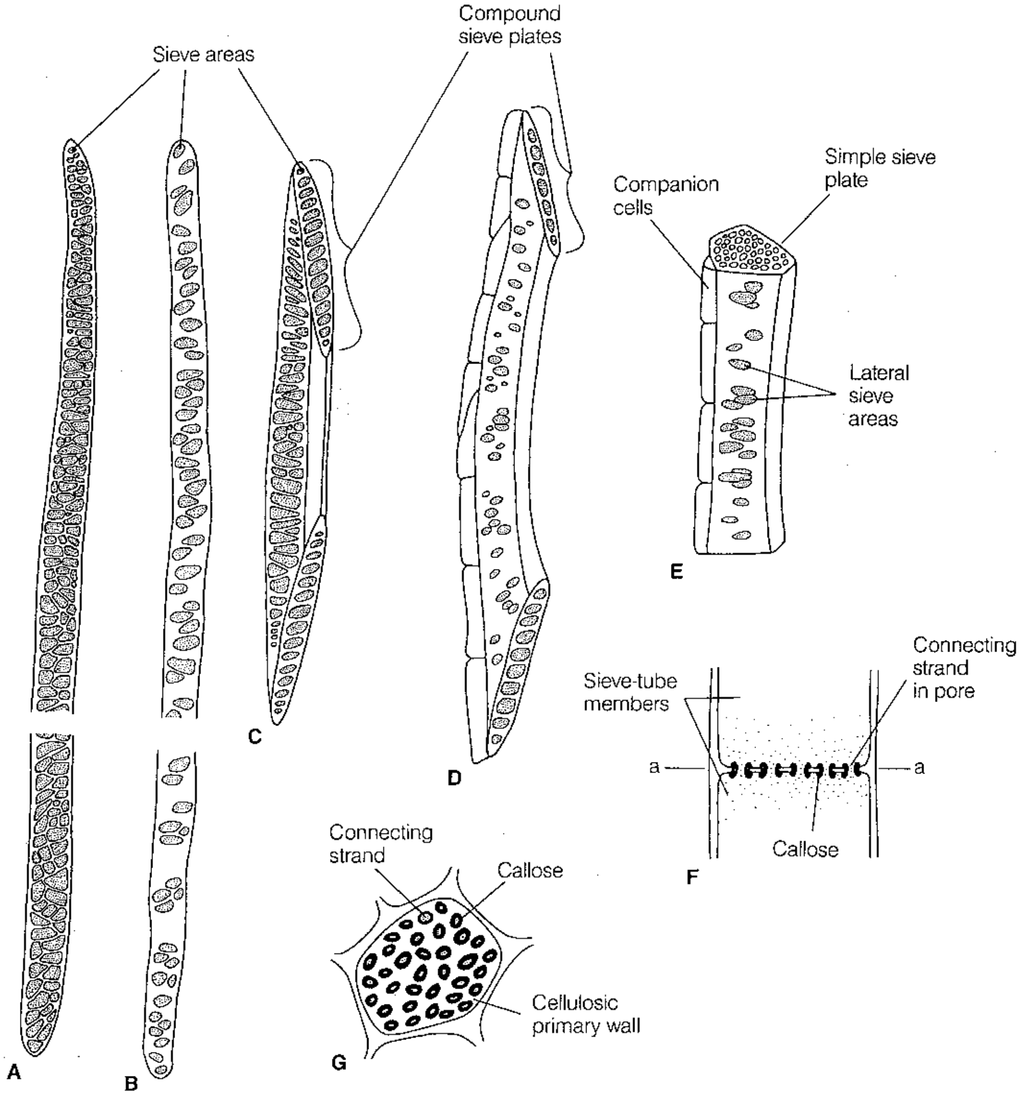


FIGURE 3-18 Sieve elements of various taxa. **A,** sieve cell, *Pteridium,* a fern (one-fourth of cell shown); **B,** sieve cell, *Tsuga,* a conifer (one-third of cell shown); **C,** sieve-tube member, Juglans, an angiosperm; **D,** sieve-tube member, *Liriodendron,* an angiosperm; **E,** sieve-tube member, *Robinia,* an angiosperm; **F,** schematic representation of a longitudinal section of a sieve plate; **G,** sieve plate in transverse section (plane a-a in **F**). [A–E redrawn from *An Introduction to Plant Anatomy* by A. J. Eames and L. H. MacDaniels. McGraw-Hill, New York. 1947.]

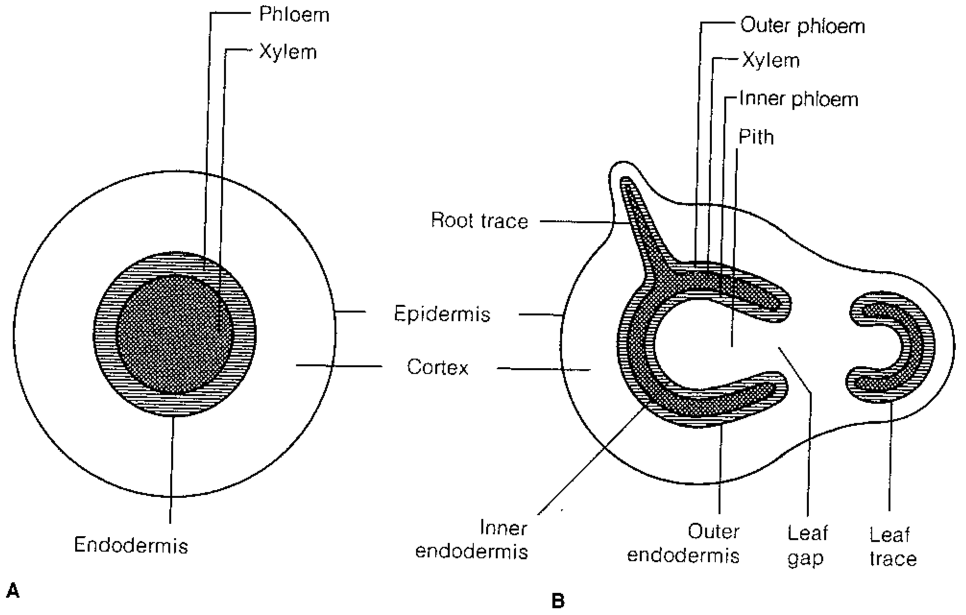


FIGURE 3-19 Types of steles in the stems of vascular plants. A, the protostele; B, the siphonostele. [Redrawn from *The Anatomy of Woody Plants* by E. C. Jeffrey. University of Chicago Press, Chicago. 1917.]

studies have shown that the so-called pericycle in the stems of many angiosperms is actually the outermost portion of the primary phloem (Blyth, 1958). In such instances there is no independent tissue zone separating the cortex from the stele.

Despite the absence of consistent histological boundaries between the cortex and stele, the value of the stelar theory as a unified concept has been widely recognized and has led to efforts to classify and interpret phylogenetically the varied types of vascular cylinders that occur in stems and roots.

Stelar Types

It is now rather generally agreed that from a phylogenetic as well as an ontogenetic standpoint the most primitive type of stele is the *protostele,* which is characterized by the absence of a central column of pith. In its simplest form the protostele is merely a central strand of primary xylem sheathed by a cylinder of phloem (see Fig. 3-19, A). This particular form of protostele is often termed a *haplostele.* In certain plants the contour of the core of xylem is lobed or star-shaped in transectional view — this form is designated an *actinostele* (Chapters 8 and 9). Interconnected strands of xylem, which in transection appear as separate plates of tissue between which occurs the phloem is a specialized type of protostele termed a *plectostele.*

A stele with a central column of pith, called a *siphonostele,* is regarded as an advance in anatomical development. There is considerable difference of opinion among morphologists concerning the phylogenetic origin of the pith which will be discussed in later chapters.

The histological structure of the siphonostele varies widely. In many fern genera the vascular cylinder consists of xylem surrounded on both sides by phloem and endodermal layers (outer endodermis, outer phloem and inner endodermis, inner phloem; Fig. 3-19). This condition is termed *amphiphloic,* and a stele with this construction is specifically termed a *solenostele.* Solenosteles commonly have *leaf gaps* (Fig. 3-19, B). A leaf gap occurs where parenchyma interrupts the vascular cylinder of the stem above the departure of a leaf trace and connects the cortex with the pith. The cylinder is complete again in the internode before another leaf trace departs at a higher level of the stem. In this case the leaf gaps are said to be nonoverlapping. In the region of the leaf gap, the inner and outer endodermal layers are continuous around the margins of the gap (Fig. 3-19, B).

Evolutionary modification of the solenostele in ferns is believed to have resulted in a type of stele with two or more overlapping leaf gaps at any given level of the stem. This type of vascular cylinder is termed a *dictyostele.* When visualized in three dimensions, a stele of this type is a network of interconnected vascular strands (Chapter 13). In some dictyosteles some of the parenchymatous regions are not truly leaf gaps, but interfascicular strips of parenchyma without a consistent relationship to the leaf trace system. This type of stele is termed a "dissected" dictyostele. A dictyostele, as viewed in transverse section of the stem, appears as a ring of separate bundles each of which is *amphicribral,* i.e., it is composed of a central strand of xylem surrounded by a sheath of phloem, followed by a pericyclic and an endodermal layer. A concentric bundle of this type is commonly called a "meristele"—a portion of the interconnected vascular system (Chapter 13). In some ferns only the outer phloem is present; this type of siphonostele is termed *ectophloic* (Chapter 13, Fig. 13-20, B).

In dicotyledons, the primary vascular cylinder also appears, in transections of the stem, as a ring of more-or-less discrete vascular bundles separated by areas of parenchyma (see Fig 3-11, A; and Chapter 19, Fig. 19-20, A). This stelar type, termed the *eustele* by Brebner (1902), is distinguished from the fern dictyostele by the collateral, or bicollateral, organization of the vascular strands. Most commonly, each vascular bundle is collateral, consisting of a strand of xylem flanked externally by a strip of phloem tissue (Fig. 3-11, A). In certain taxa of the dicotyledons (e.g., *Cucurbita*) the vascular bundles are bicollateral with phloem on both sides of xylem strands. It should be emphasized at this point that the divergence of leaf traces from a eustele is associated with parenchymatous areas that are usually regarded as leaf gaps. However, it proves very difficult to demarcate the limits of each leaf gap and, as we will show in Chapter 14, the concept of leaf gap in the eusteles of both dicotyledons and conifers has been rejected by several investigators.

In our brief account of stelar types, we have attempted to show the considerable value of the concepts of protostele, siphonostele, solenostele, dictyostele, and eustele in the interpretation of the diverse patterns of the primary vascular system of the axis. Monocotyledons, however, pose a very difficult problem because the primary vascular system of the stems in this group of angiosperms usually does not conform to any of the stelar types found in other groups of vascular plants. In place of a concentric cylinder of primary xylem and phloem, or a tube of anastomosed strands, the vascular bundles in the stems of monocotyledons appear dispersed or "scattered" in arrangement; no clear boundaries exist between cortex and pith, and the divergence of the numerous leaf traces at each node is obviously not associated with definable leaf gaps. Brebner (1902, p. 520), to whom we owe many terms used to designate stelar types, proposed the term *atactostele* (from the Greek root word "atactos" meaning "without order") for the stele in monocotyledons. He defined it as consisting of "a number of more or less irregularly arranged vascular bundles together with the ground tissue in which they are imbedded." However, in a recent review, Schmid (1982) has recommended that the term atactostele be abandoned and the term eustele be applied to monocotyledons also. Although the term "atactostele" has been widely adopted for descriptive purposes (Esau, 1965, 1977; Fahn, 1967; Zimmermann, 1959), determining the significance—ontogenetic or phylogenetic—of the scattered arrangement of bundles in monocotyledonous stems has proved a most difficult and elusive problem. The magnitude of the problem is well illustrated by reference to bundle number in certain palms. According to Zimmermann and Tomlinson (1965, p. 165), about 1,000 bundles occur in the small stem (2 to 3 centimeters in diameter) of *Rhapis excelsa,* and in stems of *Cocos,* one-half meter in diameter, there may be more than 20,000 vascular bundles "at any level"! In grasses, commonly used as examples of "typical" monocotyledons, the number of bundles is considerably less. Transections of the stem of *Secale,* for example, reveal a primary vascular system consisting of two rings of vascular bundles located in the outer peripheral region of the internode (Fig. 3-20, A). A contrasting pattern of bundle arrangement is illus-

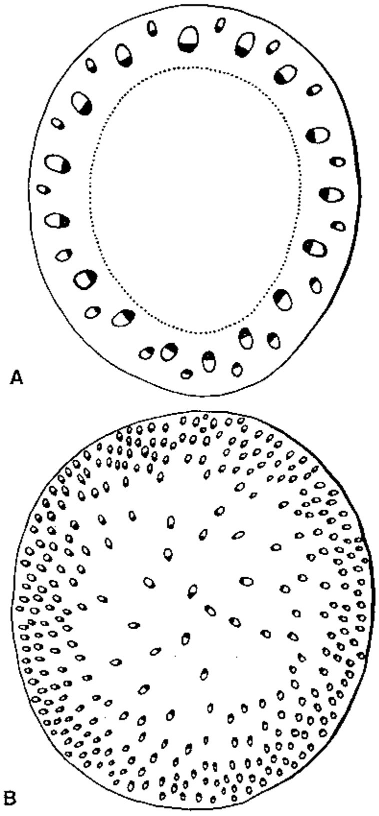


Figure 3-20 Transectional diagrams showing two patterns of vascular bundle arrangement in the stems of grasses. A, *Secale* (rye)—two "circles" of bundles at peripheral region of hollow stem; B, *Zea* (corn)—numerous bundles scattered throughout the transection. [Redrawn from *Allgemeine Botanik* by W. Troll. Ferdinand Enke Verlag, Stuttgart. 1959.]

trated by the stem of corn *(Zea)* in which numerous small bundles are closely spaced at the periphery, and larger, more widely spaced strands are distributed in the central region (Fig. 3-20, B).

To follow the course of vascular bundles in monocotyledonous stems is a difficult task. It is only in recent years that a series of studies was initiated by Zimmermann and Tomlinson designed to explain the course of vascular bundles in stems and their complex behavior with reference to the vascularization of leaves and axillary inflorescences. These investigators devised an "optical shuttle method" for photographing, by means of a motion picture camera, successive transections of the stems of *Rhapis* (Palmaceae) and *Prionium* (Juncaceae), enabling them to follow the course of vascular bundles. This method has resulted in considerable progress in reconstructing the extremely complex vascular system characteristic of these monocotyledons. Readers wishing further information should consult the original papers by Zimmermann and Tomlinson (1965, 1966, 1967, 1968, 1972) and the critical review by Beck et al. (1982).

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