CHAPTER 10

Sphenophyta

THE Sphenophyta is a well-defined group of living and extinct plants. The oldest fossil remains are from the Upper Devonian, and during the Carboniferous Period the group attained almost worldwide distribution and significant diversity of growth form. Arborescent and smaller sphenopsids coexisted during this period; however, by the end of the Jurassic Period (Mesozoic Era) only a few representatives remained, and they were relatively small plants. Today only one genus, *Equisetum,* with fifteen species, remains of this once conspicuous and diversified group. There is some evidence that *Equisetum* itself may have been present in the Carboniferous and may not have undergone any significant change since then. If this is so, *Equisetum* may be one of the oldest living genera of vascular plants in the world today.

The most conspicuous external morphological feature of the group as exemplified by *Equisetum* is the subdivision of the shoot axis into definite nodes and internodes — that is, the stem is jointed (Figs. 10-1, A, B; 10-2; 10-3). At the nodes are whorls of relatively small leaves that alternate with branches. In addition to the stem joints there are definite, easily observed longitudinal ridges on the stem. The reproductive structures of the sporophyte are terminal cones or strobili. The strobilus consists of an axis with whorls of stalklike structures (sporangiophores) with attached groups of eusporangia (Figs. 10-11, A, B; 10-12, A).

Classification

Hyenia, a fossil from the Middle Devonian, has been described as a possible early sphenopsid. The genus is now considered to be better aligned with the early ferns (order Cladoxylales) based upon the lack of the characteristic whorled arrangement of appendages, type of branching, and lack of any knowledge of its stem anatomy (Schweitzer, 1972). *Calamophyton,* a companion of *Hyenia,* also was removed from the sphenopsids (Leclercq and Schweitzer, 1965). However, Stewart (1983) believes that the two genera represent a "transitional group not far removed from their trimerophyte ancestors and sharing characteristics with the sphenopsids and Cladoxylales." Also, the extinct arborescent sphenopsids of the Carboniferous were previously placed in the order Calamitales. Paleobotanists are now inclined to combine the Calamitales with the Equisetales, based upon many morphological similarities.

SPHENOPHYTA: Living and extinct plants; sporophyte differentiated into stem, leaf, root, and eusporangium; jointed stems; monopodial

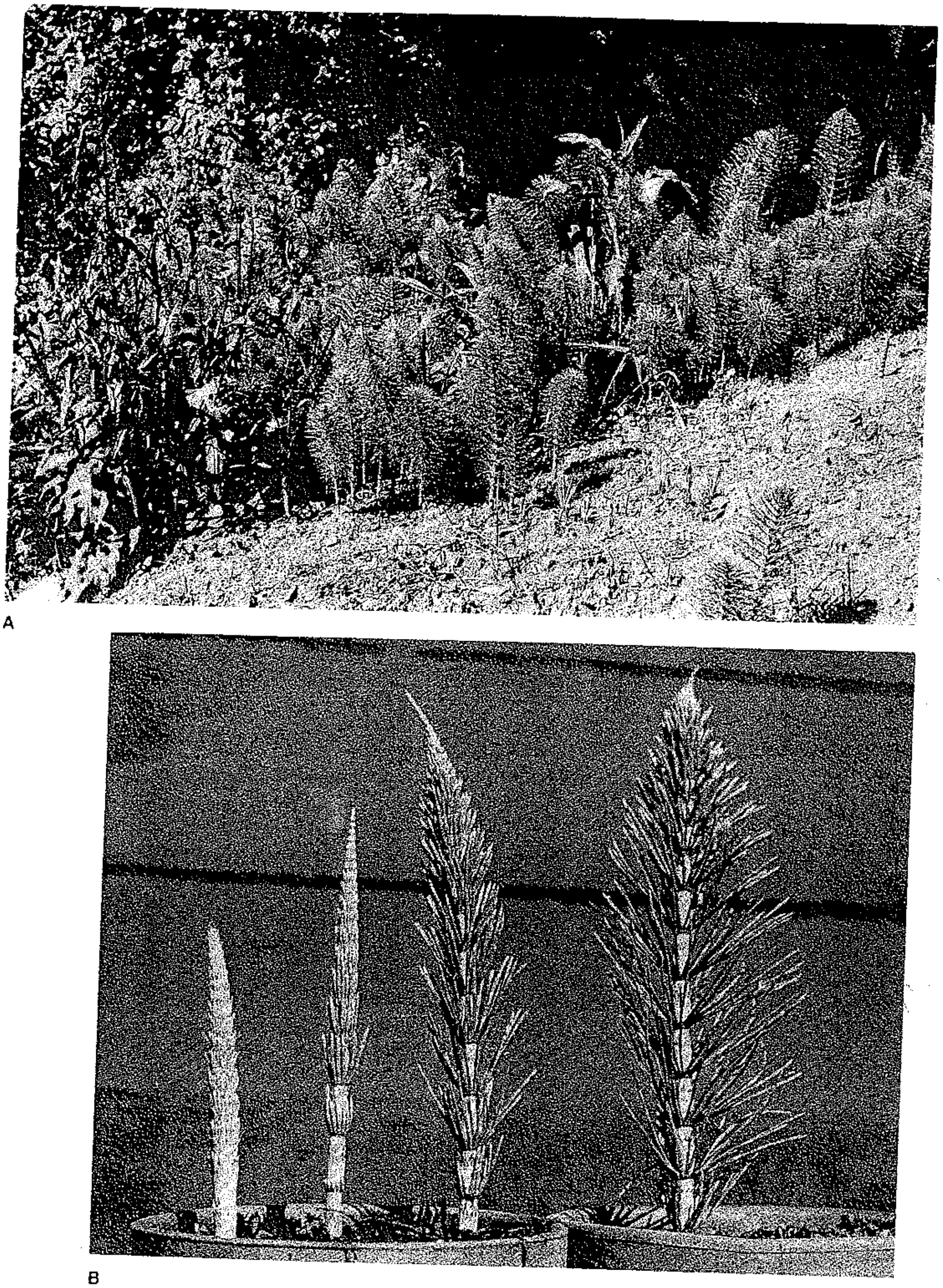


FIGURE 10-1 *Equisetum telmateia* subsp. *braunii*. **A**, colony growing along roadside embankment, Berkeley, California; **B**, series of plants arranged to show stages in the growth and expansion of vegetative shoots. [Courtesy Mr. Louis Arnold.]

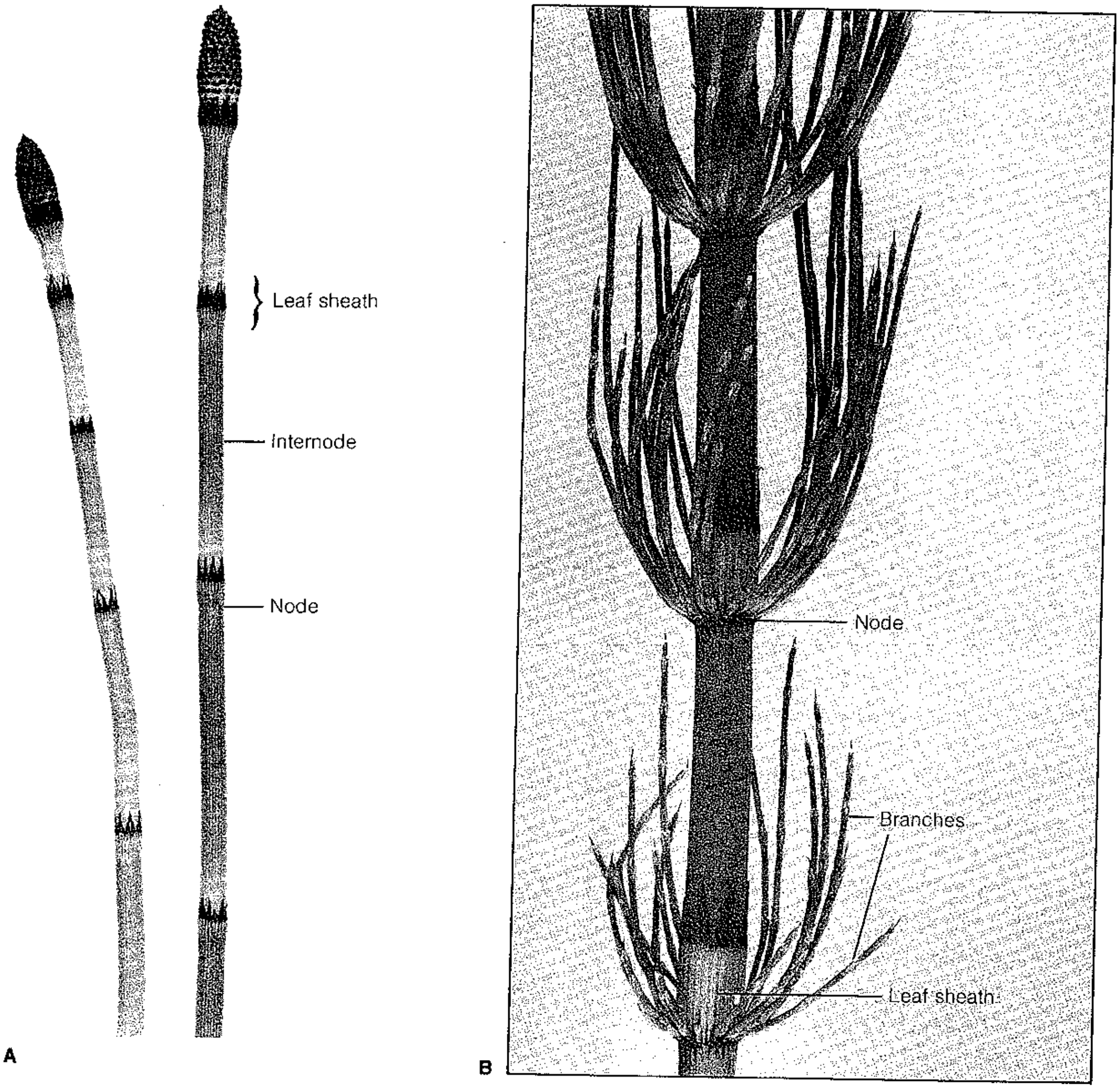


FIGURE 10-2 *Equisetum* shoots. A, *Equisetum hyemale,* portions of two unbranched shoots with terminal strobili. B, *Equisetum telmateia* subsp. *braunii,* portion of sterile (vegetative) shoot showing leaf sheaths and lateral branches.

branching; stem protostelic or siphonostelic; xylem exarch or endarch; secondary growth in some forms; sporangia borne on specialized stalks (sporangiophores) that are organized into strobili; mostly homosporous, some heterosporous (extinct).

EQUISETALES: Upper Devonian to present; living and extinct plants; ribbed stems; whorls of microphylls that are fused to form a sheath around the stem, or fused only at their bases; stems siphonostelic with endarch xylem; conspicuous protoxylem lacunae (carinal canals); internodal pith cavities; spores with elaters.

EQUISETACEAE: Permian to present; no secondary growth; microphylls fused to

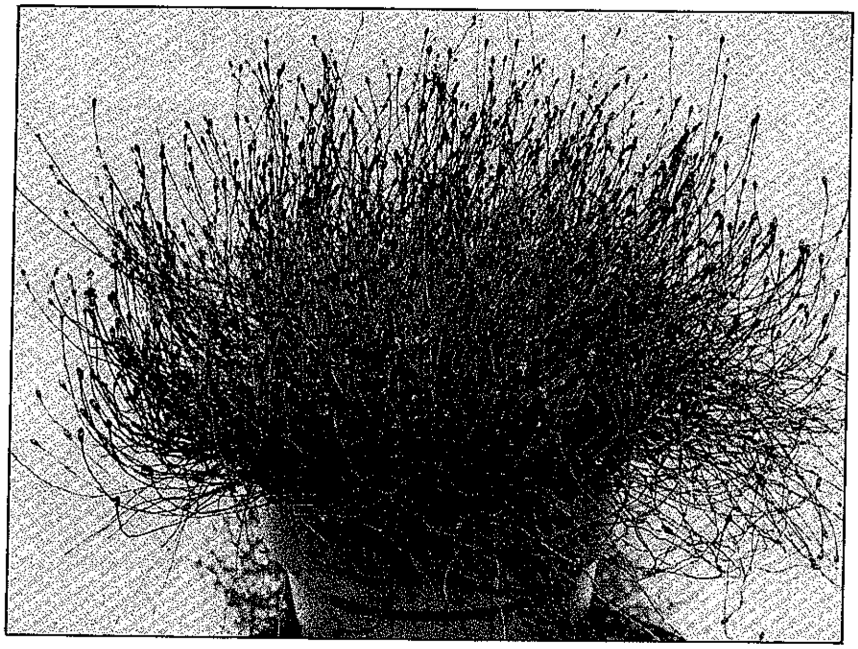


FIGURE 10-3 *Equisetum scirpoides.* A small species having unbranched aerial shoots with terminal strobili; grown under greenhouse conditions.

form a sheath around stem; strobili consisting only of whorled sporangiophores; strobili terminal on main vegetative stem, or occasionally on branches, or on a specialized strobiliferous stem; homosporous.

Equisetum, Equisetites (extinct).

CALAMITACEAE: Extinct plants from Carboniferous to Lower Permian; arborescent; secondary growth; microphylls fused at their bases to form a collar around the stem at the node; strobili consisting of (1) whorls of closely associated sporangiophores and bracts, or (2) alternate whorls of sterile bracts and sporangiophores; some heterosporous.

Calamites (pith casts, stem impressions); *Arthropitys* and *Calamodendron* (stem petrifactions); *Annularia* and *Asterophyllites* (leaves); *Palaeostachya* and *Calamostachys* (strobili).

SPHENOPHYLLALES: Extinct plants from Carboniferous to Lower Permian; small plants, either upright or trailing; stem protostelic, exarch xylem; secondary growth; leaves commonly with dichotomous venation; strobili composed of whorls of bracts and sporangiophores, the latter generally partially fused to bracts.

Sphenophyllum(stems, leaves, roots); *Bowmanites* and *Sphenostrobus* (strobili).

PSEUDOBORNIALES: Extinct plants from Upper Devonian; arborescent; three orders of branching; leaves in whorls on ultimate branches; strobili terminal on first order branches in upper portion of plant.

Pseudobornia ursina.

Equisetales - Equisetaceae: *Equisetum*

The sporophytes of *Equisetum*, with their characteristic jointed stems and rough texture, have several names—"horsetails" and "scouring rushes" are the most popular. During the American colonial period, horsetails were used as scouring agents, as they probably are today in some regions of the world. The American Indians used the stems of

Equisetum as an abrasive for polishing bows and arrows (Lloyd, 1964).

The horsetails are worldwide in distribution today, except for Australia and New Zealand. They generally grow in wet or damp habitats, being particularly common along the banks of streams or irrigation ditches (Fig. 10-1, A); some have become adapted to dry or mesophytic conditions, for at least a part of the year. In some localities they are a serious weed problem for farmers and a matter of concern for livestock owners because of the poisonous substances in the stems of some species. Horses are especially susceptible to their toxins. However, a certain species in Costa Rica is used medicinally, as a treatment for human kidney trouble (Hauke, 1969c). American Indians prepared infusions of certain species for treatment of various medical problems — to counteract diarrhea, to rid the hair of vermin, and as an eye wash (Lloyd, 1964).

Certain species are indicators of the mineral content of the soil in which they grow (Vogt, 1942). These plants accumulate minerals, including gold, up to 4½ ounces per ton (Benedict, 1941). This source of mineral information is therefore of some value in prospecting for new ore deposits.

The horsetails, despite the range of variation in branching and shoot dimorphism, are usually not mistaken for some other group, and most botanists recognize the one genus *Equisetum*. However, some specialists have proposed that at least two genera be recognized. Consequently, the genera *Equisetum* and *Hippochaete*, or even three genera, have been described. Hauke (1969a) has pointed out that there are some real and consistent differences between the two major groups of species, but that they are minor, and the number of similarities outweigh the differences. Therefore, he could see no gain in establishing two genera instead of one. Two subgenera, however, recognize the differences (Hauke, 1974). Table 10-1 summarizes the main differences between the subgenera. (For earlier literature and taxonomic analyses, see Rothmaler, 1944, and Hauke, 1961, 1962a, b, c, 1963, 1978).

Table 10-1 Subgenera of *Equisetum*

Equisetum subgenus *Equisetum*

1 Aerial stems generally branched, annual or short lived.
2 Strobili borne on chlorophyllous vegetative stems or on nonchlorophyllous stems, lacking apiculum (not pointed).
3 Stomata on stems scattered in the furrows between the ridges, or in bands one to three stomata wide.
4 Stomata flush with the epidermis.
5 Upright, platelike lamellae on gametophytes.
6 Projecting antheridia, generally with more than two opercular cells.
Examples: *E. arvense, telmateia, sylvaticum*

Equisetum subgenus *Hippochaete*

1 Aerial stems generally unbranched, and may function for several seasons.
2 Strobili borne on chlorophyllous vegetative shoots, apiculate.
3 Stomata on stems in one or two longitudinal rows in the furrows between the ridges.
4 Stomata sunken below surface of the epidermis.
5 Upright, columnlike lamellae on gametophytes.
6 Antheridia sunken, with two opercular cells.
Examples: *E. hyemale, scirpoides, laevigatum*

Organography

The shoot system of *Equisetum* consists of an aerial portion and an underground rhizome system that exhibit monopodial branching. The sporophyte is perennial, at least the rhizome is, even though the aerial shoots may die back during part of the year. In some species the rhizomes may reach soil depths of 2 to 3 meters. Some species are small, particularly those of arctic and alpine regions. Some species grow near or within the Arctic Circle in Europe, Siberia, and North America. A South American species, *E. giganteum*, may reach a height of 5 meters; the stems are relatively small in diameter, and supported partly by surrounding tall grass.

The stem of *Equisetum* has a very rough texture, and an irregular surface pattern that is especially evident in scanning electron micrographs of the stem surface (Fig. 10-4). Stomata occur in one or two longitudinal rows either in the furrows between the ridges, scattered in the furrows, or in bands one to three stomata wide. The extremely rough texture results from the deposition of silica as discrete knobs (Fig. 10-4, D) and rosettes on the epidermal surface (e.g., in *Equisetum arvense*) or in a uniform pattern (Fig. 10-4, A, B) on and in the

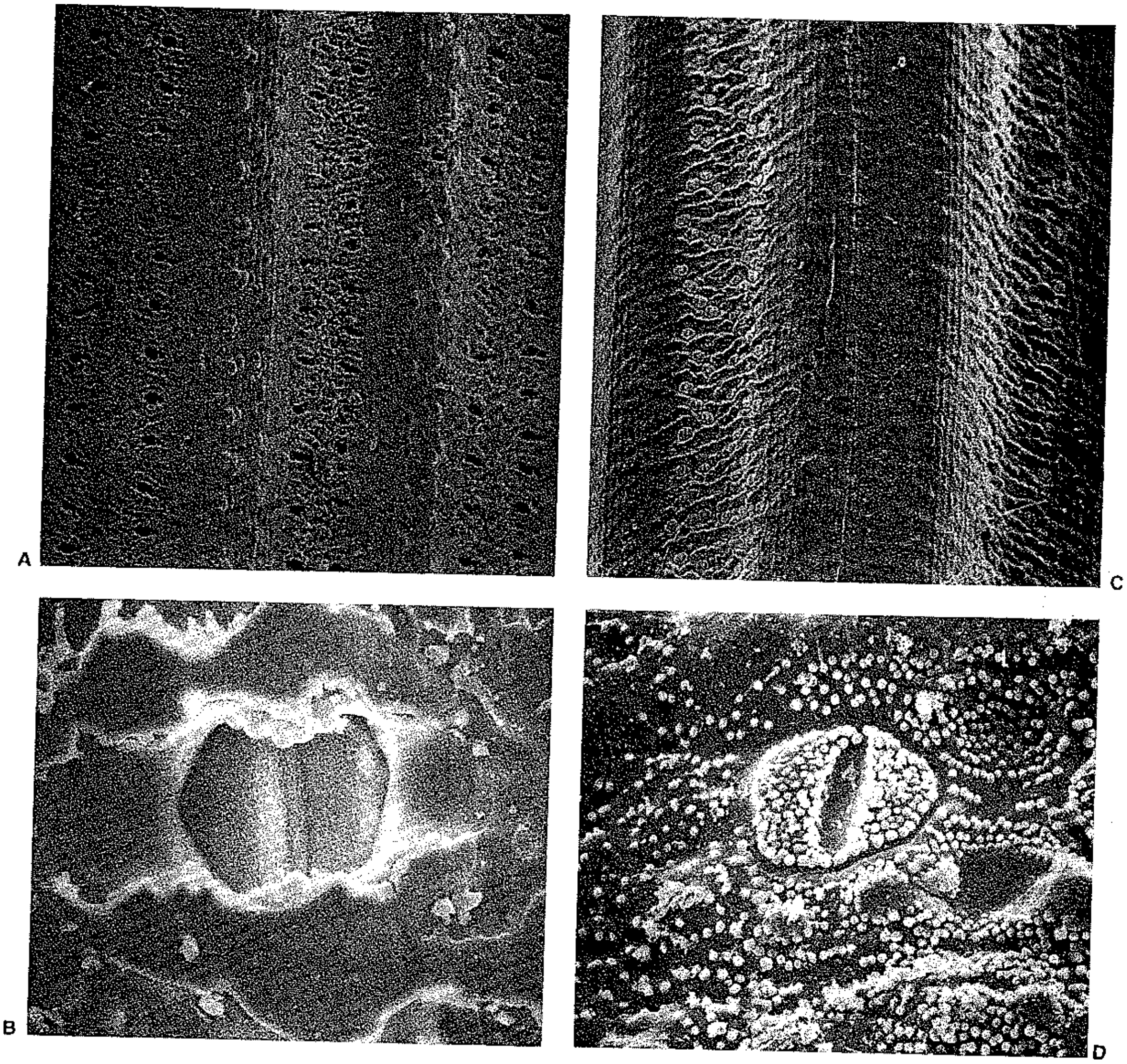


FIGURE 10-4 Scanning electron micrographs of stem surfaces. A, B, *Equisetum hyemale,* showing two rows of stomata in the valleys between the ribs (A), and one sunken stoma (B). C, D, *Equisetum telmateia* subsp. *braunii,* showing bands of stomata (C), and one stoma (D). (A, C × 50; B, D × 700)

entire outer epidermal cell walls (e.g., in *Equisetum hyemale,* Kaufman, et al., 1971). Silica is an essential element for normal growth of Equisetum (Chen and Lewin, 1969) and may play an important role in maintaining erectness of the plant, compensating for the very low lignin content of the cell walls. Other functions have been proposed: protection against pathogens and predators and prevention of excessive water loss (Kaufman et al., 1971). Silicon is necessary for the completion of the life cycle. Sporophytes, produced on gametophytes, formed viable spores only if the artificial culture medium contained at least 20 milligrams per liter of silicon (Hoffman and Hillson, 1979).

The shoot system of all species of *Equisetum,* comprising an underground rhizome and an aerial shoot, possesses the same fundamental organization. The stem is divided into definite nodes and internodes, and leaves are attached at nodes, united at least for a part of their length, forming a sheath around the stem (Fig. 10-2). The number of leaves per node varies according to the species and the position on the stem in most species. Where adjacent nodes have the same number of leaves in the leaf sheath, there is a very precise type of symmetry. The number of leaves at a node corresponds to the number of ribs on the internode below. Opposite each rib is a vascular bundle which enters the leaf that is on a line with the rib (Figs. 10-7, A; 10-10). However, careful examination of an aerial shoot reveals that the number of leaves per node generally increases from the base for some distance and then decreases. The type of vascularization just described is not observed for this growth pattern; adjustments in vascular connections occur such that some leaves of a whorl may have two vascular bundles instead of one (Bierhorst, 1959).

An internode may continue to grow for some time through the activity of an intercalary meristem located at its base. Lateral branches, when evident, are attached at the nodes and alternate with the leaves. During development, each branch breaks through the lower part of the leaf sheath in reaching the exterior. Whether a species is highly branched or not, branch and root primordia are formed at each node (Fig. 10-5). In the rhizome a root primordium develops into a root; a branch primordium may develop into an erect aerial shoot, remain as an arrested bud, develop into a new rhizome, or become abortive. In aerial shoots (if branching is a characteristic of the species) the branch primordia develop while the roots remain in an arrested condition unless the stems become procumbent and come to lie on a moist surface. This information can be used in vegetative propagation. A plant may be propagated vegetatively also in some species from arrested tuberous branches which occur at the nodes of rhizomes. The propensity for vegetative propagation is the major factor in *Equisetum* becoming a weed that is difficult to control in some localities. A small detached branch or tuber could be the start of the colonization of a very large area under favorable conditions for growth. For a farmer or cattle rancher to eradicate the last bit of rhizome is almost an impossible task!

The rhizome, and the aerial stem, can be pulled apart into internodal lengths or "pipes." In an interesting study, Treitel (1943) found that before a rhizome actually breaks under tension its elasticity closely compares with that of muscle or rubber.

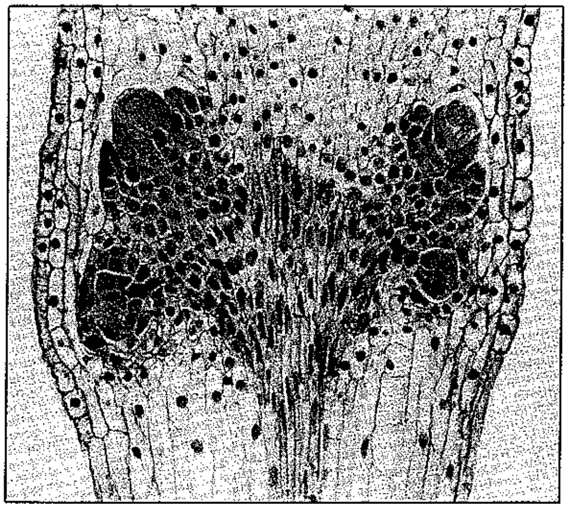


Figure 10-5 *Equisetum scirpoides*. Stem longitudinal section showing bud and root primordia at a node. Bud primordia toward top of figure.

Abnormal growths or monstrosities (teratological forms) are always of interest. Certain shoots may have unusually short internodes. Other shoots may have flexuous (snakelike) stems or have continuous spiral leaf sheaths, exhibit dichotomous branching, or produce a vegetative shoot beyond the usual terminal cone (Schaffner, 1933). All of these abnormalities undoubtedly are the result of an unbalanced growth-regulating system.

Strobili may occur terminally on many of the main vegetative axes of a highly branched species (*E. myriochaetum*), but more often a single strobilus terminates the main axis, whether the plant is branched or not (Fig. 10-2, A). Shoot dimorphism or segregation of function occurs in certain species: some shoots are green and purely vegetative (Figs. 10-1, A; 10-2, B), and others are fertile, unbranched (Fig. 10-6), brownish in color, and have terminal strobili (e.g., *E. arvense*). Still other species (e.g., *E. sylvaticum*), in addition to having purely green vegetative shoots, produce brownish, fertile shoots which may develop chlorophyll after the spores are shed; green branches then grow out from the nodes of the stem.

FIGURE 10-6 *Equisetum arvense.* Photograph taken in early spring showing unbranched fertile shoots terminated by strobili; some branched sterile (vegetative) shoots are evident to the right. [Courtesy of Dr. Richard L. Hauke.]

Anatomy of the Mature Stem

The stem of *Equisetum,* as seen in transverse section, has prominent ridges. The epidermal cell walls are thick and have a generous deposition of siliceous material. Distribution of stomata in the furrows between the ridges varies according to the subgenus (Table 10-1). In the subgenus *Hippochaete,* the stomata are sunken, consisting of two guard cells and overarching subsidiary cells; the latter have ridges on their inner walls (Hauke, 1957). Beneath the epidermis is the cortex, which exhibits a varied type of organization. The outer cortex is composed of collenchyma (Brown, 1976) and thinner-walled chlorenchyma. The distributional pattern of the two types of tissue varies according to species. Collenchyma is often excessively developed opposite the ribs (e.g., *E. hyemale,* Fig. 10-7, A), and a large longitudinal air space (vallecular canal) is present between the ridges.

Opposite each ridge is a vascular bundle of unusual interest. A transverse section of the internode of a mature stem reveals a protoxylem lacuna (carinal canal) associated with a vascular bundle (Fig. 10-7, A). The carinal canal is formed during elongation of an internode by the separation and disruption of protoxylem elements. In a mature stem one or more late-maturing tracheids can be seen along the edge of the carinal canal (Fig. 10-7, B). The parenchyma cells lining the canal develop thick walls, and the canal itself functions in water conduction (Bierhorst, 1958a), as shown by experiments with dyes. Opposite the carinal canal is the primary phloem flanked on each side by strands of xylem (Fig. 10-7, B), the ontogeny of which has been variously interpreted. In the past these strands have been considered to be the metaxylem of the bundle (Golub and Wetmore, 1948a, b), but Bierhorst (1958a) considers this portion of the xylem to be separate and distinct (developmentally) from the carinal group; he refers to the flanking strands as "lateral xylem." Authors do agree that, despite some irregularities, maturation of the tracheary elements in the lateral xylem is centrifugal. Also, vessels have been reported to occur in the lateral xylem of the rhizomes of five species (Bierhorst, 1958b).

Protophloem elements of the centripetally differentiating phloem are small in diameter, whereas those of the metaphloem are large (Fig. 10-7, B). End walls of the metaphloem sieve elements are

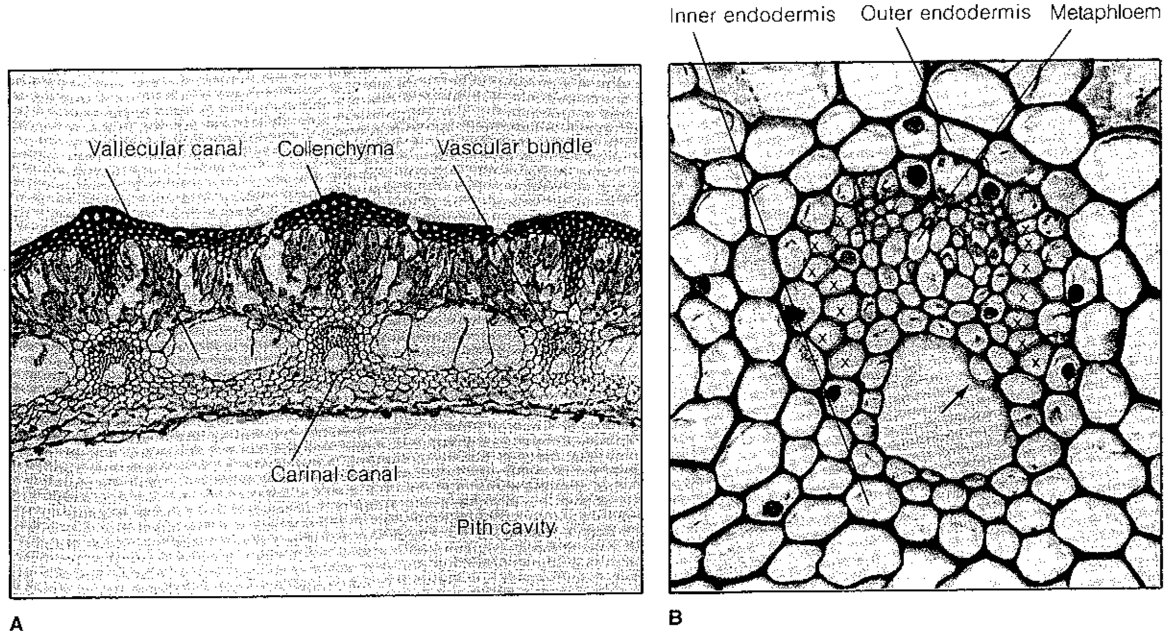


FIGURE 10-7 Stem anatomy in *Equisetum hyemale*. **A**, transection, portion of stem (note that carinal canals are opposite ridges on stem); **B**, structure of vascular bundle; one protoxylem tracheid is visible along edge of carinal canal at right (arrow); cross marks designate tracheids of the metaxylem(lateral xylem).

transverse to slightly oblique with callose-lined pores that are larger than those occurring on lateral walls (Lamoureux, 1961). Structure of a sieve element is much like a sieve-tube member of an angiosperm.

Depending on the species, one endodermal layer may be present outside the cylinder of vascular bundles (Fig. 10-8, A), or there may be, in addition, an inner endodermis (Fig. 10-8, B). In other species, an endodermis may completely surround each vascular bundle (Fig. 10-8, C). A pericycle may or may not be evident. Sometimes the pericycle cells are filled with starch. The vascular cylinder of *Equisetum* has been described as an ectophloic siphonostele of the "*Equisetum* type," or as a "perforated" ectophloic siphonostele (Schmid, 1982).

The stem nodes are unusual in that the xylem is extensively developed as a conspicuous circular ring. There are no carinal or vallecular canals. In addition, a nodal plate of pith tissue separates one internode from another.

The tips of underground rhizomes are covered by scalelike leaf sheaths, which may secrete mucilage from their abaxial epidermal cells. Trichomes may also be present on the adaxial side of the sheaths. There is collenchyma in the outer cortex. Vallecular canals and protoxylem lacunae are present. An endodermis around each vascular bundle is common (Fig. 10-8, C). There is often no consistency in the arrangement and number of endodermal layers in the aerial stem and rhizome of the same plant (Fig. 10-8, A, B).

Development of the Shoot

The shoot apical meristem is dominated by a conspicuous tetrahedral cell, the apical cell, that has three lateral ("cutting") faces that are directed downward. The fourth side is the rounded cap (Fig. 10-9, A, B). The apical cell cuts off daughter cells (segments) in a continuous sequence, so that three tissue regions are established (Gifford and Kurth, 1983). Each segment divides anticlinally. By subsequent divisions of these cells, a pith meristem and a lateral circular bulge are formed. The lateral bulge is

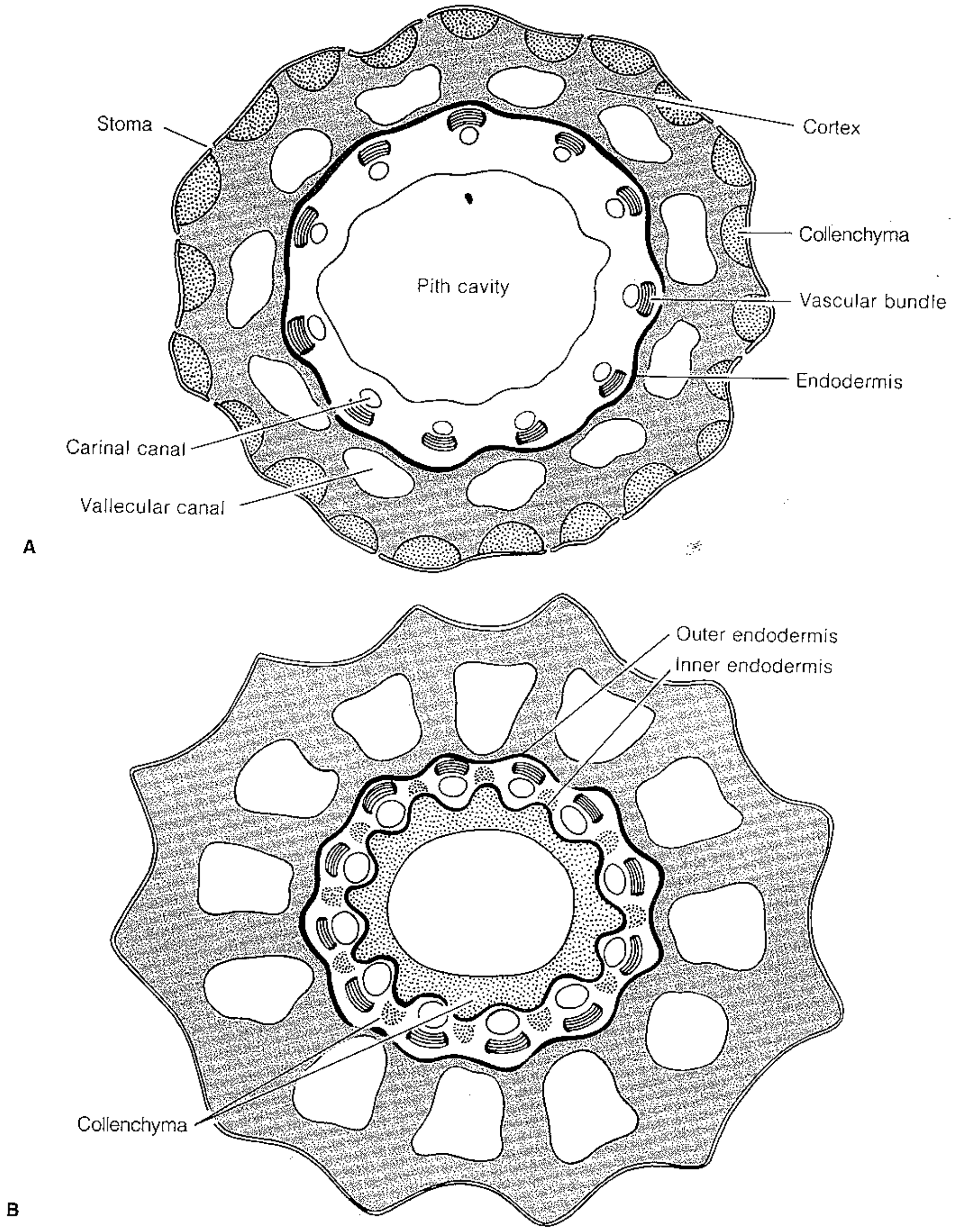
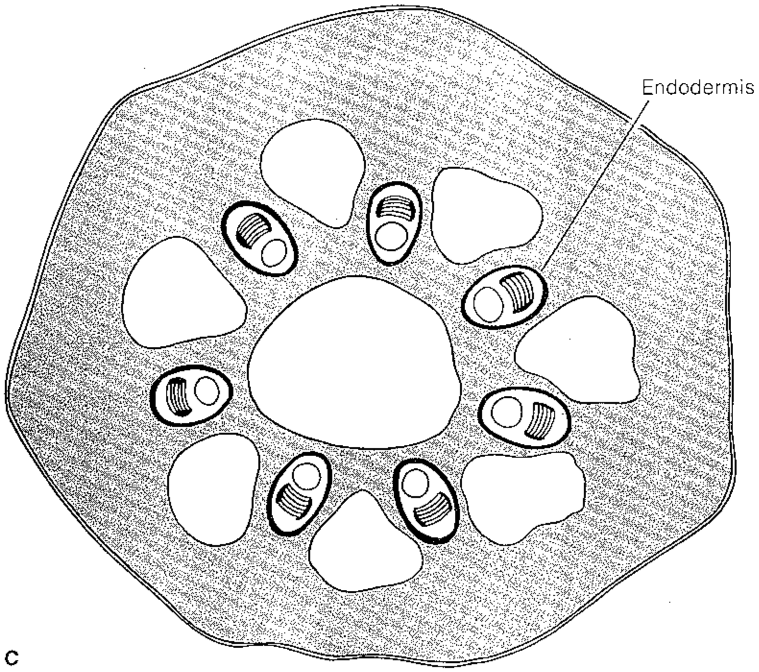


Figure 10-8 Schematic representations of variations in configuration and position of the endodermis in two species of *Equisetum*. **A**, aerial stem, *Equisetum sylvaticum;* **B**, rhizome, *Equisetum sylvaticum;* C, rhizome, *Equisetum hyemale*.



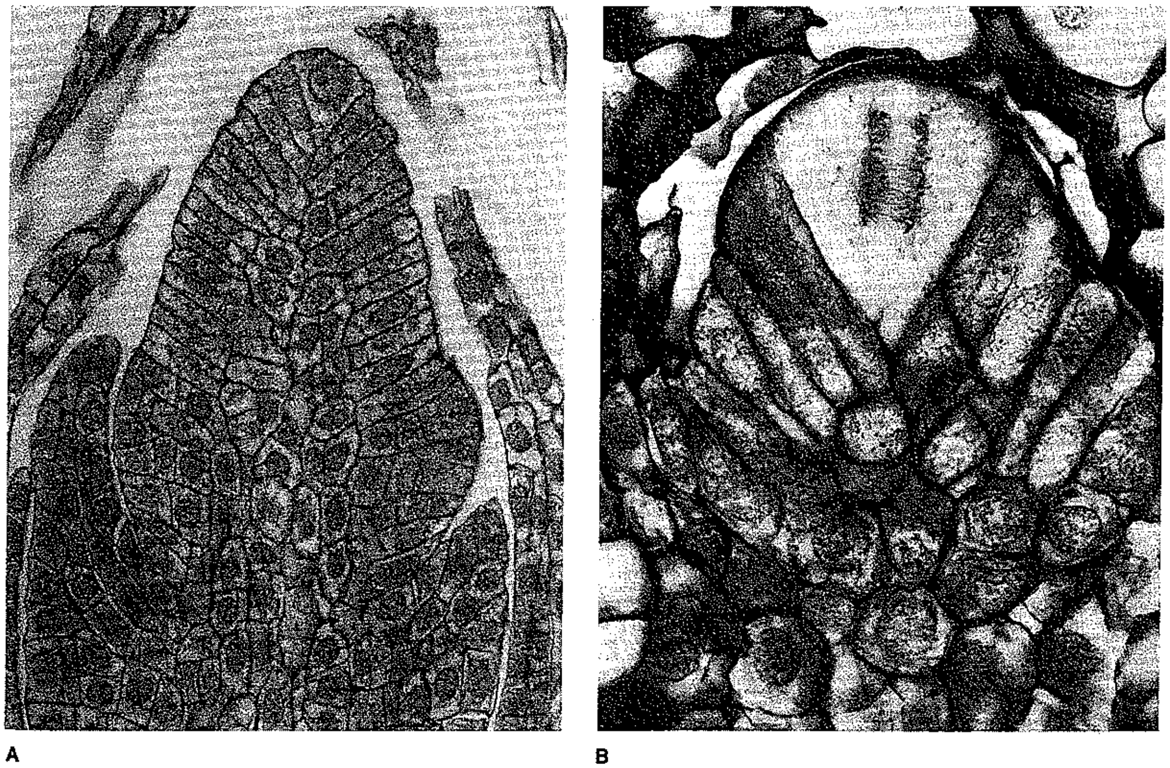


Figure 10-9 A, B, median longitudinal sections, shoot tips of *Equisetum;* note prominent apical cell in each, and the initiation of leaf primordia at the base of the apical cone in (A); apical cell in (B) is in anaphase. [B courtesy of Dr. D. W. Bierhorst.]

reported to consist of five to six layers in *E. arvense* (Golub and Wetmore, 1948a). Cells of the upper two layers will produce the future node and leaves; the lower layers will form the future intercalary meristem of the internode.

Very early in development, leaf-sheath initials can be distinguished as certain regularly placed surface cells of the upper two layers. A leaf then grows in length and widens at its base, eventually becoming fused to varying degrees with adjacent leaves, thus forming the characteristic leaf sheath (Fig. 10-2, A, B). At the time leaf initials are apparent, procambial cells become differentiated in the nodal and internodal regions near the pith. The results of one study (Golub and Wetmore, 1948b) indicate that the procambium in *E. arvense* is acropetally continuous throughout the shoot. (For additional information on mitotic activity, early shoot histogenesis, and determination of DNA content of various cells of the apical meristem, see Gifford and Kurth, 1983).

Vascularization

There has been considerable controversy regarding the longitudinal differentiation and maturation of xylem and phloem (see Golub and Wetmore, 1948b). In *E. arvense,* the differentiation of protoxylem and protophloem within a procambial strand begins at about the fourth node. Differentiation then proceeds acropetally into a developing leaf and basipetally into the internode below. In the elongation of older internodes the protoxylem and protophloem elements become stretched and torn because the intercalary meristem, located at the base of each internode, does not contribute new cells to the procambial strand. It is during this period of rapid elongation that protoxylem lacunae (carinal canals) are formed. After considerable elongation of an internode, the differentiation of the lateral xylem and metaphloem proceeds basipetally from a node through the internode below, and continuity is finally achieved with the same tissues in the node below.

During internodal elongation certain cortical cells separate from each other and form vallecular canals. The pith cavity is reported to be formed by mechanical tearing of cells (Golub and Wetmore, 1948b).

Following a vascular bundle up through an internode reveals a trichotomy of the protoxylem at the level of the leaf attachment. The median bundle enters the scale leaf, the two laterals diverge right and left, and each is joined laterally with an adjacent strand to form one of the vascular bundles of the next higher internode (Fig. 10-10).

Branches occur at nodes on radii alternating with those of the leaves. At about the sixth node from the shoot tip, a lateral branch is initiated from a single surface mother cell. An apical cell is soon established, and a branch bud with whorled leaves is formed. At about the time the first or second whorl of leaves is formed, a large cell appears near the basal end of each branch bud. This is the root apical cell which may give rise to several segments (Fig. 10-5). The branch buds may continue to develop if the species is normally branched; the roots remain arrested in development except on underground rhizomes. Of course, some of the buds on the rhizome have the potential to grow upward as new aerial shoots. The vascular tissue at the base of the branch shoot is in the form of a continuous cylinder (siphonostele) and is in continuity with the xylem and phloem of the nodal region. There is tissue continuity between the pith of the parent axis and the pith of the branch axis. These interruptions in the vascular tissue at the nodes constitute branch gaps (Jeffrey, 1899).

The leaves at each node are united to varying degrees. The thick-walled cells of the abaxial epidermis have various types of ornamentation on their outer tangential walls. Internally the mesophyll is lacunate and is traversed by one small median vascular bundle. Mesarch xylem has been reported by several workers.

One interesting feature of the *Equisetum* leaf is the presence of specialized "water stomata" (hydathodes) on the adaxial surface of the leaf along the midvein region (Johnson, 1937). *Equisetum* secretes water as it is associated with the conditions of high moisture around the roots and a saturated atmosphere.

The Root

The primary root is ephemeral; all other roots in *Equisetum* arise at the nodes of stems. Cells of the outer root cortex often have thick walls, those of

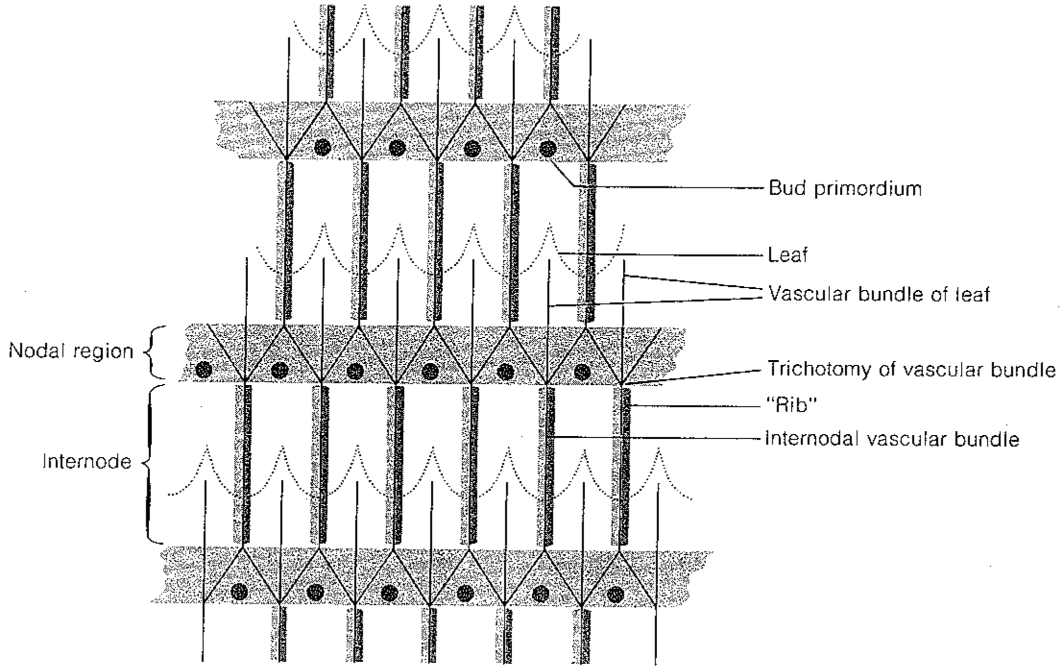


FIGURE 10-10 Schematic representation of a portion of the vascular system of *Equisetum,* shown in relationship to the "ribs," leaves, and buds.

the inner cortex are thinner. The xylem is triarch or tetrarch, or, in smaller roots, may be diarch. Small roots, as seen in transverse section, may have one large metaxylem element in the center of the root (Walton, 1944). The cells of the endodermis and pericycle occur on the same radii, indicating a common origin. Lateral roots have their origin in the endodermis.

A tetrahedral cell is the most prominent feature of the root apical meristem. A root cap is formed distally; the apical cell also produces segments laterally (proximally), each of which by two divisions gives rise to three cells, which in turn are the origin of the vascular tissue, cortex (including endodermis and pericycle), and epidermis (Johnson, 1933). Historically, the root apical cell in lower vascular plants was considered to be the ultimate source of cells of the root. In recent years evidence has been presented for the belief that the apical cell is active in cell division only during early stages of development. It then ceases to divide and the nucleus may become endopolyploid. Some surrounding cells assume the role of initials (Avanzi and D'Amato, 1967; D'Amato, 1975). Evidence from a more recent investigation on *E. scirpoides* supports the original tenet that the apical cell is active mitotically throughout root growth; it is not quiescent and does not become endopolyploid (Gifford and Kurth, 1982).

The Strobilus

The strobilus terminates an axis, whether it be on a vegetative stem or a strictly fertile nonchlorophyllous axis. The strobilus is composed of an axis with whorls of stalked, peltate structures termed sporangiophores (Fig. 10-11, A). Each sporangiophore is umbrellalike in shape, with pendant sporangia (five to ten in number) attached to the underside of the polygonal, disk-shaped shield (Fig. 10-12, A). The flattened tips of the sporangiophores fit closely together, providing protection for the sporangia during development. At maturity the cone axis elongates, separating the sporangiophores, and the sporangia open by a longitudinal cleft that is formed down the inner side of each sporangium. Additional protection during early development is provided by a rudimentary leaf sheath,

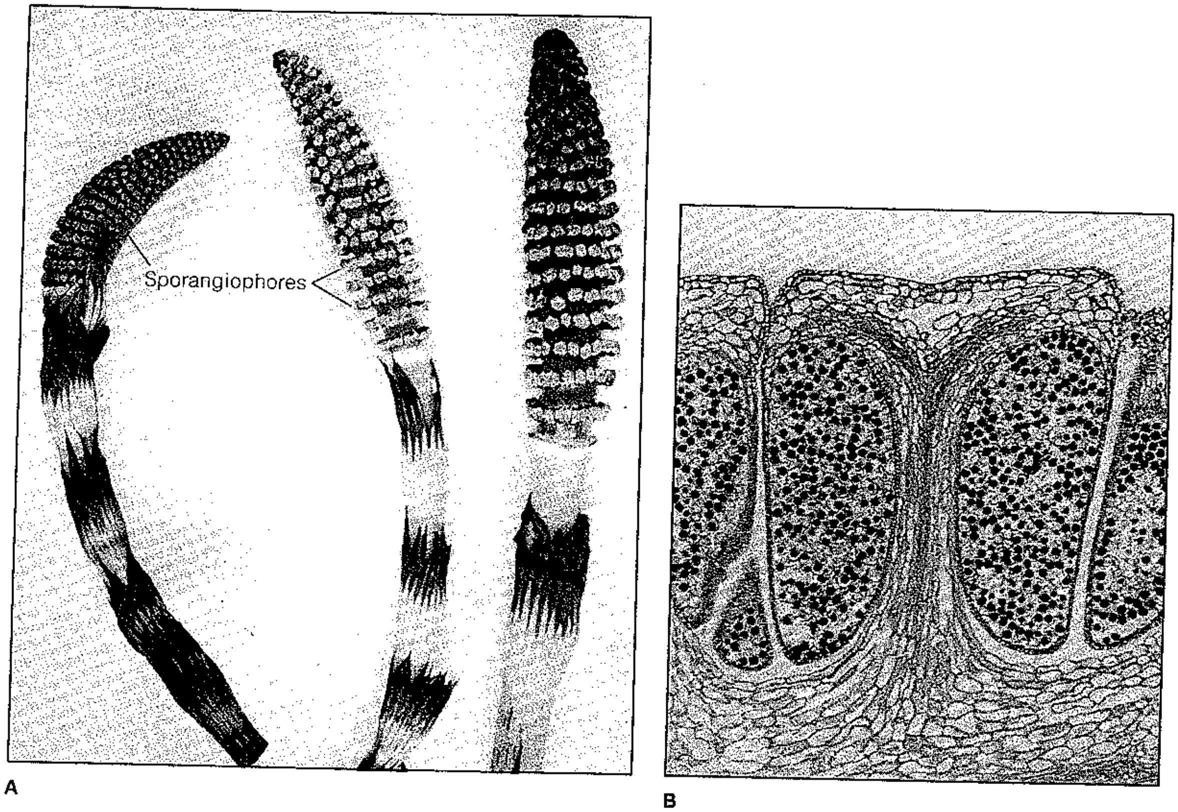


Figure 10-11 *Equisetum telmateia* subsp. *braunii*, **A**, fertile shoots (the strobili are at different stages of maturity; the youngest is to the left); **B**, median longisection of one sporangiophore showing the vascular bundle in the stalk and its mode of branching (crowded spores with elaters are evident in the sporangia).

the so-called annulus, at the base of the cone in some species.

The vascular cylinder of the cone axis is a network of interconnected vascular bundles. No large canals are formed as described for the stem. Vascular bundles (sporangiophore traces) diverge from the vascular cylinder at regular intervals and enter the successive whorls of sporangiophores. At the distal end of the sporangiophore the bundle is branched; each strand is recurved and ends near the base of a sporangium (Fig. 10-11, B).

Early in development, whorls of sporangiophore primordia arise in an acropetal manner on the flanks of the meristematic cone axis (Fig. 10-13). After enlargement of the sporangiophore primordium, sporangia are initiated in single superficial cells around the rim of the sporangiophore. The sporangium initial divides periclinally, setting aside an inner and an outer cell. The inner cell, by further divisions in various planes, produces sporogenous tissue (see Chapter 4, also Fig. 10-14). The outer cell, by anticlinal and periclinal divisions, gives rise to irregular tiers of cells, the inner of which may also become sporogenous; the outer tiers become the future sporangial wall cells. Superficial cells adjacent to the original initials may also contribute to the development of the sporangium. Before the sporocytes separate and round off prior to the meiotic divisions, two to three layers of cells adjacent to the sporogenous mass differentiate as the tapetum. In addition, not all of the sporogenous cells function as sporocytes; many degenerate and their cytoplasm, together with that of the tapetum, forms a multinucleate nourishing substance which occupies the spaces between the sporocytes.

The results of one study indicate that the first

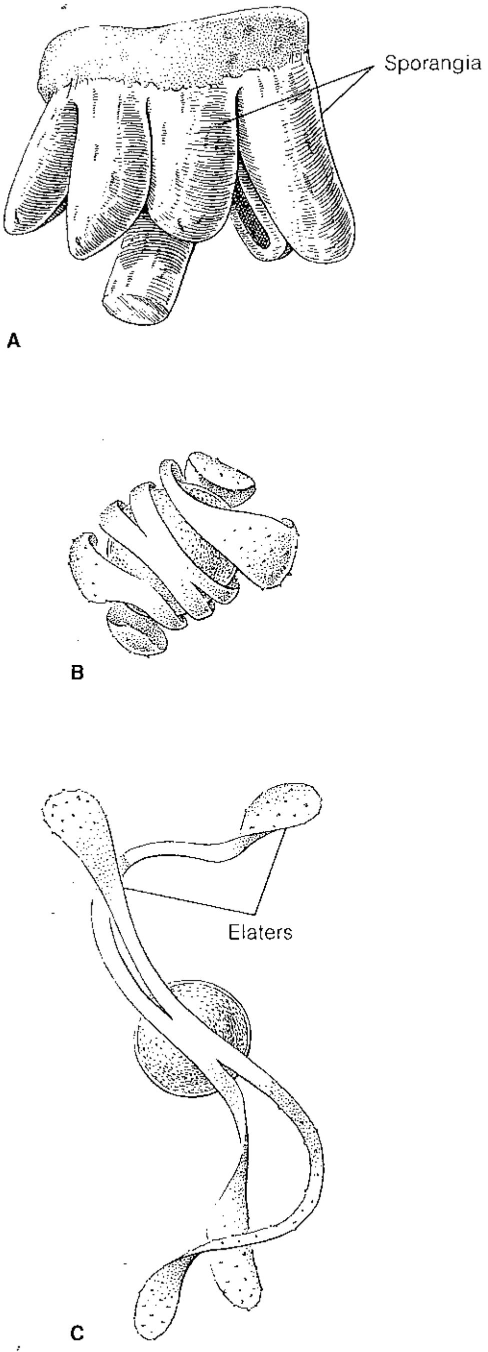


FIGURE 10-12 Sporangia and spores of *Equisetum*. **A,** a single sporangiophore with pendant sporangia; **B,** a mature spore whose coiled elaters indicate that it is moist; **C,** a spore whose uncoiled elaters indicate that it is dry.

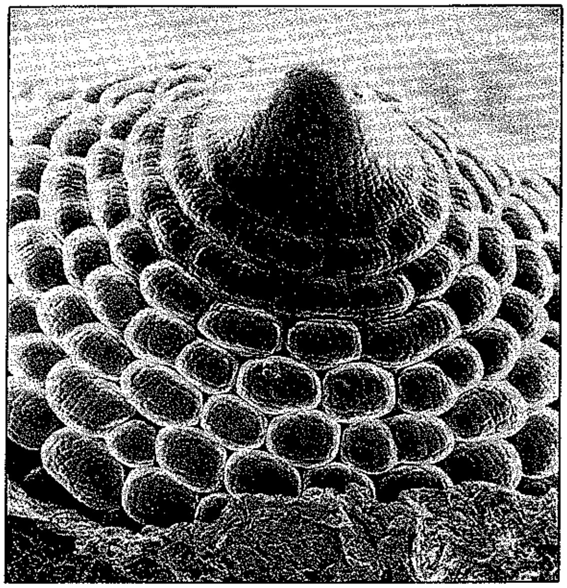


FIGURE 10-13 Scanning electron micrograph of a young strobilus of *Equisetum hyemale,* showing whorls of developing sporangiophores (×50).

sporangia to mature in a strobilus are sporangia situated in the widest part of the cone. Furthermore, within a single sporangium the sporocytes may be in various stages of meiosis. This may be related to the fact that the sporocytes are separated into pockets surrounded by the multinucleate plasma (Manton, 1950).

After the meiotic divisions have taken place, the spore tetrads separate from one another, and each spore becomes spherical. The spore wall is said to be laminated. The outer layer is deposited on the spore in the form of four bands, derived presumably from the breakdown products of the nonfunctional sporocytes and tapetal cells. The four bands are attached to the spore wall at a common point and remain tightly coiled around the spore until the sporangium is completely mature. The spores are filled with densely packed chloroplasts, a feature relatively uncommon to other lower vascular plants.

At maturity a sporangium consists of an outer wall composed of two layers of cells, the inner of which is generally compressed; the cells of the outer layer develop helical thickenings similar to tracheids which presumably are involved in sporangial dehiscence. Internal to the wall is the mass of

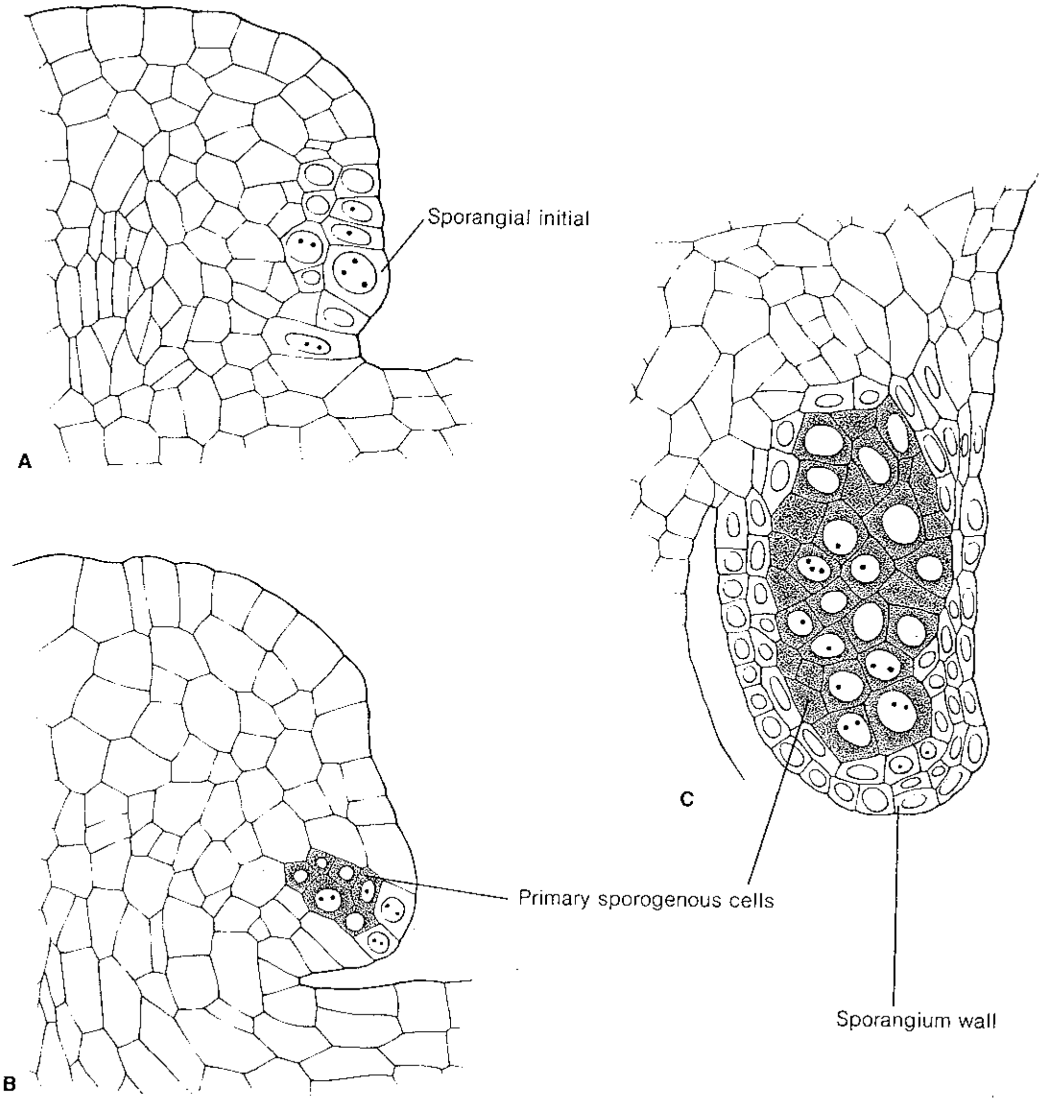


FIGURE 10-14 Early ontogeny of the sporangium in *Equisetum hyemale.* Initiation occurs in a single superficial cell (A), although lateral derivatives of the sporangial initial as well as adjacent superficial cells may contribute to the formation of primary sporogenous cells and primary wall cells. (See text for details.)

spores. At the time of dehiscence the free ends of the four bands, called elaters, separate from the spore wall. The elaters are hygroscopic, uncoiling as their water content decreases and recoiling with the addition of moisture (Fig. 10-12, B, C). It has been assumed that through this action the elaters assist in the dehiscence process and also bring about the dispersal of spores in large clumps from the sporangium.

Chromosome Numbers and Hybridity

In the species that have been studied critically, the chromosome number is $n = 108$ (Manton, 1950; Bir, 1960). Chromosomes vary in size and shape between the two subgenera (*Equisetum* and *Hippochaete;* Table 10-1), but the uniformity of the chromosome number may be indicative of a highly derived level and the extinction of lower numbers

(Tryon and Tryon, 1982). The high chromosome number could be indicative of a high degree of polyploidy. However, the data from enzyme electrophoresis of three species indicate that *Equisetum* possesses, in general, the number of isozymes typical of diploid angiosperms and gymnosperms (Soltis, 1986). Thus, for most enzymes examined, these plants are genetically diploid despite the high chromosome number. Hybridization is common in both subgenera, and this is reflected in the observed peculiarities at meiosis and the production of abortive spores. Hybridization has been responsible for much confusion in the taxonomy of the genus. In an intensive study of the subgenus *Hippochaete,* Hauke (1962c) described six hybrids between various pairs of seven species. Five hybrids in the subgenus *Equisetum* occur in North America (Hauke, 1983); also, artificial hybrids have been produced (Duckett, 1979b; Duckett and Page, 1975). Even if a hybrid produced nonviable spores, the sporophyte resulting from the initial cross could propagate itself very efficiently through fragmentation and growth of rhizomes (Hauke, 1969a).

Gametophyte Generation

Under natural conditions the gametophytic plants may be found growing in damp areas, on

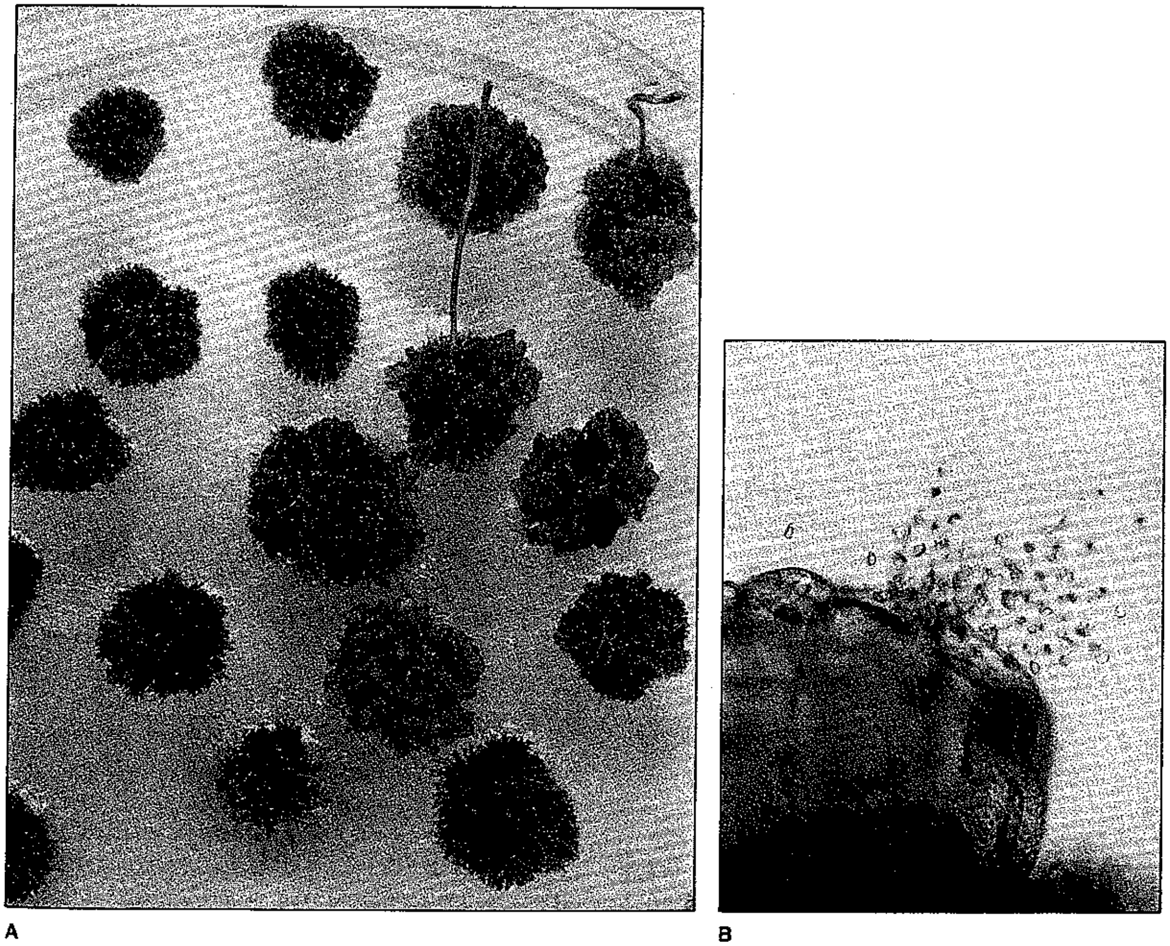


Figure 10-15 **A,** gametophytes of *Equisetum* sp. grown on simple inorganic nutrient medium; young sporophytes attached to gametophytes can be seen toward upper edge of figure. **B,** liberation of sperms from an antheridium.

mud, along creek banks, and even on the damp floors of abandoned mines and quarries. Mature plants may range in diameter from a few millimeters to 1 centimeter or more. A tropical species (Kashyap, 1914) and one from California (Mesler and Lu, 1977) may be even as large as 3 to 3.5 centimeters in diameter. An older plant may be uniform in outline; viewed from above, it resembles a miniature pin cushion (Fig. 10-15, A).

The time interval between shedding of spores and germination is quite critical. Spores germinate very readily if they land in a suitable environment; however, the limiting factor seems to be the amount of available water. If the spores do not germinate at once their viability decreases rapidly.

The first division of the spore results in two cells unequal in size. The smaller cell, which has fewer chloroplasts, elongates and forms a rhizoid (Fig. 10-16, A, B). The larger cell may divide transversely, or the division may be perpendicular to the original wall.

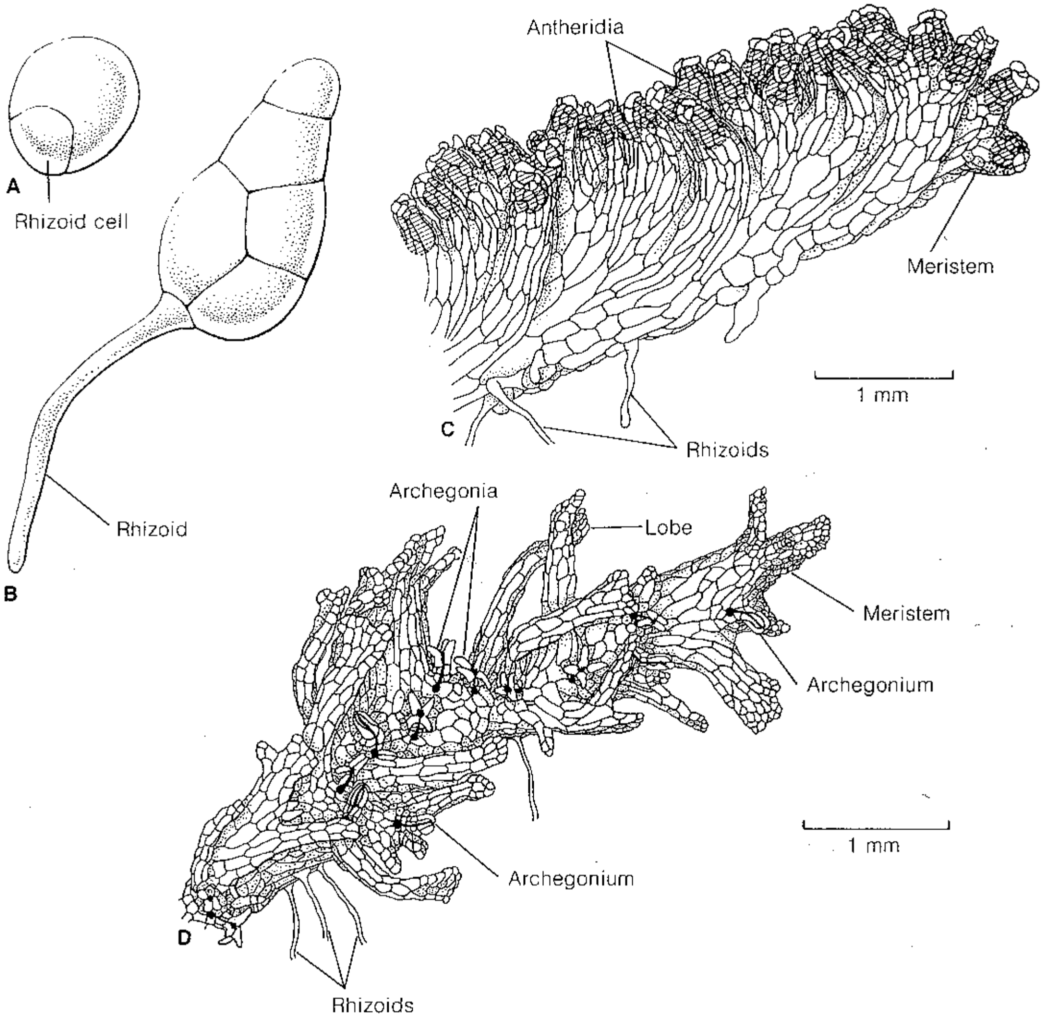


FIGURE 10-16 A, B, spore germination and early development of the gametophyte in *Equisetum hyemale;* C, apical portion, branch of male gametophyte of *Equisetum arvense;* D, branch of initially female plant. (See text for details of development.) [C, D redrawn from Duckett, *Bot. Jour. Linn. Soc.* 63(4):327–352, 1970.]

Single spore cultures of five species in subgenus *Equisetum (E. arvense, E. telmateia, E. fluviatile, E. palustre,* and *E. sylvaticum)* reveal that within 15 to 20 days after germination a developing gametophyte becomes organized into two quite different regions: (1) a basal region with rhizoids on the lower surface and (2) an upright, bright green, branched region. After 15 to 25 days in culture a localized meristem develops that gives rise to new basal cells of the "cushion" and produces derivatives which contribute to the development of upright, platelike lobes (Duckett, 1970a). Subsequent development and morphology is dependent on the type of sex organ produced.

Sexual behavior in *Equisetum* has long been a standing controversy. Some investigators reported that for the species they studied the gametophytes were either unisexual or bisexual, or were initially unisexual and then became bisexual. Heterospory was claimed to support sexual differentiation, but subsequent research failed to support this contention (Duckett, 1970b).

According to Duckett (1970a), *Equisetum* gametophytes generally are either male or female initially and the first sex organs to appear are antheridia on male plants. In the five species mentioned earlier, the male gametophytes are smaller and grow more slowly than the females. The initially female gametophytes eventually produce antheridia, generally in great numbers. The proportions of males to bisexual gametophytes are much the same within each species, but vary greatly between species.

MALE GAMETOPHYTES. The basal or cushion meristem, after producing a few upright lobes, suddenly begins forming antheridial tissue, and the gametophyte often has a distinctive coloration (Fig. 10-16, C). Old males may have several hundred antheridia.

INITIALLY FEMALE GAMETOPHYTES. Archegonia are found on the cushion and at maturity lie at the bases of the upright lobes (Fig. 10-16, D). Female gametophytes sooner or later produce antheridia. When they do, archegonia and antheridia are both present, but in older gametophytes the number of antheridia produced increases. If a culture of a bisexual gametophyte (derived from one spore) is flooded with water, homozygous sporophytes are produced (also see Sporne, 1964).

Early sex determination, at least in some species, appears to be related to environmental conditions —temperature, light, and humidity as well as the supply of nutrients. (See discussions in Schratz, 1928; Wollersheim, 1957a, b; Hauke, 1967; Duckett, 1970a, 1972.) In other experiments designed to explore sexuality in *Equisetum,* Duckett (1977) subcultured fragments of male gametophytes. Some of the fragments remained male throughout successive subcultures. Others produced archegonia, but subsequently produced antheridia in increasing numbers, supporting the contention that *Equisetum* gametophytes are potentially bisexual. In contrast to these results Hauke (1969b) reported that gametophytes of *E. bogotense* were unisexual and never changed. Duckett (1972) also found that in *E. ramosissimum* and *E. variegatum* the initially male gametophytes never became bisexual. However, for *E. giganteum* (subgenus *Hippochaete*) Hauke (1969b) reported that the gametophytes were normally bisexual, with archegonia and antheridia appearing at the same time. The pattern in *E. giganteum* was considered by Hauke to be primitive and could be correlated with primitive features of the sporophyte of the species; Duckett (1979a), however, believes that our knowledge of gametophytes does not provide definitive information to support the view that the subgenus *Hippochaete* is a more primitive group.

In the absence of clear-cut heterospory, it seemed unlikely to Duckett (1970b) that any exact sex-determining mechanism is operative in *Equisetum;* rather, sexuality is controlled by a complex set of interactions, although Hauke (1977) believes that all the available information points to a genetic basis for sex in *Equisetum* spores.

Although the gametophytes of most species of *Equisetum* are potentially bisexual, a study of sexuality in *E. arvense* revealed that intragametophytic self-fertilization is infrequent. This conclusion is based upon genetic data from enzyme electrophoresis (Soltis et al., 1988).

GAMETANGIA. Antheridia first appear on the lobes of the male gametophyte and they may occur by the hundreds on the rounded, compact surface of old bisexual gametophytes at the "pincushion" stage. An antheridium is initiated by a periclinal division in a superficial cell which gives rise to a cover or jacket cell and a primary spermatogenous cell. The jacket cell divides anticlinally, and at maturity the jacket layer may consist of two or more cells. The primary spermatogenous cell divides, and the derivative cells then undergo a series of synchronized divisions, forming spermatids. At maturity the spermatids escape through a pore (Fig. 10-15, B) created by the separation of the jacket or opercular cells (Hauke, 1968; Duckett, 1972, 1973; Bilderback et al., 1973). A sperm escapes after the spermatid wall breaks; each sperm has about 120 flagella attached to a lamellar band (Duckett, 1975; Duckett and Bell, 1977). The flagella beat with a continuous, traveling, helical wave, propelling a sperm in a unidirectional, helical path (Fig. 10-17; Bilderback et al., 1973).

An archegonium follows the common type of ontogeny displayed in other lower vascular plants (Chapter 5, Fig. 1). At maturity an archegonium may have a projecting neck frequently comprising three tiers of neck cells arranged in four rows, two adjacent neck-canal cells, often of unequal size, a ventral canal cell, and an egg at the base of the embedded venter (Chatterjee and Ram, 1968;

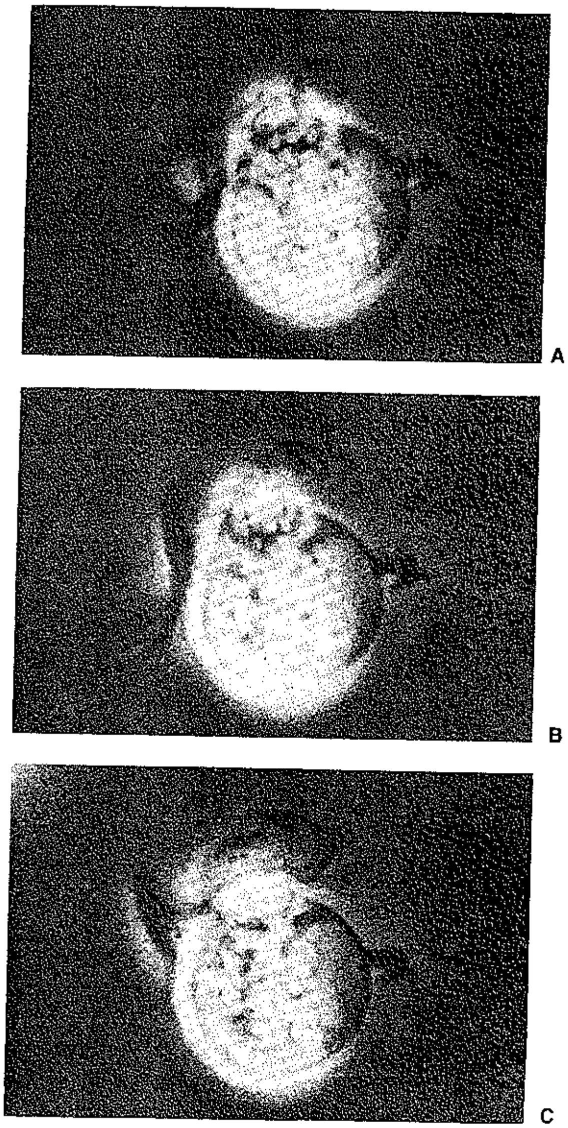


FIGURE 10-17 A–C, a sequential series of a swimming sperm of *Equisetum hyemale*, illustrating the helical nature of the flagellar beat (× 1500). [Courtesy of Dr. David E. Bilderback.]

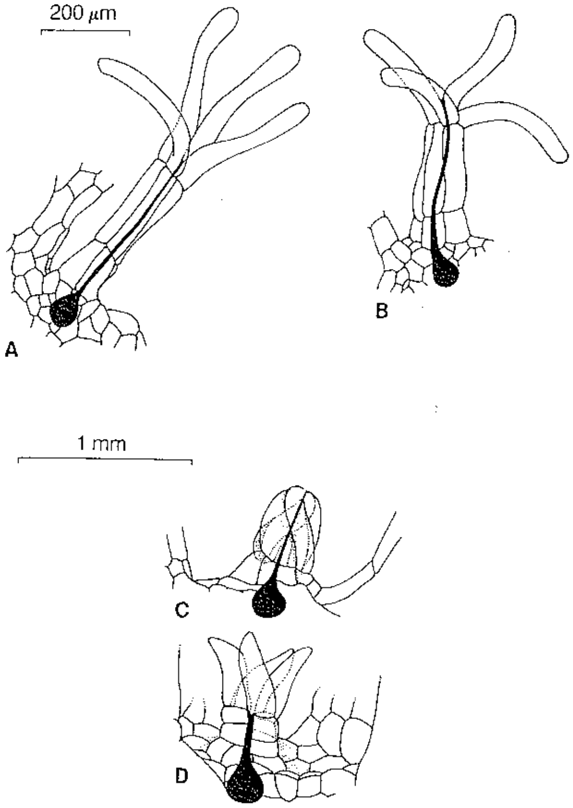


FIGURE 10-18 A, B, archegonia of *Equisetum fluviatile* showing greatly elongated terminal tier of neck cells. C, D, archegonia, *E. scirpoides,* illustrating the twisted form of the terminal tier of neck cells (C), and their spreading apart at archegonial maturity (D). [**A, B** redrawn from Duckett, *Bot. Jour. Linn. Soc.* 66:1–22, 1973; **C, D** redrawn from Duckett, *Bot. Jour. Linn. Soc.* 79:179–203, 1979.]

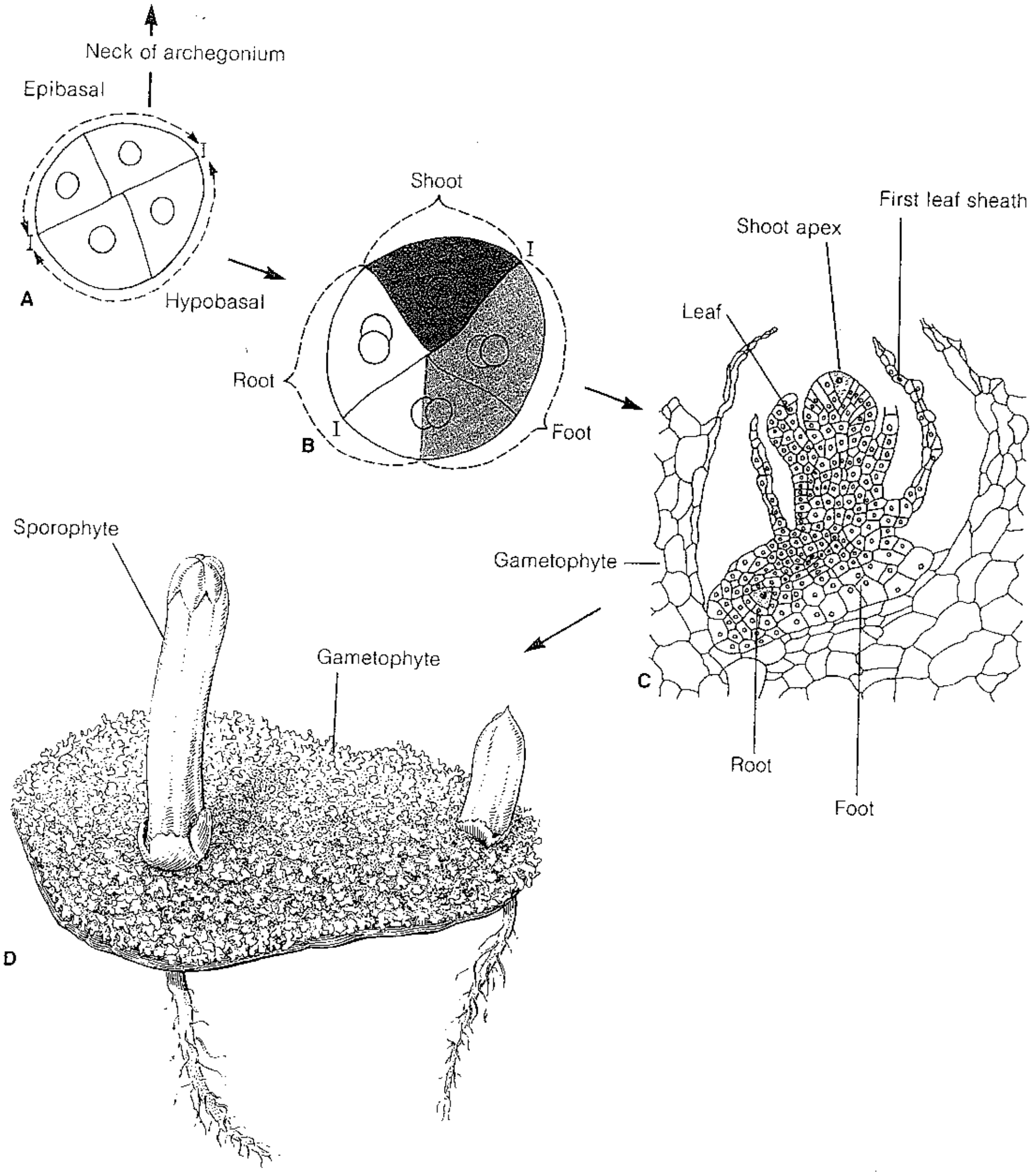


FIGURE 10-19 A–C, development of the embryo in *Equisetum* showing the first cleavage of the zygote (I–I in **A**) and derivation of shoot, root, and foot from the eight-celled embryo (**B**); **D**, dorsiventral gametophyte of *Equisetum laevigatum* with two attached sporophytes. [A, B redrawn from Laroche, *Rev. Cytol. Biol. Veg.* 31:155–216; C redrawn from *Cryptogamic Botany,* Vol. II, 2d edition, by G. M. Smith. McGraw-Hill, New York. 1955: D redrawn from Walker, *Bot. Gaz.* 71:378–391, 1921.]

Duckett, 1973). During egg maturation and degeneration of the ventral and neck-canal cells, the terminal tier of neck cells elongate considerably. In some species the subterminal neck cells may also elongate (Fig. 10-18, A, B). The terminal tier of neck cells are often twisted initially but then separate from each other and spread apart in an arching manner (Duckett, 1973; Hauke, 1980; Fig. 10-18, C, D).

To achieve fertilization the gametophytes must be covered by at least a thin layer of water in which the motile sperm swim to the archegonia. Mature spermatids are probably not released until the proper osmotic conditions are achieved. When gametophytes are flooded, water probably enters the cells of the mature antheridia because of an osmotic gradient. This would bring about swelling of the spermatids and opercular cells and is possibly the causal factor in the opening of the antheridium. The spermatid cells have elaterlike structures which may aid discharge and dispersal (Bilderback et al., 1973).

The Embryo

Observations on fertilization have indicated that numerous sperm may enter the archegonium, and even penetrate the egg cytoplasm, but only one sperm actually fuses with the egg nucleus (Chatterjee and Ram, 1968). The first division of the zygote has been described as transverse (Sadebeck, 1878) for certain species; the first division in *E. arvense* has been described as being oblique (Laroche, 1968), setting aside an upper cell, the epibasal cell, and a lower cell, the hypobasal cell. The embryo is therefore exoscopic in polarity (Chapter 6; Fig. 10-19).

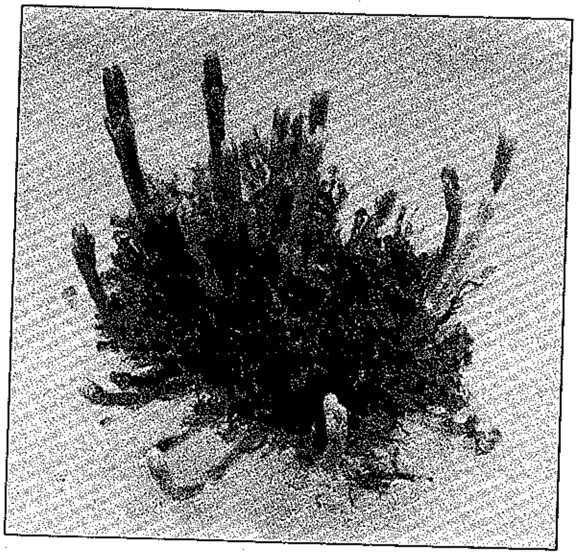


Figure 10-20 *Equisetum* gametophyte with attached sporophytes (× 4).

There are conflicting accounts of subsequent embryogeny in *Equisetum*, which may indicate variation in the genus. Earlier descriptions were presented at a time when embryogeny was considered to be a precise series of unalterable events. Assign-

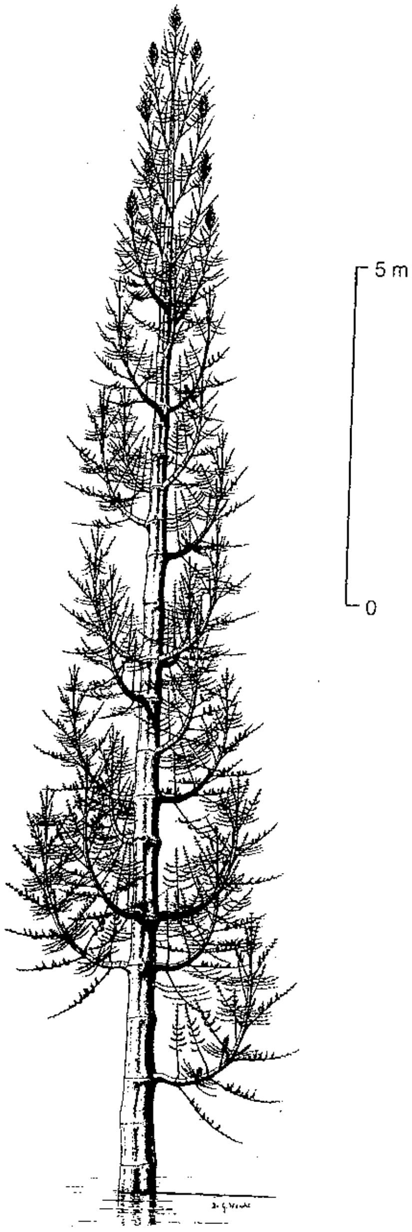


Figure 10-21 Reconstruction of *Pseudobornia ursina* from the Devonian Period. [From Schweitzer, *Palaeontographica* 120B:116–137, 1967.]

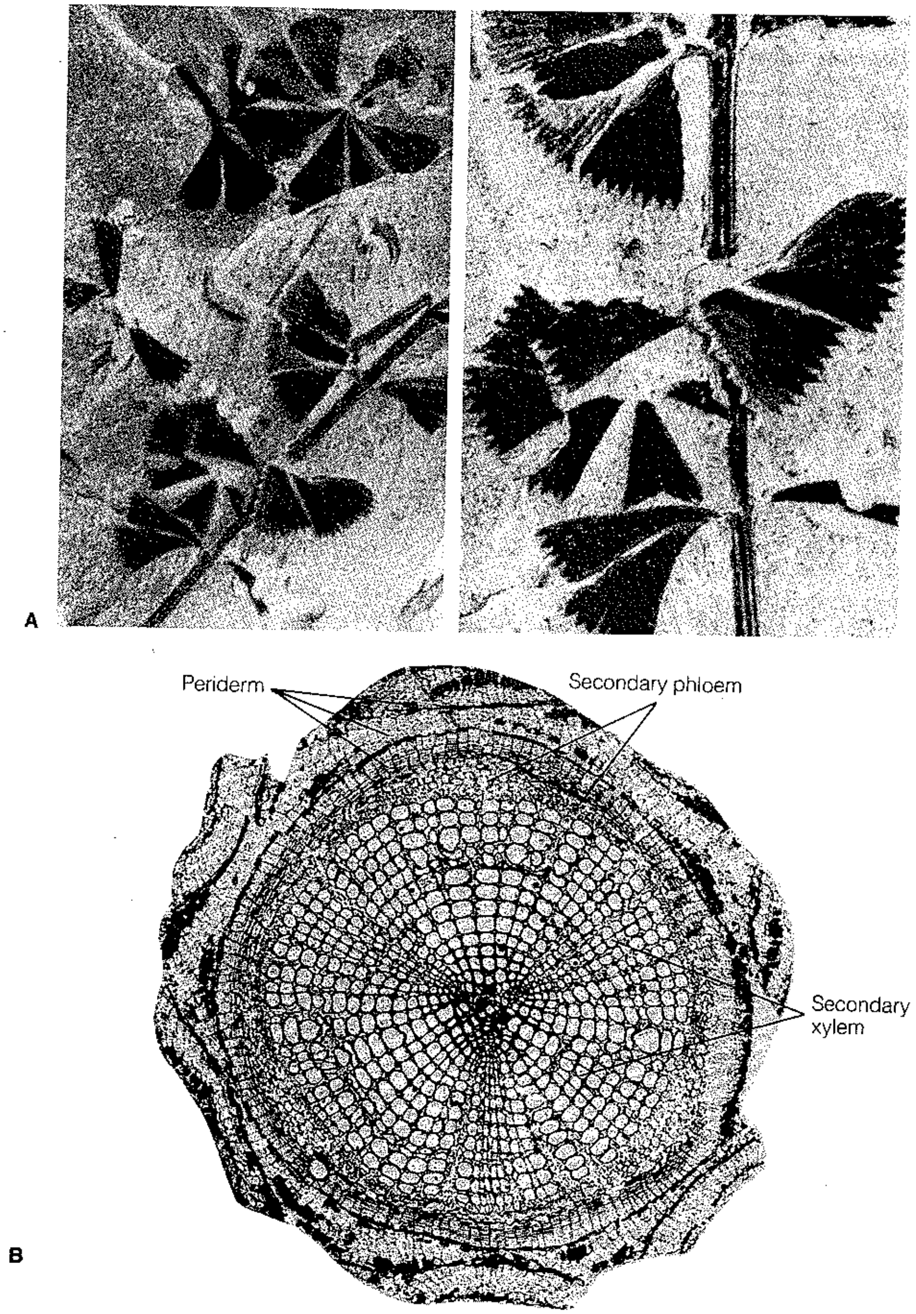


FIGURE 10-22 **A,** leaves and stems of *Sphenophyllum.* **B,** transection, stem of *Sphenophyllum plurifoliatum.* [A from Remy and Remy, *Pflanzenfossilien,* 1959; B from Eggert and Gaunt, *Amer. Jour. Bot.* 60:755–770, 1973.]

ment of the first leaf, stem (future shoot apex), root, and foot to definite segments of the embryo in the quadrant stage was described by Sadebeck (1878). The first leaf and the shoot apex were said to develop from the epibasal portion, the first root and the foot from different quadrants of the hypobasal portion. Later workers reported variations in segmentation and origin of fundamental organs. Until more complete studies are made of more species, the following general outline of development may be taken as representative for *E. arvense* (Laroche, 1968) and some other species.

Following the first oblique division, the epibasal and hypobasal cells divide at right angles to the original wall. This establishes the quadrant stage (Fig. 10-19, A). After subsequent divisions in the four cells, the future shoot apex is organized from derivatives of one quadrant of the epibasal hemisphere. The foot takes its origin from one quadrant of the hypobasal hemisphere and a portion of the other adjacent hypobasal quadrant. The first root is organized from one of the epibasal quadrants and a portion of the subjacent hypobasal quadrant (Fig. 10-19, B). The shoot then grows rapidly, forming whorls of three or four scalelike leaves (Fig. 10-19, C). Later the root penetrates the gametophytic tissue in reaching the soil or substratum (Fig. 10-19, D). Additional erect shoots are formed from buds on the primary axis of the sporophyte. Large, mature gametophytes may support several sporophytes (from multiple fertilizations) in varying stages of development (Fig. 10-20).

Fossil Sphenopsids

Pseudoborniales — *Pseudobornia*

The order Pseudoborniales is represented by one species from the Upper Devonian, *Pseudobornia ursina,* collected from Bear Island, south of Spitzenberg, and from northeastern Alaska. *Pseudobornia* was a monopodial branched tree about 15 to 20 meters in height (Fig. 10-21). The basal portion of the trunk was up to 60 centimeters in diameter. There were three orders of branching, with one or two branches at the nodes of the main axis; the ultimate branches bore leaves in whorls of four, each of which dichotomized two or three times and were finely dissected along their margins. The strobili at the ends of first order branches were about 30 centimeters long. Strobili consisted of whorled bracts and sporangiophores; the sporangiophores were upturned, divided into two segments, and bore about thirty terminal sporangia (Schweitzer, 1967). The affinities of *Pseudobornia* are obscure. Organization of the reproductive structures would appear to support a relationship with the Sphenophyllales (Stewart, 1983).

Sphenophyllales

The group Sphenophyllales was common in the Carboniferous Period; it may have existed as early as the Upper Devonian, but disappeared by the Per-

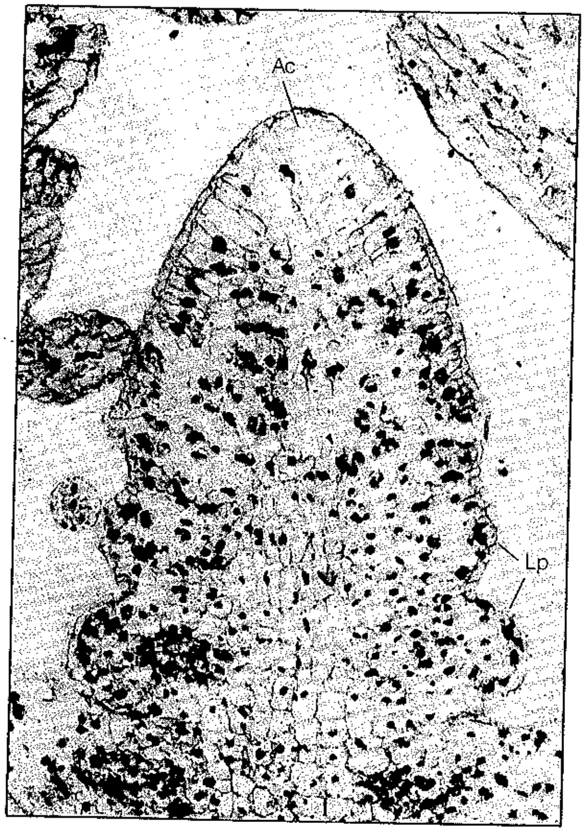


FIGURE 10-23 Median longitudinal section, shoot apex of *Sphenophyllum* showing the large inverted pyramidal apical cell (Ac) and derivative cells. Lp, leaf primordia. [Courtesy of Dr. T. N. Taylor.]

mian. These plants were probably less than 1 meter tall and are variously depicted as erect and self-supporting, or supported by surrounding vegetation. The generic name *Sphenophyllum* was originally applied to leaf compressions, but now includes extremely well-preserved stems, roots, and leaves. Similar to other sphenopsids, the stems were jointed with whorls of leaves at each node. Unlike other groups, however, the leaves were commonly wedge shaped, the distal margins toothed or deeply notched, with a dichotomously branched venation system (Fig. 10-22, A). The stem had an exarch protostele which was usually triarch (Fig. 10-22, B). In larger stems an abundant amount of secondary xylem was produced consisting of elongate tracheids (in excess of 8 millimeters) with circular to elliptical pits. Between the tracheids were longitudinal strands of narrow parenchymatous cells which become confluent in the outer part of the xylem to form a type of multiseriate ray. Eggert and Gaunt (1973) have shown that secondary phloem was formed in *Sphenophyllum plurifoliatum*. *Sphenophyllum* appears to be the only nonseed plant in which a well-documented bifacial vascular cambium has been recorded. A periderm was produced by a phellogen that probably arose early in development in tissue believed to be the pericycle.

A remarkable discovery was made of beautifully preserved shoot tips of *Sphenophyllum* by Good and Taylor (1972). The shoot apices resemble in every way those of *Equisetum*, including the prominent apical cell, derivatives, young leaves, and the initiation of intercalary meristems (Fig. 10-23). Because *Sphenophyllum* is protostelic, it formed a cyl-

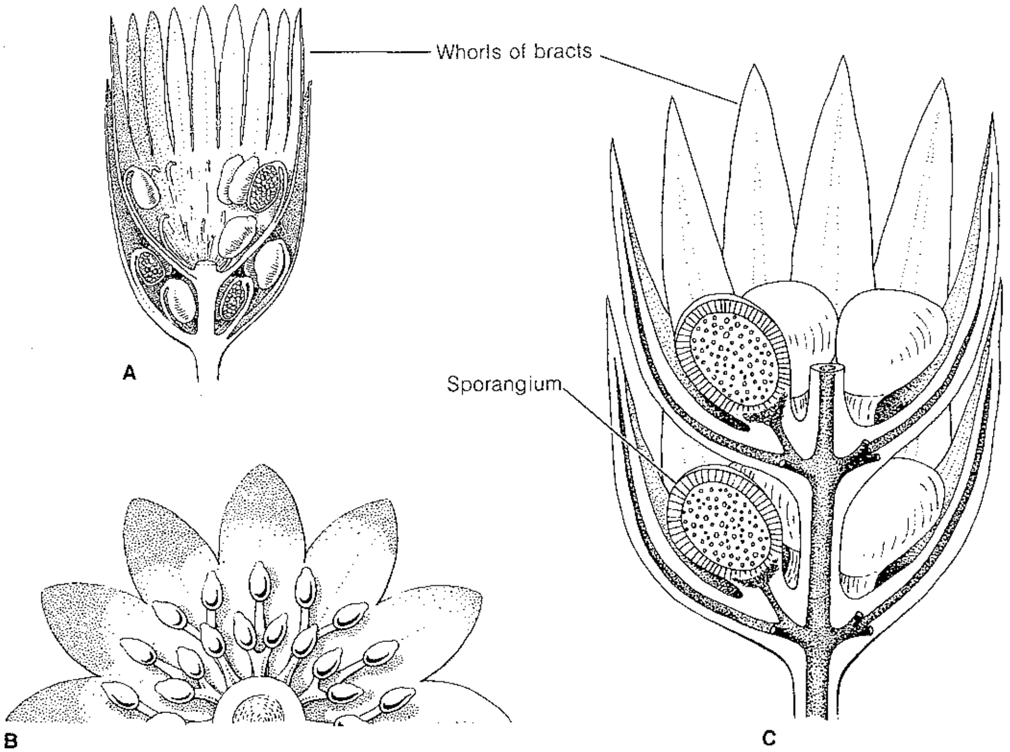


FIGURE 10-24 Sphenophyllales. **A**, longisection, strobilus of *Bowmanites dawsoni;* **B**, same as **A**, viewed from above (stalked sporangia were fused with the laterally joined bracts to variable degrees); C, strobilus of *Litostrobus iowensis* as seen in longisection. [A redrawn from *An Introduction to the Study of Fossil Plants* by J. Walton. Adam and Charles Black, London, 1953; B redrawn from *Handbuch der Paläobotanik* by M. Hirmer. R. Oldenbourg, Munich, 1927; C redrawn from Reed, *Phytomorphology* 6:261–272, 1956.]

inder of procambium in the center of the axis, rather than a pith meristem as in *Equisetum*.

Strobili consisted of alternating whorls of bracts and sporangiophores. Commonly there were one to two sporangiophores per bract which were fused to varying degrees with the adaxial sides of the bracts (Fig. 10-24, A–C).

Equisetales — Calamitaceae

Members of this family were trees reaching heights up to 20 meters and constituted a significant part of the Upper Carboniferous flora. Arborescent sphenopsids also occurred in the Upper Devonian to Lower Carboniferous and are placed in the family Archaeocalamitaceae, but we will discuss only the Calamitaceae.

If a complete calamite plant could be assembled, the plant body would consist of an aerial branch system and an underground rhizome system similar to those of *Equisetum* (Fig. 10-25). Roots, as well as aerial branches, originated at nodes along the rhizome. The aerial, articulated shoot exhibited limited or extensive branching depending upon recognized subgenera. The stems were jointed, as in *Equisetum,* but had a smooth outer surface. Whorls of linear, lanceolate, or spatulate microphylls occurred at the nodes (Fig. 10-26, A). These leaves were larger than those of *Equisetum* and were often fused at the base to form a collar around the base of an internode. In contrast to *Sphenophyllum,* the leaves had only a single unbranched vein, similar to *Equisetum.* Strobili were at the tips of side branches, not terminally on the main axis as is common in *Equisetum.*

Form or organ genera are common in the Calamitaceae. There are genera for casts of pith cavities (e.g., *Calamites*), permineralizations of stems *(Arthropitys, Calamodendron),* leaf whorls *(Annularia, Asterophyllites),* and strobili *(Calamostachys, Palaeostachya).* Not all organ genera are listed here. It is conventional to use the generic name *Calamites* in speaking of entire plants (Fig. 10-25).

The remains of a calamite stem are most commonly of two types: pith casts and permineralizations. Pith casts were formed by sediments infiltrating pith cavities and hardening there. When the surrounding organic material decayed, an image of the inner surface of the vascular cylinder remained. On the surface of a pith cast there are longitudinal furrows and ridges (Fig. 10-26, B); the furrows mark the positions of the primary xylem and can be correlated with a stem seen in transverse section (compare Figs. 10-26, B and 10-27). The permineralized stems reveal a remarkable similarity to those of *Equisetum,* except for the cylinder of secondary xylem.

Annularia is a genus for whorls of leaves attached to small stems (Fig. 10-26, A). Strobili consisted of alternate whorls of bracts and sporangiophores (*Calamostachys;* Fig. 10-28, D, E) or whorls of sporangiophores that were situated in the

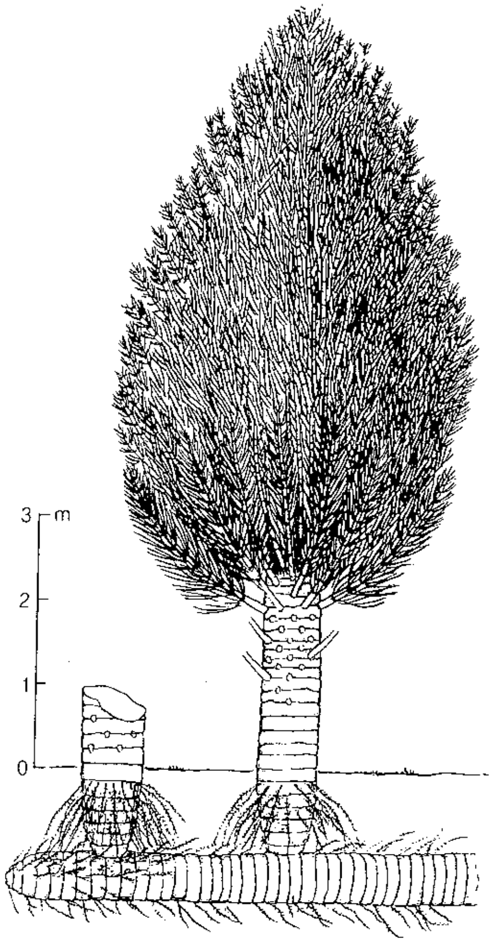


FIGURE 10-25 Schematic representation of *Calamites* showing rhizome and a tall, upright, branched portion. [Redrawn from *Les Plantes Fossiles* by L. Emberger. Masson et Cie, Paris, 1968.]

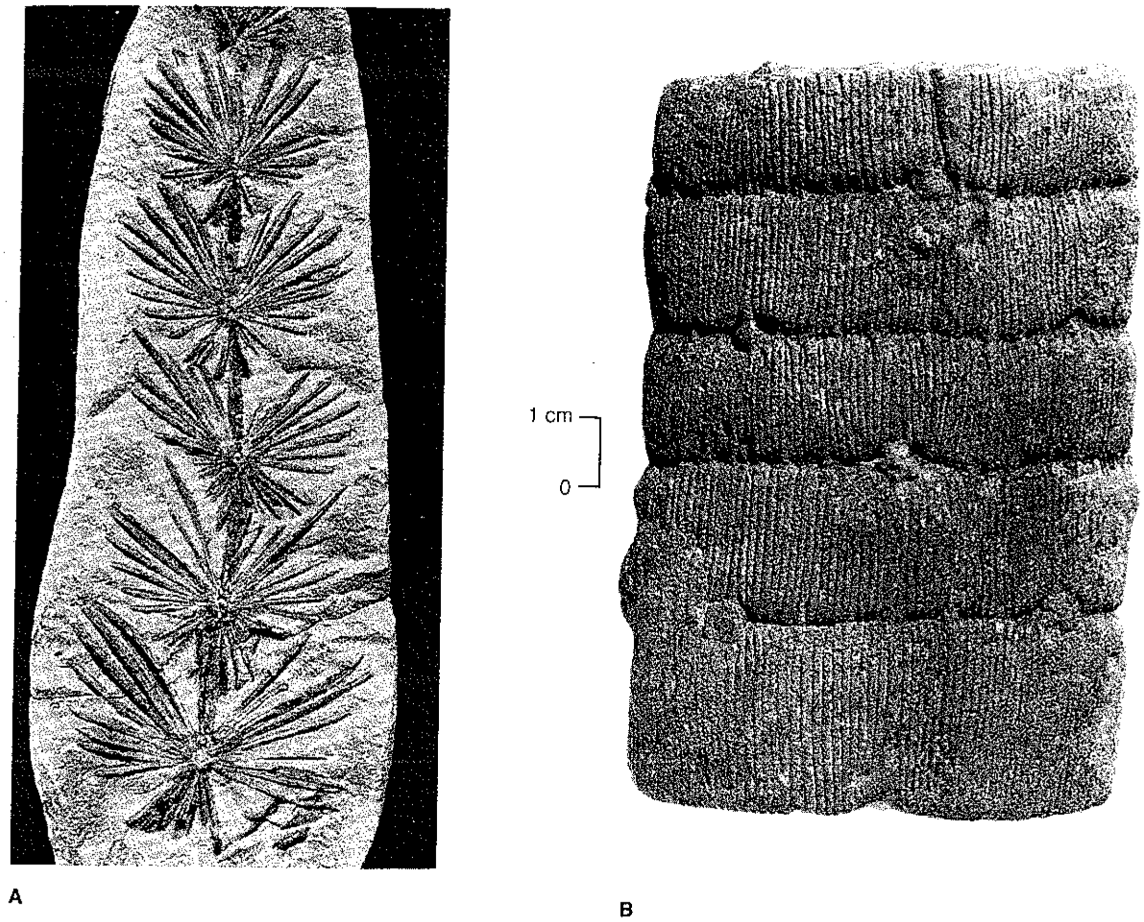


FIGURE 10-26 A, *Annularia radiata,* stem with whorls of leaves. B, pith cast of a calamite; note prominent nodes and internodes, and the presence of branch scars at the nodes. [A from R. E. Janssen, *Leaves and Stems from Fossil Forests,* Popular Series, Vol. I. Illinois State Museum, Springfield, Illinois, 1965.]

axils of sterile bracts (*Palaeostachya;* Fig. 10-28, A–C). Some calamites were heterosporous, and in one species each megasporangium retained only one megaspore (Baxter, 1963).

Equisetales — Equisetaceae: *Equisetites*

Certain sphenopsids of the Carboniferous resembled the living genus *Equisetum* and are placed in the genus *Equisetites.* However, most of the species are known from the early Mesozoic and later. The generic name *Equisetum* is used for Cenozoic fossils that are in every way similar to living species of the genus.

The reader is referred to books on paleobotany for descriptions of additional extinct genera (Taylor, 1981; Stewart, 1983).

An Appraisal

In this book we have recognized three orders in the Sphenophyta: Pseudoborniales, Sphenophyllales, and Equisetales. The latter order is comprised of two families: Equisetaceae and Calamitaceae. Some authors recognize five orders: Hyeniales, Pseudoborniales, Sphenophyllales, Calamitales, and Equisetales, although the Hyeniales are considered to be

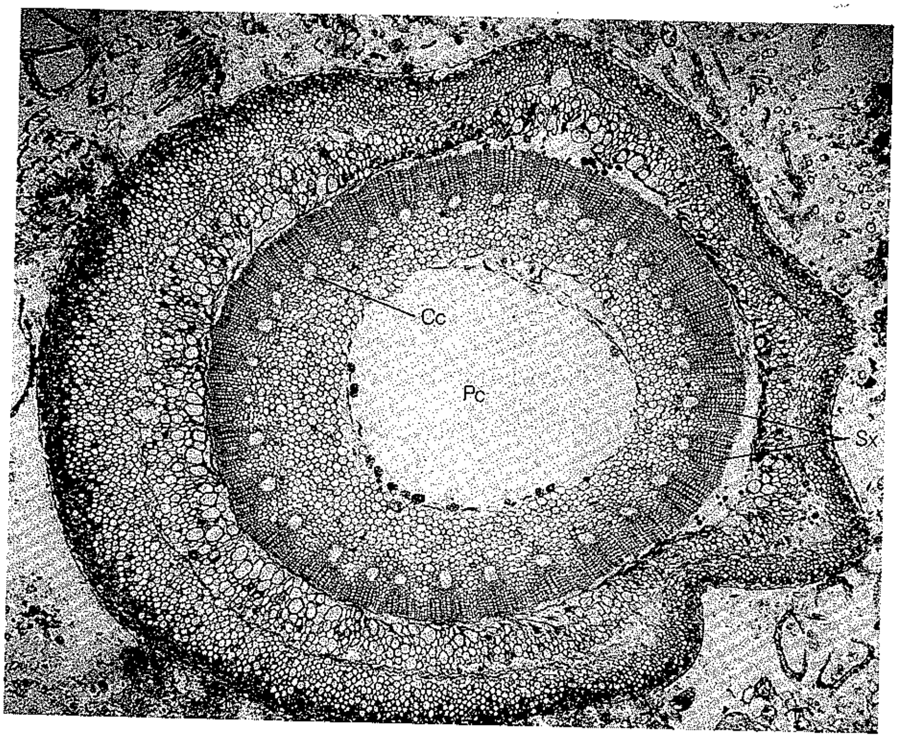


FIGURE 10-27 Transverse section of the stem of *Arthropitys* from the Pennsylvanian Epoch of the Carboniferous Period. Cc, carinal canal; Pc, pith cavity; Sx, secondary xylem. [Courtesy of Dr. T. L. Phillips.]

primitive ferns by some paleobotanists. Additionally, the Sphenophyta is designated, for example, as the Articulatae or Arthrophyta by other authors in reference to the jointed nature of the stems.

The Sphenophyllales is quite distinct from other members of the Sphenophyta in leaf morphology, possession of a protostele, and the close association of sporangiophores with bracts. In some instances the sporangiophore-bract complex is exceedingly intricate.

The general morphology of *Equisetum* and that of an extinct calamite is similar except for the great size of a calamite and the formation of secondary xylem. Morphologists are confronted with the question: Is the strobilar organization in *Equisetum* and the fossil *Equisetites* essentially primitive or is it specialized? In both genera a strobilus consists of sporangiophores without bracts. If *Equisetum* does truly represent a highly reduced calamite, then strobilar organization has involved the loss of bracts in the strobilus. In this case, the *Equisetum* strobilus would be specialized and reduced — by the loss of bracts in the course of evolution. Another way of looking at the problem is to consider sporangiophores and bracts as equivalent or serially homologous structures — perhaps both fertile in the past — the bracts having lost their reproductive structures (sporangia) in the course of time. Page (1972) has presented evidence for such a concept based upon the presence of occasional leafy sporangiophores and the occurrence of gradual transitions between typical sporangiophores to leafy ones in strobili of living species. The leaf has not evolved through a process of planation and webbing as proposed by the telome theory (Zimmermann, 1959), but has evolved by reduction and loss of dichotomies (Fig. 10-29).

It seems reasonable to assume, on the basis of morphology and anatomy, that there is an evolutionary relationship between *Equisetum* and the

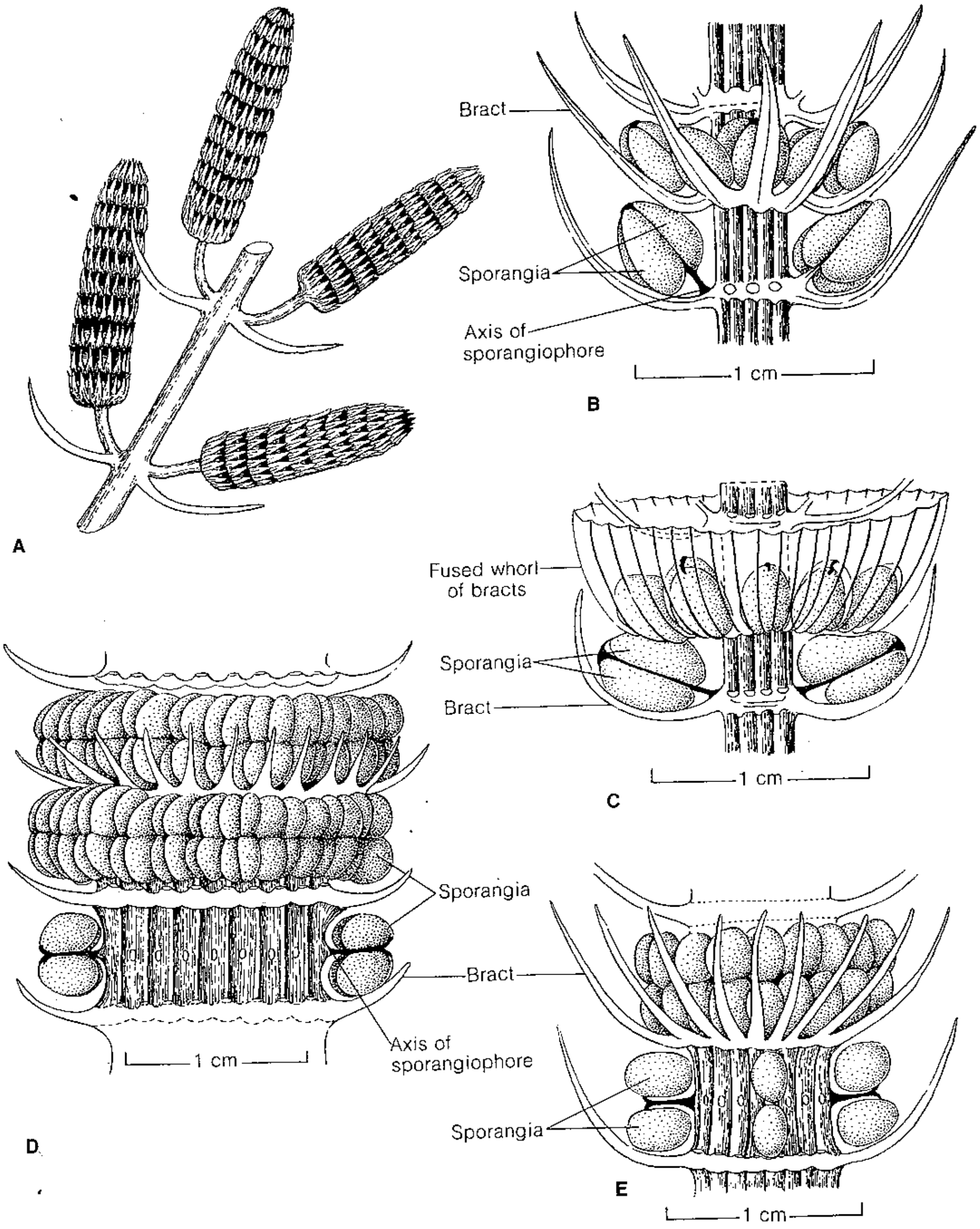


FIGURE 10-28 Diagrams of Calamitales strobili and portions of strobili showing position of sporangiophores and bracts. **A**, *Palaeostachya decacnema;* **B**, *Palaeostachya ovalis;* **C**, *Palaeostachya aperta;* **D**, *Calamostachys interculata:* **E**, *Calamostachys longibracteata.* [A redrawn from Delevoryas, *Amer. Jour. Bot.* 42:481–488, 1955; **B–E** redrawn from Abbott, *Palaeontogr. Amer.* 6:1–49, 1968.]

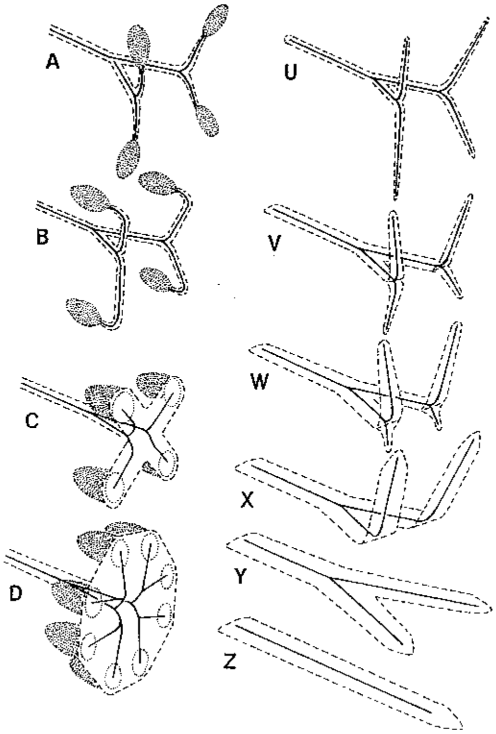


FIGURE 10-29 Diagram illustrating the suggested evolutionary stages of the *Equisetum* appendages: A–D, sporangiophores; U–Z, leaf. Broken lines indicate the outline of the appendage, stippled areas the sporangia and solid lines the vascular supply. A and U are the primitive appendages orientated in their probable planes of growth on a vertical shoot and differ from one another only in the presence or absence of sporangia. D and Z represent the morphology of sporangiophore and leaf of modern *Equisetum*, respectively. B–C and V–Y are the suggested intermediate evolutionary steps. [Redrawn from Page, *Bot. Jour. Linn. Soc.* 65:359–397, 1972.]

Calamitaceae. They probably shared a common ancestry with one line leading to the herbaceous, bractless *Equisetum*-type; the second line led to the arborescent, woody Calamitaceae with strobili having both bracts and sporangiophores.

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