CHAPTER 8

Psilophyta

THE division Psilophyta is made up of living plants comprising one order, one family, and two genera (*Psilotum,* Fig. 8-1; and *Tmesipteris,* Fig. 8-8). These plants are rather simple in organization, and traditionally they have been aligned with the extinct "psilophytes" (Chapter 7). Indeed, there are some similarities between some of the extinct early vascular plants (Chapter 7) and the Psilophyta: (1) the sporophytes are dichotomously branched with an underground rhizome system and an upright system of branches; (2) there are no roots; (3) the stems have a relatively simple vascular cylinder; (4) the sporangia are eusporangiate and homosporous; and (5) the sporangia may be interpreted as occurring at the ends of shortened axes. If this interpretation is correct, the Psilophyta resemble the ancient vascular plants in the Rhyniophyta and Trimerophytophyta (Chapter 7).

Paleobotany contributes little to proving the ancestry of *Psilotum* and *Tmesipteris* because of the lack of fossils of the two genera. If either genus is a relict form of some ancient or primitive vascular plant, we have no direct knowledge of it today. Approximately 400,000,000 years separate the Psilophyta and the earliest vascular plants and naturally, this has led to skepticism regarding the closeness of relationship. The two genera undoubtedly will be shifted from one major taxon to another in the years to come. For example, one botanist (Bierhorst, 1968a, b; 1969; 1971) would abolish a separate division or class and remove the two genera, as a family, to the leptosporangiate ferns. However, *Psilotum* and *Tmesipteris* are rootless and eusporangiate, whereas the fern (*Stromatopteris*) that is used for comparison has roots and is leptosporangiate.

Psilotin, a specific phenolic substance, has been found in *Psilotum* and *Tmesipteris* (Tse and Towers, 1967). This phenolic has not been found in the Lycophyta, which would support the conclusion that the two genera constitute a natural group. Also, the distribution of flavonoid compounds in *Psilotum*, *Tmesipteris*, and the primitive filicalean ferns shows that it is unlikely that the two genera are closely related to the ferns (Cooper-Driver, 1977).

Psilotales

Psilotaceae — Sporophyte Generation of *Psilotum*

DISTRIBUTION AND ORGANOGRAPHY. *Psilotum,* consisting of at least two species, *Psilotum nudum* (Fig. 8-1) and *Psilotum complanatum* (Reed, 1966),

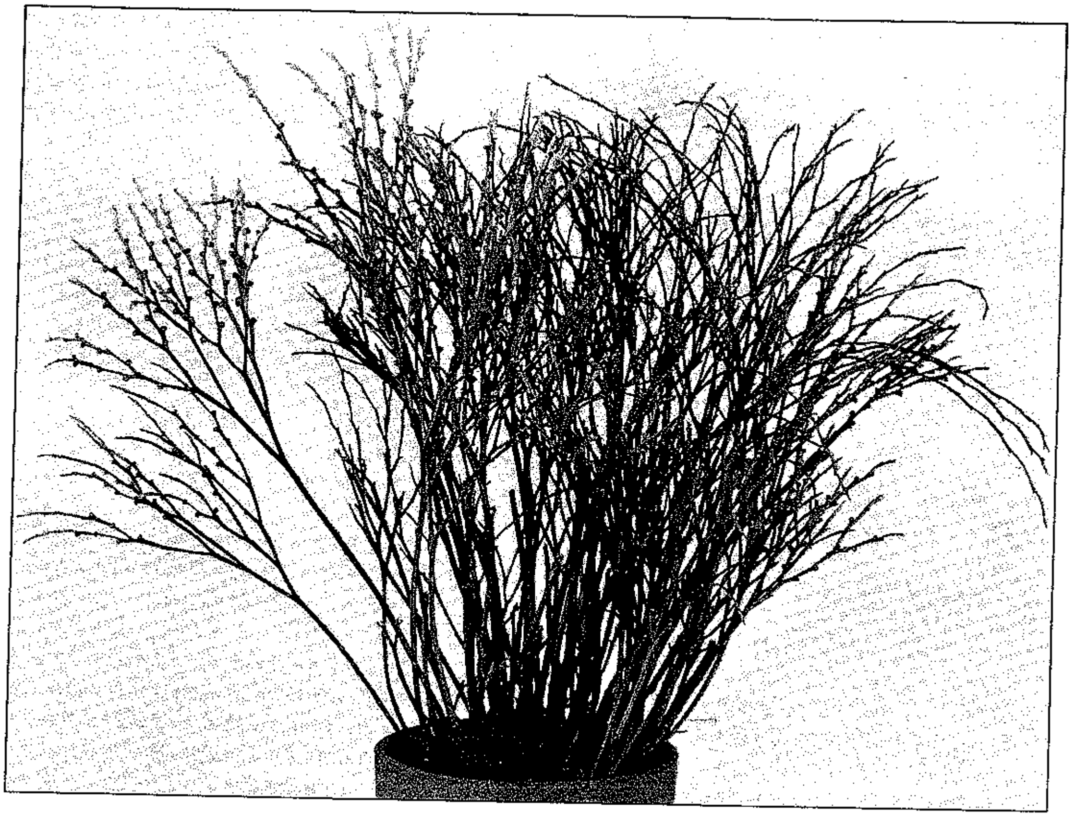


Figure 8-1 Growth habit of *Psilotum nudum* under greenhouse culture. Note dichotomies of branches at left.

is pantropical and subtropical in distribution, reaching north to Okinawa, Japan, Florida, Bermuda, and Hawaii. *P. nudum* has been reported in Nigeria (Savory, 1949), Basutoland (Morgan, 1962), Texas and Arizona (Mason, 1968), and in Spain (Allen, 1966). Its presence in some of these localities may be the result of introduction by man, intentionally or inadvertently. Plants occur as epiphytes on tree ferns, on coconut palm trunks, or at the base of trees, or they may be terrestrial, growing in soil or among exposed rocks. *P. nudum* grows remarkably well under greenhouse conditions and is cultivated in most botanical gardens in temperate regions. Depending upon its location and environment, the sporophyte of *P. nudum* may be pendent or erect and dwarfed (8 centimeters high) or as tall as 75 to 100 centimeters. The plant body consists of a basal branched rhizome system generally hidden beneath the soil or humus, and slender, upright, green aerial portions that are dichotomously branched and bear small appendages and synangia (Fig. 8-2, A, B). The branched rhizome system, which bears numerous rhizoids, grows by means of apical meristems located at the tips of ultimate branches. According to Bierhorst (1954b), the degree of branching of the rhizome is related to obstacles which the apical meristem encounters in its growth through the soil. No roots are present, although the underground rhizome system anchors the plant and rhizoids serve as absorptive structures. A mycorrhizal intracellular fungus, gaining entrance through rhizoids, is present in cells of the outer cortex (Verdoorn, 1938; Bierhorst, 1954b). This fungus may be related intimately to the physiology of the plant. Any one of the rhizome tips may turn upward and undergo several to many dichotomies that establish the basic plan of aerial branch organization. The basal part of the shoot may be

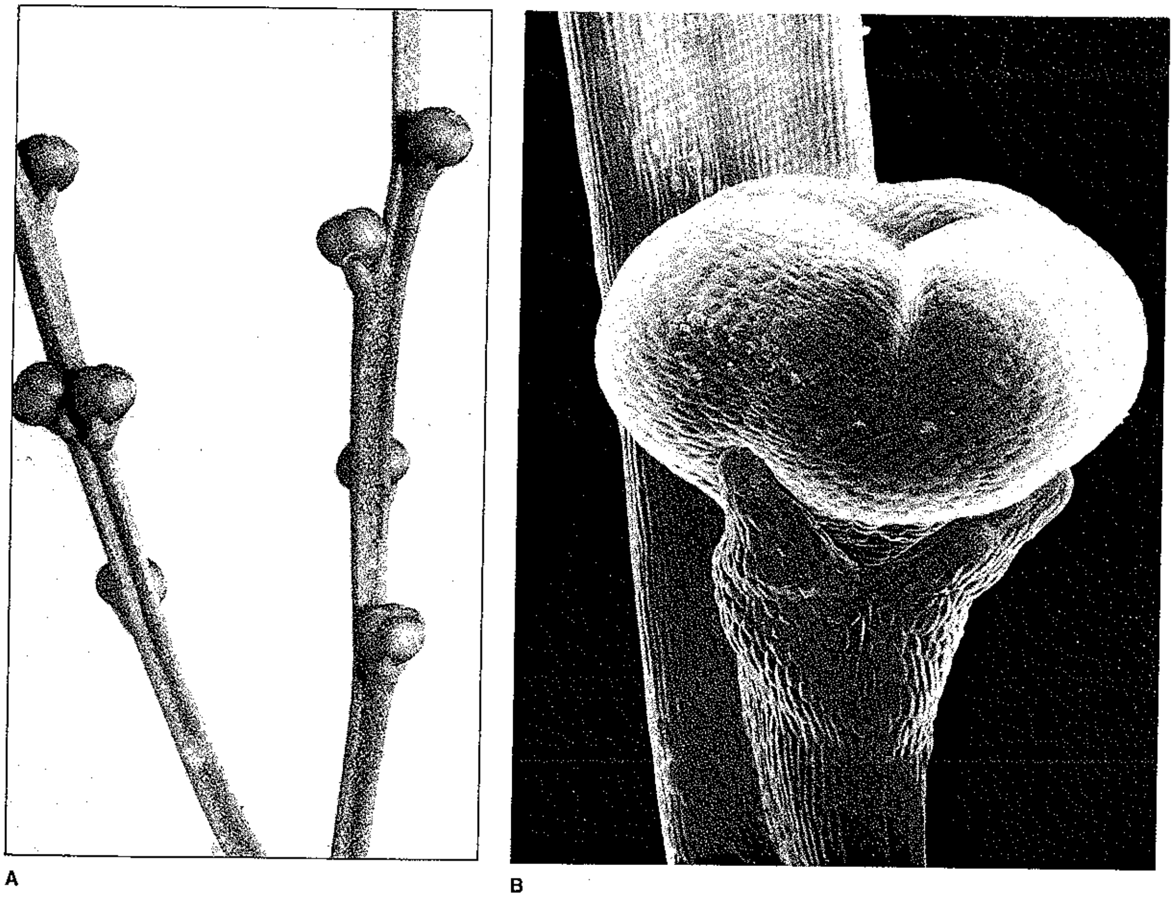


FIGURE 8-2 Organography of *Psilotum nudum.* **A,** portions of two branches showing three-lobed synangia and their associated forked appendages; **B,** scanning electron micrograph of a synangium and the forked foliar appendage.

cylindrical with longitudinal ribs, whereas the more distal aerial stems have three longitudinal ridges.

STEM ANATOMY. The apical meristem of rhizomes and aerial branches has a single, large apical cell (Bierhorst, 1954b; Marsden and Wetmore, 1954; Roth, 1963; Siegert, 1964) which divides repeatedly, giving rise to additional meristematic cells that differentiate eventually into tissues constituting the three primary tissue systems.

The aerial system is covered by an epidermis, as shown in Fig. 8-3, in which the outer tangential cell walls are heavily cutinized and covered by a cuticle. Stomata are present mainly in areas between the longitudinal ribs and are without special subsidiary cells much like the type in certain gymnosperms (Pant and Mehra, 1963). Internal to the epidermis there is a rather broad cortex which can be resolved into three regions (Fig. 8-3). The outer portion, directly beneath the epidermis, consists of elongated, lobed parenchyma cells with intercellular spaces between the vertical rows. Starch grains are present in great numbers. Internal to this zone there is a cylinder of vertically elongated and thick-walled cells, with small intercellular air spaces and few or no starch grains. In the lower portions of the aerial stems the walls of these cells apparently become lignified. In progressing from this zone to the vascular cylinder, the cell walls become thinner and thinner and less lignified with an increase in the number of starch grains per cell.

The boundary between the fundamental tissue

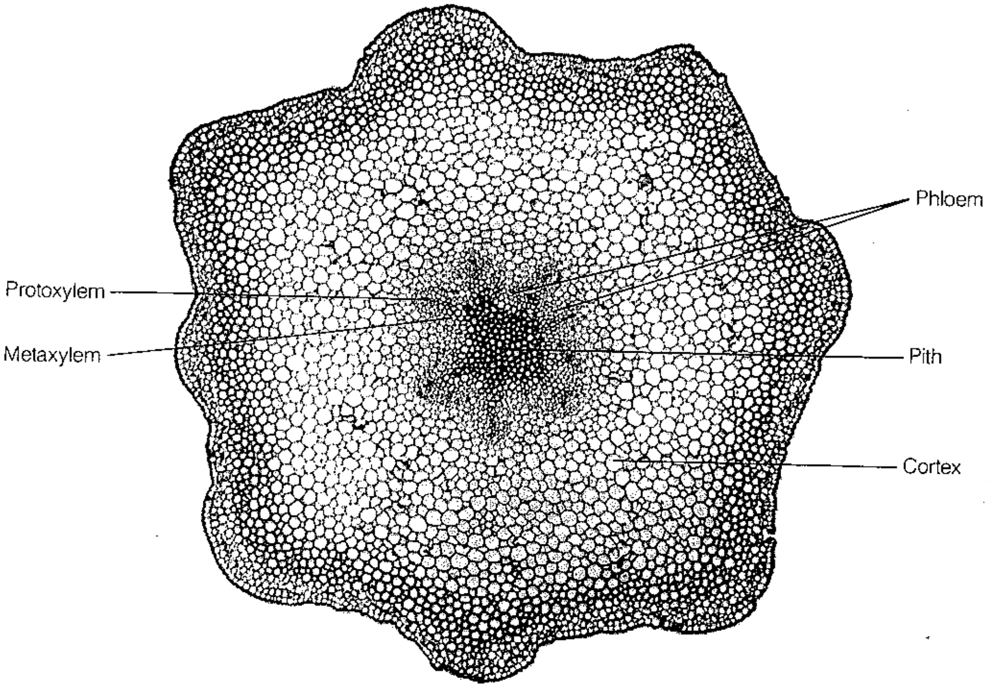


Figure 8-3 Transection of stem of *Psilotum nudum* near base of an aerial branch. Note differences in thickness of cell walls in outer and inner cortex, and xylem lobes and sclerenchymatous pith.

(cortex) system and the vascular cylinder is marked by the endodermis (Fig. 8-4, A), whose vertically elongated cells have a conspicuous casparian strip in the radial and end walls. Occupying the center of the rhizome in *P. nudum* is a slender cylinder of primary xylem which may be greatly reduced or even interrupted in small axes (Bierhorst, 1954b) and is a ridged or fluted cylinder in the aerial branches. Near the transition region from rhizome to aerial stem this cylinder may have as many as ten lobes (Bower, 1935; Pitot, 1950), whereas fewer lobes are present in the more distal parts of the aerial branch system (Figs. 8-3; 8-4, A). At levels where several xylem lobes are present, the center of the stem in *P. nudum* is generally occupied by elongate sclerenchymatous cells. Partially disorganized protoxylem tracheids, with helical or annular thickenings, occupy the extreme tips of the xylem lobes in aerial branches while the remainder is composed of metaxylem tracheids with predominantly scalariform or circular bordered pits. In summary, the rhizome is protostelic, becoming an exarch siphonostele throughout a considerable portion of the aerial branch system; the uppermost branches are, however, strictly actinostelic.

Internal to the endodermis is a cylinder of parenchyma-like cells, generally one layer thick, which is designated as the pericycle. The phloem is internal to the pericycle and occupies the regions between the lobes or flanges of the xylem. The smaller, somewhat angular cells are the sieve cells (Fig. 8-4, A). At maturity these cells are elongate, the walls are relatively thick and often lignified, and they possess many spherical bodies (refractive spherules). The sieve cells of *Psilotum* lack callose lining the pores of the sieve areas of the end walls and pores in the lateral walls (Lamoureux, 1961; Perry and Evert, 1975). However, most of the tissue in the bays between the xylem arms is composed of elongate parenchyma cells.

FOLIAR APPENDAGES. The "foliar" appendages in *Psilotum* are small scalelike structures that are helically arranged on the upper part of the aerial stem

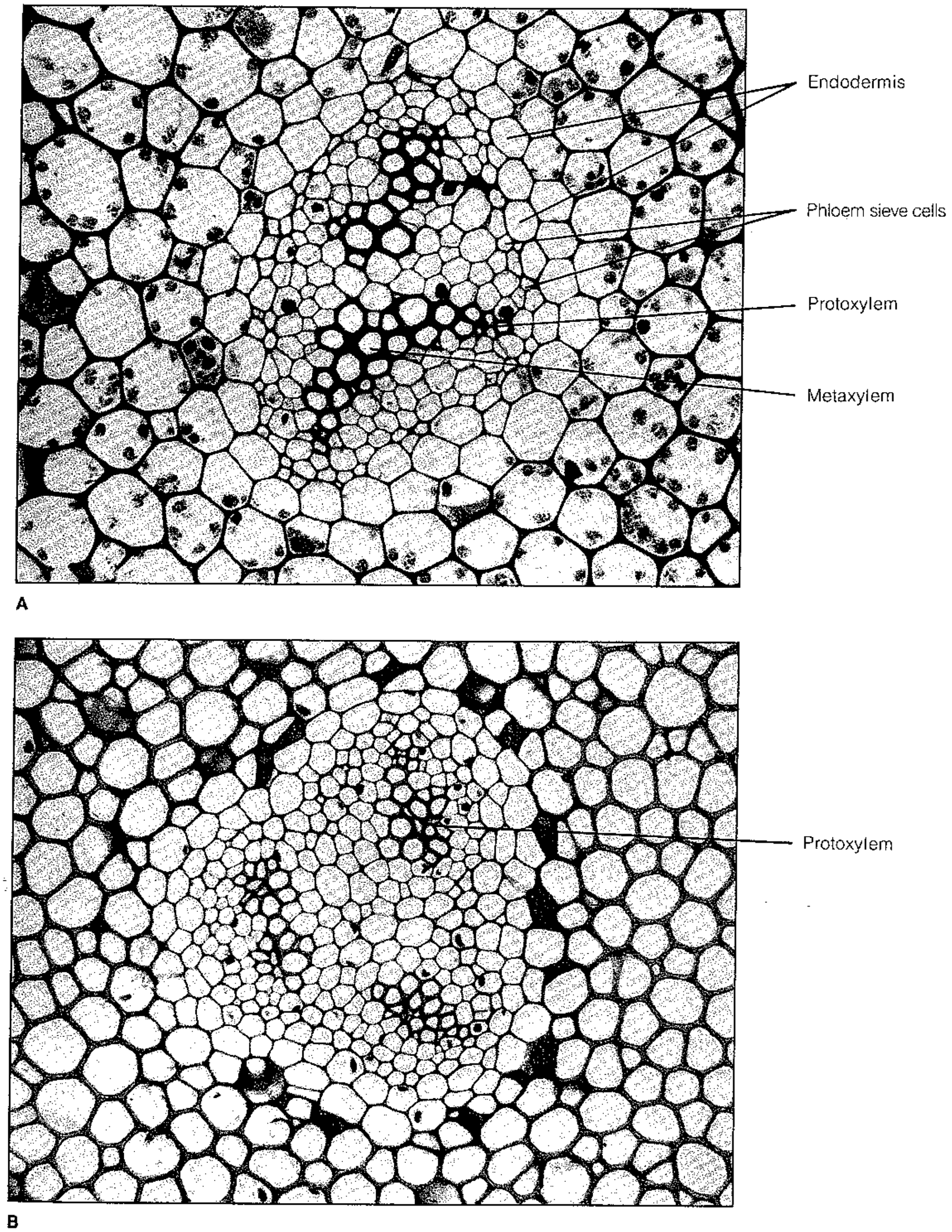


Figure 8-4 Stem anatomy of the Psilotaceae. **A,** transection of the vascular cylinder and adjacent cortex of a small aerial stem of *Psilotum nudum;* **B,** transection near the base of an aerial branch of *Tmesipteris* sp.

(Fig. 8-2, A). Internally the appendage consists of photosynthetic parenchyma cells that are continuous, lower down, with similar tissue of the stem. There is no vascular bundle in the appendage of *P. nudum,* although in *P. complanatum* a "leaf" trace ends at the base of the foliar structure. Grouped generally on the upper portions of the stems are bilobed appendages, each of which is associated with a three-lobed synangium, the fusion product of two or more sporangia. A morphological interpretation of the foliar appendages is presented in Chapter 3.

STRUCTURE AND DEVELOPMENT OF THE SYNANGIUM. Interpretations of the spore-producing structure in the Psilotales are varied and controversial; see, for example, Solms-Laubach, 1884; Bower, 1894, 1935; Eames, 1936; Campbell, 1940; Smith, 1955; Bierhorst, 1956; Zimmermann, 1959; Roth, 1963. To comment at length on all of the various theories is beyond the scope of this book. Thus, only a descriptive account will be presented with selected interpretive theories.

The spore-producing structure of *Psilotum* has been described as a trilocular sporangium and as a trisporangiate structure, i.e., a *synangium.* Results of recent investigations support the latter interpretation.

The mature synangium of *Psilotum* is generally a three-lobed structure (Fig. 8-2, A, B; and Fig. 8-5, B), 1 to 2 millimeters wide, located at the tip of a very short axis, and closely asssociated with a forked, foliar appendage. Each lobe of the synangium, corresponding to a sporangium, exhibits loculicidal dehiscence at maturity.

Some investigators believe that the short-stalked synangium arises from the adaxial side of the forked appendage or in its axil (Bower, 1894, 1935; Roth, 1963). Others have reported that the original primordium is, in fact, the "fertile axis" and that the

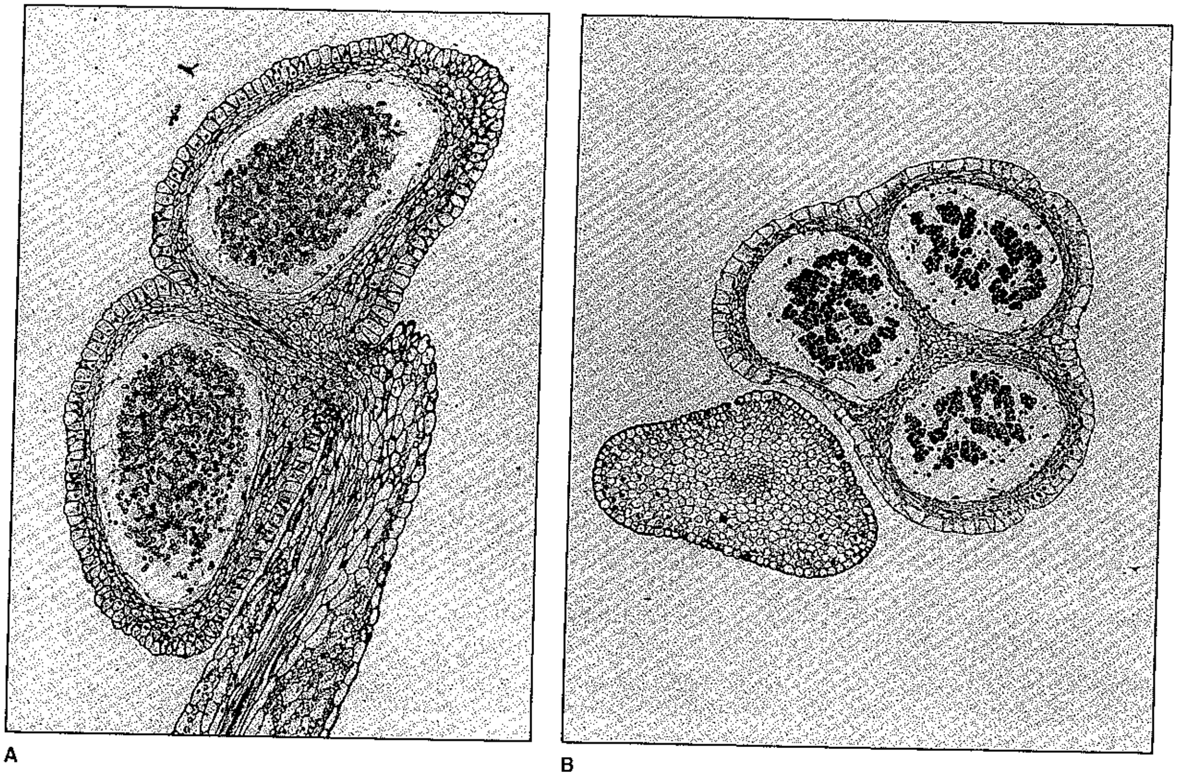


FIGURE 8-5 Synangia of the Psilotaceae. **A,** longisection, bilobed synangium of *Tmesipteris* sp.; **B,** transection, trilobed synangium of *Psilotum nudum*: note that the sporocytes are surrounded by an irregular fluid-like tapetum.

forked appendage is a lateral outgrowth on it (Bierhorst, 1956; Rouffa, 1978). Support for the latter concept is based upon experimental work. With *P. nudum* maintained on a long daily photoperiod (16 hours at 200 to 400 footcandles), the typically short fertile axes proliferated into definite branchlike structures (Rouffa, 1967). Comparable growth forms can be found occasionally under natural conditions. A variety of *Psilotum* from Japan, historically known as *Bunryu-zan,* has no sterile foliar appendages, and the synangia are borne at the tips of branches (Rouffa, 1971, 1978; Fig. 8-6).

As a result of his intensive studies on typical clones of *Psilotum* and the many varieties of *Psilotum,* such as *Bunryu-zan,* Rouffa (1978) has postulated that the fertile axes of ancestral forms may have ended in several short-stalked unfused sporangia. In the course of evolution the stalks became shortened and the sporangia became fused into synangia, culminating in the highly reduced fertile axis of the typical and more commonly known *Psilotum* clones. Ancestral forms that might provide support for this conclusion are found in the extinct group Rhyniophyta, especially *Renalia* (Chapter 7).

The development of each sporangium of the synangium in *P. nudum* is eusporangiate, i.e., separate groups of surface initials divide periclinally, setting apart primary-wall initials and primary sporogenous cells. By repeated periclinal and anticlinal divisions of the primary-wall initials, a sporangial wall of four or five layers is produced. Derivatives of the primary sporogenous cells divide in various planes to form the sporogenous tissue (Fig. 8-7). The sporogenous mass becomes irregular in outline and surrounded by a massive tapetum (Fig. 8-5, B). As is true of other plants with eusporangiate development, numerous spores are produced as a result of meiosis. Individual spores are bilaterally symmetrical and the wall has an irregular pattern of rounded, raised ridges (rugose) in some clones. Ultrastructurally, the spore-wall layers resemble more specifically those of the fern family Gleicheniaceae,

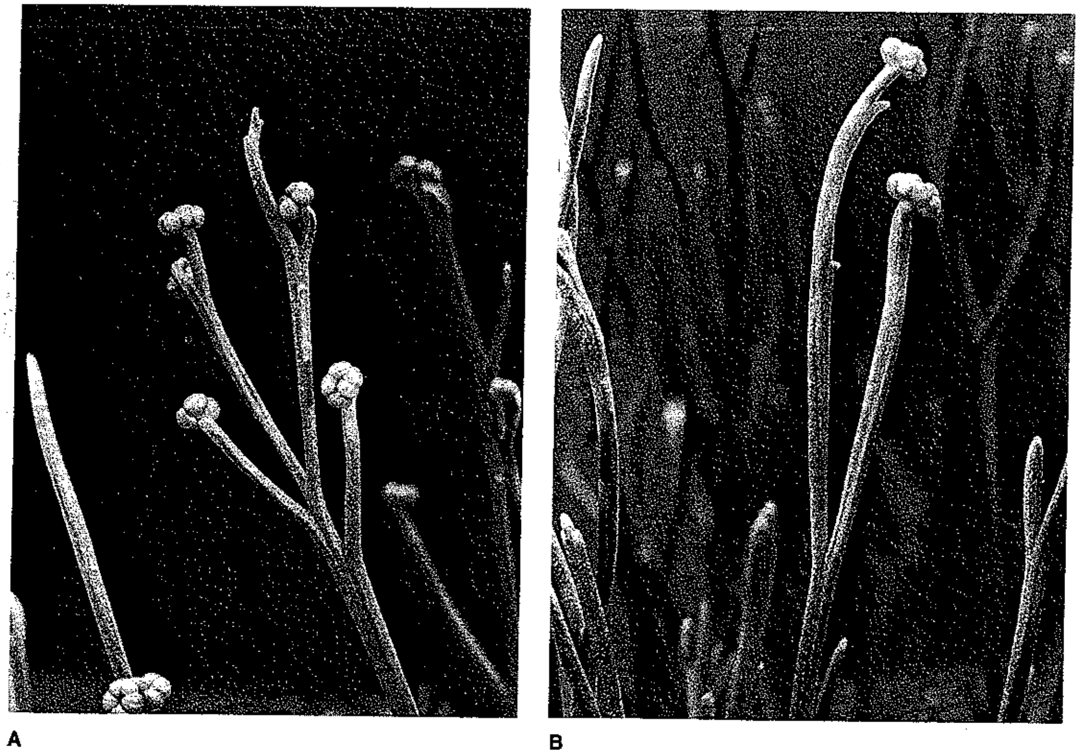


FIGURE 8-6 Two views of an appendageless form of *Psilotum* from Japan known as *Bunryu-zan*: note that the terminal synangia generally consist of more than three fused sporangia. [Courtesy Dr. A. S. Rouffa.]

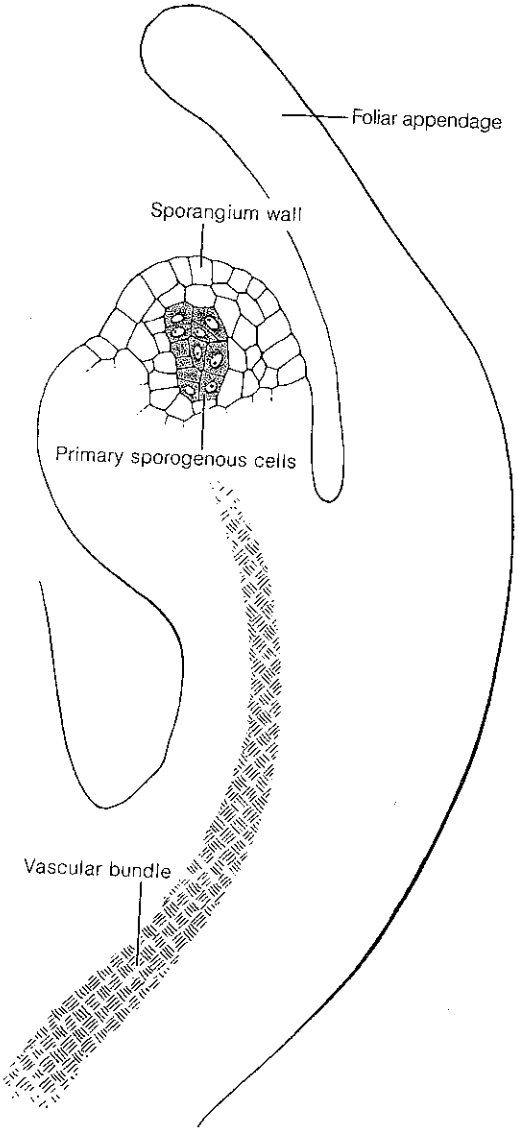


FIGURE 8-7 A young developing synangium and its associated appendage in *Psilotum nudum.* The details of only one lobe (sporangium) are shown. The vegetative stem is to the left.

but not those of the Lycophyta or *Equisetum* (Lugardon, 1979).

Unlike the foliar appendages, the fertile axis is vasculated (Fig. 8-7). A vascular bundle extends into the synangium and may become divided into three parts, corresponding to the three sporangia (Bierhorst, 1971).

Psilotaceae — Sporophyte Generation of *Tmesipteris*

DISTRIBUTION AND ORGANOGRAPHY. In contrast to *Psilotum,* which is widespread in its distribution, *Tmesipteris* is confined to Australia, New Caledonia, New Zealand, and other islands of the South Pacific Ocean. *Tmesipteris* (Fig. 8-8) generally grows as a pendulous epiphyte, 5 to 20 centimeters long, on the trunks of tree ferns or other trees, but often it may be found on mounds of humus. For many years only two species of *Tmesipteris* were recognized. *Tmesipteris tannensis* was the more widespread species. However, several forms are sufficiently different to be considered as separate species, and the five recognizable populations in southeast Australia and at least one other in New Zealand (Barber, 1954, 1957) appear to be reproductively isolated from one another.

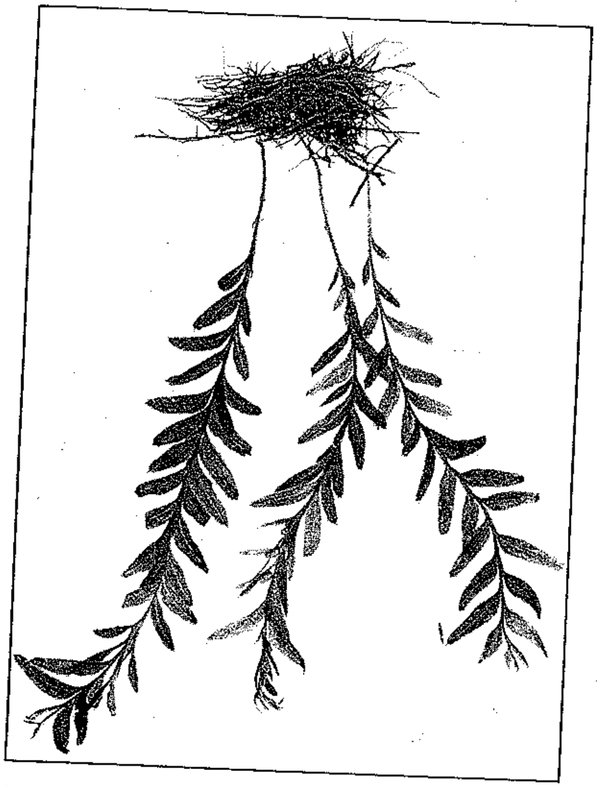


FIGURE 8-8 The pendant aerial branches of *Tmesipteris* sp. Synangia can be seen near the tip of the middle branch. In some of the appendages, the single unbranched midvein is evident.

The *Tmesipteris* sporophyte is very similar to that of *Psilotum,* with a branching rhizome system and aerial shoots. However, significant morphological differences do exist between the genera. Each aerial shoot of *Tmesipteris* may exhibit only one dichotomy. The "foliar" appendages are scalelike at the base, gradually increasing in size toward the tip. The majority of appendages are larger than those of *Psilotum,* and are flat and broadly lanceolate with a mucronate tip. The larger leaves are supplied with a single, unbranched vascular bundle. The bases of the leaves are strongly decurrent, and the distinction between stem and leaf is difficult to determine, particularly near the shoot tip, because a foliar appendage often terminates the axis. Roots are absent–a feature characteristic of ancient vascular plants (Chapter 7) and *Psilotum.*

STEM ANATOMY. The rhizome of *Tmesipteris* is protostelic, gradually becoming siphonostelic in the aerial system (Fig. 8-4, B) with three or more protoxylem poles surrounded by metaxylem. The primary xylem of aerial branches is mesarch in development, in contrast with *Psilotum* in which the primary xylem is exarch. The center of the stem consists of parenchymalike cells which may have relatively thick walls. External to the strands of xylem is a cylinder of phloem in which the sieve cells have spherical inclusions and lignified cell walls. These cells are elongate and have numerous sieve areas on their tapering end walls and lateral walls (Sykes, 1908; Lamoureux, 1961). An endodermis is present in the rhizome but lacking in the aerial portions. Between the phloem cylinder and an inner layer of cortex, cells containing brown tanniferous or phenolic substances may physiologically represent the endodermis (Fig. 8-4, B).

The cortex consists of a compact tissue of parenchymalike cells with evenly thickened walls. There may be small groups of photosynthetic parenchyma directly beneath the epidermis; the outer tangential walls of the epidermis are cutinized and covered by a definite cuticle.

FOLIAR APPENDAGES. The foliar appendages of *Tmesipteris* are larger than those of *Psilotum* and, moreover, exhibit a more diversified anatomy. The flattened appendage is covered by a uniseriate epidermis with cutinized outer tangential cell walls in which some of the thickening is laid down in the form of striations; stomata may occur on both surfaces. The internal ground tissue is uniformly arranged, consisting of lobed parenchyma cells. The single concentric vascular bundle, located centrally, is composed of several protoxylem elements surrounded incompletely by metaxylem, which, in turn, is enclosed by phloem. As in the aerial stem, no definable endodermis is present, although a compact zone of parenchyma cells occupies the expected position of such a layer.

SYNANGIUM. The mature two-lobed synangium of *Tmesipteris* is interpreted as occupying the terminus of a short lateral branch, although the axis tip is recurved and the synangium appears to be adaxial (Figs. 8-5, A; 8-9). The two foliar appendages that are attached to the fertile axis just below the synangium extend some distance beyond the synangium.

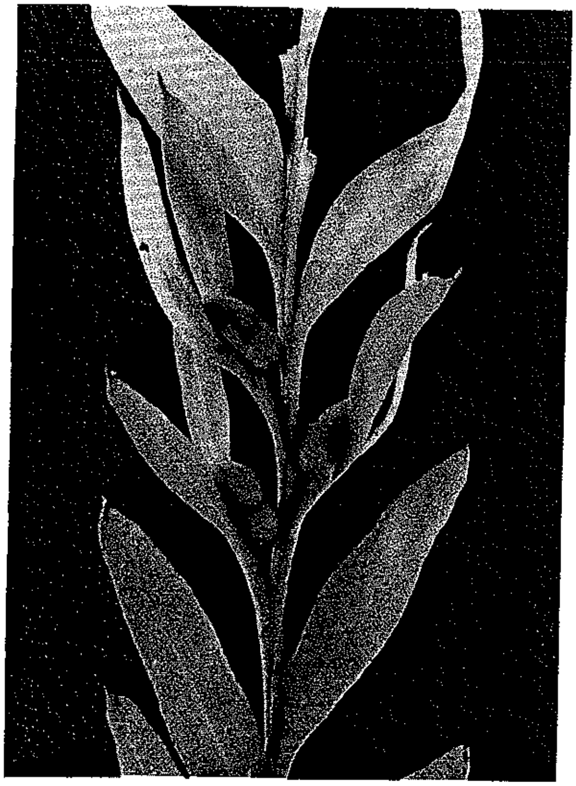
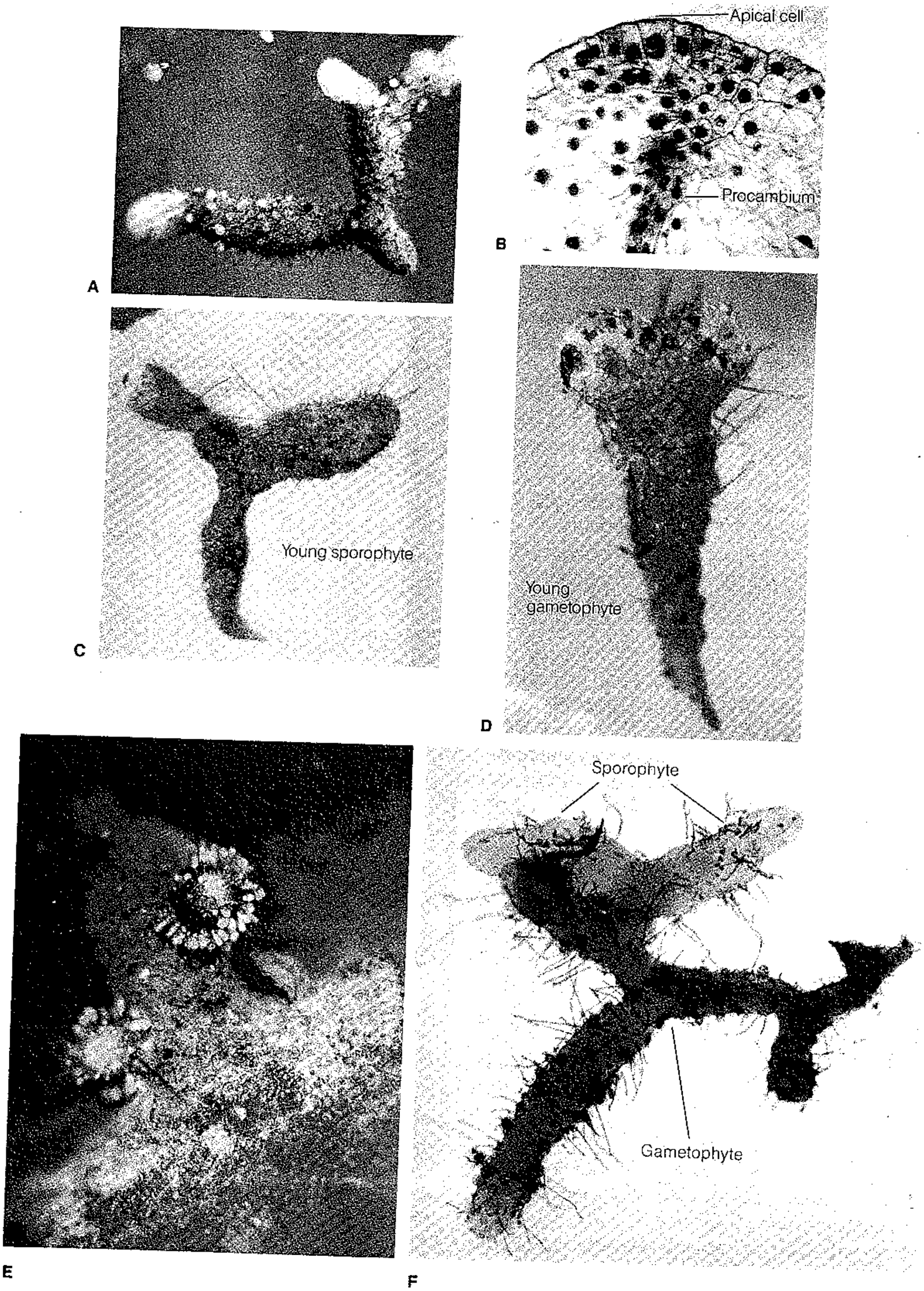


FIGURE 8-9 Small portion, branch of *Tmesipteris* sp. showing three bilobed synangia and their associated leaves.


A
Apical cell
Procambium
B
Young sporophyte
C
Young gametophyte
D
Sporophyte
Gametophyte
E
F

The single vascular bundle of the axis divides into three strands at the level of the foliar appendages. The lateral bundles traverse the appendages, whereas the median strand continues up the axis, and in some species ends in a trichotomy. The two lateral traces traverse the septum between the sporangia, and the central strand ends medianly in the septum (Sykes, 1908; Bierhorst, 1971).

According to Bierhorst (1956), the development of the fertile axis is similar to that in *Psilotum*: appearance of a primordium near the vegetative shoot tip, apical growth of the primordium, appearance of separate groups of sporangial initials, and the formation of the two foliar appendages from a common outgrowth on the original fertile axis. Subsequent development also is similar to that in *Psilotum*, with the ultimate development of a synangium with two thick-walled sporangia devoid of a well-defined tapetum and containing a large number of spores. Dehiscence of each sporangium is effected through the formation of a longitudinal cleft.

In the discussion thus far we have identified the aerial unit of *Psilotum* and *Tmesipteris* as a shoot or branch. However, Bierhorst (1968b, 1969, 1971) has interpreted each aerial entity as the morphological equivalent of a frond similar to leaves of ferns. The frond consists of sterile pinnae and fertile pinnae. The sterile pinnae are the foliar appendages not associated with synangia. The fertile pinnae are the forked appendages with synangia. On the basis of his morphological analysis, as well as upon other features of the life cycle, Bierhorst places the family Psilotaceae in the fern order Filicales (Bierhorst, 1971). The reader is referred to publications presenting arguments, pro and con, for such a concept (Bierhorst, 1977; Kaplan, 1977; Wagner, 1977).

Gametophyte Generation

The nature of the gametophyte generation in the Psilophyta long remained a gap in our knowledge of vascular plants; only in the twentieth century has it been discovered and described (*Tmesipteris*, Lawson, 1917a; *Psilotum*, Darnell-Smith, 1917, and Bierhorst, 1953). Original descriptions were based upon collections from natural habitats. The gametophytes were subterranean or grew in the crevices of rocks. In 1949 sexually mature gametophytes of *P. nudum* were discovered growing in undisturbed pots of greenhouse plants (Moseley and Zimmerly, 1949; Zimmerly and Banks, 1950; Bierhorst, 1953). Mature plants resemble pieces of the sporophyte rhizome in that they are brown, radially symmetrical, often dichotomously branched but frequently irregularly branched, and invested with rhizoids (Fig. 8-10, A, D, F). As is true of underground sporophytic axes, the branching of gametophytic plants is correlated with apical injury (Bierhorst, 1953).

There have been three successful attempts to germinate *Psilotum* spores. Darnell-Smith (1917) successfully germinated spores under simulated natural conditions. Bierhorst (1955) mixed spores in soil, and recovered young gametophytes after fifteen months. Whittier (1973, 1975) obtained germination on nutrient agar, but only after the cultures had been in the dark for six or more months. These experiments indicate that lodgment in rock crevices or burial of spores in humus or soil may be necessary for germination under natural conditions.

ANATOMY AND CYTOLOGY. Growth of a gametophyte is initiated by apical cells located at the tips of the ultimate dichotomies (Fig. 8-10, B). The gametophyte is devoid of chlorophyll, living a saprophytic existence, and is presumably aided by the presence of an endophytic fungus, which gains entrance through the rhizoids and invades nearly all cells of the plant except the apical meristems and young gametangia. The aseptate fungal hyphae may form large masses in the cells. The hyphae store quantities of lipid which appear to be released into the host cytoplasm upon fungal degeneration. The lipid may be used as an energy source by the game-

FIGURE 8-10 Gametophytes and rhizomes of *Psilotum nudum*. **A,** gametophyte showing meristematic apices (white) and prominent globular antheridia; **B,** longisection, apex of gametophyte (note large apical cell); **C,** young sporophyte of gemmaceous origin (gemmae are vegetative propagules formed both on rhizomes and gametophytes); **D,** Young gametophyte of gemmaceous origin (dark areas are presumably archegonia); **E,** clusters of gemmae on a sporophytic rhizome; **F,** gametophyte with attached sporophyte. [**A-E** courtesy Dr. D. W. Bierhorst.]

tophytes. The identity of the fungus has not been determined conclusively (Peterson, Howarth, and Whittier, 1981; Fig. 8-ll, B).

Cells of the gametophyte are parenchymatous; however, there are instances in certain races of *Psilotum* where annular and scalariform or scalariform-reticulate tracheids, surrounded by phloem and an endodermis, have been shown to occupy the center of the gametophyte (Holloway, 1938, 1939; Bierhorst, 1953). The presence of vascular tissue in the gametophytic plant is somewhat unusual among vascular plants (see Chapter 2). The external similarity of the gametophyte and the sporophytic rhizome, coupled with the presence of vascular tissue in the gametophyte, has been cited as evidence for the transformation theory as it relates to the origin of alternation of generations or phases in the life cycle (Chapter 2).

Chromosome numbers are relatively high in *Psilotum* and *Tmesipteris.* A wild "diploid" sporophyte of *Psilotum* occurs in Ceylon (Manton, 1950), and has a chromosome number $n = 52$ to 54. Bierhorst (1968b) has described similar races from Fiji and New Caledonia. Populations from widely separated regions such as India, Jamaica, Australia, New Zealand, and Japan are largely tetraploid, $n = 104$. The highest chromosome number reported, $n =$ approximately 210 (octoploid), is from New Caledonia (see Tryon and Tryon, 1982). The form commonly grown in greenhouses is tetraploid and it may have vascular tissue in the gametophyte. There is no vascular tissue in gametophytes of diploid races. That tetraploidy has been operative in the genus is supported by the presence of quadrivalents during meiosis (Ninan, 1956). A similar type of polyploid series appears to exist for *Tmesipteris* (Barber, 1957) by replications of entire chromosome sets, and is possibly based upon the theoretical basic number, $x = 13$, for both genera.

GAMETANGIA. Sex organs (antheridia and archegonia) are scattered over the surface of the gametophyte and are intermingled (Fig. 8-10, A). Young sex organs generally begin development very close to the apices of the gametophyte. The first indication of antheridial development is the presence of a periclinal division in a single surface cell, which sets aside an outer jacket initial and an inner primary spermatogenous cell (Holloway, 1918, 1939; Lawson, 1917b). By anticlinal divisions a single-layered jacket of several cells is produced enclosing a developing spermatogenous mass in which cell divisions occur in many planes. Ultimately the antheridium projects above the surface (see Fig. 8-11, A). Each spermatid eventually becomes a multiflagellate sperm and escapes through an opercular cell on the side of the antheridium (Bierhorst, 1954a).

The archegonium likewise is initiated from a single superficial cell. The initial periclinal division sets aside an outer cover cell and an inner central cell. Subsequent development is, in general, similar to that of archegonia of other lower vascular plants (Chapter 5, Fig. 5-1). At maturity there are four rows of four to six tiers of neck cells and generally one binucleate neck-canal cell (Bierhorst, 1954a). The basal two tiers of neck cells have brown, thick walls and remain in place, but the distal tiers break off with the slightest disturbance. Archegonia with only one or two tiers of neck cells are generally seen in gametophytes that have been cleaned from soil. *Psilotum nudum* gametophytes grown in vitro, however, have provided views of archegonial opening. At maturity, in the presence of water, cells of the apical tier separate and the mucilaginous contents of the neck cell are released. Within a few minutes the four rows of neck cells separate and become greatly reflexed and the apical tiers almost touch the gametophyte at the base of the archegonial neck. If undisturbed, the neck cells remain in this position for several days (Whittier and Peterson, 1980). Fertilization is accomplished by the union of a multiflagellate sperm and egg.

The Embryo

In the method of early segmentation of the zygote, and in the structure and subsequent development of the embryo, there is close similarity between *Psilotum* and *Tmesipteris* (Holloway, 1921, 1939). The first division of the fertilized egg (zygote) results in a wall formed at right angles to the long axis of the archegonium. The cell directed toward the neck of the archegonium is designated as the epibasal cell, the lower is the hypobasal cell. Members of the Psilophyta are illustrative of exoscopic polarity (Chapter 6). The apical epibasal cell will ultimately give rise to the sporophytic branch system (aerial and underground), while the hypoba-

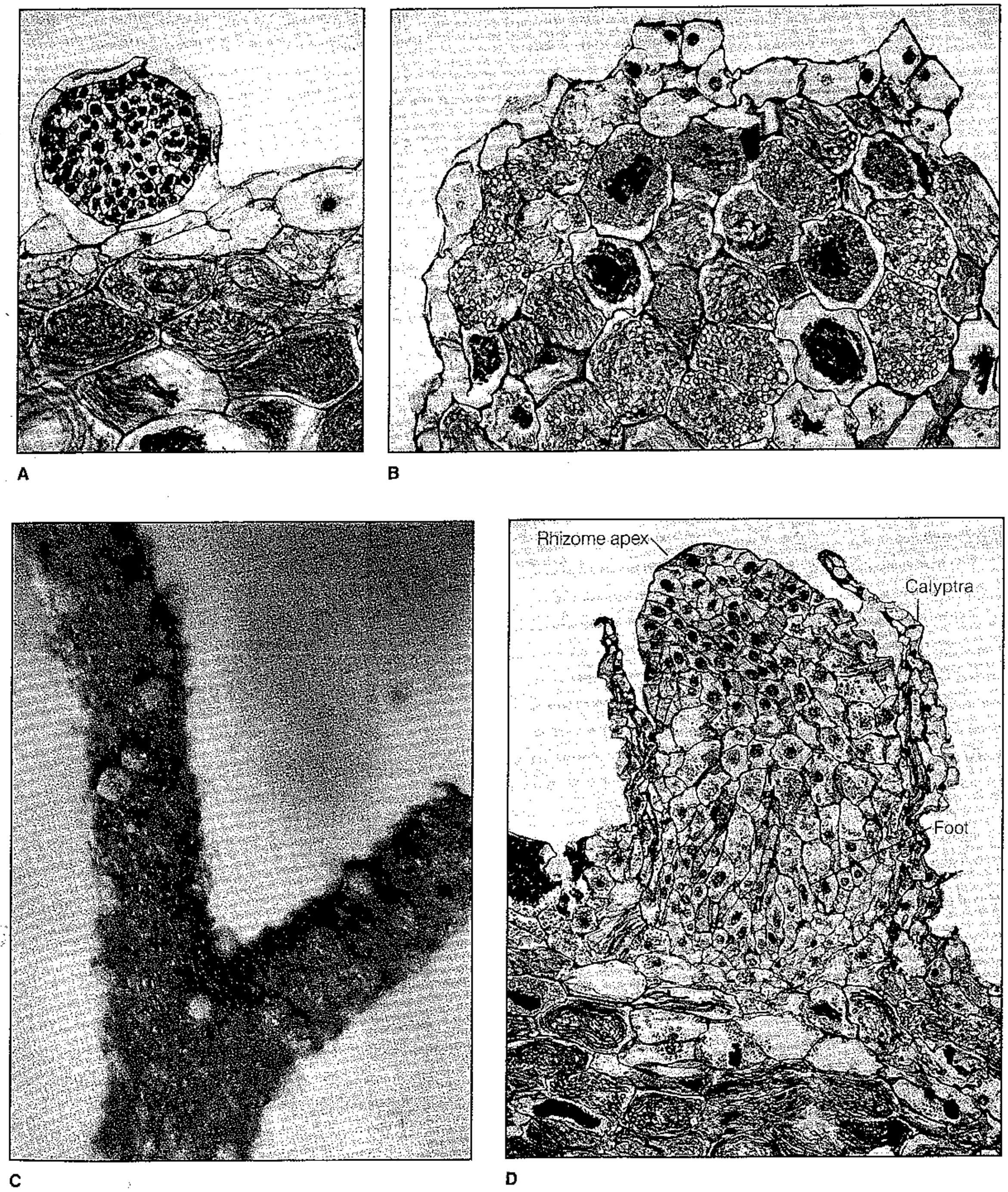


FIGURE 8-11 Gametangia and embryo of *Psilotum nudum.* **A,** section of nearly mature antheridium, showing jacket layer and spermatids; **B,** transection of gametophyte showing two mature archegonia (consult text for details of development; note that most cells of the gametophyte contain hyphae of an endophytic fungus); **C,** portion of a gametophyte with emergent antheridia; **D,** developing embryo attached to gametophyte by enlarged foot. [From slides prepared by Dr. D. W. Bierhorst.]

sal cell will produce the foot—a structure that anchors the young sporophyte securely to the gametophyte.

By repeated cell divisions the apical portion increases in size, and an apical cell is established at the distal end. Continued growth of the shoot is due in large measure to the activity of this apical cell; frequently in *Tmesipteris* two apical cells are present on the flanks of the embryo, resulting in two precociously formed horizontal branches. Concomitant with embryonic development the gametophyte forms a calyptralike outgrowth through which the young sporophyte eventually emerges (Fig. 8-11, D). While the rhizome portion is assuming form, the foot enlarges by repeated cell divisions, sending haustorial outgrowths into the gametophytic tissue. The foot, by virtue of its position and organization, is well suited for the functions of anchorage and absorption of nutrients until the sporophyte becomes physiologically independent.

Ultimately the sporophyte becomes detached from the foot and the gametophyte through a separation layer in the vicinity of the original boundary between rhizome and foot. Throughout all of the differentiation process this original boundary is clearly discernible. The rhizome continues to grow and branch, and eventually some of the rhizome tips emerge above the soil or humus and develop into photosynthetic aerial branches.

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