UNIVERSAL
LIBRARY

OU_168070

UNIVERSAL
LIBRARY

THE HYDERABAD TEXT BOOK LENDING LIBRARY

(Sponsored jointly by H. E. H. the Nizam's Charitable Trust and Rotary Club of Hyderabad)

(Name of College or Institution)

1 Anyone who shall lose, deface by writing or otherwise damage any book shall pay the full cost of the book or the entire work, if there be more than one volume,

2, Students should NOT SUB-LEND books but must return them to the Book Bank,

3, Any borrower of books, if found lending them to others shall forfeit his right of receipt of books from the Book Bank,

McGRAW-HILL PUBLICATIONS IN THE BOTANICAL SCIENCES

EDMUND W. SINNOTT, *Consulting Editor*

CRYPTOGAMIC BOTANY

Volume II

BRYOPHYTES AND PTERIDOPHYTES

McGRAW-HILL PUBLICATIONS IN THE BOTANICAL SCIENCES

EDMUND W. SINNOTT, *Consulting Editor*

ARNOLD—An Introduction to Paleobotany
AVERY ET AL.—Hormones and Horticulture
BABCOCK AND CLAUSEN—Genetics
CURTIS AND CLARK—An Introduction to Plant Physiology
EAMES—Morphology of Vascular Plants
EAMES AND MACDANIELS—An Introduction to Plant Anatomy
FITZPATRICK—The Lower Fungi
GATES—Field Manual of Plant Ecology
GÄUMANN AND DODGE—Comparative Morphology of Fungi
HAUPT—An Introduction to Botany
HAUPT—Laboratory Manual of Elementary Botany
HAUPT—Plant Morphology
HILL—Economic Botany
HILL, OVERHOLTS, AND POPP—Botany
JOHANSEN—Plant Microtechnique
KRAMER—Plant and Soil Water Relationships
LILLY AND BARNETT—Physiology of the Fungi
MAHESHWARI—An Introduction to the Embryology of Angiosperms
MILLER—Plant Physiology
POOL—Flowers and Flowering Plants
SHARP—Fundamentals of Cytology
SHARP—Introduction to Cytology
SINNOTT—Botany: Principles and Problems
SINNOTT—Laboratory Manual for Elementary Botany
SINNOTT, DUNN, AND DOBZHANSKY—Principles of Genetics
SMITH—Cryptogamic Botany
  Vol. I. Algae and Fungi
  Vol. II. Bryophytes and Pteridophytes
SMITH—The Fresh-water Algae of the United States
SWINGLE—Textbook of Systematic Botany
WEAVER—Root Development of Field Crops
WEAVER AND CLEMENTS—Plant Ecology

There are also the related series of McGraw-Hill Publications in the Zoological Sciences, of which E. J. Boell is Consulting Editor, and in the Agricultural Sciences, of which R. A. Brink is Consulting Editor.

CRYPTOGAMIC BOTANY

VOLUME II

Bryophytes and Pteridophytes

GILBERT M. SMITH

Stanford University

SECOND EDITION

ASIAN STUDENTS' EDITION

McGRAW-HILL BOOK COMPANY, INC.

New York Toronto London

KŌGAKUSHA COMPANY, LTD.

Tokyo

CRYPTOGAMIC BOTANY, Vol. II

ASIAN STUDENTS' EDITION

Exclusive rights by Kōgakusha Co., Ltd. for manufacture and distribution in Japan, South Korea, Okinawa, Taiwan, Hong Kong, the Philippines, Indonesia, Singapore, Malaya, South Vietnam, Laos, Cambodia, Thailand, Burma, Ceylon, India, Pakistan and Afghanistan. Printed in Japan.

Copyright © 1955 by the McGraw-Hill Book Company, Inc.

Copyright, 1938, by the McGraw-Hill Book Company, Inc. All rights reserved. This book, or parts thereof may not be reproduced in any form without permission of the publishers.

Library of Congress Catalog Card Number 54–8808

This book cannot be re-exported to North America, South America, Continental Europe, the United Kingdom, South Africa, Australia and New Zealand.

TOSHO INSATSU
PRINTING CO., LTD.
TOKYO JAPAN

PREFACE

In the preparation of the illustrations for this volume, many of the habit sketches of bryophytes were drawn by Mrs. Carl F. Janish, and those of pteridophytes were drawn by Maximo V. Rodrigo.

I am deeply indebted to the late Professor D. H. Campbell for placing at my disposal his extensive collections of preparations and preserved material of bryophytes and pteridophytes. These unique collections, many of them made in inaccessible tropical countries, have made possible a much fuller series of illustrations of bryophytes and pteridophytes. Professor G. S. Bryan has furnished preparations of *Andraea*, and Professor M. S. Doty has sent preserved material of *Cibotium*.

Many of the illustrations are based upon preparations made especially for me by Dr. D. A. Johansen. My thanks are again due him for helpful aid in securing illustrative material at the proper stage of development and for his technical skill in preparing it for microscopical study.

In revising the chapters dealing with bryophytes I have profited from numerous discussions about them with Professors Margaret Fulford and William C. Steere.

GILBERT M. SMITH

CONTENTS

PREFACE v

CHAPTER 1. Bryophytes and Pteridophytes 1

2. Bryophyta—Introduction 5

3. Hepaticae 14

4. Anthocerotae 87

5. Musci 96

6. Pteridophytes—Introduction 131

7. Psilophyta 159

8. Lepidophyta 179

9. Calamophyta 237

10. Pterophyta 264

INDEX 387

CHAPTER 1

BRYOPHYTES AND PTERIDOPHYTES

Bryophytes and pteridophytes stand at an evolutionary level higher than that of algae, but lower than that of seed plants. Features in which bryophytes and pteridophytes are at a higher evolutionary level than algae include multicellular sex organs with an outer layer of sterile cells, a permanent retention of the zygote within the female sex organ (archegonium), retention of the embryonic sporophyte within the archegonium and parasitism of the sporophyte upon the gametophyte for at least early stages in development. Features in which seed plants are more advanced than bryophytes and pteridophytes include migration of male gametes through a tubular connection between male and female gametophytes, permanent retention of the female gametophyte within tissues of the sporophyte, the production of seeds, and temporary cessation of growth at a certain stage in development of the embryonic sporophyte.

As between bryophytes and pteridophytes, and irrespective of phylogenetic relationships between the two (see page 131), sporophytes of pteridophytes are far more advanced than those of bryophytes. The bryophytic sporophyte is never an independent plant when mature, is more or less nutritionally dependent upon the gametophyte throughout its entire development, rarely is potentially capable of unlimited growth, and is without a conducting system differentiated into xylem and phloem. When mature, the pteridophytic sporophyte is an independent plant; is photosynthetically self-sufficient, is potentially capable of unlimited growth, and has a conducting system differentiated into xylem and phloem.

Position in a Natural System. The species is the fundamental unit (**taxon**) in classification of plants and these are grouped in taxa of different categories. Species are grouped into genera, and the genera grouped into taxa (families, orders, classes) of ascending magnitude. At first, plants were grouped in taxa based upon wholly artificial systems. Later, and long before Darwin proposed the evolutionary theory, plants were classified according to natural systems and the various taxa established upon what were thought to be their natural affinities. Not all the various natural systems proposed more than three-quarters of a century ago have been

abandoned. The system* in which the cryptogamic portion of the plant kingdom is placed in three divisions (Thallophyta, Bryophyta, Pteridophyta) was introduced about 1880. It soon became widely adopted and is still followed in a more or less modified form in many present-day textbooks. To date botanists have not questioned the validity of the Bryophyta. A decade or two after the beginning of this century botanists began raising the question of whether or not the Thallophyta and the Pteridophyta are natural divisions. These questions have been discussed in Chap. 1 of Vol. 1, but the section on the Pteridophyta is repeated here for the benefit of those who do not have Vol. 1 at hand.

Validity of the Pteridophyta. For a long time, ferns, lycopods, and horsetails were thought to be sufficiently related to be placed in a single division, the Pteridophyta. Question as to the validity of the Pteridophyta arose when Jeffrey[1] showed that there are two fundamentally different types of vascular plants. He called these two types "stocks." Ferns, gymnosperms, and angiosperms, a "stock" which he called the *Pteropsida*, have macrophyllous leaves and leaf gaps when the vascular cylinder is siphonostelic (see pages 136 and 145). Lycopods and horsetails, a "stock" which he called the *Lycopsida*, have microphyllous leaves and no leaf gaps. Jeffrey does not indicate whether these two "stocks" should be considered divisions or subdivisions of the plant kingdom. Scott[2] was the first to give them formal rank as divisions and to segregate the horsetails as a separate division, the *Sphenopsida*. Later, Scott[3] gave the Psilophytales the rank of a division but retained the ordinal name as a division name.

Ferns, lycopods, and horsetails are three series diverging from psilophytes, and seed plants are a series or group of series derived from ferns. The problem is that of what rank should be accorded diverging members of the collective series. Some botanists[4] place the collective series in a single division, the *Tracheophyta*, and segregate it into four subdivisions, *Psilopsida*, *Lycopsida*, *Sphenopsida*, and *Pteropsida*. This reduction of the four to the rank of subdivisions minimizes their marked divergence one from another. In the opinion of the writer, the differences between the psilopsidan, lycopsidan, and sphenopsidan series are of the magnitude of a division. There still remains the question of the degree of divergence

* This is frequently stated to have first appeared in the third edition of Eichler's "Syllabus" (1883). Credit for establishment of these divisions should go elsewhere since they are not recognized in the second edition of Eichler's "Syllabus" (1880) and they are to be found in a synopsis of the plant kingdom published by Schimper in 1879. The division name Thallophyta was first introduced by Endlicher (1836), who called it a kingdom. The names Bryophyta and Pteridophyta were first (?) introduced by Haeckel (1866) but he was not the first to give these groups the rank of a division.

[1] Jeffrey, 1902. [2] Scott, 1909.

[3] Scott, 1923. [4] Eames, 1936; Tippo, 1942.

among members of the pteropsidan series. Although ancestral to seed plants, the ferns seem to be sufficiently distinct from them to be placed in a separate division. Distinctive differences include gametic union by means of free-swimming antherozoids, gametophytes that are free-living from the beginning or eventually become so, uninterrupted growth of sporophyte from zygote to maturity, and absence of seed habit.

Finally, if psilophytes, lycopods, horsetails, and ferns are each to be given the rank of a division what are the names to be applied to the divisions? The International Code of Botanical Nomenclature as amended in 1950 recommends that all names of divisions end in the suffix -phyta and that subdivisions of vascular plants end in the suffix -opsida. Therefore, although Lycopsida and Sphenopsida have been used as division names[1] they are inappropriate. The earliest system in which the various classes of the Pteridophyta were each given the rank of a division used the name *Lepidophyta* for the lycopodian series, and *Calamophyta* for the equisetaceous series. The division name Pteridophyta was restricted to include only the ferns. Because of the widespread usage of the name Pteridophyta when all vascular cryptogams are grouped in a single division, the name *Pterophyta* is proposed for the division composed solely of ferns. The psilophytes should be grouped in a separate division, the *Psilophyta*.

Major Taxa of Bryophytes and Pteridophytes. There is no general agreement concerning the number of classes to be recognized among the Bryophyta. Some bryologists place liverworts and hornworts (anthocerotes) in a single class; others place them in two classes. All mosses are usually placed in a single class but some place them in three classes. The most natural classification of Bryophyta seems to be that of placing liverworts and hornworts in separate classes and including all mosses in a single class. In each of the four pteridophytic divisions there is not sufficient divergence to warrant the recognition of more than one class. The divisions and classes of bryophytes and pteridophytes may be listed as follows:

Division Bryophyta
  Class 1. Hepaticae (liverworts)
  Class 2. Anthocerotae (hornworts)
  Class 3. Musci (mosses)
Division Psilophyta
  Class 1. Psilophytinae (psilophytes)
Division Lepidophyta
  Class 1. Lycopodinae (lycopods)
Division Calamophyta
  Class 1. Equisetinae (horsetails)
Division Pterophyta
  Class 1. Filicinae (ferns)

[1] Scott, 1909.

Bibliography

Bessey, C. E. **1907.** *Univ. Nebr. Studies* **7,** No. 4: 1–99. [Classification of plants.]

Eames, A. J. **1936.** Morphology of vascular plants. Lower groups. (Psilophytales to Filicales.) New York. 433 pp. 215 figs.

Eichler, A. W. **1880.** Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik. 2d ed. Berlin. 47 pp. **1883.** *Ibid.* 3d ed. Berlin. 68 pp.

Haeckel, E. **1866.** Generelle Morphologie der Organismen. Bd. 2. clx + 462 pp. 8 pl.

Jeffrey, E. C. **1902.** *Phil. Trans. Roy. Soc. London B.* **195**: 119–146. 6 pl. [Stelar theory.]

Schimper, W. P. **1879.** Palaeophytologie. In K. A. Zittel, Handbuch der Palaeontologie. **2,** Lief. 1: 1–152. 117 figs.

Scott, D. H. **1909.** Studies in fossil botany. 2d ed. Vol. 2. London. 321 pp. 95 figs. **1923.** *Ibid.* 3d ed. Vol. 2. London. 446 pp. 136 figs.

Tippo, O. **1924.** *Chronica Botanica* **7**: 203–206. [Classification of plants.]

CHAPTER 2

BRYOPHYTA—INTRODUCTION

The Bryophyta have a sharply defined heteromorphic alternation of generations in which the diploid asexual generation (sporophyte), although morphologically distinct from the haploid sexual generation (gametophyte), is attached to it and never becomes an independent free-living plant. This condition is in contrast with that of pteridophytes and more advanced plants, where the sporophyte is always an independent plant at maturity. Sporophytes of plants more advanced than bryophytes are internally differentiated into xylem and phloem, whereas those of bryophytes lack these tissues.

The gametophyte of a bryophyte is always an independent plant at maturity and one that is nutritionally self-sufficient because of the presence of chloroplasts within it. In many cases the gametophyte is a thallus; that is, a plant body without differentiation into root, stem, and leaf. In those cases where it is externally differentiated into stem and leaves there are never any roots, only one-celled absorptive organs (rhizoids).

All bryophytes are oögamous, and with the gametes produced within multicellular sex organs in which there is an outer sterile layer of jacket cells. In this respect they are immediately distinguishable from algae since algal sex organs are usually unicellular and when multicellular have all the cells gamete-producing.

Life Cycle of Bryophyta. The life cycle of a bryophyte consists of a regular alternation of a gamete-producing generation and a spore-producing generation. This was first clearly demonstrated by Hofmeister[1] in 1851, but the periodic doubling and halving in the number of chromosomes in connection with the alternation of generations was not recognized[2] until 1894. The alternation of generations is obligatory in the sense that a zygote resulting from gametic union always grows into a sporophyte, and that spores produced by a sporophyte always germinate to form gametophytes. The alternation of generations is not obligatory in the sense that gametophyte and sporophyte must always alternate with each other, because there may be a life cycle in which vegetative

[1] Hofmeister, 1851. [2] Strasburger, 1894.

propagation of the gametophyte results in a succession of gametophytic generations before there is a formation of a sporophyte.

It should also be noted that vegetative propagation does not always result in a similar generation. Thus, vegetative budding of sporophytic tissue may result in the formation of a gametophyte. This production of a gametophyte from a sporophyte without the formation of spores is **apospory.** Conversely, a gametophyte may bud off a mass of cells which develops into a sporophyte. Production of a sporophyte from a gametophyte without any union of gametes is **apogamy.** Apospory and apogamy are of rare occurrence among bryophytes as compared with pteridophytes,* and most of the recorded cases among bryophytes are among mosses where a wounding of sporophytes[1] induces an aposporous production of gametophytes. The Anthocerotae are also known to be aposporous.[2]

Origin of the Bryophyta. In contrast with pteridophytes, there are no known fossil bryophytes more primitive than present-day forms. The nature of the primitive bryophyte and the manner in which it originated must, therefore, be based upon the comparative morphology and ontogeny of living plants. Except for the few dissenters[3] who hold that bryophytes have descended from pteridophytes, there is an almost universal belief that bryophytes arose from algae. The belief is quite general that these algae were Chlorophyceae, and confirmation of this is seen in the fact that they have been found[4] to be the only algae in which the chlorophylls and xanthophylls are identical with those of bryophytes.

At one time it was generally thought that there was a migration of an oögamous alga from water to land and that this was followed by an evolution of a bryophytic type of sexual plant with the sexual organs characteristic of bryophytes. Simultaneous with this migration was an appearance of the alternation of generations characteristic of bryophytes. However, it is not necessary to assume that the ancestral alga was oögamous. It is equally possible that the ancestor was isogamous and that the change to oögamy came after migration to land. The fact that an evolution from isogamy to oögamy has appeared in many independent lines of algae shows that such a change may occur at any time. It is also known that an alternation of generations has arisen independently in such distantly related taxa of green algae as the Chaetophoraceae, Cladophorales, and Ulvales. Thus it is possible that the alternation of generations found in bryophytes did not appear after the sexual thallus of the algal ancestor had evolved to a point where it would be considered

* See pp. 151–153 for a fuller account of these phenomena.

[1] Marchal and Marchal, 1911. [2] Bornhagen, 1926; Rink, 1935.
[3] Haskall, 1949. [4] Strain, 1948.

a bryophyte instead of an alga. Since there is this possibility it is better to discuss separately the possible origin of the two generations.

Origin of the Gametophyte. There are two diametrically opposed views concerning vegetative structure of the archaic bryophytic gametophyte. Adherents of one view[1] hold that the primitive bryophytic gametophyte was an erect leafy plant. Adherents of the other view hold[2] that it was a simple thallose structure without external or internal differentiation. If the primitive bryophytic gametophyte was an erect leafy plant it is a long jump from it to any known green alga. On the other hand, such parenchymatous terrestrial green algae as *Fritschiella*[3] show the beginning of an evolution toward the type of plant postulated by those who think that the primitive bryophyte had a simple thallose gametophyte.

Among isogamous and anisogamous multicellular green algae most cells of a thallus are capable of producing one or more gametes, and this usually takes place in several adjoining cells. This condition is markedly

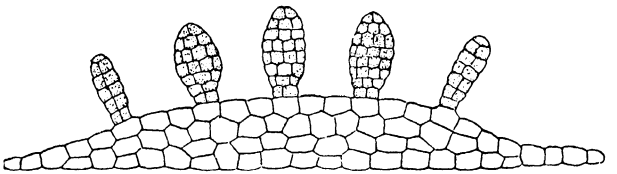

FIG. 1. Hypothetical terrestrial green alga bearing the assumed type of gametangia from which bryophytic antheridia and archegonia were evolved.

different from that in bryophytes where sex organs are multicellular and with the superficial cells differentiated into a sterile jacket layer. The most attractive hypothesis[4] explaining the origin of the sex organs characteristic of bryophytes holds that archegonia and antheridia of bryophytes are fundamentally alike and that they arose by sterilization of the outermost cells of a multicellular gametangium, similar in appearance to gametangia of *Ectocarpus*. One of the weaknesses of this hypothesis is that such gametangia, although widespread among brown algae, are not known for any green alga. However, certain branched Chaetophoraceae have their formation of isogametes restricted to small-celled branches in which each cell produces but a single swarmer. There are also filamentous green algae where the fertile portion is more than one cell broad. Thus it is not inconceivable that a green alga evolving into a bryophytic type had a massive body bearing on its upper surface cylindrical, multicellular, gamete-producing outgrowths more than one cell broad (Fig. 1). The gametangial hypothesis holds that certain of the outgrowths produced motile male gametes and others produced motile

[1] Church, 1919; Evans, 1939; Harris, 1938; Kashyap, 1919; von Wettstein, 1908.
[2] Campbell, 1891, 1918, 1936; Cavers, 1910.
[3] Iyengar, 1932; Singh, 1941, 1947. [4] Davis, 1903.

female gametes of the same or a somewhat larger size. In both kinds of outgrowth the superficial cells lost their gamete-producing capacity and evolved into a sterile layer (jacket) that enclosed the fertile cells. Retention of the gamete-producing capacity by all fertile cells within the male outgrowth resulted in the antheridium typical of Bryophyta (Fig. 2). Archegonial evolution was accompanied by a sterilization of all but the

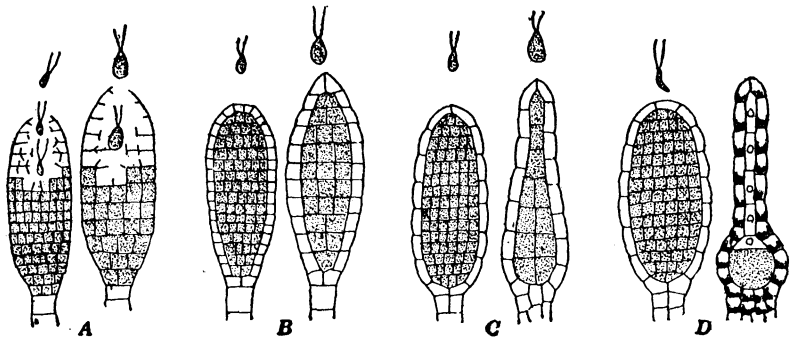

FIG. 2. Diagrams showing the hypothetical origin of sex organs of Bryophyta. (*Based upon Davis*, 1903.)

lowermost of the fertile cells within the outgrowths producing female gametes. The single cell remaining fertile lost its ability to form flagella, was retained within the female outgrowth, and thus became an egg. According to this interpretation the neck canal cells and venter canal cell of an archegonium are homologous with the first-formed fertile cells within an antheridium. The evidence supporting this hypothetical origin

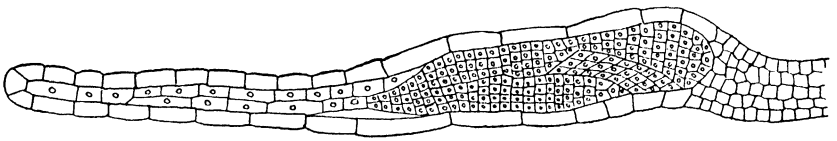

FIG. 3. Abnormal archegonium of *Mnium* showing an antheridium-like internal tissue.

of bryophytic sex organs comes largely from abnormal sex organs occasionally developed by various Hepaticae and Musci.[1] These reversionary sex organs are almost always archegonia. In some of them cells other than the lowermost become fertile. Sometimes these cells mature into eggs, but more frequently they divide and redivide to form masses of cubical cells identical in appearance with those within antheridia (Fig. 3). Reversion of superficial cells into a fertile condition is most unusual, and only a couple of such cases have been reported.[2]

[1] Bryan, 1927; Florin, 1923; Haupt, 1926, 1943; Holferty, 1904; Meyer, 1912.
[2] Meyer, 1912.

Origin of the Sporophyte. At one time there was a widespread belief that an alternation of generations did not appear in the plant kingdom until after the first land plants had arisen from an algal ancestor that had migrated onto land. We now know that an alternation of independent gametophytic and sporophytic generations has been evolved in several independent lines among aquatic algae. Therefore a migration from an aquatic to a terrestrial environment is not essential for an appearance of an alternation of generations. Some of the aquatic algae with an alternation of generations have an **isomorphic alternation** in which the two generations are vegetatively identical in size and shape; others have a **heteromorphic alternation** in which the two are dissimilar in size and structure.

Views of various writers concerning the origin of the bryophytic sporophyte are in large part influenced by how they adhere to the two conflicting theories concerning the nature of the sporophyte. According to the **modification (homologous) theory** the sporophyte is a direct modification of the gametophyte. Advocates of this theory hold that the sporophyte is to be interpreted as a neutral generation, and one whose primary function is the production of spores. Evidence supporting the modification theory has been drawn from algae, bryophytes, and pteridophytes. This includes the isomorphic alternation found in certain algae, photosynthesis in sporophytes of bryophytes, the presence of tracheids in gametophytes of pteridophytes, and apogamy and apospory. Adherents of the modification theory who have speculated upon the nature of the primitive land plant (bryophyte or archegoniate) think[1] that the two generations were isomorphic, free-living, and of somewhat complex external structure. They hold that in time the sporophyte became permanently attached to the gametophyte, partially dependent upon it, and that this resulted in a reduction in complexity of the sporophyte.

According to the **intercalation (antithetic) theory,** the sporophyte is to be interpreted as an entirely new structure intercalated between two successive gametophytic generations. It is thought that the bryophytic sporophyte did not make its appearance until after a gamete-bearing plant had evolved an archegonium. The zygote retained inside an archegonium did not divide meiotically, but divided mitotically to form a number of diploid cells, each of which divided meiotically to form four spores. The result was a rudimentary type of sporophyte vegetatively different from the gametophyte and a sporophyte in which all cells were sporogenous. From this was evolved a sporophyte in which the superficial cells were sterile instead of sporogenous. Further evolution of the sporophyte came about as a result of additional sterilization of sporogenous tissue, and in what are considered more advanced bryophytic

[1] Church, 1919; Fritsch, 1945; Zimmermann, 1932.

sporophytes resulted in a differentiation of them into foot, seta, and capsule. In contrast with the modification theory, those supporting the intercalation theory believe that there was a progression from a simple to a more complex sporophyte by a progressive sterilization of sporogenous tissue. Evidence supporting the theory of progressive sterilization is to be seen in abnormal sporophytes where, as in *Porella*,[1] internal portions of foot and seta are sporogenous.

Evolution among Bryophyta (Fig. 4). Three major evolutionary lines (liverworts, anthocerotes, mosses) are recognizable among bryophytes. The question as to which of these three lines contains the most primitive living bryophytes depends upon what one considers the primitive type of

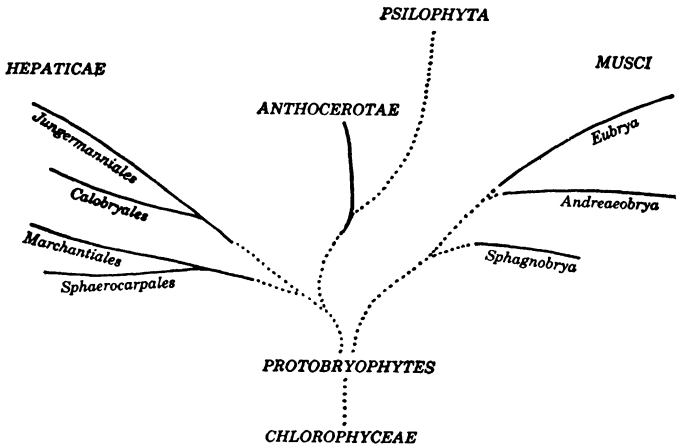

FIG. 4. Diagram showing the suggested interrelationships among the Bryophyta.

gametophyte and the primitive type of sporophyte. In the opinion of the writer there is more in favor of the view that the primitive bryophytic gametophyte was a simple thallose plant, and that the primitive sporophyte was the simple globose type postulated by the intercalation theory. According to such an interpretation the bryophytes most nearly approaching the primitive condition are to be found among the liverworts. Here the simplest gametophytes are to be found among the Sphaerocarpaceae, and the simplest sporophytes are to be found among the Ricciaceae (for a discussion of whether this sporophytic simplicity is due to primitiveness or to reduction see page 28). For hypothetical bryophytes (protobryophytes) more primitive than any known bryophyte, Lotsy[2] has suggested a type combining the simple gametophyte of *Sphaerocarpos* with the simple sporophyte of Ricciaceae to form the imaginary genus *Sphaero-riccia*.

[1] Anderson, 1923. [2] Lotsy, 1909, p. 88.

When both generations are taken into consideration the Sphaerocarpales appear to be the most primitive of living liverworts (Hepaticae). The marchantiaceous series of Hepaticae is one characterized by gametophytes of external simplicity but internal complexity. Similarities in structures of their sex organs with those of Sphaerocarpales, and similarities in jacket layers of the sporophytic capsule suggest a relationship between the two. Features in ontogeny of sex organs, especially antheridia, and structure of the sporophytic capsule indicate that relationships of Jungermanniales and Calobryales with other Hepaticae are rather remote. In the opinion of the writer these orders are of an advanced type among the Hepaticae but it should be noted that there are those who consider them the most primitive (see page 16). No matter what the evolutionary order of their interrelationships the Hepaticae seem to constitute a blindly ending evolutionary side line.

The mosses also seem to be a blindly ending evolutionary side line. Their gametophytes are externally complex and at times with some internal differentiation of tissues. Most of them have sporophytes with greater internal differentiation of tissues than do any of the Hepaticae but growth of all sporophytes of mosses is determinate. The mosses are sometimes thought to have been evolved from leafy Hepaticae (Jungermanniales, Calobryales) but this appears to be improbable when ontogeny of sex organs and the early embryology are taken into consideration. It seems more probable that mosses should be considered a divergent line from ancestors of Hepaticae instead of a line diverging from any known series among the Hepaticae.

Gametophytes of anthocerotes, except for their embedded sex organs, resemble those of thallose Hepaticae. On the other hand, the anthocerotean sporophyte with its indeterminate growth is of a much more advanced type than is found in any hepatic or moss. Because of similarities in gametophytes and ontogeny of sex organs, the anthocerotes may be considered a series which departed from primitive Hepaticae along the line leading to the Sphaerocarpales and Marchantiales.

Classification of Bryophyta. The conventional treatment of the Bryophyta is to range them in two classes, Hepaticae and Musci. In recent years there has been a growing tendency to accept the proposal[1] that the Anthocerotales be placed in a taxon coordinate with the Hepaticae and Musci.

Three distinct lines are recognized among the mosses. Differences in these three lines include origin of the sporogenous layer, mode of dehiscence of capsule, the presence or absence of a pseudopodium, and structure of the protonema. Some bryologists accept the proposal[2] that these differences warrant a segregation of mosses into three classes; but in view

[1] Howe, 1899. [2] Schaffner, 1927, 1934.

of the obvious phylogenetic relationships between the three it seems better to give each of them the rank of a subclass and to place all in a single class, the Musci. When the Bryophyta are placed in three classes they may be characterized as follows:

The *Hepaticae* have gametophytes that are dorsiventrally differentiated and either externally simple or externally differentiated into leaves and stem. The interior of a gametophyte may be homogeneous or composed of various tissues. Sex organs, except when terminal in position, are always formed from superficial cells on the dorsal side of a thallus. Sporophytes may be simple; or with foot and capsule; or with foot, seta, and capsule. In any case, they are determinate in growth and with sporogenous cells derived from the endothecium of an embryo.

The *Anthocerotae* have gametophytes that are dorsiventrally differentiated, of simple external form, and internally homogeneous. Sex organs are embedded in the gametophyte, the female being formed from superficial and the male formed from hypodermal cells on the dorsal side of a thallus. The sporophyte is differentiated into capsule and foot. The lower portion of a capsule is meristematic and is continually adding to the upper portion. Sporogenous tissue of a capsule arises from the superficial layer (amphithecium) of an embryo, and encircles a columella.

The *Musci* have a gametophyte with a transitory prostrate stage (protonema) bearing erect sexual branches which continue growth as independent plants after disappearance of the prostrate portion. The sexual branches are differentiated into stem and leaves, usually radially symmetrical, and with the sex organs developed from superficial cells at the upper end of the stem. Growth of a sporophyte is always determinate and a sporophyte may consist of foot and capsule; or foot, seta, and capsule. Sporogenous tissue of a capsule may arise in the endothecium or amphithecium of an embryo, but in either case it encircles a columella.

Bibliography

Anderson, Flora. **1923.** *Proc. Ind. Acad. Sci.* **1922**: 261–262. 1 fig. [Abnormal sporophytes.]

Bornhagen, Hedwig. **1926.** *Biol. Zentralbl.* **46**: 578–586. 7 figs. [Apospory.]

Bryan, G. S. **1927.** *Bot. Gaz.* **84**: 89–101. 20 figs. [Abnormal sex organs.]

Campbell, D. H. **1891.** *Ibid.* **16**: 323–333. [Interrelationships.]

1918. The structure and development of mosses and ferns. 3d ed. New York. 708 pp. 322 figs.

1936. *Bot. Rev.* **2**: 53–66. [Interrelationships.]

Cavers, F. **1910.** *New Phytol.* **9**: 81–112, 157–186, 193–234, 269–304, 341–353. 54 figs. [Interrelationships.]

Church, A. H. **1919.** Thalassiophyta and the subaerial transmigration. *Oxford Bot. Mem.* No. 3. 1–95.

Davis, B. M. **1903.** *Ann. Bot.* **17**: 477–492. 2 figs. [Origin of sex organs.]

Evans, A. W. **1939.** *Bot. Rev.* **5**: 49–96. [Classification.]

Florin, R. **1923.** *Ark. Bot.* **18,** No. 5: 1–58. 1 pl. 25 figs. [Abnormal sex organs.]

Fritsch, F. E. **1945.** *Ann. Bot.* N.S. **9**: 1–29. 22 figs. [Origin of Bryophyta.]
Harris, T. M. **1938.** The British Rhaetic flora. London. 84 pp. 5 pl. 26 figs.
Haskall, G. **1949.** *Bryologist* **52**: 49–57. [Origin of Bryophyta.]
Haupt, A. W. **1926.** *Bot. Gaz.* **82**: 30–54. 2 pl. 16 figs. [Abnormal sex organs.]
1943. *Bryologist* **46**: 139–141. 4 figs. [Abnormal sex organs.]
Hofmeister, W. **1851.** Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farrn, Equisetaceen, Rhizocarpeen, und Lycopodiaceen) und der Samenbildung der Coniferen. Leipzig. 179 pp. 33 pl.
Holferty, G. M. **1904.** *Bot. Gaz.* **37**: 106–126. 2 pl. [Abnormal sex organs.]
Howe, M. A. **1899.** *Mem. Torrey Bot. Club* **7**: 1–208. 35 pl. [Hepaticae and Anthocerotae of California.]
Iyengar, M. O. P. **1932.** *New Phytol.* **31**: 329–335. 1 pl. 2 figs. [*Fritschiella.*]
Kashyap, S. R. **1919.** *Proc. Asiatic Soc. Bengal* N.S. **15**: cliii–clxvi. [Origin of Bryophyta.]
Lotsy, J. P. **1909.** Vorträge über botanische Stammesgeschichte. Jena. 902 pp. 553 figs.
Marchal, E., and E. Marchal. **1911.** *Bull. Cl. Sci. Acad. Roy. Belgique* **1911**: 750–778. 1 pl. [Apospory.]
Meyer, K. **1912.** *Biol. Zeitschr. Moskau* **1912**: 177–187. 12 figs. [Abnormal sex organs.]
Rink, W. **1935.** *Flora* **130**: 87–130. 28 figs. [Apospory.]
Schaffner, J. H. **1927.** *Ohio Jour. Sci.* **27**: 249–261. [Classification.]
1934. *Quart. Rev. Biol.* **9**: 129–160. 2 figs. [Classification.]
Singh, R. N. **1941.** *New Phytol.* **40**: 170–182. 49 figs. [*Fritschiella.*]
1947. *Ann. Bot.* N.S. **11**: 159–164. 11 figs. [*Fritschiella.*]
Strain, H. H. **1948.** *Year Book Carnegie Inst. Washington* **47**: 97–100. [Pigments.]
Strasburger, E. **1894.** *Ann. Bot.* **8**: 281–316. [Alternation of chromosome numbers.]
Wettstein, R. von. **1908.** Handbuch der systematischen Botanik. 1st ed. Leipzig. 577 pp. 369 figs.
Zimmermann, W. **1932.** Phylogenie. In F. Verdoorn, Manual of bryology. The Hague. Pp. 433–464. 8 figs.

CHAPTER 3

HEPATICAE

Nature. There is great diversity in external form among gametophytes of Hepaticae but, with a very few exceptions, all are fundamentally alike in that they are dorsiventrally differentiated. The sex organs are borne dorsally, or at the anterior end, and develop from a single initial cell.

The sporophytes are determinate in growth in the sense that there is no differentiation of a meristematic tissue. In all sporophytes the sporogenous tissue is derived from the endothecium of an embryo. Different from other Bryophyta, the fertile portion of a sporophyte, the capsule, does not have a sterile region (columella) internal to the sporogenous tissue.

The class includes some 8,500 species grouped in approximately 225 genera.

Occurrence. Hepaticae of temperate climates are mostly restricted to shady terrestrial habitats where the substratum is moist throughout the summer. Such habitats include swamps and bogs; the steep banks of ravines; the shaded faces of moist cliffs; and thickly wooded areas where they grow on rotting logs, on the base of tree trunks, or on hummocks of earth.

A few hepatics are truly aquatic and grow floating on the surface of water, as in certain species of *Riccia;* or, as in *Riella*, grow entirely submerged.

Not all Hepaticae are restricted to habitats where there is a continuous supply of water. An example of this is seen in *Porella platyphylloidea* (Schwein.) Lindb. Its thalli growing on rocks or on the bark of trees can withstand desiccation for several months without apparent injury. In temperate climates where there is a long dry summer season, as in California, the liverworts of exposed fields and open valleys dry up with the onset of the dry season and remain dormant throughout the summer. Adult portions of these gametophytes are killed, but tissues of the apical region remain alive and are capable of resuming active growth when thoroughly wetted. Thus, within a surprisingly short time after the beginning of the rainy season there are well-developed thalli bearing mature sex organs.

From the geographical standpoint, the number of genera known to occur in the tropics far outnumbers that of other parts of the world; and the two areas with the richest hepatic flora are the American tropics and the East Indies. The geographical distribution of genera has been worked out most thoroughly for the leafy Jungermanniales,[1] a group comprising some 180 genera. Some of these genera are cosmopolitan and found throughout the world wherever conditions for growth are favorable. Other genera are endemic, and with a definite continuous or discontinuous geographical distribution. The map (Fig. 5) showing the distribution of endemic genera

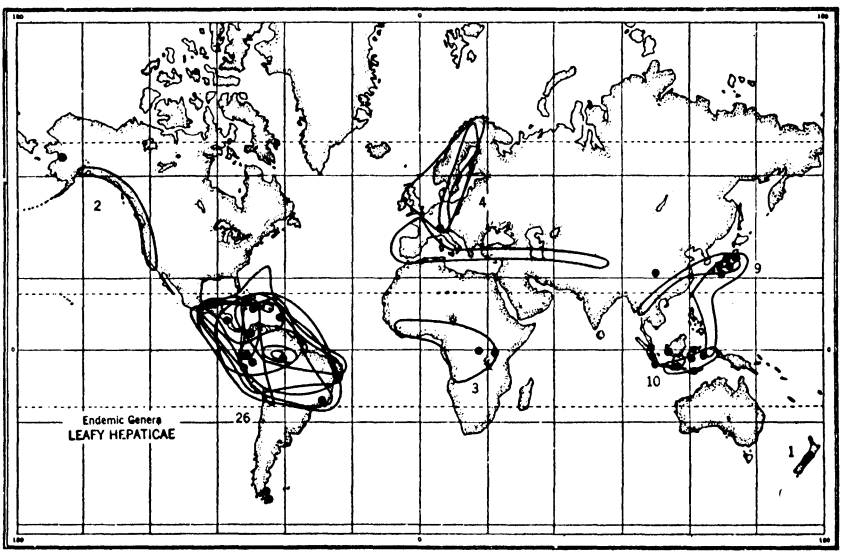

FIG. 5. Map showing the distribution of endemic genera of leafy Hepaticae throughout the world. Numerals on the map give the number of genera in each area. (*After Fulford*, 1951.)

of leafy Jungermanniales reveals the richness of the tropical hepatic flora, and shows how the tropical Americas may be considered the richest of all areas. Discontinuous geographical distribution is mostly in the Southern Hemisphere and with members of a genus found in different continents. A less frequent type of discontinuous distribution is that where a genus occurs in the north and south temperate zones, but not in the intervening tropics.

Fossil Hepaticae. Compared with the pteridophytes the known number of fossil liverworts is small and, with the exception of *Naiadita*, all are known only in a vegetative condition. The oldest known fossils are from the Upper Carboniferous.[2] These are referable to the anacrogynous Jungermanniales, and among them are species resembling such modern genera

[1] Fulford, 1951. [2] Walton, 1925.

as *Aneura* and *Treubia*. Genera referable to the Marchantiales have been found as far back as the Lower Cretaceous.[1] Fertile gametophytes of *Naiadita* with archegonia and mature sporophytes have been found[2] in abundance in Jurassic deposits. This liverwort has been placed[2] among the Sphaerocarpales, but there seem to be equally good arguments for considering it closer to the Calobryales.

Evolution among Gametophytes. Since all known fossils are comparable to present-day forms, opinions concerning the nature of primitive Hepaticae must be inferred from present-day liverworts. As previously noted (page 7), there are two irreconcilable theories concerning the nature of the primitive bryophytic gametophyte.

One theory holds that the primitive gametophyte of Hepaticae was a simple, dorsiventral, prostrate, thalluse structure. The nearest approach to it is to be seen in such present-day genera as *Aneura* or *Metzgeria;*[3] or "in *Sphaerocarpos* (but without) the envelope of the sex organs."[4] From this, with retention of the thalloid habit but with elaboration of internal differentiation and an aggregation of sex organs in receptacles, there was an evolution of the marchantiaceous series. Elaboration of external form, but retention of internal simplicity, resulted in the jungermanniaceous series and one which reached its greatest elaboration in the erect leafy forms.

The other theory concerning the nature of the primitive hepatic gametophyte was first proposed by von Wettstein[5] when he postulated that erect leafy jungermanniaceous forms are the nearest to the primitive Hepaticae. Although disagreeing in details the theory that the primitive liverworts had erect leafy gametophytes has received support in several quarters.[6] It is thought that those present-day Hepaticae with erect, radially symmetrical, leafy gametophytes of the *Calobryum* type (see page 79) are the nearest living approach to the primitive hepatic gametophyte. It is thought that such an erect thallus with leaves in three ranks became prostrate, and that the row of leaves on the ventral side gradually became reduced in size and ultimately disappeared. Associated with disappearance of leaves on the underside was a flattening of the axis, and a reduction in size of lateral leaves to papillae, or a complete elimination of them. Such a type gave rise to the marchantiaceous series by internal differentiation of tissues, and it is thought that the scales on the underside of their thalli are to be interpreted as modifications of the ventral leaves of a leafy ancestor.

There are very good reasons for thinking that the bryophytes came from green algae (Chlorophyceae) rather than from brown or other algae.

[1] Steere, 1946. [2] Harris, 1938. [3] Campbell, 1891, 1918.
[4] Cavers, 1910. [5] von Wettstein, 1908, p. 43; 1911, p. 282.
[6] Church, 1919; Evans, 1939; Harris, 1938; Kashyap, 1919.

Although there are thalli among brown and red algae where there is a differentiation into axis and leaves, this is not the case with green algae. An origin of Hepaticae among green algae is to be sought among those with branching filamentous thalli with uninucleate cells. In them, except for certain corticated Charophyceae, there is no tendency for the branches of a filament to become more than one cell in thickness. On the other hand, some filamentous green algae have more or less massive crustose thalli. Thus, there seems to be more in favor of the theory that the primitive bryophytic gametophyte was thallose rather than leafy. From this it follows that gametophytic evolution among Hepaticae has been a progressive elaboration instead of a progressive simplification.

Evolution among Sporophytes. Since practically all types of sporophyte found in Hepaticae are present in the Marchantiales, this order exemplifies the evolution that has taken place in sporophytes of Hepaticae. These sporophytes constitute a series in which the simple ones of the *Riccia* type are at one extreme, and those of the *Marchantia* at the other. Many bryologists[1] are in agreement with Goebel,[2] who, primarily on comparison of gametophytes, considered such genera as *Preissia* and *Marchantia* to be nearest the ancestors of the Marchantiales. According to such an interpretation of the order, evolution of the sporophyte has been a reduction from the complexity found in *Marchantia* to the simplicity found in *Riccia*.

Others[3] think that the sporophytic series should be read the opposite way. They hold that sporophytes of the Ricciaceae are the most primitive. Here, only the superficial cells of an embryo mature into sterile tissue and such sporogenous cells as do not divide meiotically disintegrate before a sporophyte is mature. Such sporophytes as those of Corsiniaceae and of *Plagiochasma* (Marchantiaceae) are considered the most primitive of Marchantiales with the lower (hypobasal) half of an embryo developing into sterile tissue. In them (Fig. 21*G*, page 39) the sterile hypobasal portion is a small haustorial organ (foot) and without a seta (if the seta is considered a structure capable of elongating and pushing the capsule beyond gametophytic tissues). In these sporophytes, sporogenous cells that do not divide meiotically mature into persistent nurse cells or mature into elaters. In *Marchantia* and a majority of the Marchantiaceae the sterile portion of a sporophyte consists of many cells, the majority of which constitute the seta. In these sporophytes the sterile jacket layer of a capsule may be more than one cell in thickness. Cell walls of jacket cells of the *Riccia* and *Corsinia* type of sporophyte are homogeneous; those of the *Marchantia* type have ring-like thickenings.

Nutrition of the Sporophyte. There is a widespread belief that Hepaticae differ from other Bryophyta in having the sporophyte wholly dependent

[1] Evans, 1939; Kashyap, 1919; Meyer, 1931; Verdoorn, 1932.
[2] Goebel, 1910. [3] Bower, 1908, 1935; Campbell, 1918; Cavers, 1910.

upon the gametophyte for the products of photosynthesis. Sporophytes of several Marchantiales and Jungermanniales have been shown[1] to have chloroplasts at the time they are well along in development, and with chloroplasts in cells of developing foot, seta, and capsule of jacket. In *Marchantia* no chloroplasts are evident until the embryo begins to become differentiated into foot, seta, and capsule.[2] Sporophytes of Sphaerocarpales have chloroplasts at all stages from the zygote to maturity. Water cultures of excised sporophytes[2] of *Riella* and *Sphaerocarpos* indicate the extent to which these sporophytes are photosynthetically self-sufficient. Cultures of sporophytes removed before reaching half the mature diameter remained alive for a few weeks, but did not grow to maturity. Those removed when three-fifths to three-fourths mature developed to maturity in vitro and produced functional spores, but were slightly smaller and did not contain as many spores as sporophytes growing attached to gametophytes.

Classification. Until early in the present century the Hepaticae (exclusive of the anthocerotes) were grouped in two orders, Marchantiales and Jungermanniales. The proposal[3] that the Sphaerocarpaceae be segregated from the Jungermanniales and placed in a separate order, the Sphaerocarpales, has met with the approval of most bryologists. The Haplomitriaceae (Calobryaceae) were placed among the acrogynous Jungermanniales until the distinctive nature of their sex organs and structure of their sporophytes were pointed out in connection with a study of *Calobryum*.[4] This group has been given[5] the rank of a suborder of the Jungermanniales, but the placing of it in a separate order, the Calobryales,[4] seems amply justified.

ORDER 1. SPHAEROCARPALES

There are three genera in which vegetative structure of the gametophyte is similar to that of anacrogynous Jungermanniales, but in which development and structure of sex organs, as well as structure of the sporophyte, are similar to those of Marchantiales. Because of this, these genera are placed in a separate order, the Sphaerocarpales. The chief diagnostic feature by which one may readily recognize Sphaerocarpales is the presence of a globose or a flask-shaped envelope (involucre) around each of the sex organs. The order is divided into two families.

FAMILY 1. SPHAEROCARPACEAE

The Sphaerocarpaceae have bilaterally symmetrical, thallose gametophytes without internal differentiation of tissues. Each of the sex organs is surrounded by an involucre. There are two genera, *Sphaerocarpos* and

[1] Bold, 1938. [2] Studhalter, 1938. [3] Cavers, 1910.
[4] Campbell, 1936. [5] Evans, 1939.

Geothallus. *Sphaerocarpos* has seven species, four of which occur in the United States and chiefly in the Gulf and Pacific Coast states. The monotypic *Geothallus* was known only from the original description until rediscovered 45 years later near the type locality in Southern California.[1]

The gametophyte of *Sphaerocarpos* is relatively small, orbiculate to cuneate, and simple or dichotomously branched. Annual species may often be found growing in clumps of four in which there are two male and two female gametophytes. A gametophyte has a broad midrib, several cells in thickness, and lateral to both margins of the midrib is a wing-like expansion one cell in thickness. Depending upon environmental conditions, the wings are more or less entire or incised into leaf-like lobes. The dorsal surface of a midrib is densely crowded with ovoid or flask-shaped involucres, each of which surrounds a single sex organ (Fig. 6). The ventral surface of a gametophyte lacks scales and all rhizoids growing from it are of the smooth-walled type. Multicellular glandular hairs, of the type found in many anacrogynous Jungermanniales, are frequently present on the ventral surface and just back of the growing point (Fig. 7*A*). There is no internal differentiation of tissues within a gametophyte and all vegetative cells, except the rhizoids, contain chloroplasts.

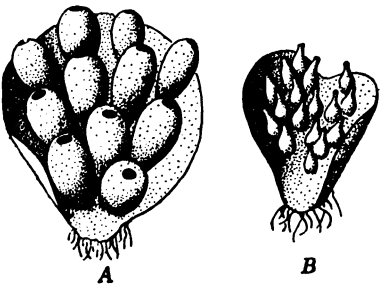

FIG. 6. *Sphaerocarpos californicus* Aust. *A*, female gametophyte. *B*, male gametophyte. (× 1½.)

Growth of a gametophyte is at the distal end and is initiated by a transverse row of wedge-shaped apical cells laterally joined to one another.[2] Segments alternately cut off from the dorsal and ventral face of each apical cell contribute to the midrib (Fig. 7*A*); segments cut off from the apical cell at each end of the row contribute to the wings. Dichotomous branching begins with vertical divisions in the median portion of the row of apical cells and this segregates the original row into two sets. The branching becomes more and more evident as vegetative tissue develops between the two sets. There is rarely a dichotomous branching in such short-lived gametophytes as those of *S. cristatus* Howe. Repeated dichotomous branching is of frequent occurrence in such long-lived gametophytes as those of *S. donnellii* Aust. Species with long-lived, dichotomously branched gametophytes have them reproducing vegetatively by the progressive death in the posterior portion of a gametophyte ultimately reaching a dichotomy and the two surviving forks continuing growth as separate plants. Vegetative multiplication may also take place by a for-

[1] Campbell, 1896, 1938. [2] Rickett, 1920.

mation of proliferous outgrowths, either from the midrib, or from the lateral wings, or from the involucres.[1]

All species are heterothallic, with sexual differentiation genotypic and due to a sex chromosome.[2] Male plants (Fig. 6*B*) may be distinguished from female ones by their smaller size, their flask-shaped involucres, and by the fact that they are tinged with purple. Antheridial development begins with the capitate enlargement of a superficial dorsal cell but two or

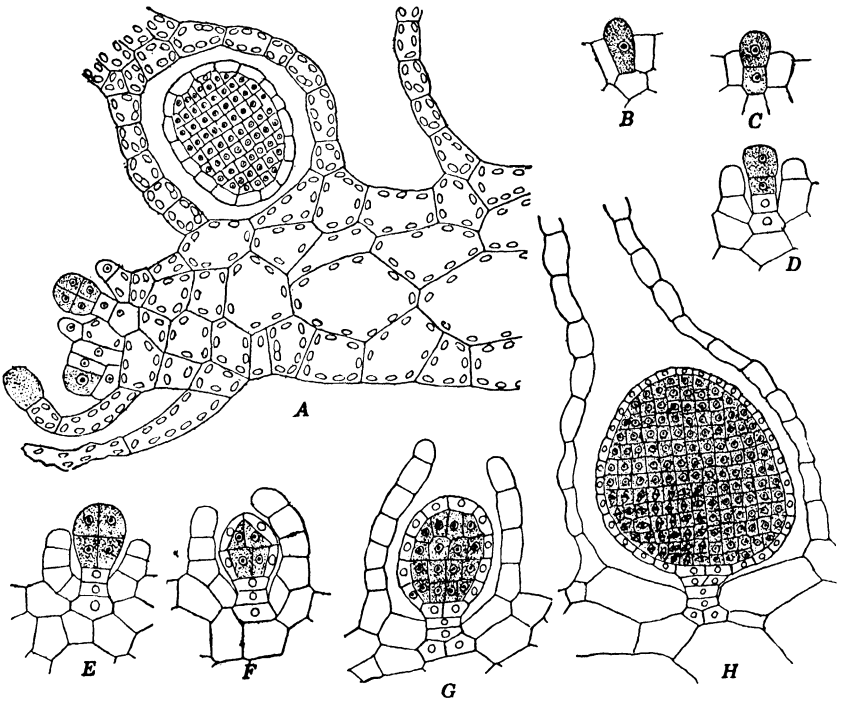

FIG. 7. *Sphaerocarpos cristatus* Howe. *A*, longitudinal vertical section through the apex of a male gametophyte. *B–H*, stages in development of antheridia. (× 325.)

three removed from an apical cell (Fig. 7*B*). This **antheridial initial** soon divides into a **basal cell** and an **outer cell** which projects somewhat above the thallus (Fig. 7*C*). The basal cell develops into the embedded portion of an antheridial stalk; the outer cell develops into the remainder of an antheridium. Successive transverse divisions of the outer cell soon result in a vertical file of three cells (Fig. 7*D*). The two upper cells are the **primary antheridial cells** which eventually produce the antheridium proper; the lowermost cell is a **primary stalk cell** which eventually produces all of the stalk except the part embedded in the gametophyte. Each of the two

[1] Rickett, 1920*A*. [2] Allen, 1919.

primary antheridial cells, by two successive vertical divisions at right angles to each other, gives rise to four cells (Fig. 7*A*,*E*). In both tiers of four cells there is next a periclinal division into four **jacket initials** that encircle four **primary androgonial cells** (Fig. 7*F*). By successive divisions at right angles to one another each of the eight primary androgonial cells gives rise to many cubical **androgonial cells** which become progressively smaller in successive cell generations. The blocks of androgonial cells derived from each of the primary androgonial cells may be recognized by their arrangement and by the fact that all descendents from a particular primary androgonial cell divide simultaneously (Fig. 7*G*–*H*). Each cell (**androcyte mother cell**) of the last cell generation of androgonial cells divides into two **androcytes,** and this division is usually in a diagonal instead of a transverse plane.[1] Shortly after the primary androgonial cells begin to divide, each of jacket initials divides anticlinally into two **jacket**

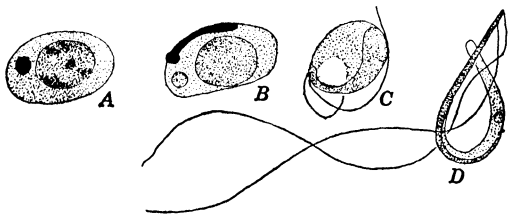

FIG. 8. *Sphaerocarpos donnellii* Aust. *A*–*C*, stages in metamorphosis of androcytes into antherozoids. *A*, just after appearance of blepharoplast. *B*, during elongation of blepharoplast. *C*, late in metamorphosis. *D*, free-swimming antherozoid. (*A*–*C*, *after Nevins*, 1933; *D*, *after Showalter*, 1926.) (*A*–*C*, × 3,800; *D* × 1,000.)

cells, and with further increase in size of the androgonial tissue the jacket cells divide and redivide anticlinally to form a **jacket layer** one cell in thickness (Fig. 7*G*–*H*).

The androcytes are cells that are metamorphosed into **antherozoids.** Metamorphosis into an antherozoid begins with the appearance of an extranuclear granule, the **blepharoplast** (Fig. 8). After increasing somewhat in size the blepharoplast begins to elongate and to develop into a rod-shaped body lying next to the plasma membrane.[1] Shortly after this, the blepharoplast begins to form two flagella at its anterior end. Eventually the nucleus migrates to the side of the blepharoplast and assumes the form of a crescent with one very blunt pole, and then blepharoplast and nucleus become so firmly united that only the apex of the blepharoplast is recognizable. During this metamorphosis of androcytes into antherozoids there is a complete disintegration of cell walls internal to the jacket layer and a production of a viscous liquid in which the antherozoids lie in an immobile condition. The antherozoids continue to remain immobile until the liquid in which they lie escapes from the antheridium and

[1] Nevins, 1933.

oozes out from the neck of the antheridial involucre. Then, if they come in contact with water, they soon become motile. Free-swimming antherozoids (Fig. 8*D*) are spindle-shaped, curved or variously coiled, and biflagellate. The two flagella are borne at the anterior end, one just ahead of the other, and the lower one is slightly longer than the upper one.[1] The elongate nucleus at one side of the body of an antherozoid is sharply delimited from the cytoplasmic portion.

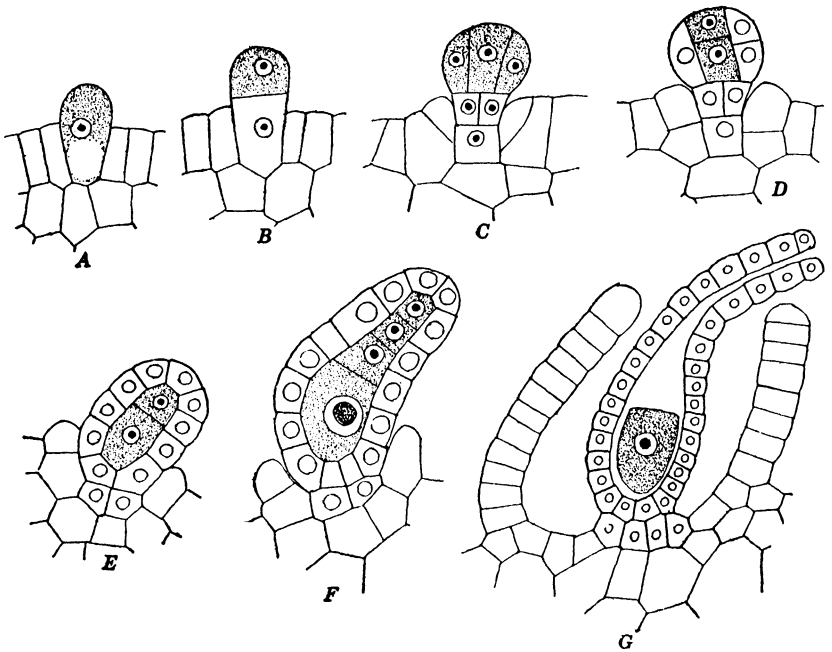

FIG. 9. *Sphaerocarpos cristatus* Howe. Stages in development of archegonia. (*A–F*, × 485; *G*, × 325.)

Archegonial development begins with a capitate enlargement of a dorsal cell (**archegonial initial**) which lies but two or three cells back from an apical cell (Fig. 9*A*). This soon divides transversely into a **basal cell** and an **outer cell** (Fig. 9*B*). The basal cell produces the lowermost portion of an archegonium, and the outer cell produces all the rest of it. The first division of an outer cell is in an asymmetrical vertical plane and cuts off **a peripheral initial.** Two further unequal vertical divisions cut off two more peripheral initials. The three peripheral initials so intersect one another that they lie lateral to a fourth cell, the **primary axial cell** (Fig. 9*C*). Vertical division of each of the three peripheral initials results in six

[1] Nevins, 1933; Rickett, 1923; Showalter, 1926.

jacket initials surrounding the primary axial cell. This is soon followed by a transverse division of each jacket initial to produce a tier of six **neck initials** which lies above a tier of six **venter initials** (Fig. 9*D*). Transverse division of neck initials and of their daughter cells ultimately forms an archegonial neck several cells in length and six cells in perimeter. The venter initials give rise to the jacket of the venter but, different from development of the jacket of the neck, division of venter jacket cells is both vertical and transverse. Thus the jacket of a mature venter may be 10 or more cells in perimeter instead of 6 as in the neck.

Coincident with division of jacket initials there is an unequal transverse division of the primary axial cell into a **primary cover cell** and a **central cell** (Fig. 9*D*). During development of the neck the primary cover cell, by two successive vertical divisions, contributes four **cover cells** to the apex of the jacket layer of the neck. Soon after it is formed the central cell divides transversely into an **upper canal cell** and a **lower canal cell** (Fig. 9*E*). At first these two cells are of equal size, but the lower canal cell eventually becomes broader and longer. The upper canal cell, by two successive transverse divisions, develops into the four **neck canal cells** within the neck of an archegonium. An asymmetrical transverse division of the lower canal cell results in a small **venter canal cell** lying above a large **egg.** Shortly before an archegonium is mature, the venter canal cell and the neck canal cells disintegrate into a mucilaginous mass and the cover cells spread apart (Fig. 9*G*). The result is an open passageway that permits swimming of antherozoids down the neck to the egg.

Development of an involucre begins shortly after the initials begin developing into antheridia and archegonia. Involucres around antheridia develop at a rapid rate and when an antheridium is less than half mature the involucre is higher than the antheridium (Fig. 7*F–H*). Development of the involucre surrounding an archegonium is at a slower rate, and when an archegonium is mature the involucre is not so tall as the archegonium (Fig. 9*G*). Thus antherozoids have little difficulty in entering an archegonium if sufficient water is present. Fertilization stimulates a rapid upward growth of the involucre and within two or three days the top of the involucre stands higher than the top of the archegonium (Fig. 10*A*).

Antherozoids swimming in the vicinity of the neck of an archegonium may enter the canal of the neck and swim down it to penetrate the egg. Entrance into the neck is undoubtedly a chemotactic response. Chemotaxis has not been demonstrated for antherozoids of *Sphaerocarpos*, but those of *Marchantia* have been shown to give a positive chemotactic response to certain proteins and to certain inorganic salts, especially salts of potassium.[1] **Polyspermy,** the entrance of more than one antherozoid into an egg, is not a rare phenomenon in *Sphaerocarpos*, and in one series

[1] Åkerman, 1910; Lidforss, 1904.

of experiments[1] it was found in about 8 per cent of the observed cases of fertilization.

The male nucleus within an antherozoid begins to enlarge and assume a spherical shape immediately after an antherozoid has entered an egg. Fusing male and female nuclei have definitely organized chromosomes, and fusion of the two nuclei begins 60 to 70 hours after entrance of an antherozoid.[1] Division of the zygote is transverse, and this is followed by transverse division of the upper (**epibasal**) and lower (**hypobasal**) cells formed by division of the zygote. This results in a filamentous four-celled

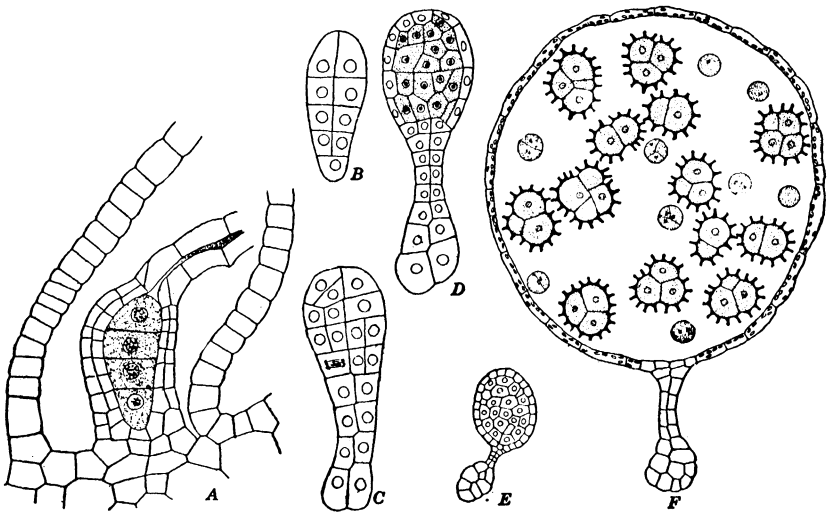

FIG. 10. *Sphaerocarpos cristatus* Howe. *A*, four-celled embryo. *B*, before differentiation of sporogenous tissue and jacket layer of capsule. *C*, during differentiation of sporogenous tissue and jacket layer. *D–E*, stages during increase in number of sporogenous cells. *F*, mature sporophyte. (*A–D*, × 215; *E F*, × 60.)

embryo (Fig. 10*A*) in which each cell, by two successive vertical divisions, gives rise to a tier of four cells. It is very probable that the two tiers of four cells in the epibasal half of an embryo ultimately develop into the capsule of a mature sporophyte, and the two tiers of four in the hypobasal half develop into remaining portions of a sporophyte. Cell division in the two upper tiers of four cells is periclinal (Fig. 10*C*) and results in an outer layer (the **amphithecium**) encircling an inner portion (the **endothecium**). The amphithecium, by anticlinal cell division, develops into the jacket layer of the capsule, a layer that remains one cell in thickness even when fully mature. The endothecium develops into the sporogenous tissue of a capsule (Fig. 10*D–E*). Some cells of the sporogenous tissue become **sporocytes** (**spore mother cells**) which divide meiotically into four spores. Other

[1] Rickett, 1923.

cells of the sporogenous tissue mature into sterile **nurse cells** which supply food to developing spores. The nucleus of a young nurse cell divides mitotically into four daughter nuclei.[1] In some species, as *S. donnellii*, the nurse cells remain quadrinucleate; in others, as *S. cristatus*, the nurse cells have internal walls separating nuclei from one another (Fig. 10*F*). Nurse cells and jacket cells of the capsule contain numerous chloroplasts, and it has been shown experimentally[2] that photosynthesis in these cells contributes materially to nutrition of sporophytes during later stages in their development. The jacket of a capsule remains intact even after the sporophyte is mature, and spores become free only after the death and decay of the jacket and surrounding gametophytic tissues.

Coincident with development of the capsule, the basal part of the hypobasal half of an embryo, by cell division in an irregular sequence, develops into a bulbous **foot.** The upper part of the hypobasal half of an embryo develops into a narrow structure two cells broad that connects the capsule and foot (Fig. 10*F*). This portion of the sporophyte is sometimes called a **seta,** but it is not functionally comparable to setae of sporophytes of Jungermanniales and certain Marchantiales since it does not elongate and push the capsule beyond adjoining gametophytic tissues.

Of the four spores formed by a sporophyte, two develop into male gametophytes, and two into female gametophytes. In species where the four spores formed by a sporocyte adhere even when mature the gametophytes grow in clusters of four, two male and two female. The first step in germination of a spore is the production of a relatively long **germ tube.**[3] Then the germ tube divides transversely into a small terminal cell densely filled with protoplasm, and a large basal cell with but little protoplasm. The basal cell does not divide. The terminal cell, by transverse and vertical division, forms a short ribbon three to four cells in length and two cells broad. The ribbon then becomes two cells in thickness by horizontal division of each of the cells. Cells in the distal tier then divide and redivide in the horizontal plane to form a **germinal disk** that lies at right angles to the remainder of the juvenile gametophyte. Growth of the disk becomes asymmetrical after a time because of a differentiation of a rapidly dividing row of **apical cells** at one side of the disk. Further growth after differentiation of these apical cells is similar to that at the apex of an adult thallus.

FAMILY 2. RIELLACEAE

The Riellaceae are separated from the Sphaerocarpaceae because of their asymmetrical gametophytes. The single genus, *Riella*, has about 17 species. In the United States, *R. americanum* Howe and Underw. is

[1] Gross and Allen, 1938. [2] Studhalter, 1938.
[3] Campbell, 1896*A*; Rickett, 1920.

known[1] from South Dakota and Texas; and *R. affinis* Howe and Underw. is known from California.[2] The scarcity of records on the occurrence of *Riella* is due to a considerable extent to the fact that it is an aquatic plant which grows entirely submerged and frequently several feet below the surface of the water.

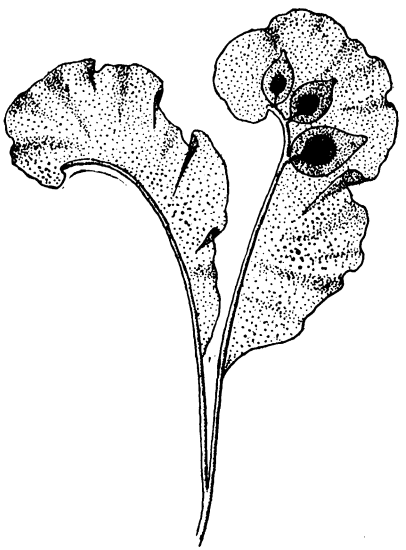

FIG. 11. *Riella americana* Howe and Underw. Gametophyte with sporophytes. (× 5.)

The gametophyte of *Riella* is erect and consists of a thickened stem-like axis bearing a single conspicuous, straight to spirally twisted, plate-like wing one cell in thickness (Fig. 11). A gametophyte bears rows of scales one cell in thickness and these are formed from a single initial cell.[3] Scales borne along the median portion of an axis are called ventral scales, and those at the juncture of axis and wing are called lateral scales. Rhizoids are restricted to first-formed portions of a gametophyte. Growth of adult portions of a thallus is at the distal end and wholly by means of a single apical cell with two cutting faces,[2] or the single apical cell may eventually be replaced by a row of apical cells.[4] The relationship of the wing to the apical cell and to the ventral scales shows that the wing is to be interpreted as a dorsal outgrowth from the axis.[4]

Vegetative propagation is by means of gemmae borne between the rows of ventral and lateral scales. A mature gemma is oval in outline, one cell in thickness, and transversely constricted into two lobes of unequal size. Because of the marked differences from gemmae of other liverworts, the gemma of *Riella* has been called[5] a **gemmaling.** After abscission from the parent plant, a gemmaling becomes meristematic in the isthmus between two lobes, and this meristem produces a juvenile phase which is eventually succeeded by the adult gametophytic phase with axis and wing.[6]

Riella may be homothallic or heterothallic; but in either case antheridia are borne in clusters in notches along the margin of the wing, and archegonia are borne singly at the juncture of wing and axis. Development of

[1] Howe and Underwood, 1903; Studhalter, 1931. [2] Thompson, 1942.
[3] Studhalter and Cox, 1941, 1941*A*. [4] Studhalter, 1931.
[5] Studhalter and Cox, 1940. [6] Studhalter and Cox, 1941*B*.

sex organs (Fig. 12*A–D*) is similar to that in *Sphaerocarpos*.[1] Development of the antheridial involucre is also similar, but development of the archegonial involucres differs in having the involucre initials arise from the stalk of an archegonium instead of from vegetative cells encircling a young archegonium.[1]

Development of the sporophyte (Fig. 12*E*) is much the same as in *Sphaerocarpos* and with the same differentiation of sporocytes and quadrinucleate nurse cells by the sporogenous tissue.[1]

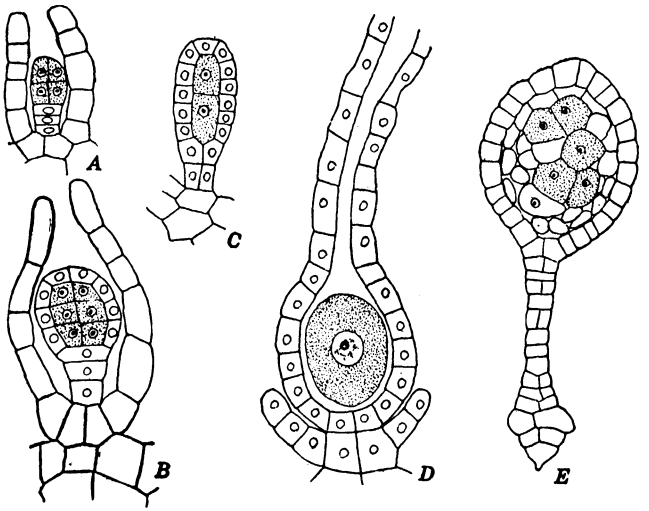

FIG. 12. *Riella affinis* Howe and Underw. *A–B*, young antheridia. *C*, young archegonium. *D*, mature archegonium. *E*, sporophyte at time of differentiation of sporocytes and nurse cells within the capsule. (*E*, *after Thompson*, 1942.) (*A–D*, × 400.)

Growth from spore to mature gametophyte is not the same in all species. It is most complex in *R. affinis* where it is sharply differentiated into three successive phases, each with a different method of growth.[1] A spore germinates to form a monostromatic phase with a pair of apical cells at the distal end. Eventually the transverse band of descendants of the first derivative formed by each of the two apical cells functions as an intercalary monostromatic meristem from which cells are matured on both the anterior and posterior faces. In time, active cell division in this second or juvenile phase becomes restricted to lateral margins of the meristem, and ultimately there is a differentiation of a single apical cell producing the adult phase with axis and wing.

ORDER 2. MARCHANTIALES

Gametophytes of Marchantiales grow prostrate upon the substratum and are ribbon-shaped, dichotomously branched, and dorsiventrally

[1] Thompson, 1943.

differentiated. Except in *Monoclea* and at times in *Monoselenium* and *Dumortiera*, the dorsal side of a thallus is internally differentiated into air chambers, each opening externally by an air pore of simple or relatively elaborate construction. The ventral portion of a gametophyte is a parenchymatous storage tissue composed of two or of three types of cells, and at times with a rudimentary conducting tissue of elongate cells in the sagittal axis. Other unique features of gametophytes of most genera are the scales borne transversely on the ventral surface and the presence of two types of rhizoids.

The ontogeny and structure of antheridia and archegonia are similar to those in Sphaerocarpales, but individual sex organs are not surrounded by an involucre.

Capsules of sporophytes of most members of the order are also similar to those of Sphaerocarpales in having a jacket layer one cell in thickness; but certain Marchantiales have, as in Calobryales, the apical portion of the jacket layer becoming more than one cell in thickness.

The order includes about 32 genera and 400 species. Grouping of genera into families is based upon nature of the receptacle, the manner in which they are borne, and the structure of the sporophyte.

Gametophytes and sporophytes of the most elaborate structure are found in the Marchantiaceae, and those of simplest construction are found in the Ricciaceae. Some bryologists[1] follow Goebel[2] in thinking that evolution among Marchantiales has been a retrogression from the type of complexity found in *Marchantia* to the simplicity found in Ricciaceae.* Advocates of the theory of reduction hold that in the gametophyte there has been a loss of assimilating filaments in the air chambers, a simplification of air pores, and an eventual elimination of stalks of special erect branches bearing sex organs so that the sex organs are borne in indefinite clusters on ordinary branches. In the sporophyte there has been an elimination of special protective structures surrounding immature sporophytes, a gradual elimination of seta and foot until the sporophyte consists wholly of capsule, a simplification of wall structure of jacket cells of the capsule, and an elimination of elaters.

Other morphologists[3] consider the Ricciaceae the most primitive and the Marchantiales the most advanced members of the order. They hold that progressive evolution of the gametophyte has included an appearance of assimilating filaments in air pores, and an evolution of air pores of more

[1] Evans, 1939; Kashyap, 1919; Verdoorn, 1932; von Wettstein, 1908.

[2] Goebel, 1910.

* In this connection it is interesting to note that most of those agreeing with Goebel think that evolution among Hepaticae has been a progressive simplification from an erect leafy ancestor (see p. 7).

[3] Bower, 1908; Campbell, 1918; Cavers, 1910.

elaborate construction. It is thought that the most primitive gametophytes produce archegonia in circumscribed areas (**receptacles**) along the entire sagittal axis of all branches; those more advanced have but one receptacle on each branch and it just posterior to the growing apex; and the most advanced have archegonial receptacles at the tips of special erect branches. Evolution of the sporophyte began with one consisting solely of a capsule. Progressive sterilization of such a sporophyte first evolved a basal haustorial organ (foot) and later there was an evolution of a seta capable of pushing the capsule beyond overlying gametophytic tissues.

In the opinion of the writer it seems more probable that evolution among the Marchantiales has been progressive rather than retrogressive. It has also been held that the plane in which the upper (epibasal) and lower (hypobasal) cell of a two-celled embryo divides is a feature of fundamental importance and has resulted in two parallel lines in evolution of sporophytes among Marchantiales.[1] In the so-called filamentous type of embryo,[2] division of the two cells is transverse. Filamentous embryos may develop into sporophytes in which the sterile portion consists largely of foot (*Plagiochasma*[3]), or into sporophytes in which the sterile portion consists of a well-developed seta and foot (*Conocephalum*[4]). Certain filamentous embryos have been shown to have an apical cell at both poles during early growth stages.[4] In the so-called[2] octant type of embryo, division of epibasal and hypobasal cells of the two-celled embryo is at right angles to the previous plane of division. Octant embryos may produce a sporophyte whose sterile appendage consists almost wholly of foot, as in *Corsinia* (Fig. 21*G*, page 39), or may produce a sporophyte with a well-developed seta and foot as in *Marchantia* (Fig. 35*A*, page 55).

The Marchantiales are variously grouped into four to six families. The families discussed on pages to follow begin with what the writer considers the most primitive and end with the most advanced.

FAMILY 1. RICCIACEAE

The Ricciaceae differ from other Marchantiales in having the sex organs borne in a sagittal strip extending the entire length of a thallus. The family is also the only one in which the sporophyte consists solely of a capsule. There are three genera in the family and some 140 species.

Riccia, a genus with more than 130 species, is the most widely distributed member of the family. Its gametophyte is typically rosette-like because of several dichotomous branchings close to one another (Fig. 13). Each branch of a thallus is linear to wedge-shaped, is thickened in the sagittal axis, and has a conspicuous median longitudinal furrow on the dorsal side. The ventral surface of the growing apex of a branch bears a

[1] Meyer, 1931. [2] Dupler, 1922. [3] Meyer, 1914. [4] Meyer, 1929.

transverse row of scales, one cell in thickness, which project forward and overlap the growing point. The scales are close together near the growing point, but back from it they are some distance apart. Posterior to the growing point, the median part of a branch increases in breadth and this splits each scale into two parts. As a result, older parts of a branch appear to have two rows of scales, one near each lateral margin. In older parts of a branch certain superficial cells of the ventral surface grow out into unicellular rhizoids. As is the case with most other Marchantiales, rhizoids are of two sorts, those with smooth walls, and those with rod-like or plate-like ingrowths of the wall which project into the lumen of the rhizoid.

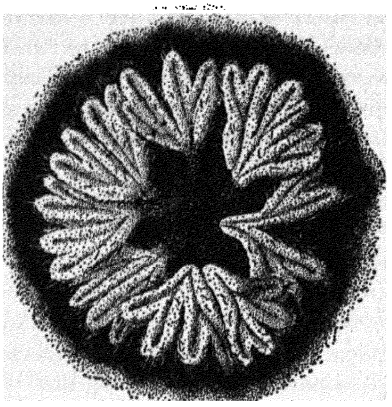

FIG. 13. *Riccia trichocarpa* Howe. (× 3.)

The lower portion of a thallus is a colorless parenchymatous tissue in which the cells may contain starch (Fig. 14). Above this is a single layer of air chambers which are vertical canals with their long axes approximately vertical. In most cases the canals are bounded by only four cells,

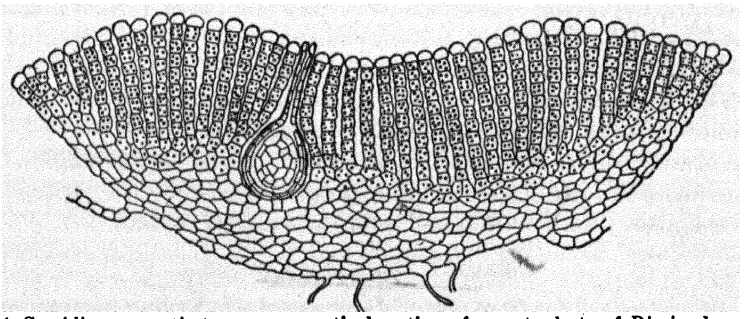

FIG. 14. Semidiagrammatic transverse vertical section of gametophyte of *Riccia glauca* L. (× 80.)

but in some cases[1] the walls of the canals are plates of variable size. The cells constituting the walls of the air chambers contain numerous chloroplasts. Unlike most Marchantiales, but similar to other Ricciaceae, the air chambers of *Riccia* have no plate-like or filamentous ingrowths which increase the photosynthetic surface of the thallus. Above the air chambers is an "epidermal" layer, one cell in thickness. The air pores, through which there is an interchange of gases between the interior and exterior

[1] Black, 1913; Juel, 1910.

of the plant, are simple intercellular spaces bounded by four to six "epidermal" cells.

The growing distal end of each branch is occupied by a transverse row of three to five or more apical cells laterally joined to one another.[1] Each apical cell is triangular in vertical longitudinal section, and rectangular in surface view or in horizontal longitudinal section. Segments are cut off largely from the dorsal and ventral faces of each apical cell, but from time to time a segment may be cut off from a lateral face. The growing apex lies in a deep notch because maturation of embryonic tissue lateral to the group of apical initials is more rapid than of embryonic tissue posterior to the initials. Now and then certain of the median members in

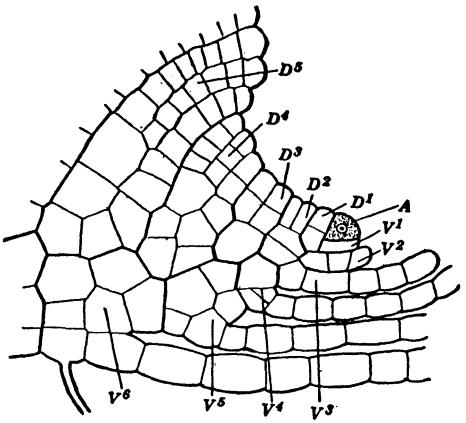

FIG. 15. *Riccia glauca* L. Longitudinal vertical section through growing apex. (The outlines of the portions derived from the last five dorsal segments (D^1–D^5) and from the last six ventral segments (V^1–V^6) cut off by the apical initial are drawn with a heavy line. (× 325.)

a row of apical cells divide vertically, and the original set of initials becomes segregated into two sets. This is the beginning of a dichotomy of the thallus and one which becomes more and more pronounced as more tissue develops between the two sets.

Although the apical initials cut off segments alternately to the dorsal and the ventral faces, the greater bulk of the thallus is derived from those produced at the dorsal face. The ventral segments have been described[2] as contributing only to the lowermost cell layer of the thallus and to its appendages (rhizoids and scales), but this seems to be too radical a statement. The first division in a segment from the dorsal face of an apical initial is parallel to the surface of the thallus (Fig. 15). The inner daughter cell, by division and redivision, contributes to the colorless parenchymatous tissue in the lower portion of a thallus. Derivatives from the

[1] Campbell, 1918. [2] Pietsch, 1911.

outer daughter cell give rise to the air chambers and to the "epidermal" layer. Differentiation of the epidermal layer takes place quite early and there are sometimes but three or four cells intervening between the apical cell and the first embryonic epidermal cell. Differentiation of the air chambers takes place farther back from the apical cells. There are those[1] who hold that air chambers are formed by a cessation of upward growth in certain surface areas of a thallus and by a vigorous upgrowth in adjoining parts of the thallus. The more widely accepted view holds that air chambers arise schizogenously, that is, by a splitting of vertical cell walls. Those finding a schizogenous formation of air chambers are in conflict as to whether the splitting begins below and extends upward,[2] or begins at the surface and extends downward.[3]

Riccia, similar to other dichotomously branching prostrate Hepaticae, reproduces vegetatively by the progressive death of older parts reaching a dichotomy, and the two surviving branches continuing growth as two separate plants. In regions with a prolonged dry season, as in California, all of a gametophyte but the branch tips is killed by the summer drought. During the succeeding rainy season, resumption of growth by surviving branch tips may result in a rosette of new plants (Fig. 13). Several species of *Riccia* produce adventitious branches from the ventral surface of a gametophyte. Detachment of these adventitious branches may result in numerous adventitiously formed gametophytes.[4] Cell division at the apices of young rhizoids may result in a gemma-like mass of cells capable of developing into a new thallus.[5]

Most species of *Riccia* are homothallic, but at least two (*R. bischoffi* Hubner and *R. curtisii* James) are known to be heterothallic. In *R. curtisii* there is a genotypic determination of sex at the time spores are formed, two spores of a tetrad developing into female and two into male gametophytes.[6]

Riccia forms sex organs in basipetalous succession in the longitudinal groove on the dorsal side of a gametophyte. Among homothallic species, there is alternately a group of a few antheridia and then a group of a few archegonia for a considerable distance back from the growing tip.

Development of an antheridium begins with the capitate enlargement of a superficial dorsal cell, the **antheridial initial,** which lies only two or three cells removed from an apical cell. Subsequent stages (Fig. 16) in development of an antheridium[7] are identical with those in *Sphaerocarpos* (see page 20). Metamorphosis of androcytes into biflagellate antherozoids[8] is also quite similar to that in *Sphaerocarpos*. At an early stage a de-

[1] Black, 1913; Hirsch, 1910; Leitgeb, 1879.
[2] Barnes and Land, 1907; Pietsch, 1911. [3] Black, 1913; Orth, 1943.
[4] Cavers, 1903. [5] Campbell, 1918. [6] McAllister, 1916, 1928.
[7] Black, 1913; Campbell, 1918. [8] Black, 1913.

veloping antheridium becomes completely encircled by upward growth of adjacent vegetative tissue and continued upgrowth of this tissue results in an **antheridial chamber** connected with the exterior by a narrow cylindrical canal (Fig. 16*C*). Mature antheridia completely fill the antheridial chamber except for the canal at its apex. When an antheridium is fully mature there is a gelatinization of its jacket layer. Discharge of antherozoids is due to imbibitional absorption of water by the gelatinized jacket, and ripe antheridia may retain their antherozoids for a considerable time if there is an insufficient supply of water. Evidence for this is to be seen in thalli bearing fairly well advanced sporophytes adjacent to antheridia

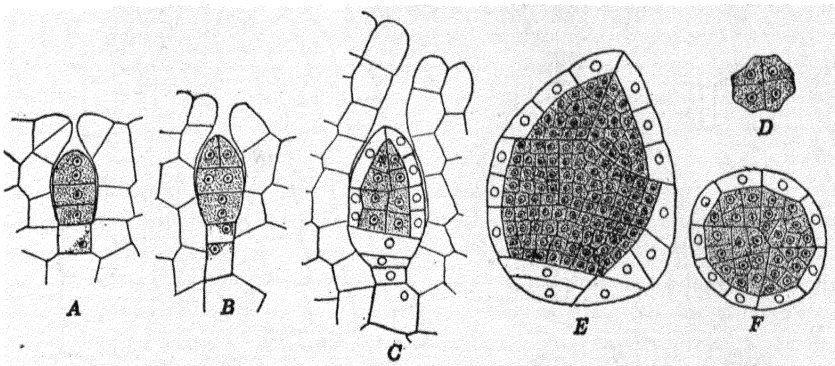

FIG. 16. *Riccia glauca* L. Stages in development of antheridia. (*A–C*, *E*, in vertical section; *D*, *F*, in transverse section.) (× 485.)

with ripe antherozoids. The exact manner in which antherozoids are discharged through the canal of an antheridial chamber is as yet unknown. It is not known whether this takes place explosively as in certain Marchantiaceae,[1] or by exudation in a gelatinous mass as in certain other Marchantiaceae.[2]

Archegonial development begins with the upward growth of a superficial dorsal cell, the **archegonial initial,** which lies but two or three cells removed from an apical cell. Subsequent stages (Fig. 17) in development of an archegonial initial into an archegonium[3] are identical with those in *Sphaerocarpos* (see page 22). Development of archegonia is accompanied by an upgrowth of adjoining vegetative tissues, but even when an archegonium is fully mature the tip of its neck stands above adjacent vegetative portions of the gametophyte (Fig. 17*I*).

Water is essential if antherozoids are to reach an archegonium. However, the gametophytes need not be inundated, since the dorsal furrow

[1] Cavers, 1903*A*; Peirce, 1902. [2] Andersen, 1931.
[3] Black, 1913; Campbell, 1918.

functions as a capillary tube which takes in sufficient water to permit swimming of antherozoids. Antherozoids swimming near an archegonium swim to and into its neck canal and down the canal to the egg. Several antherozoids may enter the venter of an archegonium, but usually only one of them penetrates the egg. It is very probable that gametic union in homothallic species is generally between antherozoids and eggs produced by the same gametophyte. The details of gametic union have not been

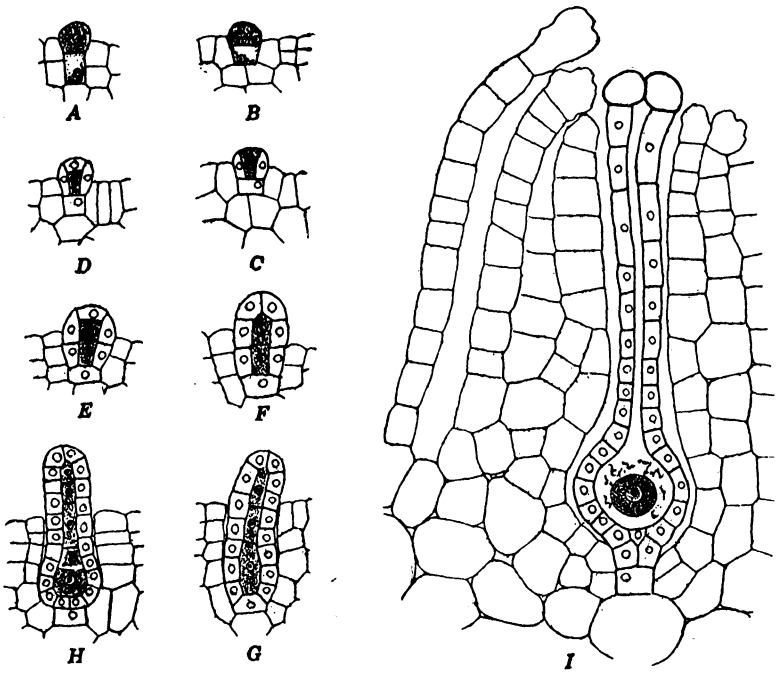

FIG. 17. *Riccia glauca* L. Stages in development of archegonia. (× 325.)

described as fully as they have for *Sphaerocarpos* and for certain Jungermanniales, but it has been shown[1] that shortly after fertilization a male gamete nucleus may be found lying close to the female nucleus (Fig. 18*A*).

Shortly after gametic union, the zygote secretes a wall and increases in volume until it nearly fills the cavity within the venter. Fertilization also stimulates division of venter cells, and even before division of the zygote, cells of the venter may begin to divide periclinally. The entire venter becomes two cells in thickness and then all further cell divisions are anticlinal. Anticlinal division is more active in the outer than in the inner layer of the venter so that the outer layer is many more cells in per-

[1] Black, 1913; Pande, 1933.

imeter (Fig. 18*F–G*). Division of the zygote is transverse or approximately so.[1] Most species regularly have a vertical division of epibasal and hypobasal cells of the two-celled embryo to form a four-celled embryo of the quadrant type (Fig. 18*B*), but certain species have epibasal and hypobasal cells dividing to form a four-celled embryo of the filamentous type.[2]

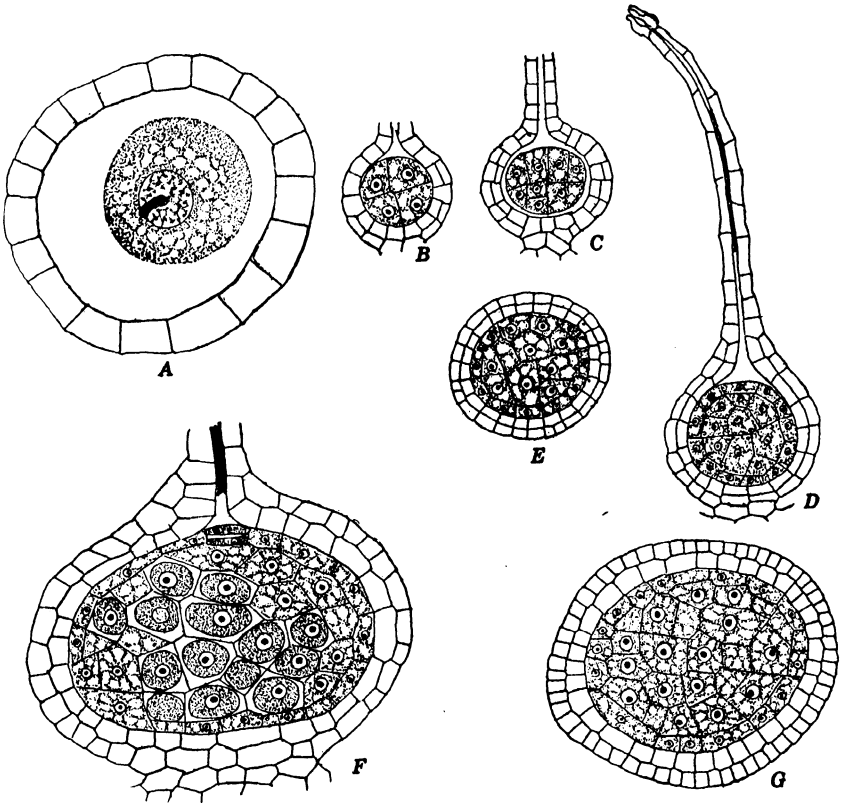

FIG. 18. *Riccia glauca* L. *A*, zygote with uniting male and female nuclei. *B*, quadrant type of four-celled embryo. *C*, before differentiation of sporogenous tissue and jacket layer. *D–E*, *G*, early and late stages in increase in number of sporogenous cells. *F*, after differentiation of sporogenous tissue into sporocytes and nurse cells. (*A*, *E*, *G*, in transverse section; *B–D*, *F*, in vertical section.) (*A*, × 650; *B–G*, × 215.)

In four-celled quadrant embryos, another series of vertical divisions at right angles to the preceding series results in a globose embryo of eight cells. Succeeding divisions are in an irregular sequence. At the stage when an embryo consists of 20 to 30 cells, there are periclinal divisions which differentiate it into an outer layer (the **amphithecium**) and an inner mass

[1] Campbell, 1918; Pagan, 1932; Pande, 1933. [2] Garber, 1904; Lewis, 1906.

(the **endothecium**). In *Riccia*, where the entire sporophyte is a capsule, the amphithecium becomes the jacket layer of the sporophyte (Fig. 18*D–G*). The endothecium is the first cell generation (**archesporium**) of the sporogenous tissue. Division and redivision in cells of this tissue result in a considerable increase in number of sporogenous cells. Eventually the sporogenous tissue becomes differentiated into two kinds of cells, **sporocytes** with densely granular cytoplasm, and **nurse cells** with a watery vacuolate cytoplasm (Fig. 18*F*). Disintegration of the nurse cells, together with disintegration of jacket cells of the sporophyte and the inner cell layer of the surrounding venter, results in a viscous fluid in which the

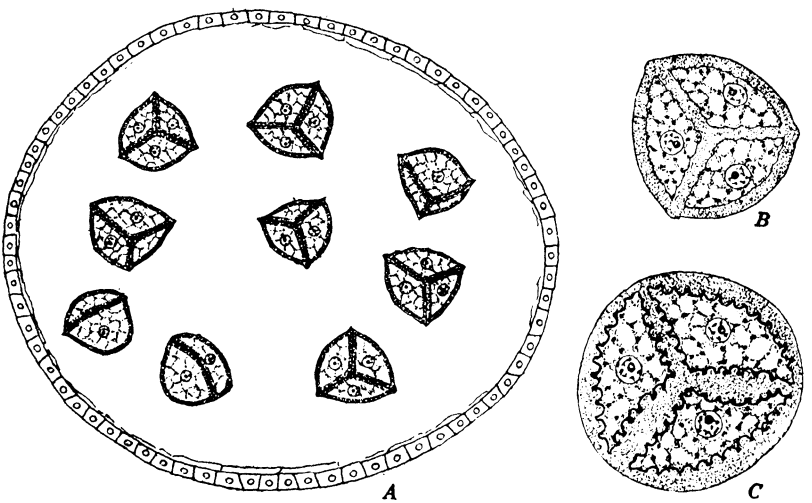

FIG. 19. *Riccia glauca* L. *A*, transverse section of a nearly mature sporophyte. *B–C*, maturing tetrads of spores. (*A*, × 215; *B–C*, × 485.)

sporocytes are suspended. This fluid serves as a food supply for sporocytes during meiosis and development of spores. The cytokinesis following the first meiotic division is incomplete, and the cell plates delimiting the four spores are formed simultaneously after completion of the second meiotic division.[1] The four spores of a tetrad remain apposed to one another and surrounded by a common spherical sheath until the spore walls are nearly mature (Fig. 19*B–C*). In one species, *R. curtisii*, the spores of a tetrad remain united to one another even after they are fully mature and have been shed.[2] Mature spore walls are composed of three layers laid down in centripetal succession. The outermost layer, the **exosporium,** is thin and strongly cutinized. The median layer (**mesosporium**) is thick and composed of three concentric zones. The innermost and last-

[1] Beer, 1906; Lewis, 1906. [2] McAllister, 1916.

formed layer (**endosporium**) is a homogeneous layer composed of pectose and callose.[1] The entire spore wall is irregularly thickened and folded.

The jacket layer of a sporophyte and the inner layer of the surrounding venter disappear long before the spores are mature (Fig. 19*A*). The spore mass, surrounded by a venter layer one cell in thickness, is usually called the sporophyte. In the strict morphological sense, this is incorrect since the structure to which the term is applied consists of a mass of spores, the first cells of the new gametophyte, surrounded by an envelope belonging to the preceding gametophyte.

The Ricciaceae, unlike other Hepaticae, do not have a liberation of the spores immediately after they are mature, and spores remain within a thallus until after the death and decay of the surrounding gametophytic tissues. Under ordinary conditions this does not take place until a year or so after the spores are formed. Germination of a spore begins with a rupture of the two outer wall layers and the protrusion of a tubular outgrowth in which the surrounding wall is continuous with the endosporium.[2] This germinal tube attains a length several times the diameter of the spore before a transverse wall is laid down near its distal end. Previous to formation of the cross wall most of the protoplasm has migrated to the distal end of the tube. Coincident with cross-wall formation, there is a development of a rhizoid near the region of emergence of the germinal tube from a spore. A second division, parallel to the first, results in two cells at the distal end of the tube. Each of these cells, by successive vertical divisions, gives rise to a tier of four cells. Further divisions in the proximal tier are transverse, and the daughter cells so formed elongate greatly in their longitudinal axes to form the distinctly cylindrical and elongate posterior portion of a young gametophyte. It is very probable that one of the four cells in the distal tier functions as an apical cell with two cutting faces. This cell functions actively and forms several derivatives. The other three cells of the tier divide but once or twice. Fairly early in development of the gametophyte, there is a replacement of the single apical cell by a transverse row of apical cells. From then onward further growth is identical with that at the apex of a mature thallus.

FAMILY 2. CORSINIACEAE

Gametophytes of Corsiniaceae have air chambers with simple pores and bear sex organs in a linear series of receptacles which lie somewhat removed from one another along the dorsal surface. The sporophytes, which lie in depressions on the dorsal surface, are differentiated into capsule and foot.

Of the three genera in the family, *Corsinia* is the best known and most thoroughly studied. It occurs in North America (Texas and Louisiana),

[1] Beer, 1906. [2] Campbell, 1918.

South America, Europe, Africa, and Japan. A gametophyte of *Corsinia* grows prostrate, is but two or three times dichotomously branched, and has the ribbon-like dichotomies widely divergent. Unlike most other Marchantiales, the scales are irregularly distributed over the entire ventral surface. The lower portion of a gametophyte consists of a relatively thick, colorless, parenchymatous tissue. Above this is a single layer of air chambers, each of which opens externally by a simple pore encircled by one or two rings of thin-walled cells. The floor of an air chamber may have short erect photosynthetic filaments or may lack them.

Most gametophytes of *Corsinia* are heterothallic, but some are homothallic. Antheridia are borne in definitely localized areas (**receptacles**) along the median axis of the dorsal surface. Each receptacle is encircled by a low ridge resulting from more active upward growth of adjacent

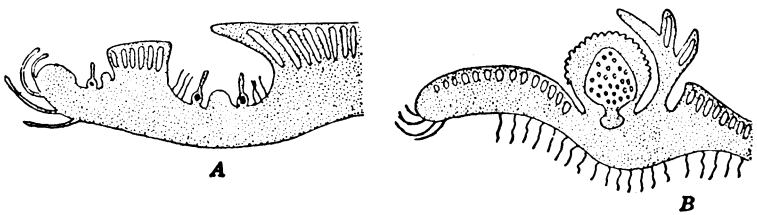

FIG. 20. *Corsinia coriandrina* (Spreng.) Lindb. *A*, vertical section of a female gametophyte before development of involucre. *B*, the same after development of involucre. (*After Leitgeb*, 1879.)

thallus tissue. Each mature antheridium[1] lies within an antheridial chamber, and the scanty evidence indicates that development of antheridia is as in other Marchantiales. Archegonia are also borne in receptacles lying in conspicuous sunken pits (Fig. 20*A*). Each receptacle contains 6 to 10 archegonia surrounded by numerous filamentous proliferations (**paraphyses**) from the surface of the receptacle.

In development of a sporophyte the zygote divides transversely into an epibasal and a hypobasal cell,[2] which then divides vertically to form a quadrant type of embryo (Fig. 21*A–B*). The epibasal half of the young embryo becomes differentiated into amphithecium and endothecium by a series of periclinal divisions (Fig. 21*D*). Cells of the endothecium (archesporium) give rise to the sporogenous tissue by division and redivision. The last cell generation of the sporogenous tissue becomes differentiated into two types of cells;[3] sporocytes and sterile cells that persist until the spores are mature (Fig. 21*F–G*). The spiral thickenings found[1] on homologous cells of another member of the family (*Funicularia*) show that the sterile cells of *Corsinia* are to be considered a primitive type of elater. The

[1] Leitgeb, 1879. [2] Meyer, 1912. [3] Meyer, 1912, 1914.

amphithecium of a young capsule develops into a jacket layer one cell in thickness and one in which walls of mature cells are without secondary thickenings. Cell divisions producing the foot portion of a sporophyte are in irregular sequence and produce a foot composed of relatively few cells (Fig. 21*G*).

Periclinal division of cells of the venter of an archegonium is more extensive than in *Riccia*, and the enlarged venter (**calyptra**) surrounding a sporophyte is a massive structure several cells in thickness. The calyptra with its enclosed sporophyte is partially ensheathed by an **involucre.** This

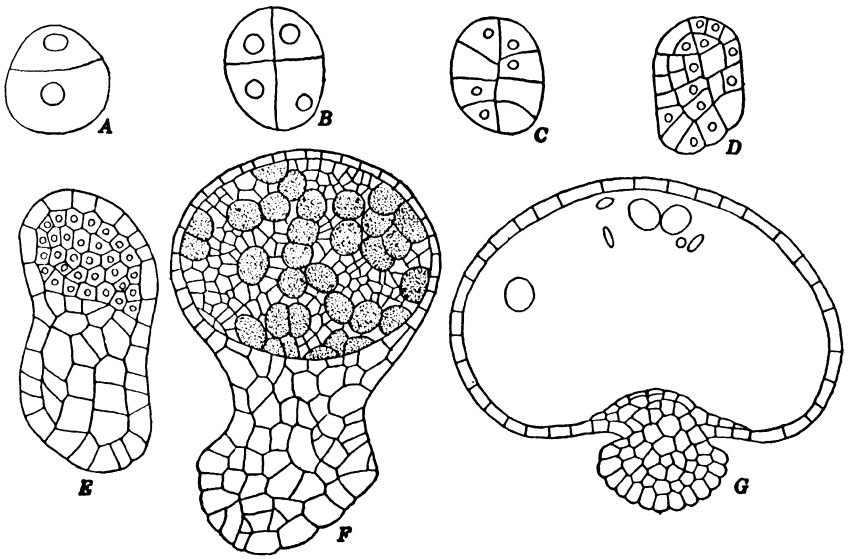

FIG. 21. *Corsinia coriandrina* (Streng.) Lindb. *A–C*, early stages in development of embryo. *D*, just after differentiation of capsular portion of embryo into jacket layer and sporogenous tissue. *E*, a somewhat later stage. *F*, after differentiation of sporogenous tissue into sporocytes and nurse cells. *G*, mature sporophyte. (*A–F*, *after Meyer*, 1912; *G*, *after Meyer*, 1914.) (*A–E*, × 130; *F*, × 140; *G*, × 50.)

structure is first evident on the receptacular floor as a small hump of meristematic tissue which lies either between or posterior to the archegonia (Fig. 20*A*). Depending upon whether the involucre adjoins one or a group of sporophytes, it either develops into a curved and irregularly branched shield (Fig. 20*B*), or it develops into a lobed umbrella-like structure in which each lobe shields a sporophyte. The upper portion of a mature involucre is differentiated into air chambers. The involucre of Corsiniaceae has been interpreted[1] as the evolutionary forerunner of the archegoniophore characteristic of Marchantiaceae, but one that differs in being developed subsequent to fertilization. This interpretation does

[1] Cavers, 1910.

not appear logical since the involucre is merely an upgrowth of tissue posterior to the growing point; whereas the archegoniophore of Marchantiaceae is formed by an upgrowth of the growing point itself.

FAMILY 3. TARGIONIACEAE

The Targioniaceae differ from other Marchantiales in having the female receptacle enclosed by a sheath (involucre) developed from tissues lateral to it. The family contains three genera, two (*Targionia* and *Cyathodium*) of world-wide distribution, and one (*Aitchinsoniella*) known only from India.

Targionia hypophylla L., the species here selected as illustrative of the family, is world-wide in distribution and is a common liverwort in the

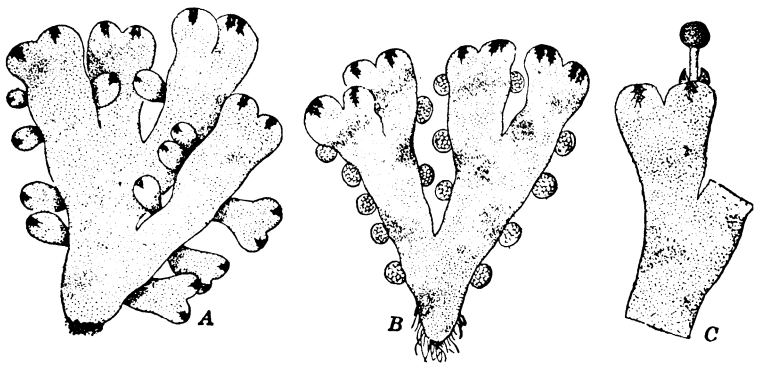

FIG. 22. *Targionia hypophylla* L. *A*, female gametophyte with adventitious branches. *B*, male gametophyte. *C*, portion of a female gametophyte with the two halves of involucre at tip of one branch spread apart and a sporophyte growing out between them.

western part of the United States. Its gametophyte (Fig. 22) is ribbon-like, is sparingly dichotomous, and has adventitious branches formed in abundance from the ventral side of the midrib. Most of these branches arise laterally, but some of them arise near the thallus apex and grow anterior to it. Death and decay of the slender connection between adventitious branches and the parent plant result in extensive vegetative propagation of the gametophyte.[1]

When viewed from above, the upper surface of a gametophyte is divided into small polygonal areas, each area indicating the position of an air chamber just beneath the epidermal layer. Each chamber opens externally by a small pore that is encircled by four to six concentric rings of cells so arranged that the pore is at the summit of a small hump. The chambers, which are formed schizogenously,[2] lie in a single layer at the upper side of a thallus and are laterally separated from one another by vertical plates one cell in thickness (Fig. 23*A*). The floor of a chamber bears numerous

[1] Cavers, 1904. [2] Deutsch, 1912.

simple or branched, erect, photosynthetic filaments. A filament is generally three cells in height, the spherical distal cell being much larger than the others. The colorless tissue below the air chambers is about 20 cells in thickness in the region of the midrib and is composed of elongate cells whose long axes parallel the long axis of the thallus. Toward the lateral margins of a branch the colorless tissue is composed of fewer and more nearly isodiametric cells, and at the extreme margin it is but one cell in thickness. Many of the cells in the colorless tissue contain starch grains. Intermingled with the starch-containing cells are isolated cells containing either mucilage or a large oil body. Isolated cells containing an oil body are characteristic of most genera in the Marchantiales. Superficial cells of the ventral surface produce obliquely inserted scales, which lie in two rows,

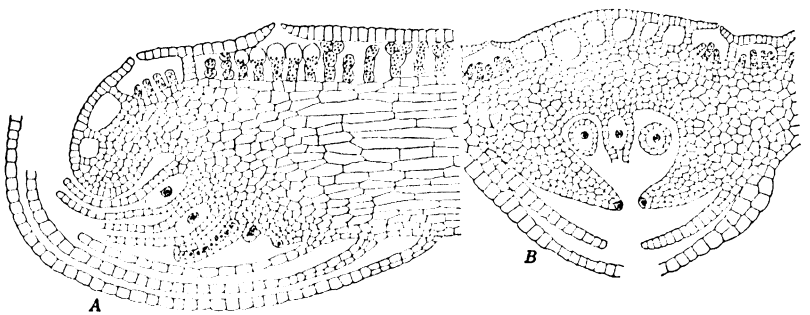

FIG. 23. *Targionia hypophylla* L. *A*, longitudinal vertical section of fertile apex of a female gametophyte. *B*, transverse vertical section of the same. Both semidiagrammatic. (× 105.)

one on either side of the midrib. The scales are one cell in thickness except in the basal portion. The ventral surface of a thallus also bears the two types of rhizoids characteristic of Marchantiales. Apical growth is due to a single wedge-shaped apical cell that alternately cuts off segments ventrally and dorsally.[1]

Antheridia are produced only on short lateral branches which arise adventitiously from the ventral surface of a midrib (Fig. 22*B*). Antheridia develop according to the same sequence as those of *Riccia*. Development of antheridia is accompanied by an upward growth of adjacent vegetative tissue, and each mature antheridium lies within an antheridial chamber (Fig. 24*A*). These chambers are externally recognizable as small pores irregularly distributed over the upper surface of an antheridial branch.

Archegonia begin to develop from superficial dorsal cells only two or three removed from the apical cell (Fig. 23*A*). The history of their development is essentially the same as in *Riccia*. As in the Corsiniaceae, there is a definitely restricted receptacular area, but unlike the Corsiniaceae, the receptacle never comes to lie a considerable distance posterior to the

[1] Deutsch, 1912; O'Keefe, 1915.

thallus apex. *Targionia* is essentially **acrogynous** (with a cessation of apical growth following the production of archegonia), but there is no proof that the last-formed archegonium is developed from the apical cell itself as in the acrogynous Jungermanniales.

Development of archegonia is accompanied by a maturation and enlargement of tissues posterior to them that push the archegonial receptacle to the ventral side of the thallus (Fig. 23*A*). However, in spite of its ventral position, the archegonial receptacle is a dorsal structure since it lies posterior to the dorsal face of the apical cell. Inversion in position of the receptacle is accompanied by the outgrowth of a conspicuous plate-like mass from either lateral flank of the receptacle. These two outgrowths eventually become apposed to each other to form a sheath, the **involucre,**

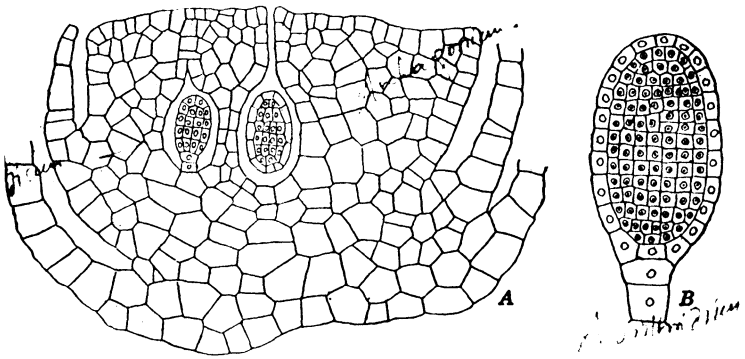

FIG. 24. *Targionia hypophylla* L. *A*, transverse vertical section near apex of an antheridial branch. *B*, vertical section of an immature antheridium. (*A*, × 225; *B*, × 400.)

which surrounds the developing sporophyte. In most cases development of the involucre takes place subsequent to fertilization, but instances have been noted where it is well along in development before fertilization.[1] Each lobe of the involucre is to be interpreted as an adventitious branch from the dorsal face of the thallus, and one which grows in length by the functioning of a single apical cell (Fig. 23*B*). Back from the growing point each lobe of the involucre develops air chambers on its morphologically dorsal surface, but these lack photosynthetic filaments. Late in development of an involucre there is a heavy cutinization of cells on the outer face. In addition to being enclosed by the involucre, the sporophyte is ensheathed by a **calyptra,** three or four cells in thickness, a structure developed from the venter of the archegonium.

Division of the zygote is transverse (Fig. 25*A*). The next step is a formation of a filamentous embryo of four cells[2] whose epibasal half ultimately develops into the capsule and whose hypobasal half develops into foot and seta of the mature sporophyte. At first, cell divisions in the epi-

[1] Deutsch, 1912. [2] O'Keefe, 1915.

basal half are transverse but periclinal divisions soon differentiate the capsular portion into amphithecium and endothecium (Fig. 25*B–C*). As in other Marchantiales, all cell divisions in the amphithecium, the future jacket layer of the capsule, are anticlinal. When mature, the jacket layer has band-like thickenings in its cell walls, and the apical portion of the jacket is differentiated into a well-defined lid. Cells of the endothecium, the first generation of the sporogenous tissue, divide in all planes to form a sporogenous tissue of many cells (Fig. 25*D*). About half of the cells of the last cell generation in the sporogenous tissue enlarge considerably

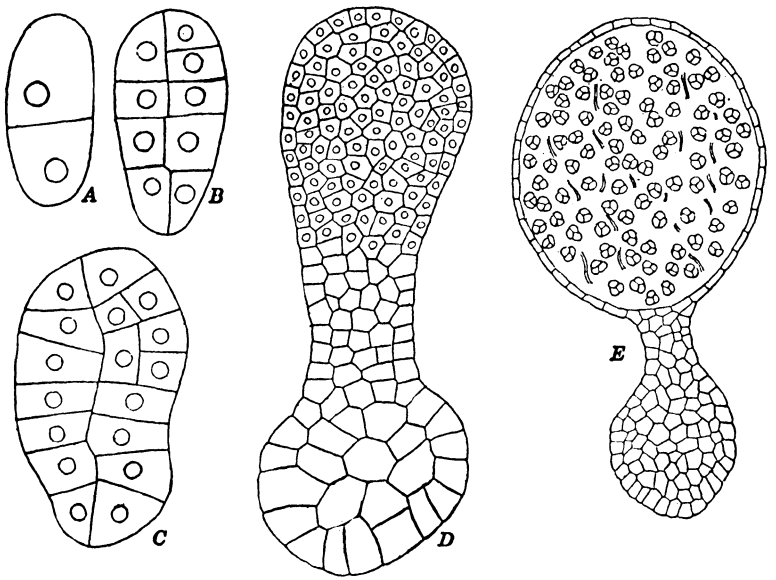

FIG. 25. *Targionia hypophylla* L. Stages in development of sporophyte. (*A–C*, × 400; *D*, × 225; *E*, × 105.)

and become sporocytes, each of which divides meiotically into four spores. The other half of the cells in this cell generation elongate greatly and mature into **elaters** with two or three spiral thickenings on their walls. Cells maturing into elaters are indiscriminately mixed with the sporocytes (Fig. 25*E*). Elaters are hygroscopically sensitive, curling and abruptly uncurling as they become alternately dry and moist after dehiscence of the capsule.

The first cell divisions in the hypobasal half of the four-celled embryo are transverse (Fig. 25*C*), but soon division is in various planes. There is an early enlargement of cells in the lower portion to form a bulbous foot (Fig. 25*D*). The portion of the embryo destined to become the seta never becomes as broad as the foot, and until relatively late in development of a

sporophyte it is composed of relatively few cells (Fig. 25*E*). Then, by a series of transverse divisions, there is a great increase in number of cells in the seta. When the spores are fully mature, the two valves of the involucre spread apart and the capsule is pushed beyond the apex of the gametophyte by elongation of the cells of the seta (Fig. 22*C*). Dehiscence of the capsule is usually by a shedding of the apical lid-like portion and a splitting of the remainder of the capsule jacket into five to eight lobes which bend back upon themselves.[1]

FAMILY 4. MONOCLEACEAE

The Monocleaceae differ from other Marchantiales in the unique hood-like sheath posterior to the female receptacle. The elongate capsule is also of different shape from those in other families of the order. The single genus, *Monoclea*, has but two species, *M. gottschei* Lindb. of the tropical Americas, and *M. forsteri* Hook. of New Zealand and Patagonia.

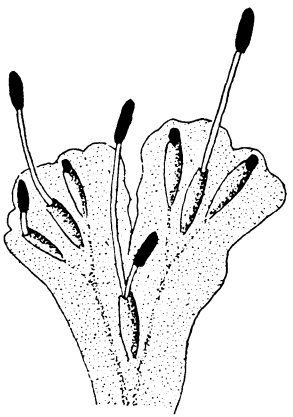

FIG. 26. *Monoclea forsteri* Hook. (*After Cavers*, 1904.)

The family has been referred both to the Marchantiales[2] and to the Jungermanniales.[3] Features showing its affinities with the Marchantiales include oil bodies in isolated cells, two types of rhizoids, structure of male receptacle, ontogeny of antheridia, structure of neck of archegonia, and structure and dehiscence of jacket of the capsule. The chief arguments for placing it among the anacrogynous Jungermanniales are lack of air chambers in the gametophyte, lack of ventral scales, and resemblance of the involucre to those of certain Jungermanniales.

The twice to thrice dichotomously branched gametophyte of *M. forsteri* (Fig. 26) is the largest known thallose gametophyte among Bryophyta. There is no distinct midrib, but the gametophyte is some 10 cells in thickness in the sagittal axis and tapering to a thickness of one or two cells along the lateral margins. The gametophyte is solidly parenchymatous and with chloroplasts restricted to the dorsal epidermis and cells immediately beneath. The lack of air chambers might be considered a justification for excluding the genus from the Marchantiales were it not known that other genera of the order (*Dumortiera*[4] and *Monoselenium*[5]) form

[1] Cavers, 1904. [2] Campbell, 1898; Cavers, 1904; Johnson, 1904.
[3] Evans, 1939; Schiffner, 1893–1895; Verdoorn, 1932.
[4] Campbell, 1918*A*. [5] Goebel, 1910.

only rudimentary chambers or may lack them entirely. Isolated cells of the gametophyte have the oil bodies characteristic of Marchantiales. Scales are never formed by segments cut off from the ventral face of the apical cells, but there is a formation of unicellular mucilage hairs which project forward and overarch the growing apex.[1] The ventral surface bears two kinds of rhizoids, smooth-walled ones and those in which the walls are irregularly thickened.

Monoclea is heterothallic. The antheridia are borne in sessile receptacles which project somewhat above the surface of the gametophyte. Since the

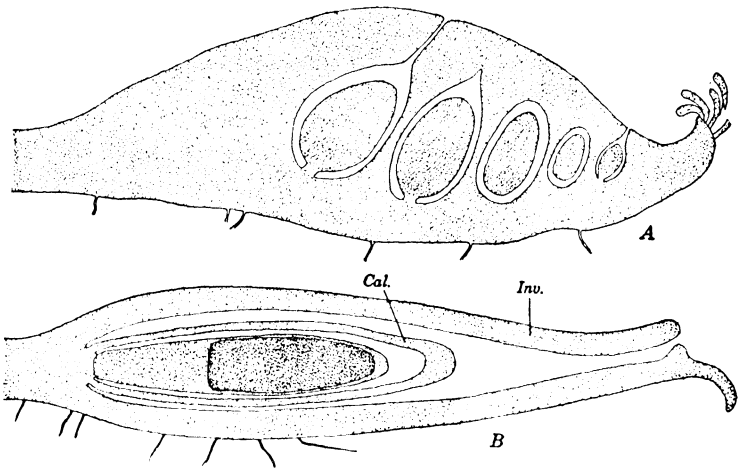

FIG. 27. *Monoclea gottschei* Lindb. *A*, longitudinal vertical section through a male gametophyte. *B*, longitudinal vertical section through a female gametophyte, showing a sporophyte surrounded by a calyptra (*Cal.*) and an involucre (*Inv.*). (*A*, × 34; *B*, × 16.)

apical initials are not destroyed in formation of a receptacle, there is continued apical growth and a production of a succession of male receptacles. Antheridia of each receptacle are produced in acropetalous succession and their ontogeny is typical of that of Marchantiales.[2] Development of antheridia is accompanied by an upward growth of adjoining vegetative tissues, so that a mature antheridium lies within an antheridial chamber opening to the exterior by a long narrow canal (Fig. 27*A*). Certain of the cells lining the chamber develop unicellular mucilage hairs similar to those on the ventral face of a gametophyte.

The first stages in development of archegonia are to be found only a few segments back from the apical initials. Production of archegonia is not long continued, only a dozen or so being formed. *Monoclea* is **anacrocynous**; that is, production of archegonia does not check apical growth. However, the portion of a thallus developed anterior to the female recep-

[1] Cavers, 1904, 1904*A*. [2] Johnson, 1904.

tacle does not subsequently form new receptacles. Shortly after the female receptacle is differentiated, there is a thickening of the portion of the thallus posterior to it, after which the front edge of the thickening grows forward to form a hood-like outgrowth. Elongation of the hood is at the same rate as that of the growing point anterior to the receptacle. The tubular **involucre** resulting from elongation of hood and thallus apex may attain a length of 15 mm. before growth ceases (Fig. 27*B*). Subsequent apical growth of a branch bearing a female receptacle is due to the activity of two new sets of initials which appear one on either side of the involucre which remains in the angle between the two new branches.[1] A mature archegonium has a swollen venter and a long neck. The neck has the six vertical rows of jacket cells typical of Marchantiales, but there may be as many as 10 neck canal cells.

The young sporophyte has an early differentiation into foot, seta, and capsule. The great length of the seta and the elongate capsule in the mature sporophyte are features more typical of Jungermanniales than of Marchantiales. However, this resemblance is only superficial since the jacket layer of the capsule is but one cell in thickness and never has the dehiscence into four valves characteristic of Jungermanniales. Late in development of the sporogenous tissue there is a vertical elongation of all the cells. Certain of these cells mature directly into elaters. Others of them divide transversely to form eight isodiametric sporocytes.[2] Thus, unlike *Targionia*, elaters and sporocytes are not members of the same cell generation. Quadripartition of sporocytes is by furrowing, a type of cytokinesis more commonly found in Jungermanniales than in Marchantiales.

FAMILY 5. MARCHANTIACEAE

The Marchantiaceae include all the genera in which archegonia are borne on special stalked vertical branches (**archegoniophores** or **carpocephala**). There are 23 genera and some 250 species. These are separated into three subfamilies, sometimes given the rank of separate families,[3] which are superficially distinguishable from one another by structure of the air pores.

The type genus, *Marchantia*, is placed among the most advanced members of the family by those who hold that Marchantiaceae are not primitive Marchantiales (see page 17). There are some 65 species in the genus, of which *M. polymorpha* L. (Fig. 28*E–F*) is the best known and most widely distributed. In certain respects this genus is not typical of the family since male gametophytes of most genera do not have the erect fertile branches (**antheridiophores**) found in *Marchantia*.

Most Marchantiaceae are readily recognized in the field by their prostrate dichotomously branched thalli in which the dorsal surface is divided

[1] Johnson, 1904; Cavers, 1904, 1904*A*.
[2] Johnson, 1904. [3] Evans, 1923, 1939.

into rhomboidal to polygonal areas, each with a small but clearly evident pore in the center. The dichotomous branching so conspicuous in *Marchantia* is sometimes obscured in other genera because of a development of adventitious branches from the ventral surface of a gametophyte.

Apical growth of most genera is initiated by a transverse row of apical cells, but there are genera[1] where there is only a single apical cell. Air chambers begin to develop very close to the growing apex. Their formation is schizogenous and by intercellular cleavage. In air chambers formed just beneath the upper epidermis the splitting begins at the surface and

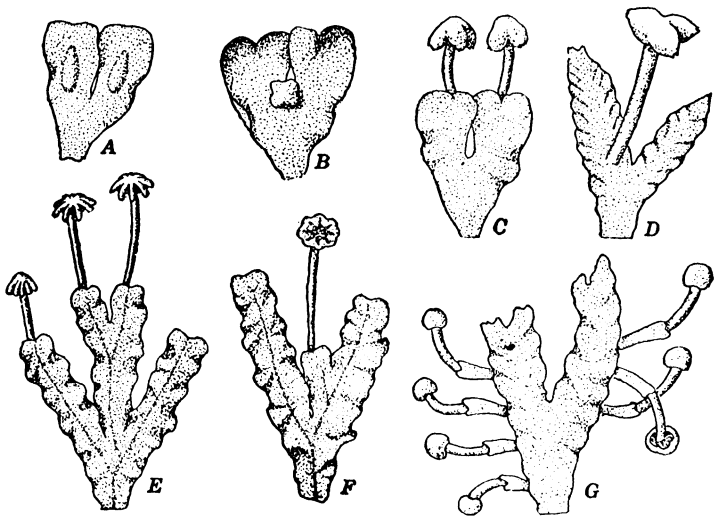

FIG. 28. *A–C*, *Asterella californica* (Hampe) Underw. *A*, male gametophyte. *B–C*, female gametophytes. *D*, *Athalamia pusilla* Kashyap, female gametophyte. *E–F*, *Marchantia polymorpha* L. *E*, female gametophyte. *F*, male gametophyte. *G*, *Grimaldia indica* Stephani, female gametophyte. (*D*, *G*, *after Kashyap*, 1929.)

progresses inward.[2] Air chambers may be formed in a single horizontal layer just beneath the upper epidermis, as in *Marchantia* (Fig. 29*A*); or in two or more layers as in *Reboulia* (Fig. 29*B*). The majority of genera have air chambers of the *Marchantia* type and in them there are usually simple or branched photosynthetic filaments arising from the floor of the chamber. Genera of the *Reboulia* type usually lack such filaments. All chambers in the *Marchantia* type and the uppermost chambers in the *Reboulia* type have well-defined air pores in which the surrounding cells are either in concentric rings or superimposed in tiers to form a barrel-like structure. Certain genera with the surrounding cells of air pores in tiers

[1] Haupt, 1926, 1929, 1942.

[2] Barnes and Land, 1907; Dupler, 1921; Evans, 1918; Haupt, 1921, 1926, 1942.

have been shown[1] to have an opening and closing of the pore due to imbibitional changes in walls of the surrounding cells. The portion of the gametophyte below the air chambers is several cells in thickness, except near the lateral margins, is parenchymatous, and usually lacks chloroplasts. These parenchymatous cells are isodiametric except along the midrib, and isolated ones among them may contain a single large oil body or be filled with mucilage. Cells comprising the midrib portion of this colorless tissue are elongate in the sagittal axis of the branches and with locally thickened walls. The ventral surface of a gametophyte bears two or more transverse rows of scales, never a single row as in Ricciaceae. Both

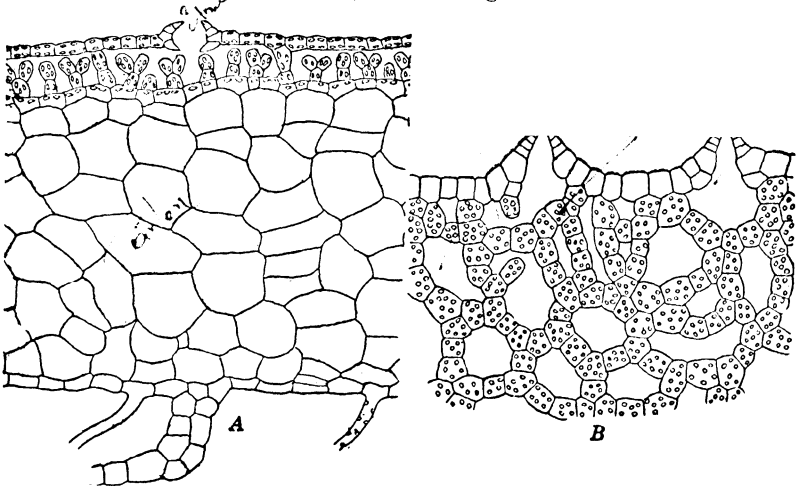

FIG. 29. *A*, vertical section through gametophyte of *Marchantia polymorpha* L. *B*, vertical section through upper portion of gametophyte of *Reboulia hemisphaerica* (L.) Raddi. (*A*, × 160; *B*, × 125.)

smooth-walled and tuberculate rhizoids arise from the ventral surface between the scales. The smooth-walled rhizoids grow forward, penetrate the soil, and absorb water from it. The tuberculate rhizoids form a capillary conducting system parallel to the thallus and thus make possible distribution of water to all absorptive parts of the gametophyte.[2]

There is regularly a vegetative reproduction of gametophytes as a result of apical growth, branching, and progressive death at the posterior end reaching a dichotomy. Vegetative multiplication is also effected by a production of adventitious branches from the ventral surface of a gametophyte, followed by death and decay of tissues connecting the branches with the parent plant.

In *Marchantia* and *Lunularia* special asexual reproductive bodies (**gemmae**) are produced in cup-like or crescent-shaped **cupules** on the

[1] Walker and Pennington, 1939. [2] McConaha, 1941.

dorsal surface of a gametophyte. The efficiency of this method of propagation is shown by the wide distribution of *Lunularia cruciata* (L.) Dum. in this country after its introduction from Europe with nursery stock. In most parts of the United States it is found only in greenhouses, but in areas with a mild climate, as California, it has become established outdoors. Each gemma is developed from a single superficial cell on the floor of a cupule. A mature gemma (Fig. 30) is attached to the cupule by a one-celled stalk and is disciform, several cells in thickness in the median portion, and with a marginal row of apical cells in a shallow indentation on either lateral margin. Most of the cells contain chloroplasts, but isolated superficial cells of the central area on both surfaces are colorless. There are also isolated cells just within the margin which contain oil bodies instead of chloroplasts. Intermingled with the gemmae are club-shaped mucilage cells growing up from the floor of the cupule. Discharge of mucilage from these cells and the swelling of the mucilage as it imbibes water break the gemmae from their stalks and force them out of the cupule. Gemmae lodging on soil develop rhizoids from the colorless cells on the face next to the soil, and the apical initials in the two marginal indentations begin to function in the same manner as those at the growing tip of a branch. Continued apical growth and dichotomous branching are in two opposite directions. Eventually death and decay of the tissue originally comprising the gemma result in two separate thalli growing in opposite directions.

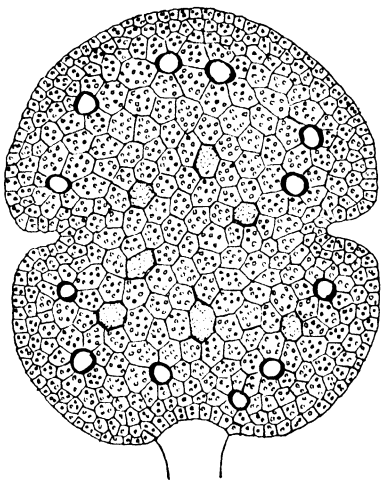

FIG. 30. Gemma of *Marchantia polymorpha* L. (× 210.)

Some Marchantiaceae are homothallic; others are strictly heterothallic and for certain of them this has been shown[1] to be due to sex chromosomes. Archegonia are borne on special stalked erect branches (**archegoniophores** or **carpocephala**) and these are structures peculiar to Marchantiaceae. They are modified prostrate branches. This is shown by the dorsiventrality of the stalk of an archegoniophore, its morphologically ventral side having one or two longitudinal furrows containing scales and rhizoids, and the morphologically dorsal side having an internal differentiation of air chambers.

[1] Lorbeer, 1934; Tatuno, 1937, 1938.

An archegoniophore begins development by an upward bending of a prostrate branch. This is usually an ordinary vegetative branch; but in some cases, as in *Grimaldia* (Fig. 28*G*) and certain species of *Asterella*, it is an adventitious branch growing out laterally from the ventral side of an ordinary branch. Although the archegoniophore is a terminal structure it does not always appear to be such. There are certain genera, for example, *Athalamia* (Fig. 28*D*), where the mature archegoniophores lie a considerable distance back from the tips of thallus branches. Such archegoniophores are said to be dorsal in origin, but for *Preissia* the base of the erect archegoniophore has been shown[1] to differentiate a new apical cell which continues prostrate vegetative growth of the thallus branch. In other cases (Fig. 28*B*), the archegoniophore seems to grow out of the base of a dichotomy. Here it has been shown[2] that the archegoniophore is in reality terminal, and that on both flanks of its base there is a differentiation of apical initials which produce prostrate growth.

In most genera, including *Marchantia*, there is a precocious dichotomy in the young archegoniophore.[3] Evidence for this is seen in the two furrows with scales and rhizoids on the morphologically ventral side of the archegoniophore's stalk. In *Marchantia* and most other genera there is soon a dichotomy of the forked swollen apex, followed by a second dichotomy in each of the four lobes. The apex of a young archegoniophore thus becomes a rosette-like eight-lobed disk, which seems to be radially symmetrical but which actually is bilaterally symmetrical (Fig. 31*A*). Other genera, including *Conocephalum*, have no branching of two of the four lobes and thus a formation of a disk with six lobes. In still other cases, there is a complete obliteration of the third series of dichotomies and thus a formation of a four-lobed disk; or as in certain species of *Asterella*, there is an obliteration of both the second and third series and thus a formation of a two-lobed disk. Shortly after apical branching ceases, archegonia are formed in acropetalous succession on the dorsal side and just back from the growing apex of each lobe of the disk. The portion of a lobe in which archegonia develop is a receptacle and the number of receptacles on a disk is the same as the number of lobes. The entire apex of an archegoniophore is frequently termed the receptacle, but this is incorrect since it really is a composite structure with two to eight receptacles.

The ontogeny of archegonia is similar to that in Ricciaceae and other members of the order. Archegonia are mature and fertilization is effected at a time when the disk of an archegoniophore is but slightly elevated above the remainder of the thallus. After fertilization, and as the stalk of an archegoniophore is elongating, there is a conspicuous upwelling of the tissues comprising the central area of the disk (Fig. 31*B*, 33*A*). This upwelling, which resembles the raising of a loaf of bread dough in a pan, in-

[1] Haupt, 1926. [2] Haupt, 1929*A*. [3] Cavers, 1904*B*.

THIS BOOK IS THE PROPERTY OF THE UNIVERSITY OF TEXAS
No. 800K

verts the marginal portion of the disk so that the archegonia lie with their necks downward. The oldest archegonia are now nearest the periphery of the disk and the youngest nearest the stalk (Fig. 31*C*). Inversion is followed by development of a plate of tissue on both sides of each receptacle. Thus each group of archegonia becomes surrounded by a pendant two-parted curtain-like **involucre.** Many species of *Marchantia* are unique among Marchantiales in having stout cylindrical processes developing from the periphery of the disk (Fig. 31*D*). In *M. polymorpha* these rays alternate with the lobes of the disk. Most individuals have nine rays, seven developing between adjacent lobes, and two developing at the margins between two lobes.

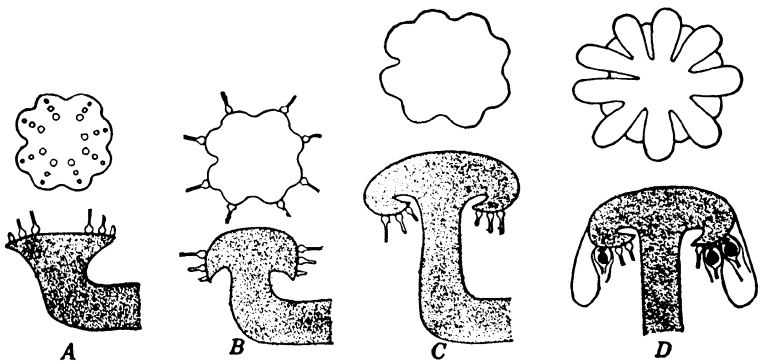

FIG. 31. *Marchantia polymorpha* L. Diagrams of top view and vertical longitudinal sections of stages in development of an archegoniophore.

The majority of genera produce antheridia in definitely circumscribed sessile areas (receptacles) on the dorsal side of the gametophyte and slightly elevated above adjacent sterile tissue (Fig. 28*A*). Receptacles are usually borne on ordinary vegetative branches but, as in certain species of *Asterella*, they may be borne on adventitious branches growing from the ventral side of a thallus. A branch may bear a single receptacle or a succession of three or four, but in either case they lie along its sagittal axis. Antheridia are formed in acropetalous succession and their ontogeny is as in *Riccia*. As in other Marchantiales, each antheridium of Marchantiaceae lies within an antheridial chamber. In *Marchantia*, antheridia are borne on special branches (**antheridiophores**) with the same dichotomy as an archegoniophore. An antheridiophore of *Marchantia* (Figs. 28*F*, 32) differs from its archegoniophore in having no inversion of the receptacular surfaces, and in the lack of rays and involucres.

Discharge of antherozoids and fertilization take place at a time when archegoniophores are but slightly elevated above the thallus. Antherozoids usually exude in a milky mass from canals of the antheridial cham-

bers, but cases have been recorded[1] where they are discharged explosively. Free-swimming antherozoids have been shown[2] to be positively chemotactic to certain substances, especially certain proteins and inorganic salts of potassium; and it seems safe to assume that entrance of an antherozoid into the neck of an archegonium is a chemotactic response. Union of antherozoid and egg takes place as in other liverworts, but union of the two gamete nuclei may take a much longer time.[3]

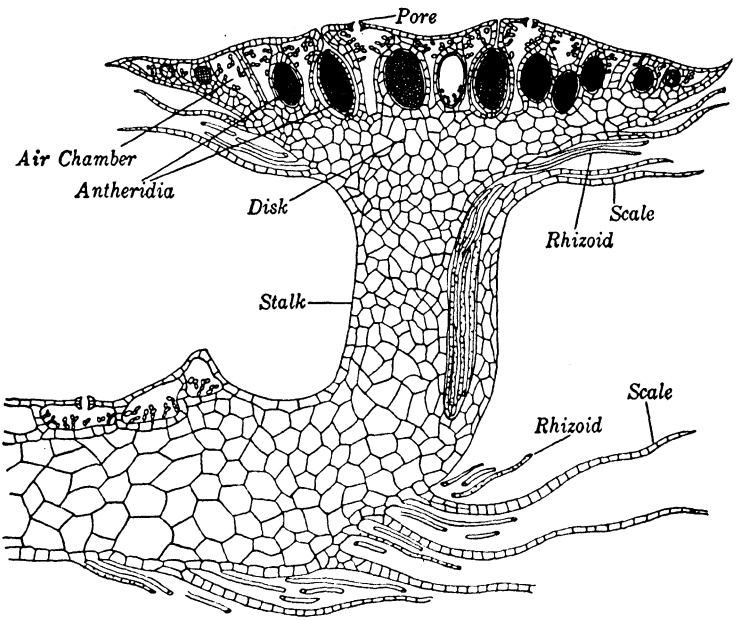

FIG. 32. *Marchantia polymorpha* L. Vertical longitudinal section through antheridiophore and adjoining portion of male gametophyte. (*From Smith et al.*, 1953.)

As is the case with many other liverworts, fertilization stimulates division of cells in the venter of the archegonium; and this tissue develops into a **calyptra,** two or more cells in thickness, that surrounds the sporophyte until maturity. In some genera, including *Marchantia* and *Conocephalum*, fertilization also stimulates division of cells immediately below the archegonium and their division and redivision produce a cylindrical outgrowth, the **pseudoperianth,** that is one cell in thickness (Fig. 34). These genera have three concentric protective sheaths around a sporophyte, the calyptra, the pseudoperianth, and the involucre. Other genera do not produce a pseudoperianth.

[1] Cavers, 1903*A*; Peirce, 1902. [2] Åkerman, 1910; Lidforss, 1904.
[3] Andersen, 1929.

Division of the zygote is transverse or approximately so (Fig. 34*A*). In some genera (including *Conocephalum*,[1] *Reboulia*,[2] *Grimaldia*,[3] and *Asterella*[4]) the two daughter cells of a zygote also divide transversely and thus form a filamentous type of four-celled embryo. In other genera (including *Marchantia*[5] and *Preissia*[6]) division of the two daughter cells is vertical and results in a quadrant type of embryo. The first four cells of the filamentous type of embryo cannot be related with absolute certainty to parts

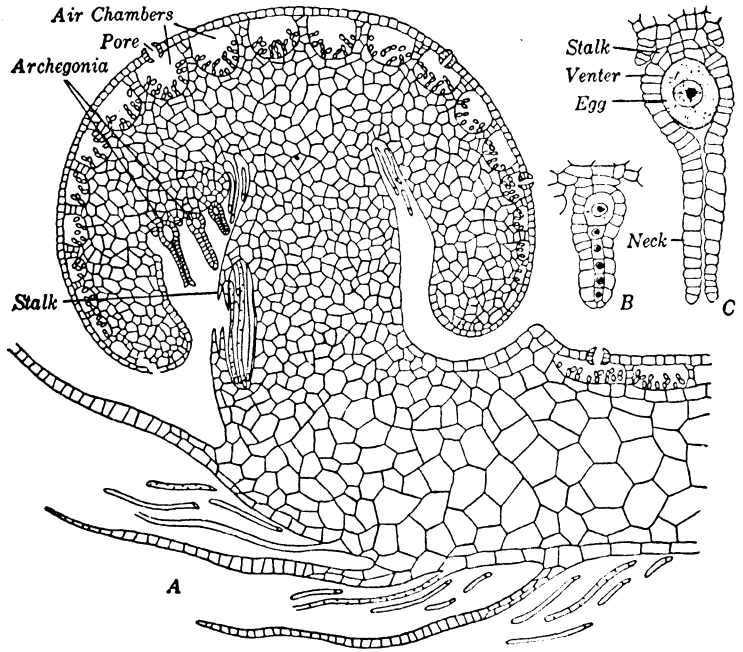

FIG. 33. *Marchantia polymorpha* L. *A*, vertical longitudinal section through archegoniophore and adjoining portion of female gametophyte. *B*, young archegonium. *C*, mature archegonium. (*From Smith et al.*, 1953.)

of the mature sporophyte, but it is thought[7] that the lowermost one gives rise to the foot, the one next above produces the seta, and the two upper cells produce the capsule. For the quadrant type of embryo the hypobasal half is thought to give rise to foot and setae of a mature sporophyte, and the epibasal half to give rise to its capsule.

Formation of a four-celled filamentous embryo is usually followed by two successive divisions of each of the four cells to produce four superimposed tiers of four cells each. Then by transverse cell division the em-

[1] Meyer, 1929. [2] Dupler, 1922; Haupt, 1921*A*. [3] Meyer, 1931.
[4] Haupt, 1929*A*. [5] Durand, 1908. [6] Haupt, 1926.
[7] Dupler, 1922; Haupt, 1929, 1942.

bryo may become a dozen or more cells in height before periclinal divisions in the capsular portion differentiate amphithecium and endothecium. Early growth of filamentous embryos of certain genera is in part due to a cutting off of a few derivatives by an apical cell at each pole.[1] In the quadrant type of embryo the cell divisions immediately following the eight-celled stage are not in regular succession.

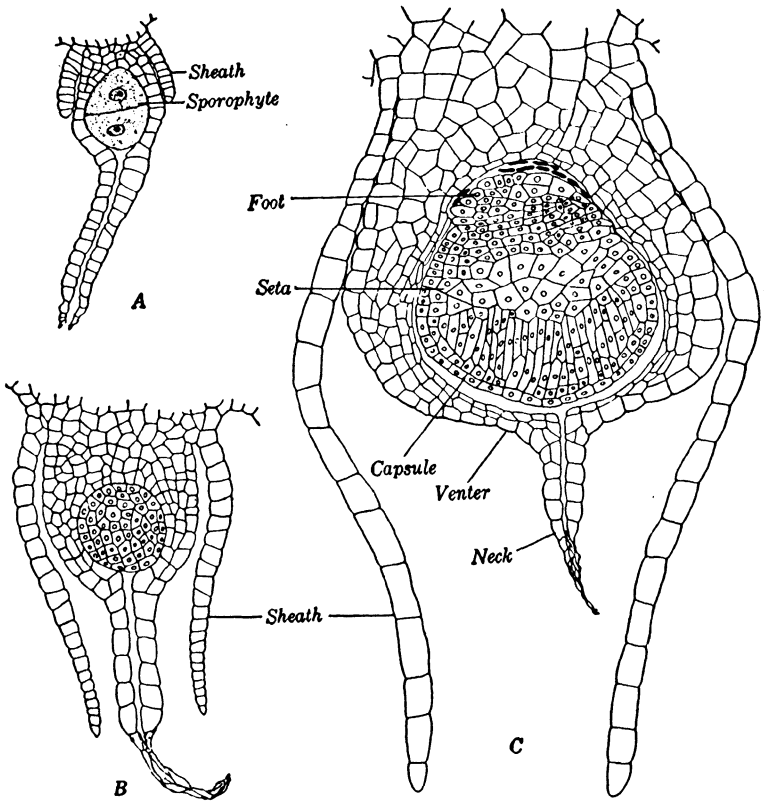

FIG. 34. *Marchantia polymorpha* L. *A*, two-celled embryo within venter of an archegonium. *B*, a somewhat older embryo. *C*, a considerably older embryo. All drawn to the same scale as Fig. 33*B–C*. (*From Smith et al.*, 1953.)

Development of seta and foot after early embryonal stages is approximately the same in both quadrant and filamentous types of embryo. Early in development of the seta, cell division changes almost exclusively to one plane and results in a seta composed of vertical rows of cells (Figs. 34*C*, 35*A*). Late in development of a sporophyte there is a rather sudden increase in length of the seta by an elongation of its cells. Growth in length

[1] Dupler, 1922; Meyer, 1914, 1929, 1931.

of the seta ruptures the calyptra and pushes the capsule beyond such enveloping structures as involucre and pseudoperianth. Cell divisions in development of a foot are at various angles to one another. When mature,

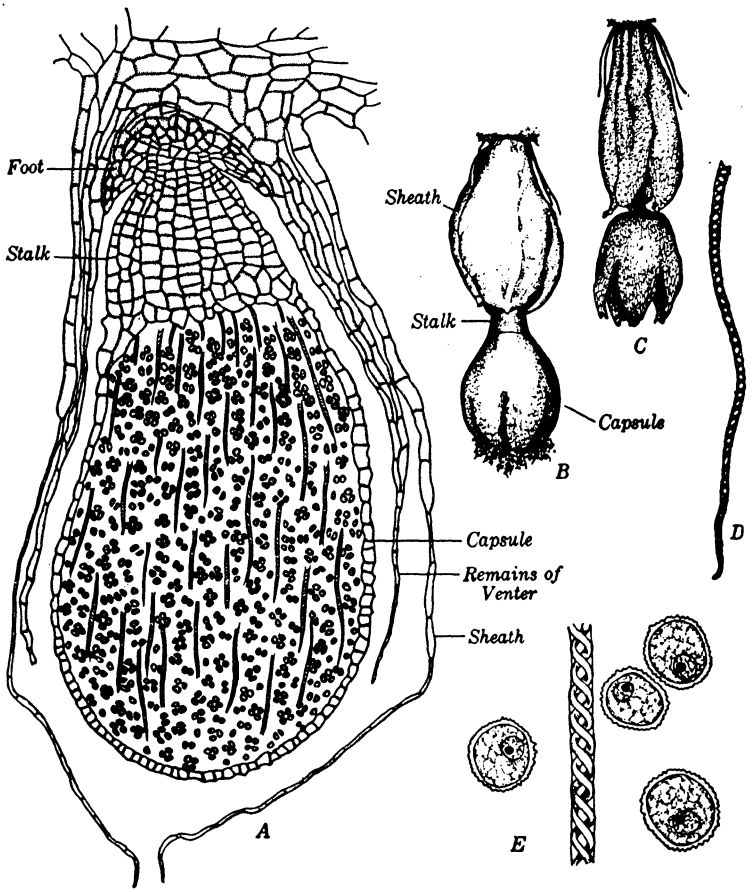

FIG. 35. *Marchantia polymorpha* L. *A*, longitudinal section of a nearly mature sporophyte. *B–C*, surface views of sporophytes during and after shedding of spores and elaters. *D*, portion of an elater. *E*, spores and portion of an elater. (*From Smith et al.*, 1953.)

the foot may be bulbous or, as in *Marchantia polymorpha*, it may be expanded into a mushroom-like structure. The foot serves as an organ for anchorage and for absorption of food from adjoining gametophytic tissues. However, the presence of chloroplasts in cells of foot, seta, and capsule of *Marchantia* shows that the sporophyte is not wholly dependent upon the gametophyte for the products of photosynthesis.[1]

[1] Bold, 1938.

Young embryos soon have periclinal cell divisions that differentiate the capsular portion into amphithecium and endothecium. The jacket layer (amphithecium) remains but one cell in thickness throughout further development of the capsule. Maturation of jacket cells is accompanied by a deposition of ring-like thickenings on their walls. When fully mature the jacket splits longitudinally from apex to about the middle, and into an indefinite number of segments. There are no definite predetermined longitudinal lines of dehiscence as in Jungermanniales.

Cells of the archesporial tissue (the endothecium) divide and redivide at various angles to form a massive sporogenous tissue. Frequently the apical cells of the sporogenous tissue become sterile so that the apex of the jacket appears to be more than one cell in thickness.[1] In certain Marchantiaceae, as *Reboulia*[2] and *Cryptomitrium*,[3] sporocytes and elaters belong to the same cell generation of sporogenous cells. Sporocytes and elaters of other Marchantiaceae do not belong to the same cell generation. *Marchantia* exemplifies this. Here, all sporogenous cells are vertically elongate and divide diagonally (Fig. 34*C*). Eventually there comes a time when about half of the sporogenous cells divide and redivide transversely to form vertical files of approximately cubical sporocytes. Typically, by five successive series of divisions, each of these sporogenous cells forms 32 sporocytes.[4] Sporogenous cells which do not divide into sporocytes elongate still further and mature into elaters with spiral thickenings on their walls (Fig. 35*E*). Since each sporocyte divides meiotically into four spores there are theoretically 128 spores to each elater. Spore output per capsule varies greatly from genus to genus among Marchantiaceae. The average output for *Reboulia*[5] has been estimated as 2,500, and that for *Marchantia*[4] as 300,000.

Liberation of spores after dehiscence of a capsule (Fig. 35*B–C*) is assisted by the coiling and uncoiling of elaters as a result of hygroscopic changes in their walls. Spore germination in *Marchantia*[6] begins with a considerable increase in size. There is no formation of a germinal tube as in *Riccia*, but the spore immediately produces an irregular filament of six to eight cells which may be two cells broad at the apex. A cell at the apex of the filament then begins to function as an apical cell with two lateral cutting faces that alternately produce five to seven segments right and left. Derivatives from the first-formed segments divide but two or three times; those from later-formed segments divide to form a large number of cells. After cutting off a few segments the two-faced apical cell divides and redivides to form a many-celled sheet in which there is soon an establishment of the transverse row of apical initials typical of Marchantiales.

[1] Andersen, 1929; Cribbs, 1918; Heberlein, 1929; McNaught, 1929.
[2] Haupt, 1921. [3] Haupt, 1942. [4] O'Hanlon, 1926. [5] O'Hanlon, 1930.
[6] Menge, 1930; O'Hanlon, 1926.

ORDER 3. JUNGERMANNIALES

Gametophytes of Jungermanniales may be of a simple thallose type or may be foliose and differentiated into stem and leaves. In either case there is but little internal differentiation of tissues. Early stages of antheridial development are of a distinctive type and result in a globose to subglobose antheridium that is usually borne on a long stalk. Archegonia differ from those of other Hepaticae in that the neck is composed of five vertical rows of cells and is nearly as broad as the venter. Unique features of the sporophyte include a jacket layer more than one cell in thickness and one which usually dehisces longitudinally into four parts. The order includes some 190 genera and 8,000 species, the great majority of which are known only from the tropics.

The Jungermanniales are often called the leafy liverworts because the vast majority of them have gametophytes with a sharp differentiation into stem and leaves. However, the order also includes genera in which the gametophyte is strictly thallose, and includes genera which are intermediate between thallose and leafy.

Growth of a gametophyte is always initiated by a single apical cell and the thallose or foliose structure of the gametophyte is due to subsequent development of segments cut off by the apical cell. Mature gametophytes are without internal differentiation of tissues except for a few thallose genera in which there are elongate cells in the sagittal axis.

As in other Hepaticae, vegetative multiplication of the gametophyte may be by progressive growth followed by death in the posterior portion. Several genera also produce adventitious branches which develop into independent plants after becoming detached from the parent thallus.[1] Many Jungermanniales form gemmae. Among thallose genera these are usually formed from any superficial cell of the gametophyte but certain genera produce them on special gemmiferous branches (*Metzgeria*) or in flask-shaped structures (*Blasia*).

Sex organs are regularly produced by most genera, but in temperate regions there is generally a definite correlation between climate and the time of year at which they are formed. In parts of the United States where the winter is severe, as in the North Central States, sex organs are usually produced in the spring, development of sporophytes continues until late in the autumn, and spores are shed the following spring or summer. In areas of the United States with a rainy winter and a long dry summer, as in California, development of sex organs begins late in autumn after start of the rainy season and the sporophytes mature and shed their spores early in the spring before the dry season begins.

Antheridia develop from superficial cells close to the apical cell. The

[1] Cavers, 1903; Goebel, 1930.

first evidence of antheridial development is a protrusion of a superficial cell somewhat above adjoining ones. This **antheridial initial** soon divides transversely into a **basal cell,** which lies embedded in the thallus, and an **outer cell,** which projects above the thallus (Fig. 41*A*). Transverse division of the outer cell results in a **primary antheridial cell** and a **primary stalk cell** (Fig. 41*B*). In most cases the primary stalk cell develops into a stalk two cells in diameter and several cells in height, but there are genera in which the stalk is a single file of four to eight cells in height.

The primary antheridial cell divides vertically into two daughter cells of equal size. Each of the daughter cells also divides vertically but in a plane diagonal to that of the first division (Fig. 41*D*). In each pair of unequal-sized daughter cells, one is a **jacket initial** which contributes only to the jacket layer of the antheridium; the other is a cell which divides periclinally into an outer cell, a **jacket initial,** and an inner cell, a **primary androgonial cell** (Fig. 41*C*, *E*). At this stage of development, best seen in vertical view, the body of an antheridium consists of two primary androgonial cells enclosed by four jacket initials.

The foregoing sequence in early stages of antheridial development has been found in all investigated species of Jungermanniales, but atypical individuals are sometimes present in which there is a different sequence of development. Instances have been recorded[1] where antheridia have the same sequence of development as in *Calobryum* (page 80) and in which the primary antheridial cell, by successive vertical divisions, gives rise to three jacket initials surrounding a single primary androgonial cell.[1] Cases have also been reported where development is as in the Marchantiales where the primary antheridial cell divides into four daughter cells, each of which divides periclinally into a jacket initial and a primary androgonial cell. Possibly the Jungermanniales do have such a marchantiaceous type of antheridial development, but it has also been held[2] that the reported cases are due to a misinterpretation of typical jungermanniaceous antheridia.

Successive division and redivision of the two primary androgonial cells (Fig. 41*F–H*) eventually result in the formation of the **androcyte mother cells,** each of which divides diagonally into two **androcytes.** Computations based upon measurements of antheridia of *Fossombronia*[2] show that there are 12 cell generations from the primary androgonial cells to the androcytes. If all the androgonial cells divide every time, this would result in 9,792 androcytes. Division of the androgonial tissue is accompanied by division and redivision of the jacket initials, and the combined result of the two is the globose antheridium characteristics of the Jungermanniales (Fig. 41*G*). Metamorphosis of androcytes into antherozoids is much the same as in other bryophytes, and the blepharoplast does not

[1] Hutchison, 1915. [2] Chalaud, 1929–1931.

appear until the androcyte mother cell stage. Mature antherozoids are biflagellate, and several genera have been shown to have the flagella ununequal in length and attached to different parts of the body of the antherozoid.[1]

Cells in the jacket of a mature antheridium are strongly hygroscopic and have a marked tendency to separate from one another when moistened. Separation of jacket cells begins at the apex of an antheridium and is due to an outward curvature immediately after they are wetted. The exposed mass of antherozoids emerges from the antheridium as a cloud-like mass in the surrounding water, and within a short time the antherozoids begin to move freely in all directions. Several of the Marchantiales are known to have an explosive discharge of the antherozoids into the air, but this has not been observed in any of the leafy liverworts.[2]

Archegonia may be borne on lateral branches or on the main axis. The initials giving rise to archegonia almost always lie close to an apical cell; in the suborder *Jungermannineae* the apical cell itself also develops into an archegonium. Genera with the apical cell developing into an archegonium always have the archegonia terminal in position; those which do not have the apical cell developing into an archegonium may have the archegonia coming to lie some distance back from the growing point by the time they are fully mature. Some of the thallose genera and practically all the foliose genera have the group of archegonia surrounded by one or another type of protective structure.

Development of the archegonium up to the stage where three **peripheral cells** surround a **primary axial cell** is identical with that of the Marchantiales and of other orders (Fig. 42*A–C*). During subsequent development, vertical divisions are restricted to two of the three peripheral cells, probably the first two formed. As a result the jacket layer surrounding the primary axial cell in Jungermanniales is composed of five **jacket initials,** instead of six as in the Marchantiales. Transverse division of each of the jacket initials results in the differentiation of five **neck initials** and five **venter initials** (Fig. 42*D*). In most cases division of the neck initials and their daughter cells is only in a transverse plane, so that the neck of the archegonium is composed of five rows of cells (Fig. 42*J*). Occasionally there may be a vertical division at an early or a late stage in neck development that results in the entire neck, or only the lower portion of it, containing more than five vertical rows of cells. The venter developing from the five venter initials is usually only slightly greater in diameter than the base of the neck. Archegonia of the Jungermanniales also differ from those of other Hepaticae in that previous to fertilization there is often a peri-

[1] Showalter, 1926; Steil, 1923.

[2] Campbell, 1918; Chalaud, 1929–1931; Horne, 1909; Humphrey, 1906; Showalter, 1926.

clinal division of all venter cells, and sometimes the lower neck cells, to form a tissue of two or more cells in thickness (Fig. 42*K*).

As in other liverworts, the primary axial cell divides transversely into a **primary cover cell** and a **central cell** (Fig. 42*D*); after which the central cell divides transversely into a **primary canal cell** and a **primary venter cell** (Fig. 42*E*). The extent to which the primary neck canal cell divides and redivides is much more variable in Jungermanniales than in other Hepaticae. According to the genus concerned, there may be a formation of 4, 8, or 16 neck canal cells; or the number may vary from individual to individual in a given species. All species investigated have a division of the primary venter cell into a **venter canal cell** and an **egg cell,** but there is great variation from genus to genus both in the time at which this division takes place and in the time at which the venter canal cell degenerates (Fig. 42*I–J*). The primary cover cell generally divides to form a cover composed of four cells quite similar in appearance to neck cells. Dehiscence of an archegonium is usually effected by a spreading apart and folding back of the cover cells, but it may be due to an internally developed hydrostatic pressure. Dehiscence due to hydrostatic pressure causes a bursting of the cover cells, or neck cells immediately beneath them.[1]

Entrance of antherozoids into archegonia is undoubtedly in response to chemotactic stimuli, but specific chemical compounds exerting such stimuli have not been determined as they have for Marchantiales (page 52). However, contrary to general opinion, it has been shown[1] that the seat of the chemotactic stimulation is not in the gelatinous slime resulting from disintegration of the neck canal cells.

Antherozoids entering the venter of an archegonium soon penetrate the egg.[2] After penetrating it, they may move immediately to the egg nucleus and become applied to it, or they may remain in the peripheral portion of the cytoplasm of the egg for some time.[3] Fusion of male and female nuclei takes place 24 to 48 hours after the entrance of the antherozoid. **Polyspermy,** the entrance of more than one antherozoid into an egg, is a common phenomenon, but there is rarely a fusion of more than one male nucleus with that of the egg.

The first division of the zygote is transverse and into an upper (**epibasal**) and a lower (**hypobasal**) cell. For certain genera (*Fossombronia*,[2] *Frullania*[4]) it has been shown that the epibasal cell also divides transversely; and that the upper, median, and lower cell of the resultant three-celled embryo develop, respectively, into capsule, seta, and foot of the mature sporophyte. Other genera have been shown to have the hypobasal cell developing into a haustorium and the entire mature sporophyte

[1] Showalter, 1928. [2] Showalter, 1926*A*, 1927, 1927*A*.
[2] Chalaud, 1929–1931. [4] Campbell, 1918.

coming from the epibasal cell (*Riccardia*,[1] *Pallavicinia*,[2] *Symphyogyna*,[3] *Treubia*[4]).

There are no essential differences between foot and seta of mature sporophytes of Jungermanniales and those of sporophytes of other Hepaticae, but the capsules differ in several respects. Capsules of Jungermanniales have a jacket layer either two, three, four, or more cells in thickness. There is always a sclerification of cells in the jacket layer, and most genera have the mature capsule dehiscing into four valves at the time when the spores are shed. All genera have a differentiation of the sporogenous tissue into elaters and spore mother cells, and in many genera the elaters are radially oriented either to the base or to the apex of a capsule. The orientation may be centered around a columella-like mass of sterile cells (**elaterophore**), or an elaterophore may be lacking. Another distinctive feature of the sporophyte, although not exclusively restricted to those of the Jungermanniales, is the quadripartition of the sporocytes to form the spores.

There is so much variation from genus to genus in the method of spore germination that no one method may be considered typical for the Jungermanniales. In one genus (*Pellia*) the spore develops into a six- to nine-celled gametophyte while still within the capsule, but this is not of particular significance since the same precocious germination is also found in one of the Marchantiales. Germinating spores of Jungermanniales may immediately develop into a massive gametophyte, or the first-formed portion may be distinctly protonema-like in structure. Thallose genera usually have the germinating spore developing immediately into a thallose structure, but sometimes[5] there is a small protonemal stage. When the germling is thallose from the beginning, there is an early differentiation of the apical cell, and this may even be recognizable as early as the three-celled stage (*Riccardia*).[6] Germlings of foliose genera usually undergo considerable development before the appearance of a definite organization into stem and leaves. The juvenile phase may be protonemal at first and then thallose (*Fossombronia*),[7] or it may be thallose from the beginning. In certain tropical foliose genera the juvenile phase constitutes the dominant portion of the gametophyte generation, and the adult phase is found only in the erect leafy branches producing the sex organs. The permanent juvenile phases of this type may be thallose structures,[6] or they may be protonemal.[8]

When the Haplomitriaceae (Calobryaceae) are removed from the order, the Jungermanniales fall into two distinct series: the **anacrogynous** series in which the apical cell of a gametophyte does not develop into an archegonium at the time sex organs are formed, and the **acrogynous** series in

[1] Clapp, 1912. [2] Campbell and Williams, 1914.
[3] McCormick, 1914. [4] Campbell, 1916. [5] Goebel, 1889.
[6] Showalter, 1925. [7] Chalaud, 1929–1931. [8] Spruce, 1884.

which the apical cell of a branch or the main stem develops into an archegonium and thus checks further growth. Some bryologists think that this difference, together with certain other differences, justifies segregation of the two series into separate orders. However, since both series have the same distinctive ontogeny of antheridia and archegonia, and have the same unique type of sporophyte, it seems more logical to follow those who place the two as suborders of the same order.

The suborder *Metzgerineae*, to which the anacrogynous forms are referred, has both thallose gametophytes and those with a stem bearing two lateral rows of leaves. The suborder *Jungermannineae*, to which the acrogynous forms are referred, has leafy gametophytes in which the great majority have three rows of leaves along the stem.

The relationship between the two suborders is a matter of dispute. Some hepaticologists[1] derive the Jungermannineae from the Metzgerineae and think that such anacrogynous genera as *Treubia* and *Fossombronia* (Fig. 40) lie on the road leading to the acrogynous series. Others[2] read the series the opposite way and hold that the foliose acrogynous forms gave rise to anacrogynous forms by condensation of leaves and stem, and by a shifting of the terminal cluster of archegonia to the dorsal side. As will be shown on a later page (page 74) there is evidence showing that certain foliose Jungermannineae have evolved toward a thallose condition. However, it does not necessarily follow that this leads to the thallose anacrogynou series. Certain fundamental differences in structure of apical cells of the two, and in the method by which segments formed by them develop into stem and leaves, seem to show that there is a considerable gap between present-day members of the two series. Thus, instead of being derived one from the other, it is equally possible that the two represent divergent evolutionary lines from an unknown ancestral type.

Suborder 1. Metzgerineae

Members of this suborder do not have the apical cells developing into archegonia at the time sex organs are formed. Because of this, mature sporophytes lie some distance back from the growing apex of a gametophyte. The suborder includes certain thallose genera in which the mature sporophytes are borne terminally, but among them the apical cell does not develop into an archegonium. Sex organs are borne laterally and on the dorsal face of a thallus. They may be produced on any branch of the gametophyte or only on special branches. The suborder includes about 20 genera and 500 species.

Some genera, as *Riccardia* (Fig. 36), have strictly thallose gametophytes. Other genera, as *Fossombronia* (Fig. 40), have species with game-

[1] Campbell, 1918; Cavers, 1910. [2] Evans, 1939; Harris, 1938; Kashyap, 1919.

tophytes differentiated into stem and lateral leaves. Gametophytes of most Metzgerineae are without internal differentiation of tissues, but certain genera have a central strand composed of axially elongate thick-walled cells with simple pits in the walls. For one such genus there has been an experimental demonstration[1] that this central strand functions as a water-conducting tissue. The ventral surface of a gametophyte, or the entire surface of rhizome-like portions, bears smooth-walled rhizoids. Superficial ventral cells near the apex may also bear uni- or multicellular mucilage hairs. These overarch and protect the apical region in much the same manner as do the ventral scales of Marchantiales. Growth of a gametophyte is initiated by a single apical cell. In some genera it has two lateral cutting faces alternately producing segments right and left. In other genera the apical cell has four cutting faces.

The older systems of classification[2] grouped anacrogynous genera (Metzgerineae) into two or into three families. More recent systems recognize six[3] or seven[4] families.

Of the two genera described below one (*Riccardia*) has a thallose gametophyte; the other (*Fossombronia*) has the gametophyte differentiated into stem and leaves.

Riccardia (*Aneura*), a genus of over 250 species, has gametophytes that are wholly thallose or have thallose terminal branches. The thallus is dichotomously branched, but unequal growth of dichotomies results in a gametophyte in which the branches seem to be lateral appendages.[5] A gametophyte may be wholly prostrate or partially prostrate and partially erect. Species with wholly prostrate gametophytes, among which *R. pinguis* (L.) S. F. Gray (Fig. 36) is the commonest in the United States, rarely have a differentiation into a midrib and lateral wings. Species with partially erect gametophytes, as *R. thaxteri* Evans,[5] have the prostrate portion rounded and the erect branches with a well-defined midrib bearing lateral wings one cell in thickness. *R. pinguis* and related species have no internal differentiation of tissues; several of the partially erect species have a well-defined system of elongate thick-walled cells. There is also a division of function in gametophytes of the latter type, the ultimate

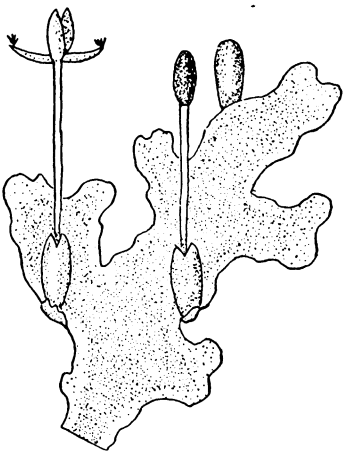

FIG. 36. *Riccardia pinguis* (L.) Gray. Gametophyte and mature sporophyte.

[1] Tansley and Chick, 1901. [2] Cavers, 1910; Schiffner, 1893–1895.
[3] Verdoorn, 1932. [4] Evans, 1939. [5] Evans, 1921.

branches being photosynthetic organs and the main axis a mechanical or conducting organ. The ventral surface of a thallus bears smooth-walled rhizoids and mucilage hairs. Young rhizoids may contain chloroplasts; old rhizoids lack them.

Riccardia has a wedge-shaped apical cell with two cutting faces which alternately form primary segments right and left.[1] The apical cell lies in a depression at the anterior end of a branch and each depression usually contains two or more apical cells. Primary segments from an apical cell divide in the same manner as a two-faced apical cell; but one which cuts off segments above and below, not right and left. Now and then a segment from an apical cell cuts off three or four derivatives above and below, and then begins to function as a true apical cell cutting off segments right and left. This is the beginning of a dichotomy of a branch.

Gametophytes multiply vegetatively by progressive growth and death. Vegetative multiplication is also by means of two-celled reproductive bodies within any superficial cell of a thallus. A cell producing one of these bodies has a rounding up of its protoplast and a secretion of an entirely new wall around the protoplast, followed by a division into two daughter cells firmly united to each other. The two-celled body thus formed is liberated by a gelatinization of the original cell wall. The two-celled structures, peculiar to *Riccardia*, are frequently called "endogenous gemmae," but they have much more in common with aplanospores of Chlorophyceae than with gemmae of other Hepaticae.

Species of *Riccardia* may be heterothallic or homothallic, but in either case the sex organs are borne on short lateral branches. In some species the sex organs are borne along the entire length of a branch; in other species they are restricted to the terminal portion.

Successive segments cut off by an apical cell may develop into antheridia, and in most species these lie in a double row on the dorsal side of a branch. In *R. pinguis* the antheridia lie in three or four irregular rows because of displacement during later growth stages. Development of an antheridium[2] is according to the type characteristic of Jungermanniales (see page 58). The stalk of a mature antheridium differs from that in most members of the order in being but two or three cells in length. Unlike most other Metzgerineae, but similar to most Marchantiales, upward growth of adjoining vegetative cells keeps pace with development of an antheridium, and results in a sunken antheridial chamber connected with the thallus surface by a narrow canal (Fig. 37*A*).

Archegonial branches are generally shorter than those bearing antheridia. Each successive segment cut off by the apical cell develops into an archegonium, but the arrangement of mature archegonia is much more irregular than that of antheridia. Development of archegonia is according

[1] Clapp, 1912; Showalter, 1923. [2] Clapp, 1912; Florin, 1922.

to the manner characteristic of Jungermanniales.[1] Typically there is a formation of five vertical rows of neck cells and a formation of four to six neck canal cells. One minor distinctive feature is the very early division of primary venter cell into egg and venter canal cell (Fig. 37*B*). There is also a precocious periclinal division of jacket cells so that mature archegonia have a neck two cells in thickness and a venter two or three cells in thickness. This results in a massive archegonium and one with little external differentiation into neck and venter (Fig. 37*C*).

Fertilization takes place in the usual manner.[2] Division of the zygote is transverse (Fig. 38*A*). The hypobasal cell immediately starts elongating

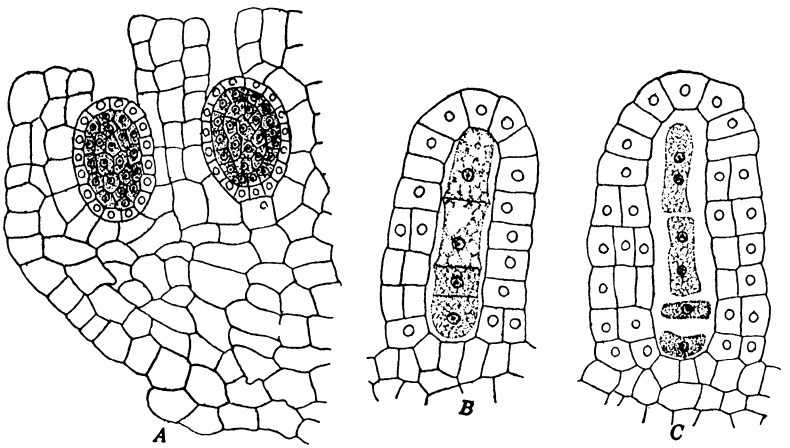

FIG. 37. *Riccardia pinguis* (L.) Gray. *A*, vertical section of antheridia within antheridial chambers. *B–C*, stages in development of archegonia. (*A*, × 120; *B–C*, × 325.)

into a haustorium that grows deeper and deeper into gametophytic tissues below the archegonium.[3] In many cases there is no division of the haustorial cell (Fig. 38*B–E*.) The epibasal cell divides transversely and the upper daughter cell soon divides transversely. These three superimposed cells develop, respectively, into foot, seta, and capsule of the mature sporophyte. The cells developing into foot and seta first undergo two successive vertical divisions, after which there are vertical and transverse divisions in an irregular sequence (Fig. 38*D–E*). The cell developing into the capsule also undergoes two successive vertical divisions and then the four cells thus formed each divide transversely. Each cell in the resultant two four-celled tiers divides periclinally into an archesporial (primary sporogenous) cell and a jacket initial cell (Fig. 38*E–F*). Divisions of sporogenous cells are in an irregular sequence, but rather early there is a

[1] Clapp, 1912; Florin, 1922; Showalter, 1923.
[2] Showalter, 1926*A*, 1928. [3] Clapp, 1912; Florin, 1922.

differentiation of an apical mass of somewhat larger cells, the future **elaterophore** (Fig. 38*F*). Sporogenous cells not developing into the elaterophore eventually give rise to sporocytes and elaters. Jacket cells divide anticlinally two or three times, after which each cell divides periclinally

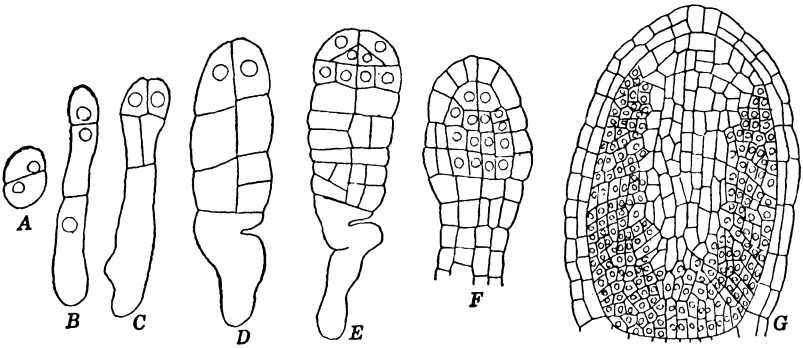

FIG. 38. *Riccardia pinguis* (L.) Gray. *A–D*, early stages in development of embryo. *E*, just after differentiation of jacket layer and sporogenous tissue in capsule of the sporophyte. *F*, a somewhat older capsule. *G*, after differentiation of elaterophore from sporogenous tissue. (*After Clapp*, 1912.) (*A–F*, × 520; *G*, × 260.)

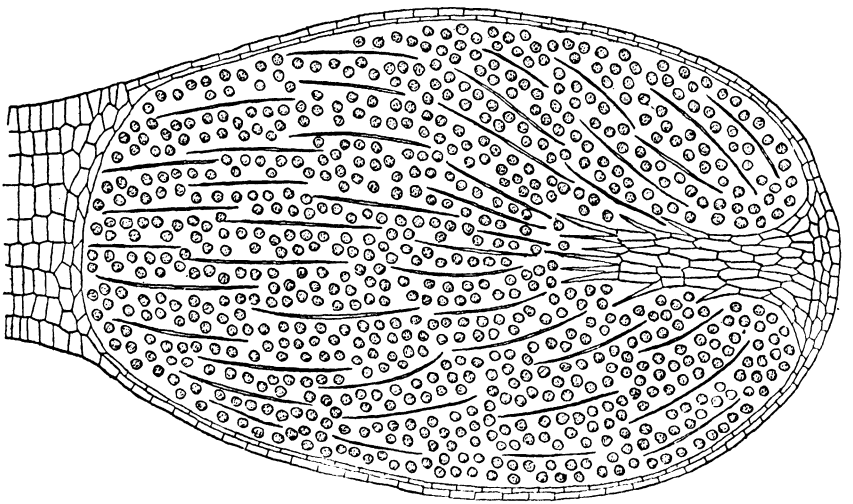

FIG. 39. *Riccardia pinguis* (L.) Gray. Longitudinal section of a nearly mature capsule. (Semidiagrammatic.) (× 70.)

(Fig. 38*F–G*). This results in a jacket layer which remains two cells in thickness throughout further development of the capsule (Fig. 39). Later in development of the jacket layer there is a considerable thickening of the cell walls, except in four vertical strips of cells—the future lines of dehiscence of the mature capsule.

For a considerable time a developing sporophyte is surrounded by a massive sheath of gametophytic tissue. The apical portion of this sheath is derived from the venter of the archegonium; the major portion of it is derived from vegetative portions of the female branch immediately below the archegonium. Thus the conventional practice of calling the sheath a calyptra is inaccurate. Eventually, by an elongation of the seta, the capsule is pushed through for a considerable distance above the "calyptra" and the capsule dehisces (Fig. 36). Dehiscence begins at the apex of a capsule and the four parts (valves) into which it divides, each with a portion of the elaterophore, bend back with a jerk. This expels the spores and elaters in a catapult-like manner.

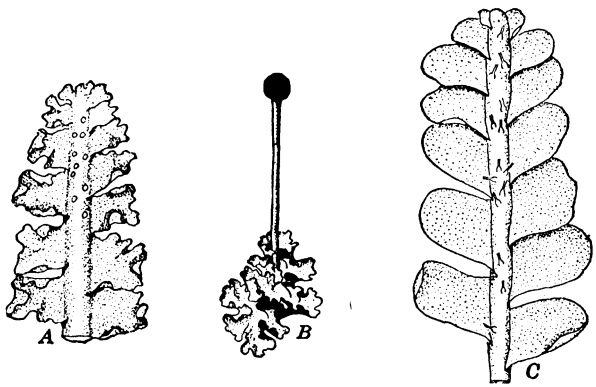

FIG. 40. *A–B, Fossombronia longiseta* Austin. *A*, male gametophyte. *B*, female gametophyte with a mature sporophyte. *C, F. intestinealis* Taylor, female gametophyte with archegonia. (*C, after an unpublished drawing by F. Stephani.*)

Spores germinate immediately after they are shed and by a transverse division into two daughter cells of unequal size.[1] The larger daughter cell rarely divides again; the smaller daughter cell divides by a diagonally vertical wall and thus differentiates a wedge-shaped apical cell which begins to function immediately. Rhizoids appear quite early on the germling and are borne toward the posterior end of it.

Fossombronia, a widely distributed genus with some 50 species, is representative of the genera in which the gametophyte is foliose. The thallus is almost wholly prostrate and with a sparse or profuse branching. A branch consists of a well-defined stem portion which bears a single row of leaves along both lateral margins. In some species it is clearly evident that leaves near the growing apex are vertically inserted and that those farther back lie so that the posterior margin of each leaf overlaps the anterior margin of the next older leaf (Fig. 40*C*). In other species the leaves are so greatly convoluted that this arrangement is obscure (Fig. 40*A*). The basal portion

[1] Showalter, 1925.

of a leaf is two or three cells in thickness; elsewhere it is but one cell in thickness. The stem is a fairly massive structure, but one without any indication of internal differentiation. Smooth-walled rhizoids are borne along the ventral face of the stem. Near the apex there are also multicellular mucilage hairs which overarch and protect the apical region, but these are not present on older parts of the stem.

Growth of the main axis and of its branches is by means of an apical cell with two cutting faces that alternately cut off segments right and left. As seen in vertical longitudinal section an apical cell is semicircular in outline; as seen in horizontal longitudinal section it is narrowly triangular.

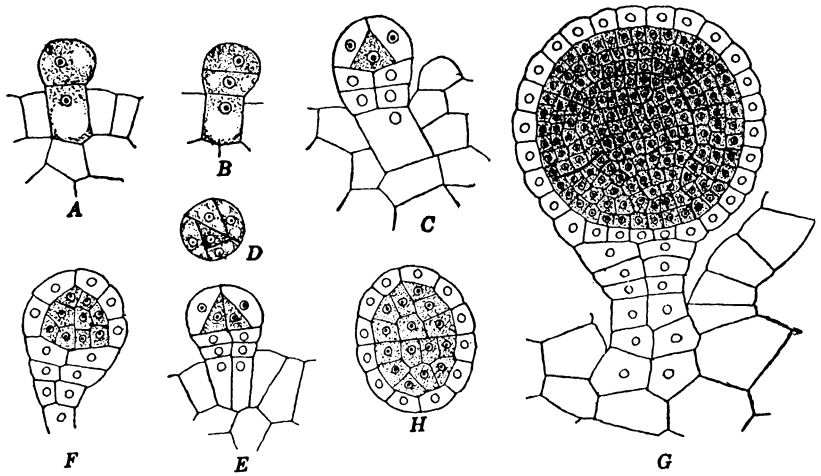

FIG. 41. *Fossombronia angulosa* (Dicks.) Raddi. Stages in development of antheridia. (× 325.)

The first division in a segment cut off by an apical cell is in a horizontal plane. The ventral daughter cell gives rise to the ventral portion of the stem. The dorsal daughter cell gives rise to the dorsal portion of the stem and to a leaf. Division of this cell is also horizontal, the upper daughter cell being the initial of a dorsal portion of the stem and the lower daughter cell functioning as the initial cell of a leaf.[1] Unlike most other Metzgerineae, branching is not initiated by a vertical division of the apical cell into two cells of equal size. Instead, there is a differentiation of a second apical cell in a very young segment derived from the apical cell. Combined growth from the original apical cell and the newly formed one bring about what appears to be a true dichotomy, but what is really a false dichotomy.

[1] Chalaud, 1929–1931.

Development of antheridia (Fig. 41) is according to the manner typical of Jungermanniales[1] (see page 58). An antheridium bursts suddenly when it is mature, but this is not accompanied by an explosive discharge of the antherozoids. The antherozoids are relatively large and have the two flagella inserted at different points near the anterior end.[2] The development of archegonia is also in the manner typical for the order (Fig. 42). A mature archegonium has six to eight neck canal cells surrounded by five vertical rows of neck cells. The venter of an archegonium is only slightly broader than the neck and has a jacket layer two cells in thickness.

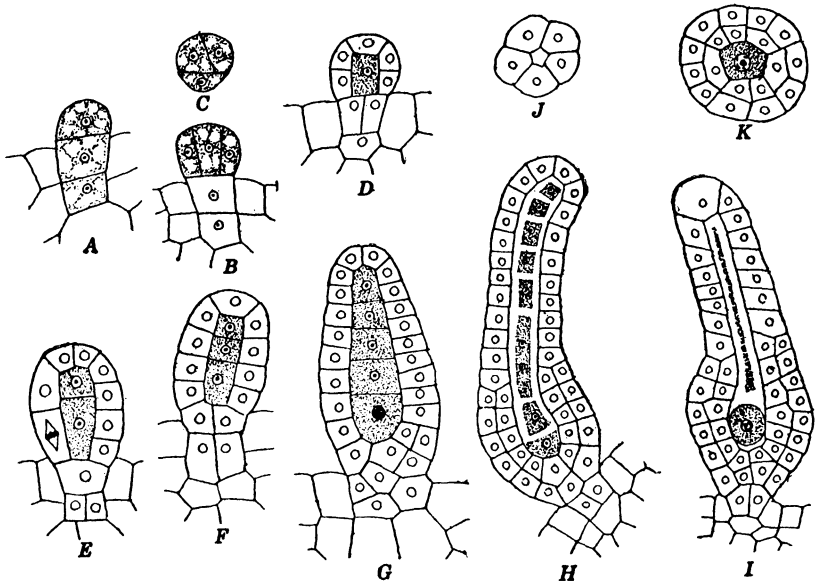

FIG. 42. *Fossombronia angulosa* (Dicks.) Raddi. Stages in development of archegonia. (*A–B*, *D–I*, in vertical section; *C*, *J–K*, in transverse section.) (*A–G*, × 325; *H–K*, × 215.)

Fertilization[3] is effected in the usual manner and division of the zygote takes place six to nine days after gametic union. Division of the zygote is always transverse and the epibasal cell is somewhat larger than the hypobasal cell (Fig. 43*A*). The hypobasal cell eventually develops into the foot of a mature sporophyte. Division of the epibasal cell is usually transverse, the upper daughter cell eventually developing into the capsule and the lower daughter cell into the seta of a mature sporophyte[4] (Fig. 43*B–E*). However, in exceptional individuals there may be a vertical division of epibasal and hypobasal cells and then a transverse division of their daughter cells.[3] The periclinal divisions differentiating the jacket layer

[1] Chalaud, 1929–1931; Haupt, 1920, 1929*A*. [2] Showalter, 1926.
[3] Showalter, 1927. [4] Chalaud, 1929–1931.

(amphithecium) and archesporium (endothecium) of the capsule occur quite early. Soon afterward the jacket layer becomes two cells in thickness, and there may be further periclinal divisions in the apical portion of the jacket. The archesporium develops into a sporogenous tissue of many cells. Differentiation into elaters and sporocytes does not take place until the last cell generation of the sporogenous tissues. Thus elaters are homologous with sporocytes instead of being homologous with rows of sporocytes as is usually the case. Elaters of *Fossombronia* are unusual in that thickenings on their walls may be laid down in five to nine rings instead of the usual two or three longitudinal spirals. An elaterophore, when present in *Fossombronia*, is a very indistinct structure.

The young sporophyte is surrounded by a calyptra (the old archegonium) and this, in turn, is ensheathed by a cup-like **involucre** produced

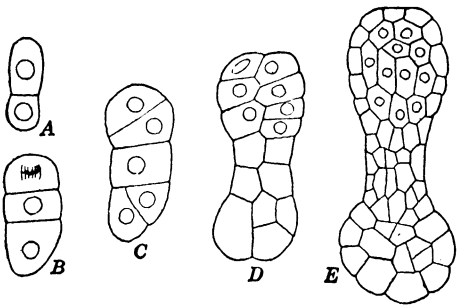

FIG. 43. *Fossombronia pusilla* Dum. Early stages in development of embryo. (*After Chalaud*, 1929–1931.)

by upgrowth of gametophytic tissue adjacent to the base of the archegonium. The seta of a sporophyte remains about a millimeter in length until the spores are mature. Then it elongates rapidly and pushes the capsule through the calyptra to a considerable distance above the perianth (Fig. 40*B*). In *F. pusilla* Dum. the elongating seta lengthens at the rate of about a millimeter for six or seven days, and the capsule dehisces 18 to 36 hours after elongation is completed.[1] According to the species, a capsule dehisces into four valves or dehisces irregularly.

Germination of a spore results in a filamentous protonema of 2 to 12 cells in which those nearest the old spore wall often bear rhizoids. Termination of the protonematal phase is marked by the distal cell dividing irregularly into a globose mass of cells, one of which soon begins to function as an apical cell with two cutting faces.[1] For some time the segments cut off by the apical cell develop into a distinctly thallose structure without any differentiation into stem and leaves. Portions of the thallus formed somewhat later have each derivative cut off by the apical cell differentiation into a leaf and a portion of the stem.

[1] Chalaud, 1929–1931.

Suborder 2. Jungermannineae

Gametophytes of Jungermannineae are always foliose and with the leaves borne in a regular spiral succession along the stem. Archegonia are always restricted to the apices of the stem and its branches, and the last-formed archegonium is developed from the apical cell itself. Because of this acrogynous formation of archegonia, the sporophytes are always terminal in position. Antheridia are borne singly or in small numbers in the axils of leaves. There are some 180 genera and 7,500 species.

With one exception (*Pleurozia*[1]), all members of the suborder have a pyramidal apical cell with three lateral cutting faces. An apical cell lies with one cutting face toward the ventral side of a thallus, and two cutting

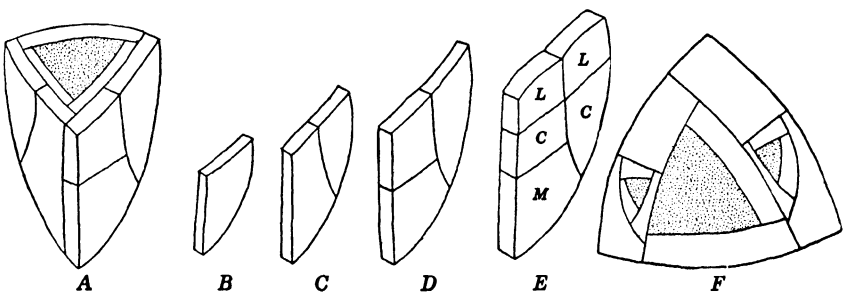

Fig. 44. *A*, stereodiagram of the thallus apex of Jungermannineae showing the apical cell and early stages in development of merophytes. *B–E*, stereodiagrams of development of a segment from an apical cell into a five-celled merophyte in which two cells (*L,L*) ultimately produce the leaf, two cells (*C,C*) ultimately produce the cortical portion, and one cell (*M*) ultimately produces the medullary portion of the mature merophyte. *F*, diagram of a transverse section of a stem apex showing formation of apical cell of lateral branches by one of the two leaf initial cells of a merophyte.

faces toward the dorsal side. Derivatives are cut off in a regular spiral succession from the three cutting faces of an apical cell, but these may be cut off in a clockwise or counterclockwise sequence. In the majority of genera the leaves are borne spirally and in three vertical rows because each derivative produced on both ventral and dorsal faces on an apical cell ultimately gives rise to a single leaf and to the portion of the stem subtending it. The leaf and the underlying portion of the stem produced by a single derivative from an apical cell jointly constitute a **merophyte.** Early cell divisions in development of an apical cell derivative into a merophyte are all perpendicular to the flat surface of the derivative. A derivative divides asymmetrically into two daughter cells, one about double the size of the other.[2] There is next a division of the larger daughter cell. The merophyte now consists of three cells of approximately the same size, and so arranged that two lie toward its free face. Next, the two cells toward

[1] Goebel, 1893. [2] Evans, 1912.

the free face divide in a plane parallel to the free face. The developing merophyte now consists of five cells, and the various parts of the mature merophyte are derived from specific cells of the five-celled merophyte. The two outermost cells jointly give rise to the leaf; the two cells below them give rise to the cortical region of the stem portion; and the innermost cell gives rise to the medullary region of the stem portion (Fig. 44*A–E*).

Leaves produced by merophytes on the dorsal face of the thallus are **lateral leaves,** and those produced by merophytes in the ventral face are **under leaves.** In rare cases, both lateral and under leaves are approximately the same size and shape (Fig. 46*D*), but in most cases the under leaves are of smaller size than lateral leaves, and different in shape (Fig. 45). All leaves are transversely inserted when first formed. Under leaves

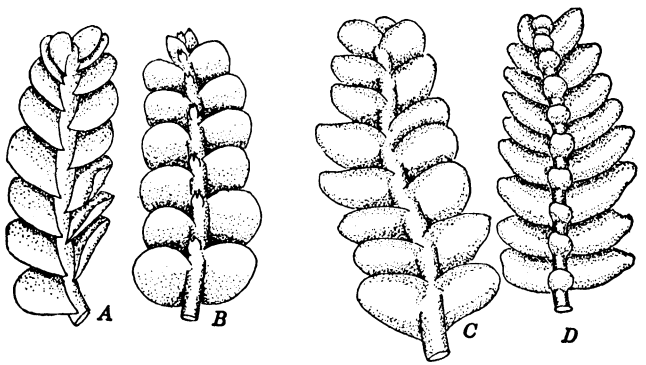

FIG. 45. *A–B*, dorsal and ventral views of succubous leaves of *Chiloscyphus rivularis* (Schrad.) Loeske. *C–D*, dorsal and ventral views of incubous leaves of *Calypogeia neesiana* (Mass. and Carr.) Müll. (*After Steere*, 1940.) (*A–B*, × 2½; *C–D*, × 3½.)

remain so, but lateral leaves become more or less diagonal in insertion as a result of unequal elongation of dorsal and ventral sides of the stem. Greater elongation of the dorsal side results in a **succubous** arrangement of lateral leaves, and one in which the posterior margin of each leaf **overlies** the next older leaf (Fig. 45*A–B*). Greater elongation of the ventral side of the stem results in an **incubous** arrangement of lateral leaves and one in which the posterior margin **underlies** the next older leaf (Fig. 45*C–D*). Arrangement of lateral leaves may be compared to the manner in which shingles may be laid on a roof. When laid with the thick end toward the eaves, shingles lie succubously and the water runs off; when laid with the thick end away from the eaves shingles lie *in*cubously and the water runs *in*.

Capillary conduction of water along the surface of a gametophyte is an important factor in distribution of water to all parts of it, and it has been shown experimentally[1] that arrangement of lateral leaves affects the rate

[1] Clee, 1937.

of movement. Upward movement of water is much more rapid in succubous than in incubous forms; whereas downward movement is more rapid in incubous than in succubous forms. This correlates to a certain extent with the natural habitat of gametophytes. Succubous forms tend to grow where there is an abundance of ground or surface water which would be supplied from below. Incubous forms tend to grow where the

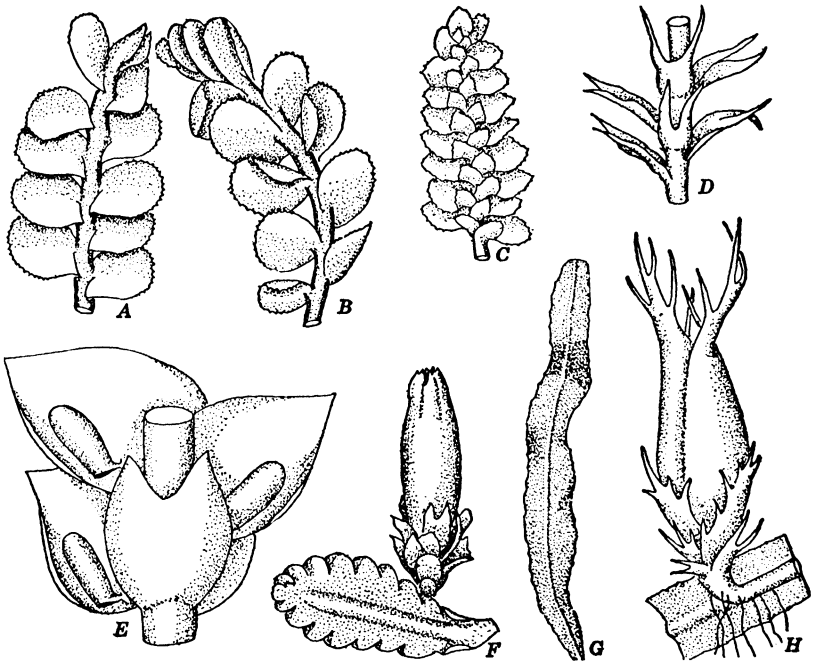

FIG. 46. *A–B*, dorsal and ventral views of *Plagiochila asplenioides* (L.) Dum., a species without under leaves. *C*, dorsal view of *Scapina nemorosa* (L.) Dum. *D*, ventral view of *Herbertia adunca* (Gray.) Lindb. *E*, ventral view of *Frullania armitiana* St., a species with water sacs on lateral leaves. *F*, dorsal view of *Schiffneria hyalina* St. *G–H*, *Pteropsiella frondiformis* Struce. *G*, dorsal view of a sterile gametophyte. *H*, ventral view of a female gametophyte with a branch bearing perichaetial bracts and a perianth. (*A–C*, *after Steere*, 1940; *D*, *after Müller*, 1912–1916; *E*, *after Verdoorn*, 1930; *F*, *after Stephani*, 1894; *G–H*, *after Spruce*, 1884.)

water comes from above, as is the case with those growing vertically on trunks of trees.

Lateral leaves of many genera have a well-marked differentiation into two lobes, one toward the dorsal side of the stem, the other toward the ventral side. This formation of two lobes is due to more or less independent growth from the two outer cells of the five-celled stage in development of a merophyte. According to the independence of their development, the two lobes are nearly free from each other or are restricted to the apex of a leaf. Among genera in which the two lobes are practically independent

of each other, the two may be of equal or unequal size. In the latter case the dorsal lobe of a lateral leaf may be smaller than the ventral lobe, or vice versa. Genera with ventral lobes larger than lateral lobes, as *Scapina* (Fig. 46*C*), seem to have four rows of lateral leaves when the gametophyte is viewed from above. A further complexity in structure of leaves is found in those whose leaves have **water sacs**—bladder-like structures where water enters by capillarity through more or less distinct openings. Only one lobe of a leaf may enter into the formation of a water sac (Fig. 46*E*), or both lobes may jointly form a sac.

In evolution within the Jungermannineae the disappearance of under leaves among forms with leaves in three rows has resulted in forms without under leaves (Fig. 46*A–B*). Evidence for this is seen in those genera where the under leaves are vestigial in nature. Further evidence is seen in those genera where vegetative portions of the gametophyte lack under leaves, whereas the more conservative fertile portions have three rows of leaves. There are also a few genera where flattening of the axis and a reduction in size of leaves have resulted in an approach to a thallose condition. Here, as in *Schiffneria* (Fig. 46*F*), the leaves may be clearly evident; or, as in *Pteropsiella* (Fig. 46*G–H*), they may have been reduced to vestigial marginal papillae. In these genera the fertile portions are much more conservative and they retain the sharp differentiation into stem and leaves so generally found in vegetative parts throughout the suborder.

As far as form of leaf is concerned, it is very probable that genera (Fig. 46*D*) with simple bifid leaves and with under leaves nearly the same size and shape as lateral leaves approach most nearly the primitive type. Evolution from such a condition has been in two directions. On the one hand are those genera where gradual obliteration of the bifid condition has resulted in simple leaves. On the other hand there are those genera where evolution has been in the opposite direction and has resulted in leaves where the lobes are dissimilar.

Branching of a gametophyte is never truly dichotomous because the apical cell never divides vertically into two apical cells which become the initials of a dichotomy.[1] Branches produced at the distal end of a stem arise from a new cell differentiated by one of the two outer cells of the five-celled stage in development of a merophyte (Fig. 44*F*). In this pair of cells the new apical cell may be formed by the cell toward the dorsal face or by the cell toward the ventral face of the gametophyte. In either case, its sister cell develops into a leaf somewhat different in appearance from other leaves. Equal growth of the axis and the new branch results in what appears to be a true dichotomy; more vigorous growth of the axis results in lateral branches along the axis. Apical cells producing lateral branches may also be differentiated from cells in mature portions of the axis.

[1] Evans, 1912, Leitgeb, 1871.

Branches developed from these apical cells are essentially adventitious in origin.

Stems and branches have little differentiation of tissues other than superficial (cortical) cells being of larger diameter than internal (medullary) cells, or vice versa. When the ventral surface of stem or branch is in contact with a substratum it may produce smooth-walled rhizoids, especially in portions just posterior to under leaves. Erect branches generally lack rhizoids.

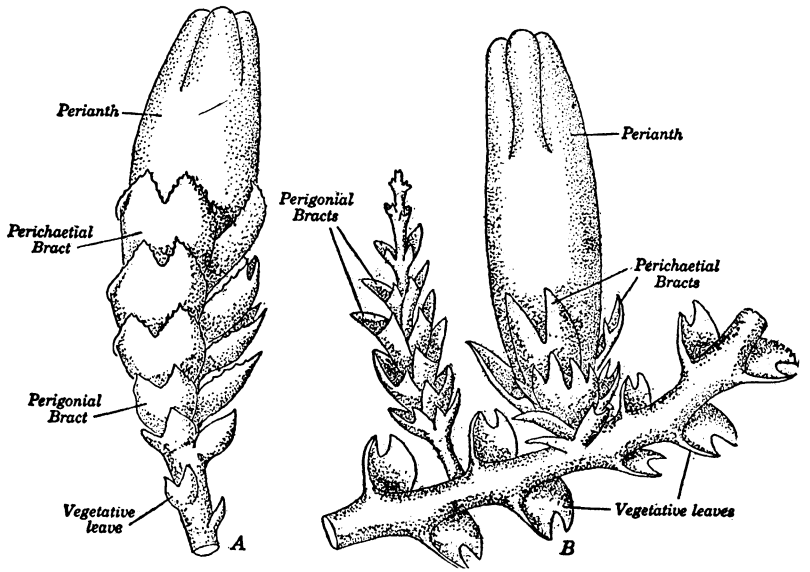

FIG. 47. *A*, *Cephaloziella rubella* (Nees) Warnst., a paroecious species. *B*, *Cephalozia pleniceps* (Aust.) Lindb., an autoecious species. (*After Schuster*, 1949.) (B, somewhat modified.)

Jungermannineae may be homothallic or heterothallic, and with sex organs borne upon major branches or restricted to special short lateral branches. Leaves associated with sex organs are called **bracts** and they usually differ in size and shape from leaves borne on vegetative portions of a gametophyte. When sex organs are restricted to special lateral branches all leaves on them are usually bracts, but when bracts are borne on a major branch they are usually restricted to its terminal portion. Bracts associated with archegonia are **perichaetial bracts.** In most genera the three or two uppermost perichaetial bracts are laterally fused to form a **perianth** surrounding the calyptra and its enclosed embryonic sporophyte. Bracts associated with antheridia are **perigonial bracts** (Fig. 47).

Homothallic species may be **autoecious** and with perichaetial and perigonial bracts borne on separate branches (Fig. 47*B*); or they may be

paroecious and with both borne on the same branch (Fig. 47*A*). Paroecious species always have the perichaetial bracts above the perigonial bracts.

In heterothallic and autoecious homothallic species the number of perigonial bracts borne in succession along a stem or branch varies from half a dozen to nearly a hundred. Antheridia develop in the axils of these bracts (Fig. 48*A–B*), and according to the genus there is a single antheridium or up to five or six antheridia in the axil. An antheridial initial seems to be a cell belonging to the stem rather than to the leaf, but these arise so close

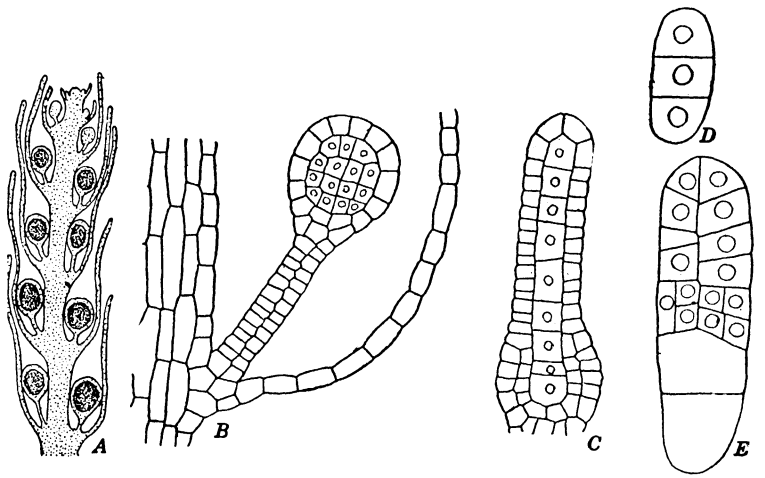

FIG. 48. *A*, *Plagiochila adiantoides* (Sw.) Dum., apex of a male gametophyte with an antheridium in the axil of each perigonial bract. *B–E*, *Porella bolanderi* (Aust.) Pears. *B*, antheridium. *C*, archegonium. *D–E*, embryos. (*A*, *after Johnson*, 1929.) (*A*, × 12; *B–E*, × 225.)

to the stem apex that the point cannot be determined with certainty. Development of the antheridial initial into an antheridium is in the manner typical of Jungermanniales and with the usual differentiation of two primary androgonial cells.[1] Mature antheridia are globose and with a long stalk. In some genera the stalk consists of a single row of cells; in other genera it consists of a double row of cells (Fig. 48*B*); and in still other genera it consists of four vertical rows of cells.

Archegonia are produced at the apex of a branch and with only the apical cell of the branch functioning as the archegonial initial, or both it and the last segments cut off may be archegonial initials. Development of archegonia is the same as in the Metzgerineae, and with a formation of five rows of neck cells.[1] Most Jungermannineae have the venter and lower por-

[1] Campbell, 1918; Johnson, 1929; Manning, 1914.

tion of the neck becoming two cells in thickness before fertilization (Fig. 48*C*).

Division of the zygote is transverse. Some genera, including *Porella* (Fig. 48*D–E*), have the hypobasal cell developing into a small haustorium of two or more cells, and have the mature sporophyte developing entirely from the epibasal cell. In other genera both the epibasal and hypobasal cells contribute to the mature sporophyte.[1]

Capsules of mature sporophytes are usually globose and with a jacket layer two to six cells in thickness (Fig. 49). Sporogenous tissue of a capsule usually has a differentiation of elaters several cell generations before the divisions forming the sporocytes. The orientation of elater-producing cells

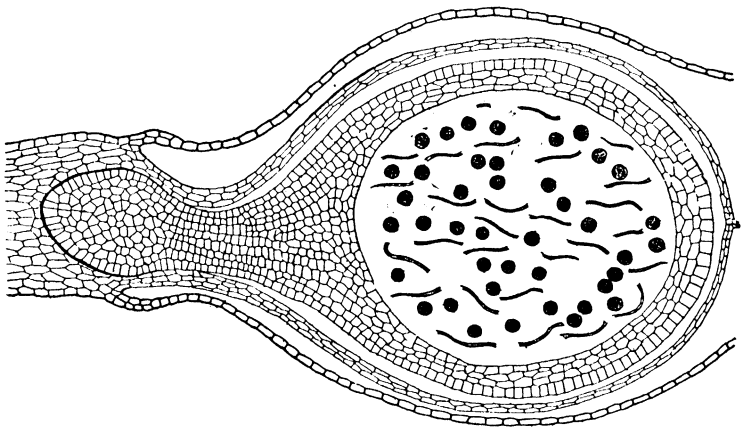

FIG. 49. *Porella bolanderi* (Aust.) Pears. Longitudinal section through a nearly mature sporophyte. (× 45.)

with respect to other sporogenous cells is not the same throughout the suborder. Usually the two do not have a definite orientation with respect to each other but elater-producing and sporocyte-producing cells may lie in vertical series as in *Frullania*[2] or in horizontal series as in *Cephalozia*.[3]

The venter of the archegonium develops into a calyptra that surrounds the sporophyte until it is nearly mature. In addition to being enclosed by a calyptra the sporophyte is also ensheathed by other protective structures. Usually this is a perianth resulting from the fusion of the three (or two) uppermost perichaetial bracts. The apical portion of the branch may also develop into ensheathing structures.[4] This may be only the receptacular portion of the stem apex (Fig. 50*B–C*), or it may include bract-bearing portions of the stem apex (Fig. 50*D*). Such sac-like envelopes produced by an upgrowth of the margin of the stem are often called

[1] Cavers, 1910; Ellwein, 1926. [2] Cavers, 1910.
[3] Goebel, 1927. [4] Knapp, 1930.

marsupia. The most striking of all marsupia are those which come to lie at right angles to the long axis of the gametophyte or become bent back upon the stem apex (Fig. 50*E*). The older hepaticologists grouped all marsupial genera in a separate family, but it is now realized that the ability to produce marsupia has arisen in several unrelated families.

The bases for grouping genera into families include characters of lateral leaves, under leaves if present, and features of the bracts and perianth. The number of families that should be recognized in the suborder is a

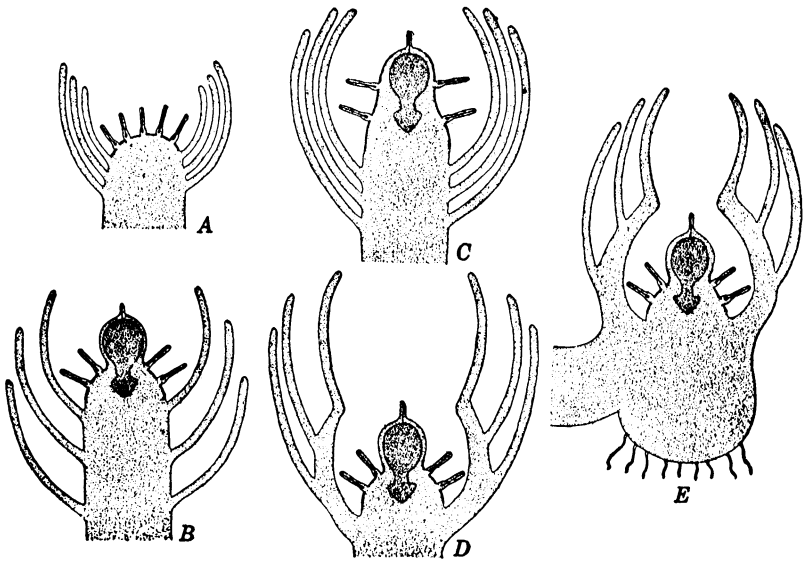

FIG. 50. Diagrams showing some of the types of protection of the sporophyte found in the Jungermannineae. The receptacle and portions derived from it are outlined with a heavy line. *A*, receptacle before development of sporophyte. *B*, a sporophyte surrounded by a calyptra. *C*, a sporophyte surrounded by a calyptra plus the receptacle. *D–E*, marsupia. (*Diagrams based upon Knapp*, 1930.)

matter of opinion. In two of the more recent systems, one[1] recognizes 15 families and another[2] recognizes 17.

ORDER 4. CALOBRYALES

Members of this order have erect leafy gametophytes with leaves in three vertical rows and all approximately alike. The antheridia are ovoid, stalked, borne at the apex of the stem, and develop in a distinctive manner. Archegonia differ from those of other Hepaticae in that the jacket of the neck has only four vertical rows of cells. The sporophyte has an elongate capsule whose jacket layer is only one cell in thickness except at the apex.

[1] Verdoorn, 1932. [2] Evans, 1939.

These liverworts are frequently placed among the Jungermanniales and either as a family of the Jungermannineae or as a separate suborder, but the distinctive characters noted above justify the placing of them in a separate order.

There is but one family, the Haplomitriaceae (Calobryaceae) and it contains two genera. The type monotypic genus, *Haplomitrium*, is known from several localities in northern Europe and is also known[1] from the United States. The three species of the other genus (*Calobryum*) are known chiefly from the tropics. Both genera have a pale, subterranean, sparingly branched rhizome from which arise erect leafy branches (Fig. 51). The erect branches bear their leaves in three vertical rows, and all leaves may be of the same size and shape, or those of one row may be slightly smaller than those of the other two. The smaller leaves are thought to be homologous with under leaves of Jungermannineae, and the side of the stem bearing them is considered the morphologically ventral side. Erect branches bearing sex organs have the uppermost leaves close together and in more than three rows. Such branches have a strong superficial resemblance to the erect gametophores of mosses.

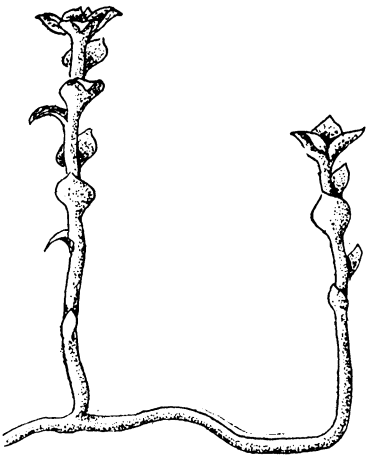

FIG. 51. Male gametophyte of *Calobryum blumei* Nees. (× 1½.)

Terminal growth in a branch of *Calobryum*[2] is due to a pyramidal apical cell with three cutting faces, one slightly narrower than the other two. It is thought that this narrower face gives rise to the ventral file of leaves. The first division in a segment from the apical cell is transverse and perpendicular to the cutting face of an apical cell. The lower daughter cell develops into the thick leaf base and the portion of a stem between it and the next leaf. The upper daughter cell develops into the portion of a leaf that is one cell in thickness. Early growth of this portion of a leaf is by means of an apical cell with two cutting faces; later growth is by intercalary cell division in the basal region.

Rhizoids are lacking on both the subterranean and erect portions of the stem. Superficial cells anywhere on the stem may develop into short two- or three-celled mucilage hairs in which the terminal cell is clavate. The axial portion of a stem of *Calobryum* contains a sharply delimited conducting tissue 10 to 15 cells in diameter. External to the conducting

[1] Evans, 1917. [2] Campbell, 1920; Goebel, 1891.

tissue are large parenchymatous cells in which there are numerous starch grains. Branches of a rhizome are intercalary in origin. A newly formed branch grows horizontally for a time, then grows upward and develops leaves.

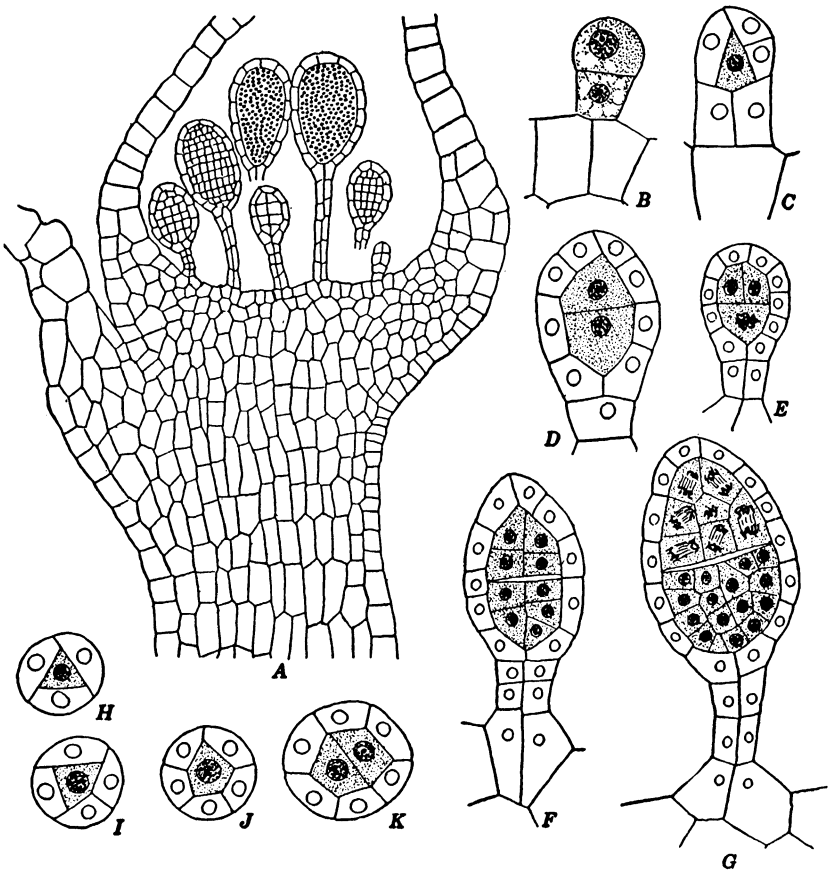

FIG. 52. *Calobryum blumei* Nees. *A*, vertical section through fertile apex of a male gametophyte. *B–K*, stages in development of antheridia. (*B–G*, in vertical section; *H–K*, in transverse section.) (*A*, × 70; *B–D*, *H–K*, × 485; *E–G*, × 325.)

Both genera are heterothallic, and with the sex organs produced in abundance on flattened apices of leafy branches (Fig. 52*A*). Leaves surrounding antheridia of male plants are larger than the others. As a result these fertile branches resemble gametophores of mosses. The details of antheridial development have been followed only in *Calobryum Blumei* Nees.[1] Here, the initial cell of an antheridium divides transversely into

[1] Campbell, 1920.

a basal cell, embedded in the thallus, and an outer cell, which projects above the thallus. The outer cell then divides transversely into a primary antheridial cell and a primary stalk cell (Fig. 52*B*). In most antheridia there then follow three successive vertical divisions of the primary antheridial cell. The sequence of division is similar to that in an archegonium and results in three jacket initials completely enclosing a single primary androgonial cell (Fig. 52*C*). The first division of the primary androgonial cell is transverse (Fig. 52*D–E*). After this, the two daughter cells divide transversely and longitudinally (Fig. 52*F–G*). The primary stalk cell develops into a stalk composed of several superimposed tiers of four cells each. Occasionally antheridia of *Calobryum* may have the primary antheridial cell dividing vertically and in the same sequence as in the Jungermanniales.

Female plants of *Calobryum* have a development of archegonia from about a half dozen recently formed segments from the apical cell and then the apical cell itself develops into an archegonium. *Calobryum*, therefore, is acrogynous. *Haplomitrium* is anacrogynous and without any disappearance of the apical cell when the archegonia are formed. *Calobryum* has the usual three vertical divisions of the primary archegonial cell to form three jacket initials that surround a primary axial cell. In most cases the jacket initials intersect one another to completely enclose the primary axial cell. Consequently the primary axial cell functions directly as a central cell and without cutting off a primary cover cell (Fig. 53*A–B*). Most archegonia have a vertical division of only one of the three jacket initials and a resultant development of an archegonial neck composed of only four rows of cells (Fig. 53*J*). The neck of a *Calobryum* archegonium is very long, markedly twisted, and surrounds a vertical row of 16 to 20 canal cells. The venter is not much broader than the neck, and its jacket is two cells in thickness at maturity (Fig. 53*C–F*).

Except for a massive calyptra there are no protective structures surrounding a developing sporophyte. Early cell divisions in development of a *Calobryum* embryo are in irregular sequence. The hypobasal portion of the embryo develops into a haustorium; the epibasal portion gives rise to foot, seta, and capsule of the mature sporophyte. The mature sporophyte has a cylindrical capsule, a long seta, and an acuminate foot. Except for the apical portion, the jacket layer of the capsule is one cell in thickness, with the thickening of the cell walls localized in a median annular band perpendicular to the surface of the capsule (Fig. 53*L–M*). Opening of the capsule is by a dehiscence into four valves, which may remain more or less united.[1] Sporogenous tissue within the young capsule does not have a partial sterilization to form an elaterophore, but it does have an early differentiation into elaters and cells that are destined to form the spores.

[1] Andreas, 1899.

The Calobryales seem to be a group which arose along the same evolutionary line as the Jungermanniales but which departed quite early from that line. Gametophytes of Calobryales exhibit a strange combination of advanced and primitive features. The gametophyte has attained a degree of differentiation unequaled by any other liverwort as far as external

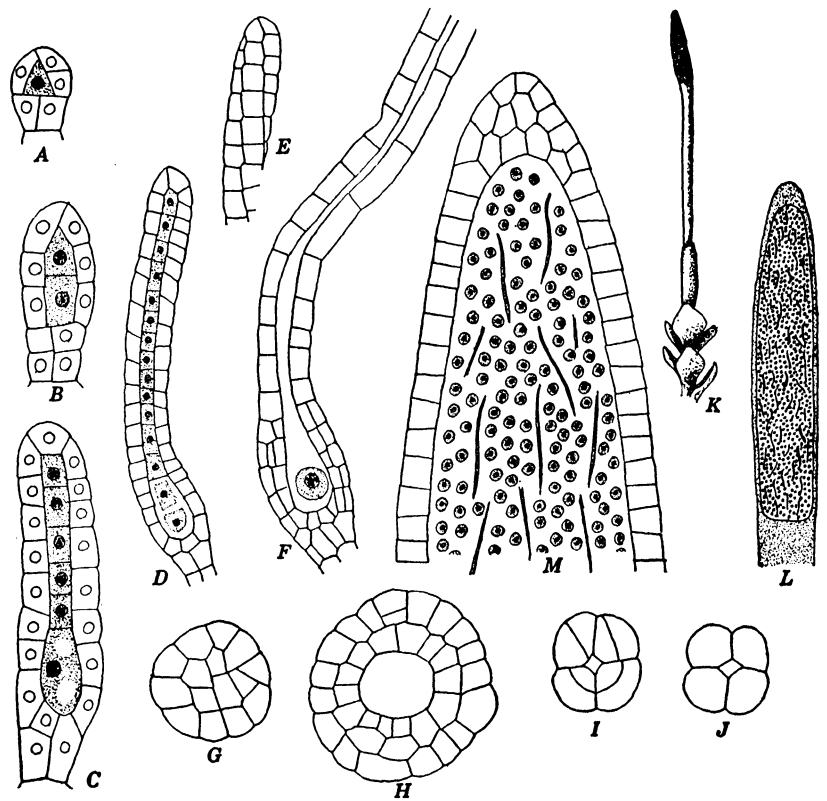

FIG. 53. *Calobryum blumei* Nees. *A–D*, longitudinal sections through archegonia at various stages of development. *E–F*, surface view of apex of neck and longitudinal section through base of the same mature archegonium. *G–J*, transverse sections through base, venter, and neck of a mature archegonium. *K*, apex of a female gametophyte bearing a mature sporophyte. *L–M*, longitudinal sections through capsule of a nearly mature sporophyte. (*A–C*, × 325; *D–J*, × 215; *K*, × 1½; *L*, × 18; *M*, × 60.)

and internal complexity are concerned. However, evolution of these complex vegetative features has not been accompanied by a corresponding evolution of the sex organs. The similarity in early ontogeny of antheridia and archegonia is a decidedly primitive feature, and one giving the best evidence for the theory that antheridia and archegonia are homologous structures. In fact, from the standpoint of early ontogeny, the sex organs of Calobryales are the most primitive of any in the Hepaticae.

Bibliography

Åkerman, Å. **1910.** *Zeitschr. Bot.* **2**: 94–103. [Chemotaxis of antherozoids.]

Allen, C. E. **1919.** *Proc. Amer. Phil. Soc.* **58**: 289–316. 28 figs. [Sex inheritance, *Sphaerocarpos.*]

Andersen, Emma N. **1929.** *Bot. Gaz.* **88**: 150–166. 34 figs. [*Marchantia.*]

1931. *Ibid.* **92**: 66–84. 19 figs. [Discharge of antherozoids.]

Andreas, J. **1899.** *Flora* **86**: 161–213. 1 pl. 29 figs. [Sporangia of Calobryales.]

Barnes, C. R., and W. J. G. Land. **1907.** *Bot. Gaz.* **44**: 197–213. 22 figs. [Air chambers.]

1908. *Ibid.* **46**: 401–409. 14 figs. [Cupule of *Marchantia.*]

Beer, R. **1906.** *Ann. Bot.* **20**: 277–291. 2 pl. [Spores, *Riccia.*]

Black, Carolina A. **1913.** *Ibid.* **27**: 511–532. 2 pl. [*Riccia.*]

Bold, H. C. **1938.** *Amer. Jour. Bot.* **25**: 551–557. 25 figs. [Nutrition of sporophyte.]

Bower, F. O. **1908.** The origin of a land flora. London. 727 pp. 359 figs.

1935. Primitive land plants. London. 658 pp. 449 figs.

Campbell, D. H. **1891.** *Bot. Gaz.* **16**: 323–333. [Interrelationships, Hepaticae.]

1896. *Ann. Bot.* **10**: 489–510. 2 pl. [Sphaerocarpales.]

1896A. *Erythea* **4**: 73–78. 1 pl. [*Sphaerocarpos.*]

1898. *Bot. Gaz.* **25**: 272–274. [*Monoclea.*]

1916. *Amer. Jour. Bot.* **3**: 261–273. 6 figs. [Anacrogynae.]

1918. The structure and development of mosses and ferns. 3d ed. New York. 708 pp. 322 figs.

1918A. *Ann. Bot.* **32**: 319–338. 2 pl. 10 figs. [Marchantiaceae.]

1920. *Ibid.* **34**: 1–12. 1 pl. 6 figs. [*Calobryum.*]

1936. *Bot. Rev.* **2**: 53–66. [Interrelationships, Hepaticae.]

1938. *Ann. Bryol.* **11**: 34–36. [Sphaerocarpales.]

Campbell, D. H., and Florence Williams. **1914.** *Leland Stanford Junior Univ. Publ. Univ. Ser.* **15**: 1–44. 23 figs. [Jungermanniales.]

Cavers, F. **1903.** *New Phytol.* 2: 121–133, 155–165. 8 figs. [Asexual reproduction.]

1903A. *Ann. Bot.* **17**: 270–274. 1 fig. [Discharge of antherozoids.]

1904. Contributions to the biology of the Hepaticae. Part I. Targionia, Reboulia, Preissia, Monoclea. Leeds. 47 pp. 12 figs.

1904A. *Rev. Bryol.* **31**: 69–80. 4 figs. [*Monoclea.*]

1904B. *Ann. Bot.* **18**: 87–120. 2 pl. 5 figs. [Marchantiaceae.]

1910. *New Phytol.* **9**: 81–112, 157–186, 193–234, 269–304, 341–353. 54 figs. [Interrelationships, Hepaticae.]

Chalaud, G. **1929–1931.** *Rev. Gen. Bot.* **41**: 24–34, 95–105, 129–141, 213–236, 293–306, 353–364, 409–423, 474–497, 541–554, 606–621, 679–699. 8 pl. 189 figs. **42**: 31–45, 99–114, 159–163, 219–232, 297–312, 366–377, 429–438, 505–512, 553–588. 61 figs. [*Fossombronia.*]

1931. *Ann. Bryol.* **4**: 49–67. 4 figs. [Gametophyte development, Jungermannineae.]

Church, A. H. **1919.** Thalassiophyta and the subaerial transmigration. Oxford. Bot. Mem. No. 3. 1–95.

Clapp, Grace L. **1912.** *Bot. Gaz.* **54**: 177–193. 4 pl. [*Riccardia.*]

Clee, D. A. **1937.** *Ann. Bot.* N.S. **1**: 325–328. 2 figs. [Water conduction.]

Cribbs, J. E. **1918.** *Bot. Gaz.* **65**: 91–96. 2 pl. [*Marchantia.*]

Deutsch, H. **1912.** *Ibid.* **53**: 492–503. 13 figs. [*Targionia.*]

Dupler, A. W. **1921.** *Bull. Torrey Bot. Club* **48**: 241–252. 22 figs. [Air chambers.]

1922. *Bot. Gaz.* **74**: 143–157. 47 figs. [Embryology, Marchantiaceae.]

Durand, E. J. **1908.** *Bull. Torrey Bot. Club* **35**: 321–335. 5 pl. [*Marchantia.*]

Ellwein, H. **1926.** *Bot. Archiv* **15**: 61–131. 148 figs. [Jungermanniales.]

Evans, A. W. **1912.** *Ann. Bot.* **26**: 1–37, 36 figs. [Apical cells, Jungermannineae.]
1917. *Rhodora* **19**: 263–272. [Calobryales.]
1918. *Bull. Torrey Bot. Club* **45**: 235–251. 14 figs. [Air chambers.]
1921. *Trans. Conn. Acad. Arts. and Sci.* **25**: 93–209. 13 figs. [*Riccardia.*]
1923. Marchantiales. In North American Flora. Vol. 14, Part. 1. New York. Pp. 9–66.
1939. *Bot. Rev.* **5**: 49–96. [Classification, Hepaticae.]
Florin, R. **1922.** *Ark. Bot.* **18**: No. 5: 1–58. 1 pl. 25 figs. [*Riccardia.*]
Fulford, Margaret. **1951.** *Evolution* **5**: 243–264. 14 figs. [Geographical distribution.]
Garber, J. F. **1904.** *Bot. Gaz.* **37**: 161–177. 2 pl. 4 figs. [*Riccia.*]
Goebel, K. **1889.** *Flora* **72**: 1–45. 2 pl. 6 figs. [Juvenile gametophytes.]
1891. *Ann. Jard. Bot. Buitenzorg.* **9**: 1–40. 4 pl. [*Calobryum.*]
1893. *Flora* **77**: 423–459. 2 pl. 18 figs. [Leaves of Jungermannineae.]
1910. *Ibid.* **101**: 43–97. 45 figs. [Marchantiaceae.]
1927. *Ibid.* **122**: 33–56. 11 figs. [Spore formation, Jungermannineae.]
1928. *Ann. Jard. Bot. Buitenzorg.* **39**: 1–116. 14 pl. [Jungermannineae.]
1930. Organographie der Pflanzen. 2d Teil. Bryophyten-Pteridophyten. Aufl. 3. Jena. 736 pp. 850 figs.
Gross, Catherine, and C. E. Allen. **1938.** *Ann. Bryol.* **11**: 76–83. 8 figs. [*Sphaerocarpos.*]
Harris, T. M. **1938.** The British Rhaetic flora. London. 84 pp. 5 pl. 26 figs.
Haupt, A. W. **1920.** *Bot. Gaz.* **69**: 318–331. 6 pl. 1 fig. [*Fossombronia.*]
1921. *Ibid.* **71**: 61–74. 21 figs. [Marchantiaceae.]
1921A. *Ibid.* **71**: 446–453. 1 pl. 11 figs. [Marchantiaceae.]
1926. *Ibid.* **82**: 30–54. 2 pl. 16 figs. [Marchantiaceae.]
1929. *Ibid.* **87**: 302–318. 1 pl. 21 figs. [Marchantiaceae.]
1929A. *Ibid.* **88**: 103–108. 1 pl. [*Fossombronia.*]
1942. *Ibid.* **104**: 264–272. 28 figs. [Marchantiaceae.]
Heberlein, Enid A. **1929.** *Ibid.* **88**: 417–429. 21 figs. [*Marchantia.*]
Hirsch, Pauline E. **1910.** *Bull. Torrey Bot. Club* **37**: 73–77. 6 figs. [Air chambers.]
Horne, A. S. **1909.** *Ann. Bot.* **23**: 159–160. 3 figs. [Discharge of antherozoids.]
Howe, M. A., and L. M. Underwood. **1903.** *Bull. Torrey Bot. Club* **30**: 214–224. 2 pl. [*Riella.*]
Humphrey, H. B. **1906.** *Ann. Bot.* **20**: 83–108. 2 pl. 8 figs. [*Fossombronia.*]
Hutchinson, A. H. **1915.** *Bot. Gaz.* **60**: 134–143. 4 pl. 1 fig. [Metzgerineae.]
Johnson, D. S. **1904.** *Ibid.* **38**: 185–205. 2 pl. [*Monoclea.*]
1929. *Ibid.* **88**: 38–62. 3 pl. 4 figs. [Antheridia, Metzgerineae.]
Juel, O. **1910.** *Svensk. Bot. Tidsskr.* **4**: 160–166. 1 pl. 5 figs. [*Riccia.*]
Kashyap, S. R. **1919.** *Proc. Asiatic Soc. Bengal* N.S. **15**: cliii–clxvi. [Interrelationships, Hepaticae.]
1929. Liverworts of the western Himalayas and the Punjab Plain. Lahore. 129 pp. 25 pl.
Knapp. H. **1930.** *Bot. Abhandl.* **16**: 1–168. 214 figs. [Protection of sporophyte, Jungermannineae.]
Leitgeb, H. **1871.** *Bot. Zeitg.* **29**: 557–565. 3 figs. [Branching of Jungermannineae.]
1877. Untersuchungen ueber die Lebermoose. III Hefte. Die frondose Jungermannieen. Jena. 144 pp. 9 pl.
1879. *Ibid.* IV Heft. Die Riccieen. Graz. 101 pp. 9 pl.
1881. *Ibid.* VI Heft. Die Marchantiaceen und allgemeine Bemerkungen über Lebermoose. Graz. 158 pp. 11 pl.
Lewis, C. E. **1906.** *Bot. Gaz.* **41**: 109–138. 5 pl. [*Riccia.*]
Lidforss, B. **1904.** *Jahrb. Wiss. Bot.* **41**: 65–87. [Chemotaxis of antherozoids.]
Lorbeer, G. **1934.** *Ibid.* **80**: 567–817. 1 pl. 110 figs. [Sex chromosomes.]

McAllister, F. **1916.** *Bull. Torrey Bot. Club* **43**: 117–126. 1 pl. [Ricciaceae.]
1928. *Ibid.* **55**: 1–10. 11 figs. [Sex ratios, *Riccia.*]
McConaha, Marjorie. **1941.** *Amer. Jour. Bot.* **28**: 301–306. 8 figs. [Movement of water.]
McCormick, Florence A. **1914.** *Bot. Gaz.* **58**: 401–418. 3 pl. [Jungermannineae.]
McNaught, Helen N. **1929.** *Ibid.* **88**: 400–416. 22 figs. [Sporophyte, *Marchantia.*]
Manning, Florence L. **1914.** *Ibid.* **57**: 320–323. 2 pl. [Sex organs, Jungermannineae.]
Menge, F. **1930.** *Flora* **124**: 423–476. 5 pl. 7 figs. [Spore germination, *Marchantia.*]
Meyer, K. **1912.** *Bull. Soc. Imp. Nat. Moscou* N.S. **25**: 263–286. 1 pl. 22 figs. [Sporophyte, Marchantiales.]
1914. *Ber. Deutsch. Bot. Ges.* **32**: 262–266. 4 figs. [Sporophyte, *Corsinia.*]
1914A. *Bull. Soc. Imp. Nat. Moscou* N.S. **27**: 597–615. 1 pl. 16 figs. [Sporophyte, Marchantiaceae.]
1929. *Planta* **8**: 36-54. 36 figs. [Sporophyte, Marchantiaceae.]
1931. *Ibid.* **13**: 193–209. 33 figs. [Sporophyte, Marchantiales.]
Müller, K. **1912–1916.** Die Lebermoose. In L. Rabenhorst, Kryptogamen-Flora von Deutschlands, Österreichs und der Schweiz. 2 Aufl. Bd. 6. Abt. 2. 947 pp. 207 figs.
Nevins, Beatrice I. **1933.** *Cellule* **41**: 293–334. 3 pl. [Antheridia, *Sphaerocarpos.*]
O'Hanlon, Sister Mary Ellen. **1926.** *Bot. Gaz.* **82**: 215–222. 4 pl. [Spore germination, *Marchantia.*]
1930. *Amer. Jour. Bot.* **17**: 765–769. 1 pl. 1 fig. [Spore germination, Marchantiaceae.]
O'Keefe, Lillian. **1915.** *New Phytol.* **14**: 105–116. 2 figs. [*Targionia.*]
Orth, R. **1930.** *Flora* **124**: 152–203. 78 figs. [Air chambers.]
1943. *Bot. Arch.* **44**: 544–550. [Air chambers.]
Pagan, F. M. **1932.** *Bot. Gaz.* **93**: 71–84. 24 figs. [Sporophyte, *Riccia.*]
Pande, S. K. **1933.** *Jour. Indian Bot. Soc.* **12**: 110–121. 3 pl. 2 figs. [*Riccia.*]
Peirce, G. J. **1902.** *Bull. Torrey Bot. Club* **29**: 374–382. 5 figs. [Discharge of antherozoids.]
Pietsch, W. **1911.** *Flora* **103**: 347–384. 21 figs. [Air chambers.]
Rickett, H. W. **1920.** *Amer. Jour. Bot.* **7**: 182–194. 4 pl. 1 fig. [Thallus, *Sphaerocarpos.*]
1920A. *Bull. Torrey Bot. Club* **47**: 347–357. 25 figs. [Regeneration, *Sphaerocarpos.*]
1923. *Ann. Bot.* **37**: 225–259. 2 pl. 3 figs. [Fertilization, *Sphaerocarpos.*]
Schiffner, V. **1893–1895.** Hepaticae. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. Teil 1. Abt. 3. 1 Hälfte, Pp. 3–141. 73 figs.
1913. *Oesterr. Bot. Zeitschr.* **63**: 29–33, 75–81, 113–121, 154–159. 1 fig. [*Monoclea.*]
Schuster, R. M. **1949.** *Amer. Midland Nat.* **42**: 513–712. 18 pl. [Hepaticae of New York.]
Showalter, A. M. **1923.** *Amer. Jour. Bot.* **10**: 148–166. 4 pl. 3 figs. [*Riccardia.*]
1925. *Bull. Torrey Bot. Club* **52**: 157–166. 1 pl. 2 figs. [Spore germination, Metzgerineae.]
1926. *Ann. Bot.* **40**: 691–707. 1 pl. 3 figs. [Antherozoids.]
1926A. *Ibid.* **40**: 713–726. 3 pl. 4 figs. [Fertilization, *Riccardia.*]
1927. *Ibid.* **41**: 37–46. 2 pl. 4 figs. [Fertilization, *Fossombronia.*]
1927A. *Ibid.* **41**: 409–417. 3 pl. [Fertilization, Metzgerineae.]
1928. *Cellule* **38**: 295–349. 5 pl. 29 figs. [Fertilization, *Riccardia.*]
Smith, G. M., *et al.* **1953.** A textbook of general botany. 5th ed. New York. 606 pp. 429 figs.
Spruce, R. **1884.** *Trans. and Proc. Bot. Soc. Edinburgh* **15**: 1–588. 22 pl. [South American Hepaticae.]
Steere, W. C. **1940.** Liverworts of Southern Michigan. Bloomfield Hills, Mich. 97 pp. 22 pl.
1946. *Amer. Midland Nat.* **36**: 298–324. [Fossil Bryophytes.]

Steil, W. N. **1923.** *Bull. Torrey Bot. Club* **50**: 197–210. 5 figs. [Antherozoids.]
Stephani, F. **1894.** *Oesterr. Bot. Zeitschr.* **44**: 1–5. 1 pl. [Thallose Jungermannineae.]
Studhalter, R. A. **1931.** *Bot. Gaz.* **92**: 172–191. 25 figs. [*Riella.*]
1938. *Ann. Bryol.* **11**: 153–154. [Nutrition of sporophyte.]
Studhalter, R. A., and Martha E. Cox. **1940.** *Bryologist* **43**: 141–157. 28 figs. [Gemmae, *Riella.*]
1941. *Ibid.* **44**: 19–27. 17 figs. [Scales, *Riella.*]
1941A. *Ibid.* **44**: 29–40. 26 figs. [Scales, *Riella.*]
1941B. *Ibid.* **44**: 77–93. 10 figs. [Gemmae, *Riella.*]
Tansley, A. G., and Edith Chick. **1901.** *Ann. Bot.* **15**: 1–38. 2 pl. [Conducting tissues.]
Tatuno, S. **1937.** *Bot. Mag. Tokyo* **51**: 860–866. 30 figs. [Sex chromosomes.]
1938. *Ibid.* **52**: 374–379. 19 figs. [Sex chromosomes.]
Thompson, R. H. **1941.** *Amer. Jour. Bot.* **28**: 845–855. 67 figs. [*Riella.*]
1942. *Ibid.* **29**: 275–281. 37 figs. [*Riella.*]
Verdoorn, F. **1932.** *Ann. Bryol. Suppl.* **1**: 1–187. 304 figs. [Jungermannineae.]
1932. Classification of Hepatics. In F. Verdoorn, Manual of Bryology. The Hague. Pp. 413–432.
Walker, R., and W. Pennington. **1939.** *New Phytol.* **38**: 62–68. 2 figs. [Movement of air pores.]
Walton, J. **1925.** *Ann. Bot.* **39**: 563–571. 1 pl. 1 fig. [Fossil Hepaticae.]
1928. *Ibid.* **42**: 707–716. 1 fig. 1 pl. [Fossil Hepaticae.]
Wettstein, R. von. **1908.** Handbuch der systematischen Botanik. 1st ed. Leipzig. 577 pp. 369 figs.
1911. *Ibid.* 2d ed.

CHAPTER 4

ANTHOCEROTAE

The Anthocerotae differ from other Bryophyta in a number of respects. Among these are cells with large chloroplasts and each chloroplast containing a pyrenoid, a development of antheridia from hypodermal cells on the dorsal side of a gametophyte, archegonia almost completely embedded in the gametophyte, and a sporophyte whose growth is indeterminate because of a meristematic region continually adding to the base of the capsule.

There is but one order, the *Anthocerotales*. This order is often placed among the Hepaticae, but because of the distinctive features enumerated above it is better to follow the proposal[1] that it be placed in a class coordinate with Hepaticae and Musci. There are approximately 300 species. Genera are based primarily on sporophytic characters, and according to one's concept of generic limits either five or six genera are recognized. All genera are usually placed in a single family, the Anthocerotaceae; but sometimes *Notothylas* is placed in a separate family, the Notothylaceae.

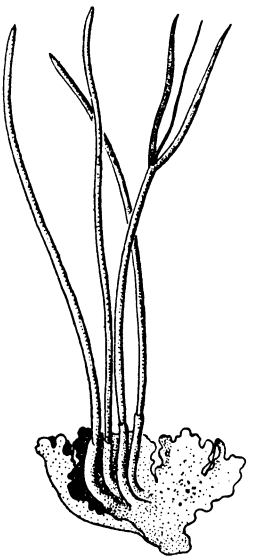

FIG. 54. *Anthoceros fusiformis* Aust. Gametophyte with sporophytes. (× 2.)

Gametophytes of Anthocerotae are thallose, somewhat lobed or radially dissected, and sometimes have a tendency toward a dichotomous branching (Fig. 54). The gametophytes are always dorsiventrally differentiated and have numerous smooth-walled rhizoids on the ventral surface. The ventral surface lacks both scales and mucilage hairs. One genus (*Dendroceros*) has certain species with the gametophyte differentiated into a thick midrib and lateral wings one cell in thickness. Lateral margins of other genera are more than one cell in thickness. Aside from a more regular

[1] Howe, 1899.

arrangement of superficial dorsal cells, there is no internal differentiation of tissues. The ventral portion of a thallus has mucilage-filled intercellular cavities on the dorsal side and opening to the surface by narrow slits. Very often these cavities contain colonies of the blue-green alga *Nostoc*. As a result, the gametophyte has a greasy dark green color, instead of the bright green characteristic of Hepaticae. Presence of the endophytic alga is not essential for growth of a gametophyte, and it has been shown[1] that thalli without *Nostoc* grow better than those containing the alga. In addition, certain species of *Anthoceros* contain tubular cavities running longitudinally through the gametophyte that are generally filled with a mucilaginous substance. Other species of *Anthoceros* lack these cavities.[2]

Cells of the gametophyte usually contain a single large chloroplast, but deep-lying cells of certain genera[3] may contain two to eight of them. Chloroplasts of superficial cells are usually larger than those in other cells and are lens-shaped. The chloroplasts differ markedly from those of other *Bryophyta* in each having a single large pyrenoid. Pyrenoids of Anthocerotae are not homologous with those of green algae since they consist of a crowded mass of 25 to 300 disk- to spindle-shaped bodies,[4] each of which may be transformed into a rudimentary starch grain without changing its shape or position.

Growth of a thallus is initiated by a single apical cell. In most genera the apical cell has two cutting faces which alternately form dorsal and ventral derivatives; but in *Dendroceros*[5] it has a convex posterior cutting face and two lateral cutting faces. Here, derivatives from the posterior face contribute to the midrib; those from the lateral faces contribute to the wings. Now and then an apical cell of *Anthoceros* and of other genera gives rise to a transverse row of cells by a series of vertical divisions. A cell near each end of the row begins to function as an apical cell, and the two growing points thus initiated separate farther and farther from each other as growth continues. Continued repetition of this dichotomous branching results in a compact rosette-like thallus. More active growth of one arm of a dichotomy, as in *Anthoceros halli* Aust.,[6] results in a long, narrow, pinnately branched thallus.

Vegetative multiplication may be by progressive growth and death reaching dichotomies, but this is of much less frequent occurrence than in Hepaticae. In addition, certain genera have the gametophyte becoming thickened in areas along the margin and with the superficial cells of the mass developing into a cork-like protective layer. Such "tubers" remain alive when drought causes a death of other portions of a thallus, and with a return of favorable conditions the "tubers" develop into new thalli.

Most Anthocerotae are homothallic, but certain species of *Anthoceros*

[1] Peirce, 1906. [2] Proskauer, 1951. [3] Campbell, 1907.
[4] McAllister, 1914, 1927. [5] Campbell, 1898, 1908. [6] Bartlett, 1928.

have been shown to be heterothallic.[1] In these heterothallic species sex determination is genotypic, two spores of a tetrad developing into male and two into female gametophytes. Here mature gametophytes show a slight sexual dimorphism, female plants having broader fertile lobes than male plants. Homothallic species are frequently protandrous.

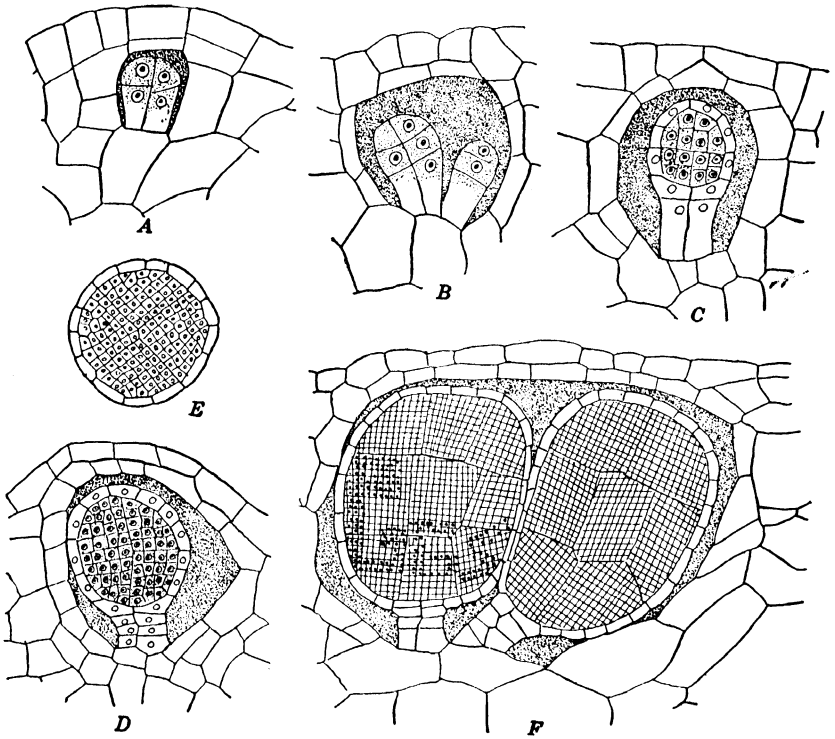

FIG. 55. *Anthoceros fusiformis* Aust. Stages in development of antheridium. (*A–D*, *F*, in vertical section; *E*, in transverse section.) (*A–C*, × 485; *D–E*, × 325; *F*, × 215.)

One fundamental difference between Anthocerotae and Hepaticae is the fact that an antheridial initial is the inner daughter cell produced by periclinal division of a superficial dorsal cell of the gametophyte. The discovery of atypical individuals in which the outer daughter cell functions as an antheridial initial[2] suggests that Anthocerotae are derived from ancestors in which antheridia developed from superficial dorsal cells. Immediately after division of a dorsal cell into an antheridial initial and a sterile cell that lies external to it, there is a development of a mucilage-filled space between the two that eventually enlarges to form the antheridial

[1] Proskauer, 1948. [2] Lampa, 1903; Leitgeb, 1879.

cavity. The sterile cell above the antheridial initial divides and redivides to form a sterile layer overroofing the antheridial chamber. This layer may be one or more cells in thickness. In certain genera, including *Anthoceros*, the antheridial initial may divide vertically into two or four daughter cells, each of which develops into an antheridium (Fig. 55*B*, *F*). Thus the antheridial chamber frequently contains two or four antheridia. This number may be increased by budding of secondary antheridial initials from the base of the two or four primary antheridia.[1] Proliferation of secondary antheridia may result in 25 or more antheridia within an antheridial chamber.[2] Transverse division of the antheridial initial (or of daughter cells formed by vertical division of it) is into a **primary antheridial cell** and a **primary stalk cell.** The primary stalk cell develops into a stalk two cells broad and several cells in height. Development of the primary antheridial cell into the antheridium proper is according to the same sequence as in Sphaerocarpales and Marchantiales. There is first a vertical division into four cells and then a transverse division to produce two tiers of four cells each. Periclinal division in the two tiers results in a formation of **primary androgonial cells** and **primary jacket cells.** The primary androgonial cells divide repeatedly to form a large number of androgonial cells (Fig. 55*D–F*) and cells of the last cell generation of androgonial cells are **androcytes.** Spermatogenesis[3] is much like that of other Bryophyta and involves a metamorphosis of androcytes into biflagellate antherozoids.

Archegonia are embedded in the gametophyte and in direct contact with vegetative cells lateral to them. In Anthocerotae the archegonial initial functions directly as a **primary archegonial cell** instead of dividing into primary archegonial cell and primary stalk cell. Obliteration of this division is the main reason for the embedded archegonium and its lateral contact with vegetative cells of a thallus. The first divisions of an archegonial initial are vertical and into three **jacket initials** surrounding an **axial cell.** The axial cell divides transversely into a **cover initial** and a **central cell,** after which the central cell divides transversely into a **primary canal cell** and a **primary venter cell** (Fig. 56*A*). Transverse division and redivision of the primary canal cell result in a vertical row of four to six **neck canal cells.** These are much smaller in diameter than are the **venter canal cell** and **egg** formed by transverse division of the primary venter cell (Fig. 56*B–C*). Development of the row of axial cells is accompanied by transverse division of the jacket initials. It is not clear whether the jacket layer of a mature archegonium is lateral to the neck canal cells alone, or lateral to all derivatives from the central cell. In either case the cells next to the lower face of the egg cannot be considered a part of the archegonium since they have not been derived from the archegonial initial. Mature arche-

[1] Bhardwaj, 1950; Campbell, 1895. [2] Proskauer, 1951. [3] Bagchee, 1924.

gonia have the usual gelatinization of neck canal and venter canal cells (Fig. 56*D*). During development of an archegonium, there is a vertical division of the cover initial into **four cover cells** which become separated from the archegonium shortly after gelatinization of canal cells.

At the time of fertilization an egg does not completely fill the venter of an archegonium. Shortly after fertilization the zygote swells to completely

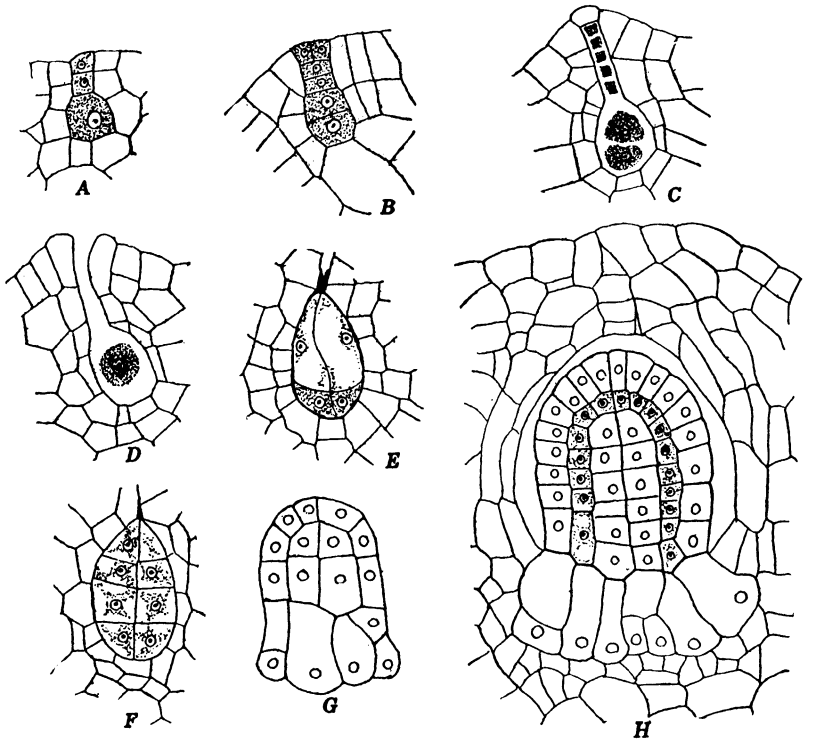

FIG. 56. *Anthoceros laevis* L. *A–D*, stages in development of archegonia. *E–G*, early stages in development of embryos. *H*, an embryo after differentiation of the archesporium. (× 325.)

fill the venter, after which it secretes a wall. The first division of a zygote is vertical, but cases have been found[1] where it is transverse. If the first division is vertical it is followed by a transverse division of the two daughter cells (Fig. 56*E*). Transverse division may be into two daughter cells of either equal[2] or unequal[3] size. In the latter case the larger cells are toward the neck of the archegonium. The next series of divisions is vertical, and the resultant eight-celled embryo is composed of two tiers of four cells each. The lower tier of four cells develops into the sterile portion (foot)

[1] Bhardwaj, 1950; Pande, 1932. [2] Campbell, 1898, 1907. [3] Campbell, 1895.

of a sporophyte. The first divisions in the foot tier are transverse, but very soon divisions begin to take place in all planes (Fig. 56*F–H*). At this time, or even earlier, the lowermost cells of the foot grow into short rhizoid-like projections which increase the absorptive surface obtaining food from adjoining gametophytic tissues. Eventually the foot becomes a globose mass or a massive inverted cap (Fig. 57*B*).

Development of the capsule from the upper four cells of an eight-celled embryo begins with one or two transverse divisions (Fig. 56*F*). The periclinal divisions differentiating **amphithecium** and **endothecium** occur at a time when the capsule is not more than two or three tiers of cells in height (Fig. 56*G*). In all genera except *Notothylas* the entire endothecium gives rise to the sterile tissue comprising the **columella.** This is also true of most species of *Notothylas*,[1] but in one species[2] the endothecium develops into sporogenous tissue. Young embryos have a columella composed of four vertical rows of cells (Fig. 56*G–H*). Somewhat older embryos have one composed of 16 vertical rows of cells, so arranged that they form a solid square when seen in transverse section. Columella cells in the mature part of a capsule are vertically elongate and have somewhat thickened walls (Fig. 57*A,C*).

Division of the amphithecium is periclinal. Except in one species of *Notothylas*,[2] the outer layer functions as the initial layer of the **jacket** and the inner layer as the **primary sporogenous layer** (**archesporium**) (Fig. 56*H*). Periclinal divisions in the jacket layer eventually make it four to six cells in thickness. The outermost layer of the jacket matures into an **epidermis** in which the cells are vertically elongate and with their walls strongly cutinized (Fig. 57*C–D*). In some genera certain of the young epidermal cells divide vertically, and the daughter cells mature into a typical pair of **guard cells** surrounding a **stoma.** Other genera lack stomata. Cells beneath the epidermal layer mature into a parenchymatous tissue with intercellular spaces. If the species is one with gametophytic cells containing a single chloroplast, there are two chloroplasts in sporophytic cells. If the species is one with more than one chloroplast in gametophytic cells, the number in sporophytic cells is greater than in gametophytic cells but is not double the number.

The layer of sporogenous tissue formed by periclinal division of the amphithecium overarches the columella. It may extend to the base of the columella or only part way to its base. The sporogenous layer may remain one cell in thickness throughout its further development (*Anthoceros hawaiensis* Howe); it may become two cells in thickness (*A. pearsoni* Howe); or it may become three or four cells in thickness.[3] In any case, alternate transverse tiers of sporogenous cells develop into sporocytes and

[1] Campbell, 1895; Lang, 1907; Mottier, 1894; Pande, 1932.
[2] Pande, 1933. [3] Bartlett, 1928.

into sterile cells. The sterile cells are joined end to end in simple or branched filaments (**pseudoelaters**) of three to five cells. Mature pseudoelaters are without protoplasts and, according to the genus, have smooth walls, irregularly thickened walls, or walls with the spiral thickenings typical of elaters. Sporocytes divide meiotically into four spores. Spores

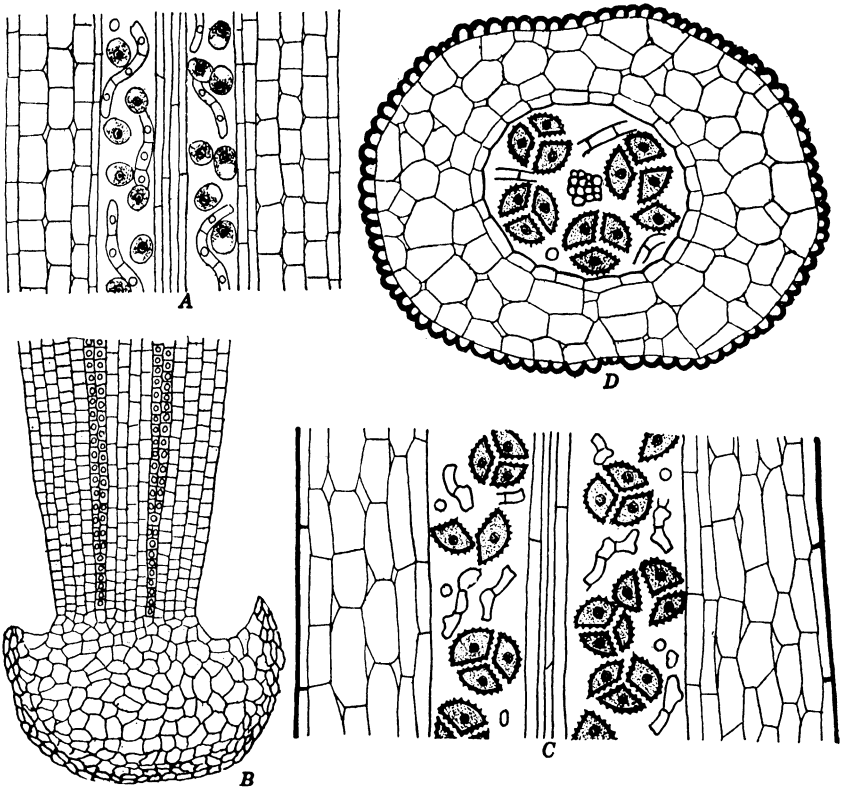

FIG. 57. *Anthoceros laevis* L. *A–B*, longitudinal sections through upper and basal portion of an immature sporophyte. *C–D*, vertical and transverse sections through the mature portion of a sporophyte. (× 160.)

in the upper part are the first to mature. As they are maturing, and beginning just below the tip of the capsule, vertical strips of cells in the jacket become differentiated into vertical zones of dehiscence.[1] Depending upon the species there may be a formation of one, two, four, or more than four dehiscence zones. The segments into which the jacket splits rarely diverge from one another because the tip of the capsule does not split. Discharge of spores after opening of a capsule is accelerated by

[1] Proskauer, 1948*A*.

twisting and untwisting of the pseudoelaters as a result of hygroscopic changes.

Early growth of a sporophyte is accompanied by an upward growth of the archegonium and adjoining gametophytic tissue. This surrounding sheath is sometimes called a calyptra, but involucre is a more appropriate designation for it. For a time, upward growth of involucre and sporophyte keep pace with each other, but eventually the sporophyte grows faster and its capsule pushes up through the involucre. At this time the jacket cells of the capsule contain chloroplasts which contribute to the nutrition of the sporophyte. The extent to which the sporophyte is photosynthetically self-sufficient has been studied by dissecting them out from the gametophyte and culturing them on nutrient agar or on soil.[1] Excised sporophytes may remain alive for months but they increase in length but little. For example, in one series of experiments[2] excised sporophytes lengthened less than 2 mm. while control sporophytes attached to gametophytes lengthened 35 to 40 mm. In experiments so devised that either light or carbon dioxide was excluded from the sporophyte, but not from the gametophyte to which it was attached, growth of sporophytes was equal to that of sporophytes growing normally.[2] Correlations have also been made between longevity of gametophytes and growth of sporophytes.[3] These show that there is a distinct correlation between the two and that when gametophytes live past their usual life span the sporophytes grow to unusual lengths. All these data seem to show that sporophytes of *Anthoceros* are nutritionally more dependent upon gametophytes than are those of certain Hepaticae (see page 25).

One unique feature of Anthocerotae is that cells of a capsule do not mature at the same rate and that cells in the basal portion of a capsule remain embryonic even after those in the apical portion are fully mature. The embryonic region at the base of a capsule is not wholly undifferentiated, but shows the beginning of a differentiation into columella, sporogenous tissue, and jacket layer (Fig. 57*B*). Maturation of derivatives from these three regions of the embryonic region continually add new cells to the corresponding mature regions of the sporophyte, and this continues as long as there is food for the sporophyte.

Bibliography

Bagchee, K. **1924.** *Ann. Bot.* **38**: 105–111. 1 pl. [Spermatogenesis, *Anthoceros.*]
Bartlett, Emily M. **1928.** *Ibid.* **42**: 409–430. 1 pl. 9 figs. [Sporophytes, *Anthoceros.*]
Bhardwaj, D. C. **1950.** *Jour. Indian Bot. Soc.* **29**: 143–163. 43 figs. [*Anthoceros.*]
Campbell, D. H. **1895.** The structure and development of mosses and ferns. London. 544 pp. 266 figs.

[1] Campbell, 1917; Proskauer, 1948; Rink, 1935. [2] Rink, 1935.
[3] Campbell, 1924; Proskauer, 1948.

1898. *Jour. Linn. Soc. Bot. London* **33**: 467–478. 2 pl. [*Dendroceros.*]
1907. *Ann. Bot.* **21**: 467–486. 3 pl. [Structure of Anthocerotae.]
1908. *Ibid.* **22**: 91–102. 2 pl. 2 figs. [Structure of Anthocerotae.]
1917. *Proc. Nation. Acad. Sci.* (U.S.) **3**: 494–496. [Self-sustaining sporophytes.]
1918. The structure and development of mosses and ferns. 3d ed. New York. 708 pp. 322 figs.
1924. *Ann. Bot.* **38**: 473–483. 8 figs. [Self-sustaining sporophytes.]
Howe, M. A. **1899.** *Mem. Torrey Bot. Club* **7**: 1–208. 35 pl. [Anthocerotae of California.]
Lampa, Emma. **1903.** *Oesterr. Bot. Zeitschr.* **1903**: 436–438. 5 figs. [Sex organs, *Anthoceros.*]
Lang, W. H. **1907.** *Ann. Bot.* **21**: 201–210 1 pl. [*Notothylas.*]
Leitgeb, H. **1879.** *Untersuchungen über die Lebermoose.* Heft V. Die Anthoceroteen. Graz. 60 pp. 5 pl.
McAllister, F. **1914.** *Amer. Jour. Bot.* **1**: 79–95. 1 pl. [Pyrenoid.]
1927. *Ibid.* **14**: 246–257. 2 pl. [Pyrenoid.]
Mottier, D. M. **1894.** *Ann. Bot.* **8**: 393–402. 2 pl. [*Notothylas.*]
Pande, S. K. **1932.** *Jour. Indian Bot. Soc.* **11**: 169–177. 5 pl. [*Notothylas.*]
1933. *Current Sci.* **1**: 272. 3 figs. [Formation of archesporium.]
Peirce, G. J. **1906.** *Bot. Gaz.* **42**: 55–59. [*Nostoc* in gametophyte.]
Proskauer, J. **1948.** *Ann. Bot.* N.S. **12**: 237–265. 1 pl. 9 figs. [*Anthoceros.*]
1948A. *Ibid.* **12**: 427–439. 1 pl. 9 figs. [*Anthoceros.*]
1951. *Bull. Torrey Bot. Club* **78**: 331–349. 38 figs. [Anthocerotae.]
Rink, W. **1935.** *Flora* **130**: 87–130. 28 figs. [Nutrition of sporophyte.]

CHAPTER 5

MUSCI

Musci, the class to which mosses are referred, differ from other Bryophyta in vegetative features of gametophyte, in early ontogeny and mature structure of sex organs, and in early ontogeny and mature structure of sporophytes.

Among the distinctive vegetative features of gametophytes is a filamentous or simple thallose **protonema** producing upright branches (**gametophores**) which bear the sex organs. Typically, the protonemata die after gametophytes are formed, and each of the latter continues growth as an independent plant. Gametophores are differentiated into stem and leaves, and almost always all vegetative leaves are of the same size and structure. Rhizoids borne by both protonema and gametophore are multicellular and with diagonal cross walls. Sex organs are unique in having early growth stages initiated by an apical cell with two cutting faces.

Sporophytes have capsules with a greater proportion of sterile tissue and frequently have the sterile portion differentiated into a variety of tissues. Unlike other Bryophyta, mosses do not have a differentiation of elaters or nurse cells by the sporogenous tissue.

The class includes approximately 660 genera and 14,500 species. The genera are of three morphologically distinct types; but, as noted elsewhere (page 11), it is better to consider the magnitude of difference that of a subclass rather than that of a class.

SUBCLASS 1. SPHAGNOBRYA

The bog mosses (Sphagnobrya) differ from other Musci in the following respects: The protonema is broadly thallose and produces but one gametophore. Leaves of gametophores are without a midrib and usually composed of two markedly different types of cells. Antheridia are borne in the axils of leaves and differentiation of the fertile portion is in a distinctive manner. Archegonia are formed acrogynously. Unlike other Musci, the sporogenous tissue of a sporophyte is formed from the amphithecium. In common with Andraeobrya, elevation of a sporophyte above the gametophyte is due to an elongation of a stalk of gametophytic tissue, the

pseudopodium, rather than to an elongation of a seta. The single order of the subclass, the Sphagnales, contains but one family, the Sphagnaceae, and this, in turn, has but one genus, *Sphagnum*. There are some 320 species.

All species of *Sphagnum* grow in ponds, swamps, or other moist places and usually only in soft-water regions where there is but little lime. Growth of gametophores is continuous from year to year. *Sphagnum* usually grows in water so acid that there is but little decay of dead basal portions of gametophores. The compacted mass of dead gametophytic tissue accumulating as growth continues from year to year, together with the remains of other plants, is **peat.**

FIG. 58. Gametophyte (gametophore) of *Sphagnum recurvum* Beauv. (Natural size.)

In some northern countries, and especially in Ireland, peat is used extensively as a fuel. Specially designed spades with long and narrow blades are used to dig blocks of peat from peat bogs. Because peat has a great capacity for retaining moisture, the blocks of peat must be dried for several months before utilization as fuel. In other cases, advantage is taken of its capacity to retain moisture. Examples of this are the nursery-man's using peat as a packing material when shipping live plants, and the gardener's use of it to improve the water-retaining quality of soil.

Sphagnum is of considerable ecological importance in modifying the landscape in regions with small lakes. When it becomes established on the shores of a morainal lake, it may encroach more and more on the lake and eventually cover the entire lake surface. The result of this encroachment is a quaking bog. The time interval required for conversion of a lake into a bog is relatively short. At several localities in the eastern United States where maps made a hundred years ago show lakes, the lakes are now quaking bogs in which there is no open water. The floating mat of vegetation comprising the bog has certain angiosperms in addition to *Sphagnum*. As the mat becomes drier through the accumulation of organic matter, the *Sphagnum* eventually disappears and the hydrophytic angiosperms are replaced by those of a more mesophytic type. Lakes bordered by gently sloping banks may have the *Sphagnum* invading the shore and occupying land several feet above the water. Such "creeping bogs" are due to the extraordinary water-absorbing and water-retaining capacity of *Sphagnum*.

The erect perennial portion of the gametophyte, the gametophore, is differentiated into stem and leaves (Fig. 58). Terminal growth of the stem is due to an apical cell with three cutting faces (Fig. 59*A*). Each segment cut off by the apical cell eventually gives rise to a single leaf and the subtending portion of the stem. When first formed, the leaves are in three vertical rows, corresponding to the three cutting faces of the apical cell, but growth of the stem soon displaces this three-ranked arrangement. A young leaf primordium grows by means of an apical cell with two cutting faces that alternately cut off segments right and left (Fig. 60*A*). Maturation of derivatives from the segments sometimes results in a leaf in which all cells are alike, but more often it results in a leaf with two types of cells. In leaves of the latter type each cell of a young leaf divides asymmetrically into a small cell, which lies toward the margin of a leaf, and a large cell (Fig. 60*C*). The large daughter cell then divides asymmetrically into a large cell and a small cell which lies toward the apex of a leaf. The two small cells formed by these divisions mature into long narrow cells which remain alive and which contain chloroplasts. The third cell enlarges in all directions and develops spiral thickenings on its walls (Fig. 60*D–F*). Its protoplast disappears after enlargement is completed and after there has been a development of large circular pores in the walls. The green photosynthetic and the hyaline cells have a regular reticulate arrangement with respect to one another in a mature leaf. The hyaline cells of leaves and similar cells in the cortex of a stem play an important role in the absorption and retention of water. Leaves of *Sphagnum* frequently have one or more axillary glandular hairs, but these disappear as the leaves become mature.

Every fourth leaf of the stem usually bears a group of three to eight lateral branches in its axil. Near the apex of a stem the branches are short and densely crowded in a compact head. Lower down on the stem they are in tufts. In many cases, especially when the plant does not grow submerged, the branches comprising a tuft are of two sorts, those which are upwardly divergent, and those which are drooping and lying next the stem. Occasionally one of the branches in a tuft continues upward growth to the same height as the main stem and becomes similar to it in structure. These branches eventually become independent plants through progressive death at the base of the axes bearing them. Vegetative propagation by this method is the main reason for the large number of individuals at any station where *Sphagnum* has become established.

The stem is internally differentiated into a central cylinder and an ensheathing layer, the cortex. When first formed, the cortex is but one cell in thickness. Later on the cortex of the main axis becomes four to five cells in thickness, and, as the cells mature, they may develop spirally thickened walls similar to those in hyaline leaf cells. The cortex of lateral branches

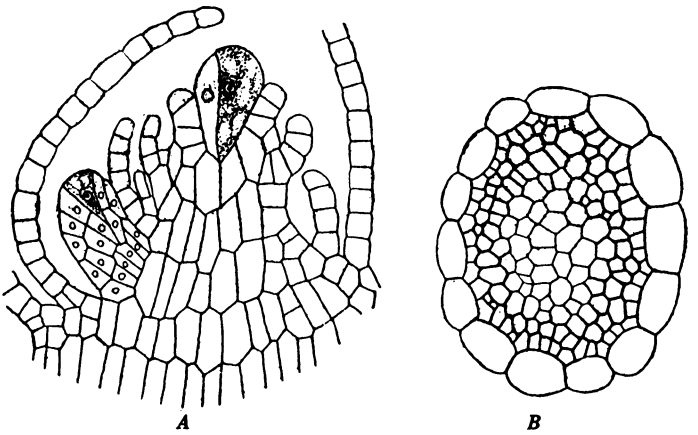

FIG. 59. *Sphagnum subsecundum* Nees. *A*, longitudinal section through apex of a gametophore bearing the primordium of a lateral branch. *B*, transverse section of a lateral branch of a gametophore. (*A*, × 325; *B*, × 215.)

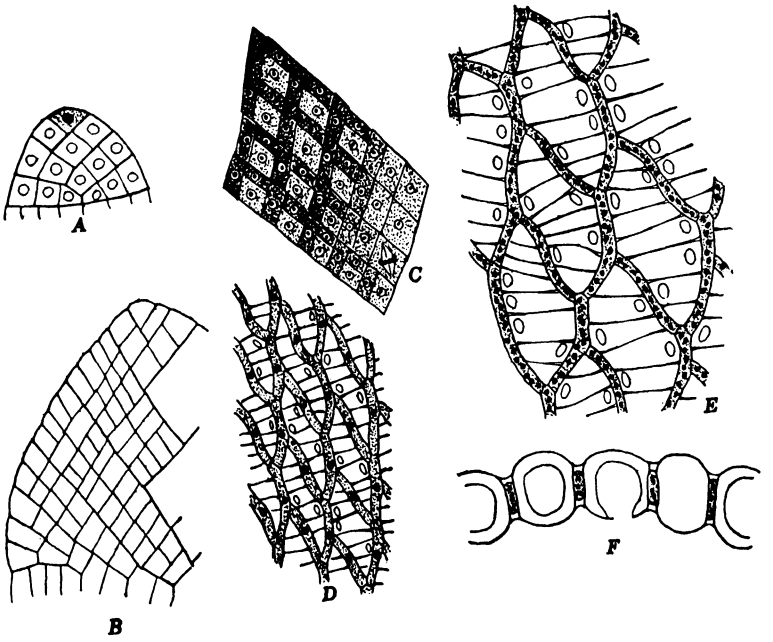

FIG. 60. Development of leaf of *Sphagnum subsecundum* Nees. *A–B*, surface views of a very young and a slightly older leaf. *C–E*, surface views of leaves at successive stages of development. *F*, transverse section of a portion of a mature leaf. (*A*, *C*, × 650; *B*, × 485; *D–F*, × 325.)

never becomes more than one cell in thickness (Fig. 59*B*). Cells toward the exterior of a central cylinder are thick-walled; those at the interior may be thin- or thick-walled.

Mature gametophores have no rhizoids and all intake of water is by direct absorption. Upward movement of water to the apex of a stem is through the cortex in species in which the cortical cells have pores and spirally thickened walls. In species without such cortical cells upward movement of water is by capillarity and in the wick-like system of pendant branches clothing the stem. Proof of this is to be seen in the lack of water movement when stems of such species are denuded of their branches but have their lower ends in water.

According to the species, *Sphagnum* is heterothallic or homothallic. The sex organs are borne on short lateral branches inserted near the apex of a gametophore. The antheridial branches are spindle-shaped and with the leaves in three rows. They are often distinguishable from other branches by their reddish, purplish, or brownish color. Archegonial branches are also inserted just below the apex of the stem. They are more or less globose and sometimes they are a yellowish to a reddish brown.[1] In the Middle West the sex organs begin to develop in the fall, but they are not mature and fertilization does not take place until the following spring.

Antheridia are produced in acropetalous succession and in the axils of leaves on an antheridial branch. The antheridial initial is a superficial cell of the stem. Although not demonstrated beyond all doubt, there seems to be good reason for believing that initials of antheridia and of leaves are homologous. Successive transverse divisions of an antheridial initial result in a filament of a few cells. As growth continues in the filament the terminal cell functions as an apical cell with two cutting faces (Fig. 61*A*). After a young antheridium has become 12 to 15 cells in height, there are two successive vertical divisions in each of the last two to five derivatives from the apical cell (Fig. 61*B–D*). These divisions[2] are similar to those in antheridia of Jungermanniales; that is, an asymmetrical diagonal vertical division divides each cell into a jacket initial and a larger sister cell which soon divides vertically into a jacket initial and a primary androgonial cell. Thus, the body of a young antheridium consists of two to five primary androgonial cells surrounded by a layer of jacket initials. One of these jacket initials is the old apical cell. Further development of the antheridium consists of a division and redivision of the androgonial cells, with compensating divisions in the jacket layer (Fig. 61*E–F*). There may also be vertical division of the stalk cells to form a stalk that is two cells broad. The antherozoids have two flagella of equal length and a structure much the same as in Hepaticae.[3]

Archegonia are borne at the apex of an archegonial branch. Typically

[1] Bryan, 1915. [2] Melin, 1915. [3] Mühldorf, 1930.

there are three of them, a primary archegonium formed from the apical cell of the branch, and two secondary archegonia formed from the last two segments cut off by the apical cell. The first step in development of an archegonium is the production of a short filament of cells (Fig. 61*G–H*). In the primary archegonium this may be by successive transverse divisions, or the terminal cell of the filament may function as an apical cell with two cutting faces.[1] There is no differentiation of an apical cell in

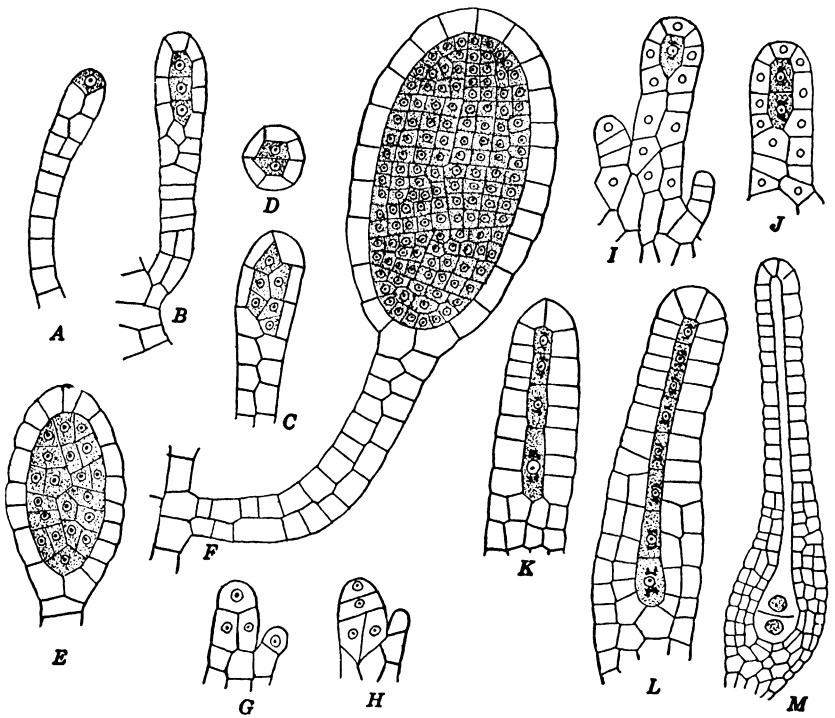

FIG. 61. *Sphagnum subsecundum* Nees. *A–F*, stages in development of antheridia. *G–M*, stages in development of archegonia. (*A–L*, × 325; *M*, × 160.)

the formation of secondary archegonia. No matter how developed, after the filament is four to six cells in length, there is a vertical division of the terminal cell to form three jacket initials and an axial cell. Transverse division of the axial cell produces a cover initial and a central cell (Fig. 61*I*). As in archegonia of other Bryophyta, the central cell divides transversely into a primary canal cell and a primary venter cell (Fig. 61*J*). The primary canal cell ultimately gives rise to a row of eight or nine canal cells (Fig. 61*K–L*). Late in the development of archegonium, there is a transverse division of the primary venter cell into two cells of approxi-

[1] Bryan, 1915.

mately the same size—the venter canal cell and the egg.[1] There is also the usual disintegration of canal cells and venter canal cell late in development of the archegonium, but the nucleus of the venter canal cell may persist until just before fertilization (Fig. 61*M*). The jacket portion of the archegonium is derived from the primary cover cell and the three jacket initials. A mature archegonium does not have a well-marked differentiation into neck and venter. The venter and lower portion of the neck are two or three cells in thickness. The upper part of the neck is but one cell in thickness. The terminal portion of the neck is derived from the primary cover cell, but this cover portion is not sharply differentiated as in archegonia of Hepaticae.

Usually the zygote is formed by union of an egg and an antherozoid, but under certain conditions there may be a gametic union of egg and venter canal cell.[2] The first division of a zygote is transverse and transverse division continues until the embryo is a filament 5 to 12 cells in length.[3] The upper half of the filament develops into the capsule of a mature sporophyte; the submedian portion develops into the foot and seta; and the lowermost portion develops into a haustorium which becomes obliterated as the sporophyte approaches maturity. Each cell in the portion destined to become the capsule undergoes two successive vertical divisions. Periclinal division in each tier of four cells thus formed results in the differentiation of an endothecium and an amphithecium. Division and redivision of the endothecium produce the dome of sterile cells (the **columella**) at the center of a capsule. Periclinal division of the amphithecium divides it into an outer sterile layer and an inner fertile layer (the **archesporium**), both overarching the top of the columella. The archesporium gives rise to a sporogenous layer two to four cells in thickness, after which each sporogenous cell divides meiotically[4] into four spores. The outer sterile layer formed by division of the amphithecium becomes three or four cells in thickness (Fig. 62). The sterile jacket layer thus formed is a homogeneous tissue, except for division of certain superficial cells into a pair of guard cells which lack the usual stomatal opening. All cells of the jacket contain chloroplasts until the capsule is nearly mature.[5] Thus, the sporophyte is not wholly dependent upon the gametophyte for carbohydrates. During later stages in development of a capsule there is a differentiation of a transverse ring in the upper portion of the jacket that delimits the lid (**operculum**) of the capsule. At the same time there is a pronounced thickening of walls of other superficial cells of the jacket.

Ripening of sporophytes in northern parts of the United States, as shown by black color of capsules, is completed by midsummer. Sporophytes are regularly produced by *Sphagnum*, but one rarely finds them in

[1] Bryan, 1915; Melin, 1916. [2] Bryan, 1920*A*. [3] Bryan, 1920.
[4] Melin, 1915. [5] Bold, 1940; Campbell, 1895.

the abundance typical of other mosses. This is due to the fact that sporophytes and associated structures shrivel and become inconspicuous immediately after shedding of spores. Thus, one frequently finds that no sporophytes are evident when one returns to a clump of *Sphagnum* where numerous sporophytes were observed the week before.

Development of a sporophyte is accompanied by a differentiation of the subtending portion of the gametophore into a leafless stalk, the **pseudopodium.** This remains relatively short until the sporophyte is mature, after which it elongates rapidly and pushes the sporophyte above the leaves at the summit of the gametophore. There is an explosive dehiscence of the capsule, and one which may hurl the operculum and spores several inches upward. The explosive dehiscence is due to air pressure developed in the cavity containing the spores.[1]

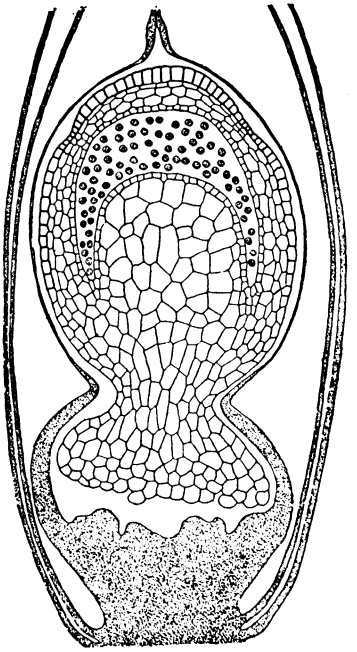

FIG. 62. *Sphagnum subsecundum* Nees. Longitudinal section of a sporophyte and the surrounding gametophytic tissue. (× 60.)

Spores germinate immediately after they are shed if conditions for germination are favorable, but they may remain viable for at least six months.[2] A germinating spore first gives rise to a short filament of a few cells (Fig. 63*A*). Sooner or later the terminal cell of the filament divides diagonally to form an apical cell with two lateral cutting faces which alternately form segments right and left (Fig. 63*B*). The flat plate (**protonema**) thus formed is one cell in thickness. The apical cell soon loses its dominance as the meristematic region of the protonema, and later stages of growth are largely confined to localized regions at the margin of the protonema.[3] This results in an irregularly lobed plate, still one cell in thickness, and a plate in which cells toward the posterior end may give rise to multicellular rhizoids (Fig. 63*C–D*). Any marginal cell may produce a filament which, in turn, may develop into a thallose protonema. As a consequence there may be considerable vegetative multiplication of the thallose protonematal stage.[4]

Erect leafy branches (gametophores) are produced from marginal cells

[1] Nawaschin, 1897. [2] Bold, 1948.
[3] Bold, 1948; Rhuland, 1924. [4] Rhuland, 1924.

near the base of a protonema. Unlike other mosses, only one gametophore is formed by a protonema. A gametophore differentiates an apical cell with three lateral faces and each derivative from the apical cell develops into a leaf and a portion of the stem. In species with leaves composed of

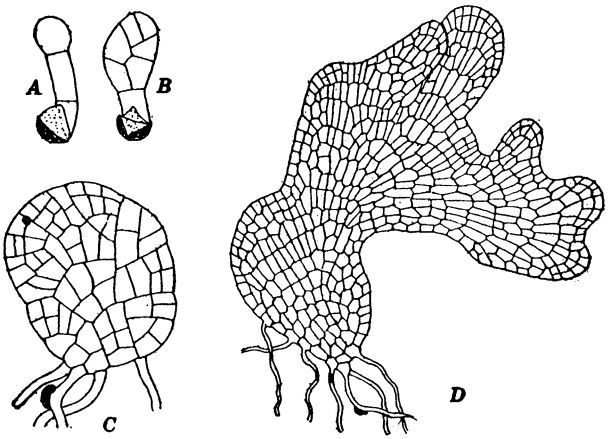

FIG. 63. *Sphagnum cymbifolium* Ehrb. Stages in development of protonema. (*After Müller in Rhuland*, 1924.)

two kinds of cells, the formation of leaves with two kinds of cells does not begin until four or five leaves have been produced.[1]

SUBCLASS 2. ANDREAEOBRYA

The granite mosses (Andreaeobrya) have some features characteristic of Eubrya and others that are characteristic of Sphagnobrya. Gametophores have a vegetative structure similar to that of Eubrya. As in Eubrya, sporogenous tissue of a sporophyte is derived from the endothecium, but in Andreaeobrya it completely overarches the columella. Mature sporophytes are like those of Sphagnobrya in becoming elevated above the gametophore by means of a pseudopodium. The one unique character of Andreaeobrya is the longitudinal dehiscence of the capsule into four valves.

This subclass contains but one order (the Andreaeales) with a single family (the Andreaeaceae) in which there are but two genera, *Andreaea* and *Neuroloma*. The former has about 120 species, the latter a single species.

Andreaea is a genus of small, dark brown to blackish mosses which grow exclusively on siliceous rocks. It is usually restricted to regions with a cold climate and grows either in arctic regions or on the tops of high mountains.

[1] Bold, 1948.

The general structure of a gametophore is like that of Eubrya. The stem grows prostrate along the surface of a rock and with a sympodial branching in which one fork grows more strongly than the other (Fig. 64*A*). The stem bears numerous rhizoids, and these are cylindrical or plate-like accordingly as they grow in crevices of the rock or upon its surface. There is not the internal differentiation into cortex and central conducting

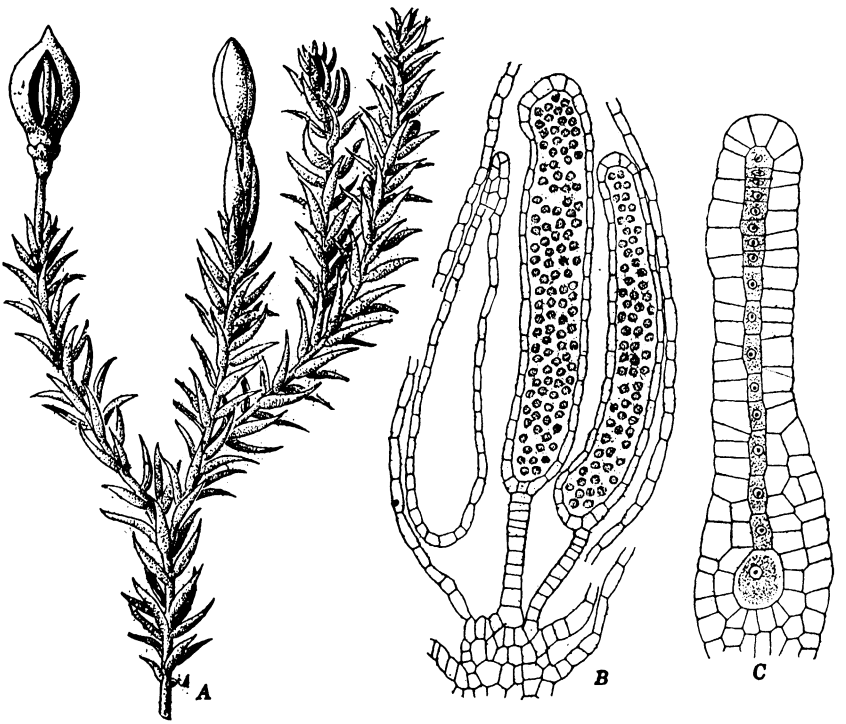

FIG. 64. *Andreaea rupestris* Hedw. *A*, gametophore with mature and immature sporophytes. *B*, longitudinal section through apex of a male plant bearing antheridia. *C*, archegonium. (*A*, × 3; *B*, × 215; *C*, × 430.)

strand that is found in stems of some other mosses, but there may be differences in wall structure of deep-lying and superficial cells.[1] Terminal growth of a stem is by means of an apical cell, and leaves are formed in three rows corresponding to the three cutting faces of the apical cell.[2] Some species have leaves one cell in thickness; others have the median longitudinal axis of the leaf differentiated into a midrib more than one cell in thickness.[2]

The gametophores are usually homothallic and have the antheridia and archegonia in terminal groups on separate branches. So far as known,[3]

[1] Lorch, 1931. [2] Pottier, 1921. [3] Kühn, 1870.

the development of sex organs is similar to that of other Musci. Antheridia have an ellipsoidal body subtended by a long stalk either one or two cells broad (Fig. 64*B*). Archegonia have a short stalk and a long neck (Fig. 64*C*).

The venter of the archegonium increases somewhat in thickness after fertilization and develops into a calyptra which surrounds the sporophyte until it is nearly mature. *Andreaea* is similar to *Sphagnum* in that there is a differentiation of a pseudopodium at the apex of the gametophyte (Fig. 65*C*).

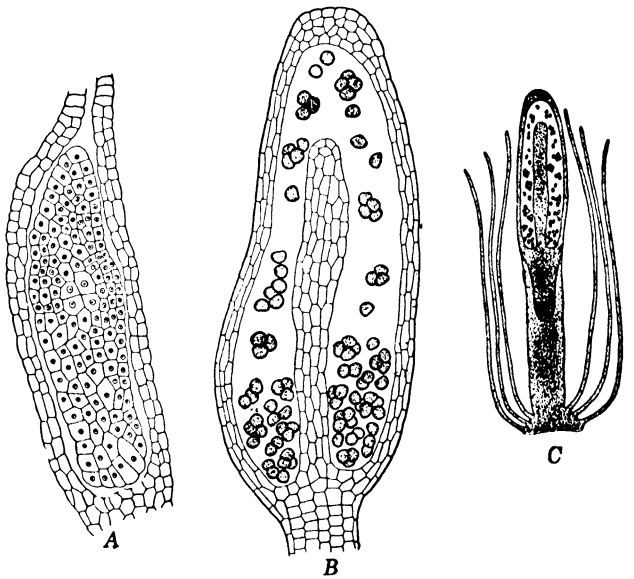

FIG. 65. *Andreaea rupestris* Hedw. *A*, longitudinal section through an embryo. *B*, semidiagrammatic longitudinal section through capsule of a nearly mature sporophyte. *C*, longitudinal section through a mature sporophyte and showing elongation of pseudopodium at the apex of the gametophore. (*A*, × 215; *B*, × 105; *C*, × 30.)

The first division of a zygote is transverse.[1] The hypobasal daughter cell gives rise to an irregularly arranged mass of cells that is haustorial in nature (Fig. 65*A*). The epibasal daughter cell functions as an apical cell with two cutting faces. Each segment from an apical cell divides vertically. The outer daughter cell is an initial cell of the amphithecium, and the inner daughter cell is an initial cell of the endothecium. The amphithecial initials develop into the jacket portion of the capsule and a jacket that eventually becomes three to eight cells in thickness (Fig. 65*B*). Most of the superficial cells of the jacket become thick-walled; but there are four vertical strips of cells, the future lines of dehiscence, that remain small

[1] Waldner, 1887.

and thin-walled. Periclinal division of endothecial initials results in an outer fertile layer, the archesporium, and an inner sterile layer, the primordium of the columella. The archesporium is a dome-shaped layer which eventually develops into a sporogenous layer two cells in thickness. Large chloroplasts have been observed in sterile cells and in sporocytes of developing sporophytes.[1] This indicates that, as in other mosses, the sporophyte is not wholly parasitic on the gametophyte.

When a sporophyte is mature there is an elongation of a pseudopodium that pushes it above enveloping leaves (Fig. 65*C*). Dehiscence of a mature capsule is longitudinal. In most species the four slits formed by rupture of thin-walled jacket cells do not extend to the apex of a capsule (Fig. 64*A*). As in the Eubrya, there is an opening and closing of the ruptured capsule jacket in response to hygroscopic changes, and there is a liberation of spores only at a time favorable for their dispersal.

The protoplast of a spore of *Andreaea* divides several times while still within the spore wall. This is comparable to spore germination in certain Hepaticae, except that in *Andreaea* these divisions take place after the spore is shed. Eventually there is a rupture of the outer spore wall layer (**exosporium**) and a development of a short filament from one or more superficial cells of the exposed globular spore mass. A filament becomes three to five cells in length and then its terminal cell begins to function as an apical cell with a single convex posterior cutting face. There is great variation in structure of the protonema resulting from activity of this apical cell. It may be a much-branched strap-like structure in which certain of the finer branches function as rhizoids; or it may be a leaf-like plate quite similar to the protonema of *Sphagnum*. Protonemata of *Andreaea* are unusual in being able to enter into a dormant stage if conditions for growth become unfavorable. The protonemal stage may develop buds on any portion, center as well as margin. The bud becomes a globose mass of 20 to 30 cells, and then one of them begins to function as an apical cell with three cutting faces. Further growth is apical and similar to that at the apex of a gametophore.

SUBCLASS 3. EUBRYA

The true mosses (Eubrya) differ from other Musci in the following respects: The protonemata are almost always filamentous and gametophores produced by them usually have leaves with a midrib more than one cell in thickness. Sporophytes never become elevated above the gametophore by means of a pseudopodium, but quite frequently the capsule becomes elevated by elongation of the seta. Sporogenous tissue of a capsule is derived from the endothecium and does not overarch the columella. Mature capsules are generally internally differentiated into several tis-

[1] Bold, 1940.

sues. There is no uniformity in mode of opening of capsules but the great majority of genera have the spore cavity covered by a peristome.

There are some 650 genera and 14,000 species. In addition, a number of fossil species are known. Practically all fossil members of the subclass found in North America[1] have been from the Lower Cenozoic (Miocene) and none from periods older than the Upper Cretaceous. The same holds for other continents.

In the case of taxa higher than the genus, bryologists generally follow Brotherus,[2] who recognizes some 80 families. There is less unanimity when it comes to grouping families into orders. For example, in a system based primarily on sporophytic characters only seven orders are recognized;[3] whereas in systems[4] taking into consideration both gametophytic and sporophytic characters the families have been grouped into 14 orders.

Occurrence. Eubrya are found in abundance from polar regions to tropics, wherever there are suitable habitats. They may be found growing in ponds and streams, in bogs and marshes, on soil of firm or loose texture, on rocks and cliffs, and as epiphytes on trunks of trees or on leaves of certain perennial plants. In relation to water they may be hydrophytes, mesophytes, or xerophytes. Their growth in aerial habitats is affected by moisture conditions both of the atmosphere and of the substratum. Many Eubrya grow vigorously in light of moderate or low intensity. Localized light relations in any particular habitat may not be so much a direct effect of light intensity as due to the influence of sunlight on moisture conditions. For example, the greater abundance of mosses on the north side of trees and on cliffs and banks facing north is usually ascribed to more favorable conditions of moisture than to lower light intensities. The hydrogen-ion concentration (pH) of the substratum is another important factor influencing the distribution of mosses, and components of the moss flora of calcareous and siliceous rocks in the same geographical area differ markedly. This factor may also affect distribution of epiphytic mosses. Thus, the differences between the moss floras on bark of coniferous and deciduous trees are correlated with the greater acidity of coniferous bark.

Colonization of a suitable habitat may be rapid or slow. Colonization of moist bare soil, as on a recently plowed field or on a bank of soil exposed by building of a road, is rapid and within a few weeks the soil may be covered with a felt of protonemata bearing young gametophores. Colonization of rocky surfaces is slow. This has been demonstrated experimentally by removing all mosses from a rocky surface and noting the time required for recolonization. In one such experiment[5] there was but little recolonization in five years.

Pioneer species colonizing any habitat may be succeeded by other spe-

[1] Steere, 1946. [2] Brotherus, 1924–1925. [3] Schaffner, 1938; Sharp, 1939.
[4] Brotherus, 1924–1925; Dixon, 1932. [5] Sharp, 1939.

cies in the course of time. The bark of trees is an especially favorable habitat for studying succession since this may be done by comparing the moss flora on young and old trees growing side by side in the same environment. Certain studies[1] on trees of the eastern United States may be cited as representative of this method of investigation. In general, these studies show that the pioneer species disappear sooner or later after they are succeeded by other mosses.

Vegetative Structure of Gametophore. Gametophores of Eubrya are differentiated into two portions, a prostrate **protonema** and upright

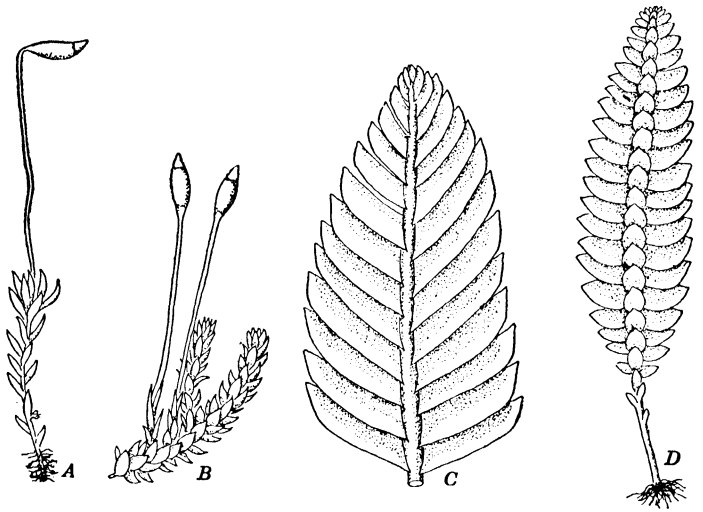

FIG. 66. Gametophores with and without sporophytes. *A*, *Mnium orthorhynchum* Bridw. *B*, *Leskea pulvinata* Wahlenb. *C*, *Phyllogonium fulgens* (Sw.) Bridw. *D*, *Cyathophorum bulbosum* (Hedw.) C.M. (*C–D*, *after Schimper*, 1836–1855.) (*A*, × 1½; *B*, × 5; *C*, × 7; *D*, × 1¼.)

gametophores. Except for a comparatively few genera, the protonema is a transitory structure, and the adult plant consists only of persistent gametophores. The gametophore may be branched or unbranched; with all branches erect, or with certain of them erect and others prostrate. In the latter case the prostrate branches may grow above or below the surface of the substratum.

Gametophores are differentiated into stem and leaves (Fig. 66). Young leaves at the apex of a stem are arranged in a definite manner. Typically, the arrangement is directly correlated with the number of cutting faces of the apical cell of the stem. Most genera have an apical cell with three cutting faces, the young leaves being spirally arranged in three vertical rows. Mature leaves, back from the apex, may not be definitely arranged because of torsions and displacements appearing during the maturation of

[1] Billings and Drew, 1938; Cain and Penfound, 1938; Phillips, 1951; Sharp, 1939.

the stem. Erect branches of a few genera, including *Phyllogonium* (Fig. 66*C*), have an apical cell with two cutting faces, but prostrate branches of these genera generally have apical cells with three cutting faces. Here the leaves on erect branches are in two vertical rows, and this arrangement usually persists in older parts of the stem. However, stems with the young leaves in three rows may have what appears to be a two-ranked arrangement of the older leaves. This bilateral symmetry is usually due to an asymmetric bending of the leaves so that the shoot is distinctly flattened. Many of the creeping mosses growing on trunks of trees have stems of this

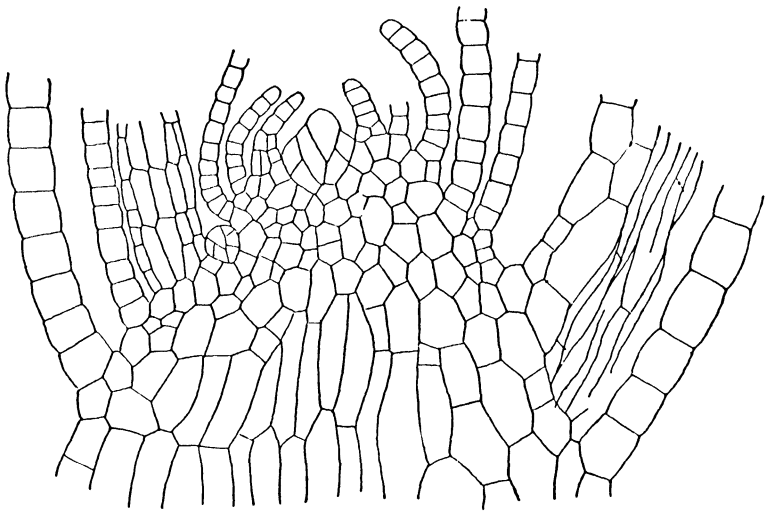

FIG. 67. *Amblystegium riparium* Bruch and Schimp. Median longitudinal section through apex of gametophore and showing the apical cell of the stem and the apical cell of an embryonic lateral branch. One leaf on each side of the stem is cut diagonally. (× 225.)

type. A flattening of the shoot may also be due to the fact that the leaves of two vertical rows become large, whereas those of the third row remain small. Mosses of this type, as *Cyathophorum* (Fig. 66*D*), have a superficial resemblance to acrogynous Jungermanniales.

When the apical cell is three-sided, segments are cut off in regular sequence from the three cutting faces. The first division in a segment is periclinal (Fig. 67). The inner daughter cell contributes to the inner portion of the stem; the outer daughter cell develops into a leaf and the subtending outer portion of the stem.[1]

The first division of the outer daughter cell is approximately perpendicular to the preceding plane of division. The superior daughter cell thus formed develops into a leaf; the inferior daughter cell gives rise to the cortical portion of the stem. Very early in development of a leaf there is an

[1] Lorch, 1931; Rhuland, 1924.

establishment of an apical cell whose two cutting faces alternately cut off segments right and left. The leaf thus formed may be but one cell in thickness throughout, but more often the axial portion becomes differentiated into a midrib that is more than one cell in thickness (Fig. 68*B*). In some genera the midrib extends only part way to the apex of the leaf; in other genera it extends to the apex of the blade; in still other genera it continues as an apical projection beyond the blade. Midribs, when present, are always composed of elongate cells in which the walls are usually conspicuously thickened. Leaves with a midrib have the chloroplasts restricted to the laminate portion one cell in thickness. Some leaves have a supplemental photosynthetic tissue of longitudinal lamellae borne

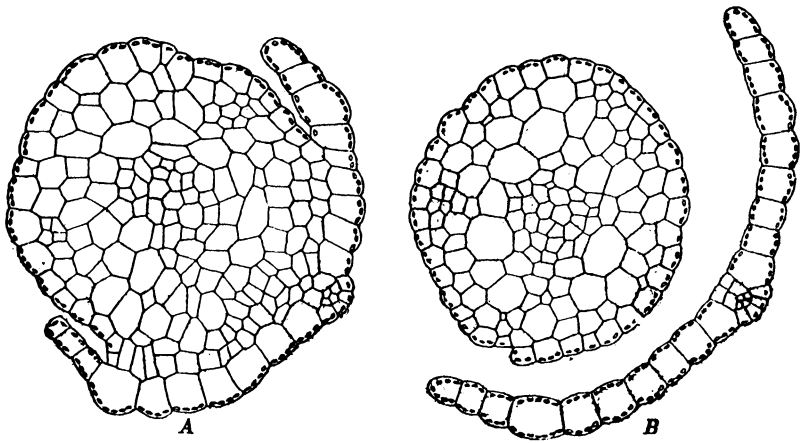

FIG. 68. *Funaria hygrometrica* Hedw. *A*, transverse section of a gametophore at the level of juncture of a leaf with the stem. *B*, the same leaf and stem cut at a slightly higher level. (× 160.)

chiefly in the region of the midrib. These lamellae are usually several cells in height and one cell in thickness (Fig. 69). Differences in the structure of the midrib and in the structure of cells at the margin of a blade, together with differences in concavity of the blade and the extent to which it is twisted, are of major taxonomic importance. Because of this the systematist keeps mounted leaves along with his herbarium material.

Leaves borne on different portions of the gametophore may also differ from one another. Those borne on prostrate branches and on the lower portion of erect branches are often scale-like, nearly colorless, and of simpler construction than those on the upper portion of an erect branch. The **perichaetial leaves** immediately next to the sex organs may also be different in size and shape from the **foliage leaves** lower on the stem. However, in passing down a stem the transition from perichaetial to foliage leaves is gradual, not abrupt.

A mature stem of a moss is differentiated into central cylinder, cortex, and epidermis. Cells of the central cylinder are vertically elongate, are of smaller diameter than those of the cortex, and have greatly thickened or relatively thin walls (Fig. 68). In most cases the central cylinder is a fairly uniform tissue except for differences in thickness of the walls. In certain mosses, as *Polytrichum*,[1] the axial portion of the central cylinder contains thick-walled cells with living protoplasts (**stereids**) and empty thin-walled cells (**hydroids**) intermingled with each other. The outer portion of such cylinders consists of an incomplete pericycle-like sheath of thin-walled living cells.

Cortical cells in young portions of a stem usually contain chloroplasts; those in older portions of the stem lack them. A fully mature cortex

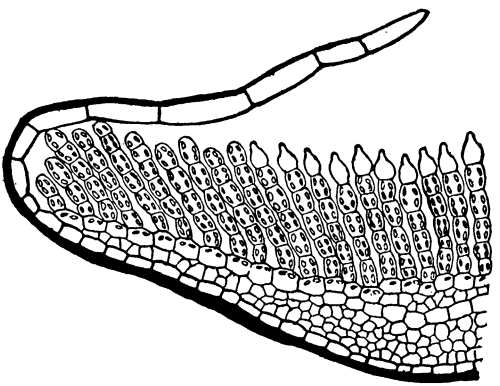

FIG. 69. Transverse section of a leaf of *Polytrichum juniperum* L. (× 215.)

usually grades off from thick-walled cells at the exterior to thin-walled cells next the central cylinder. In mosses whose leaves have midribs the cortex usually contains "leaf traces" running diagonally from the leaves to the central cylinder. These traces may be homogeneous in structure or differentiated into stereids and hydroids. The epidermis may be one or more cells in thickness and have thick or thin walls. There is never a differentiation of guard cells in the epidermis.

Although it is gametophytic in nature, the moss stem has an internal differentiation comparable to that of the stem in sporophytes of vascular plants. This resemblance has led to the assumption that conduction of water up the stem of a moss is through the central cylinder and that hydroids, when present, are special water-conducting elements. Later investigations[2] seem to show that, irrespective of whether a moss is growing in a wet, moist, or dry habitat, only a relatively small amount of water moves up through the central cylinder. Most upward movement

[1] Tansley and Chick, 1901. [2] Bowen, 1933, 1933*A*, 1933*B*.

is external and by means of capillary films of water between leaves and stem. These experiments seem to show that the major function of the central tissue, and of the midrib of the leaf, is that of a mechanical tissue, but this has been denied by others who hold[1] that internal tissues of stems are also of importance in the conduction of water.

Primordia of branches arise a short distance back from the growing apex of a stem. Each primordium is the result of the differentiation of a superficial stem cell into an apical cell. The cell thus differentiated lies below a young leaf, not axillary to it.[2] Development of a branch is identical with development at a stem apex, the apical cell successively cutting off segments from its cutting faces (Fig. 70).

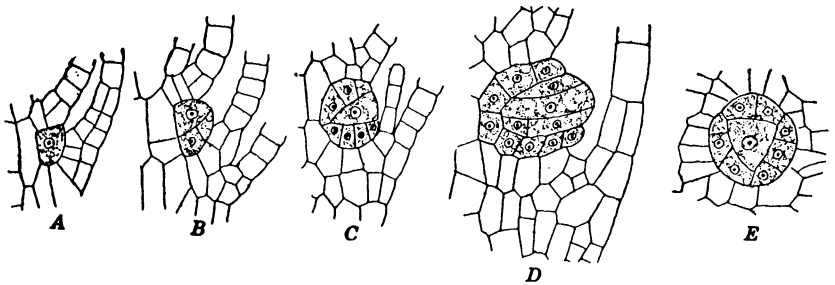

FIG. 70. *Amblystegium riparium* Bruch and Schimp. *A–D*, vertical sections of a stem showing branch primordia in longitudinal section. *E*, the same with a branch primordium in transverse section. (× 325.)

Vegetative Multiplication. When mosses grow in favorable habitats, they are usually in dense stands produced by extensive vegetative multiplication. There are certain rather widely distributed mosses which have never been observed with sporophytes and in which all reproduction seems to be by vegetative propagation of the gametophyte. Vegetative multiplication takes place in a variety of ways, including:

1. *Progressive Growth and Death of the Gametophore.* This method of asexual reproduction so characteristic of Hepaticae is largely restricted to Eubrya with prostrate rhizomes bearing erect branches. After death of the prostrate branch each erect aerial branch persists as an independent plant. Sometimes separation of erect branches from the parent plant is due to the development of a special abscission layer.

2. *Gemmae.* A rather large number of mosses produce small multicellular gemmae. These are formed in groups and either at the tips of leaves, along the midrib, along the sides of branches, or at the stem apex. Solitary gemmae may be formed on rhizoids, either those of protonemata or those of the leaf shoot. Subterranean gemmae of this type are usually called bulbils.

[1] Mägdefrau, 1935. [2] Rhuland, 1924.

3. *Primary Protonemata.* A protonema developing from a spore usually forms several buds. Development of the buds into leafy shoots, followed by death of the protonema, results in several independent gametophores. The number of gametophores may also be increased by multiplication of the protonemal stage. Death of cells here and there in a protonema results in short fragments, each of which may grow into a new protonema.

4. *Secondary Protonemata.* When growing in light, rhizoids of a leafy shoot may become protonemal in nature and produce buds just as do protonemata from germinating spores. Development of the buds into gametophores, followed by death of the protonema-like rhizoids, results in new independent gametophores. Secondary protonemata may also be developed from wounded portions of the leafy shoot. The wounded tissue may be that of a leaf or a stem.

5. *Apospory.* Wounding of sporophytic tissue may result in the production of a protonema. The gametophytes thus developed are aposporous in origin, since they are formed from the sporophyte without a production of spores. Notwithstanding the fact that their cells have the diploid number of chromosomes, the aposporously produced protonemata and gametophores are normal in appearance and with fertile gametes. Fertilization may take place between gametes from two diploid gametophores, or between gametes from a diploid and a haploid gametophore. According to the origin of the gametes, the new sporophyte has $4n$ or $3n$ chromosomes.[1]

Sexuality of Gametophores. Sex organs are borne terminally on gametophores and almost always there is a development of more than one of them at the end of a branch. A gametophore may be **acrocarpous** and with sex organs borne terminally on the main axis and its major branches (Fig. 66*A*), or it may be **pleurocarpous** and with sex organs restricted to the apices of short lateral branches (Fig. 66*B*). Perichaetial leaves adjoining sex organs may differ somewhat from foliage leaves lower on the stem and they may lie close together in a distinct "floral envelope," the **perichaetium.**

Gametophores of Eubrya may be homothallic or heterothallic. Homothallic species bear their sex organs in a variety of ways. Most conspicuous among these are: the **autoicous mosses** in which antheridia and archegonia are borne on separate branches; the **paroicous mosses** in which antheridia and archegonia are borne in the same head but in separate groups that are sometimes segregated from one another by perichaetial leaves; and the **synoicous mosses** in which antheridia and archegonia are intermingled in the same head. When the protonema connecting gametophores of an autoicous moss has disappeared it is impossible to tell by examining the gametophores whether the moss is autoicous or heterothallic. Conclusive proof of heterothallism can be established only by

[1] Marchal and Marchal, 1911; von Wettstein, 1923.

growing a species in pedigreed cultures, each derived from a single spore, to show that all gametophores produced by a protonema are of the same sex.[1]

Among the most interesting of mosses are the sexually dimorphic ones in which female gametophores are markedly larger than male gametophores. The most striking of these is *Buxbaumia aphylla* L., whose green persistent protonema bears gametophores with but little chlorophyll. The stem of a female gametophore bears a few leaves (Fig. 71*A*) and terminates in a single archegonium. Male gametophores have but one leaf, shaped much like a clamshell and overarching one antheridium (Fig.

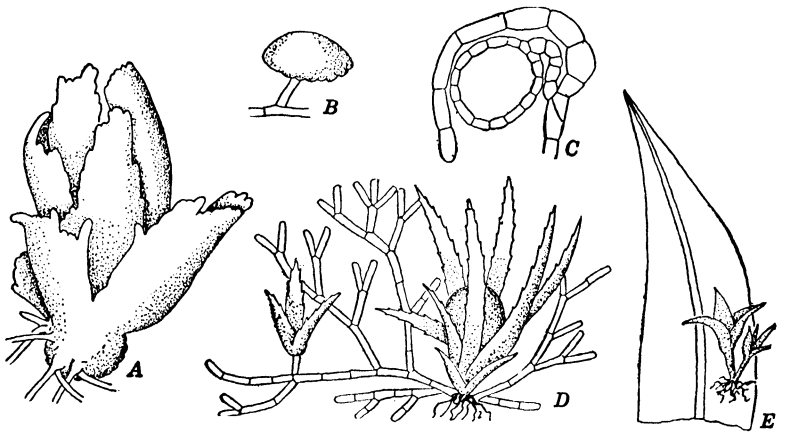

FIG. 71. Sexual dimorphism. *A–B*, *Buxbaumia aphylla* L. *A*, female gametophore. *B*, male gametophore. *C*, *Buxbaumia indusiata* Bridw., vertical section of a male gametophore and showing the single antheridium. *D*, *Ephemerum serratum* Hampe, protonema with mature male and female gametophores. *E*, *Micromitrium salakanum* C.M., leaf from a female gametophore with a mature male gametophore growing upon it. (*A–B*, *after Dening*, 1935; *C*, *after Goebel*, 1892; *D*, *after Schimper*, 1836–1855; *E*, *after Fleischer*, 1902–1904.) (*A–B*, × 70; *D*, × 20; *E*, × 25.)

71*B–C*). *B. aphylla* is heterothallic and with a genotypic determination of sex.[2] A number of markedly dimorphic tropical mosses have the dwarf male plants generally growing on leaves of female plants.[3] In one genus of this type, *Micromitrium*, certain species are heterosporous, the small spores producing male plants (Fig. 71*E*), and the large spores producing female ones.[4] Homothallic species may also have a dimorphism of gametophores. The most frequently cited example of this is *Ephemerum serratum* (Schreb.) Hampe, an acrocarpous moss whose protonemata are persistent and in which a single protonema bears both mature male and female gametophores (Fig. 71*D*). Male gametophores have but three to four leaves and produce three to four antheridia. Female gametophores have

[1] Brown, 1919. [2] Dening, 1935. [3] Fleischer, 1920.
[4] Ernst-Schwarzenbach, 1939, 1944.

six to twelve leaves, somewhat larger than those on male gametophores, and produce two or three archegonia.

Ontogeny of Sex Organs. The production of sex organs at the end of a branch, especially that of antheridia, is not simultaneous, and in actively growing gametophores all stages in development may be found in the same head. In certain cases the first sex organ to appear comes from the apical cell, and later-formed ones come from segments previously cut off by the apical cell. In other cases this is very doubtful. Many mosses have multicellular hairs (**paraphyses**) intermingled with the sex organs, especially

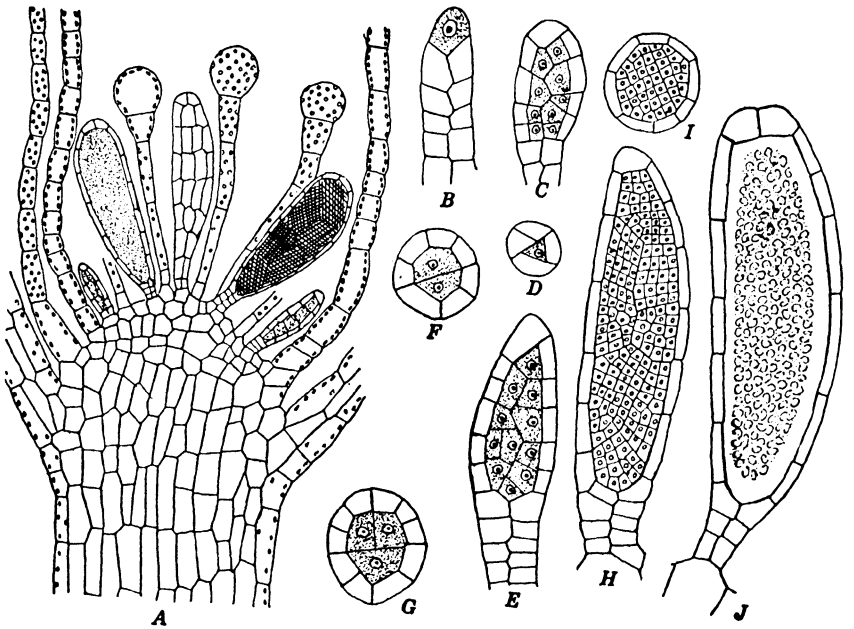

FIG. 72. *Funaria hygrometrica* Hedw. *A*, vertical section through the apex of a fertile male gametophore. *B–J*, stages in development of antheridia. (*B–C*, *E*, *H*, *J*, in longitudinal section; *D*, *F–G*, *I*, in transverse section.) (*A*, × 120; *B–G*, × 485; *H–J*, × 325.)

the antheridia (Fig. 72*A*). Paraphyses may be one or more than one cell in breadth and have a pointed or globose apex. Their function is not definitely established, but it is not improbable that water held between them by capillarity helps prevent undue desiccation.

The initial of an antheridium is a superficial cell at the apex of a stem or branch. This cell soon becomes a papillate projection, after which it divides transversely. The outer daughter cell develops into all of the mature antheridium except the lower embedded portion of the stalk. The outer cell divides transversely to form a filament two or three cells in length and then the terminal cell begins to function as an apical cell with

two cutting faces (Fig. 72*B*). Five to fifteen regularly arranged segments are cut off by the apical cell, and the last three to six cut off may have much denser protoplasts than the others. Even before the apical cell has ceased functioning, a segment three or four removed from it divides in a diagonally vertical plane. One daughter cell is a jacket initial. The other cell is one that divides into another jacket initial and a primary androgonial cell (Fig. 72*C–D*). Thus the sequence in division in upper segments from the apical cell resembles that in primary antheridial cells of Jungermanniales.[1] All the upper segments cut off by the apical cell eventually divide periclinally in this manner. It is not known whether the apical cell contributes only to the antheridial jacket, or divides periclinally to form a jacket cell and a primary androgonial cell. In the case of *Funaria* it seems to contribute only to the opercular portion of the jacket layer (Fig. 72*C*, *E*, *H*). Each of the primary androgonial cells divides and redivides to form a large number of androcyte mother cells. These divisions are accompanied by compensating divisions in the jacket layer (Fig. 72*C–H*). The typical club-shaped body of a moss antheridium, as contrasted with the ovoid or globose body in Hepaticae, results from the fact that there are several superimposed elements which give rise to the body of an antheridium. *Funaria* also differs from the Hepaticae in that the division of each androcyte mother cell into two androcytes is not diagonal.[2] Metamorphosis of the androcytes into biflagellate antherozoids is essentially the same as in Hepaticae.[3]

Mature antheridia have the jacket apex differentiated into an **operculum** whose cells are readily distinguished by their larger size, thicker walls, and more hyaline contents (Fig. 72*J*). The operculum may consist of one, two, or several cells.[4] As already indicated, it seems to be derived from the apical cell of a young antheridium. Dehiscence of antheridia does not take place until after they have been moistened and have absorbed considerable water. The intake of water by the jacket cells causes them to become more turgid, and the resultant hydrostatic pressure of the antheridial contents ruptures the operculum and forces out the mass of antherozoids. Except for the lack of an operculum and for their more hyaline appearance, empty antheridia look very much like those which have not discharged their contents.

The early development of an archegonium is also effected by an apical cell with two cutting faces, but it cuts off only four to eight segments (Fig. 73*A–D*). Division and redivision of these segments eventually produce the long columnar stalk of the mature archegonium. After it has cut off four to eight segments, the apical cell changes abruptly in nature and de-

[1] Campbell, 1918; Rhuland, 1924. [2] Allen, 1912.
[3] Allen, 1912, 1917. [4] Goebel, 1898.

velops three cutting faces.[1] Only one segment is cut off from each of the three faces (Fig. 73*E*). These three segments are the three **peripheral initials** which encircle the **axial cell** (the former apical cell). There then follows a vertical division of each peripheral initial to produce the six **jacket initials** encircling the axial cell. Different from the Hepaticae, there is no transverse division of the jacket initials to form a tier of neck initials and a tier of venter initials. During further development of an archegonium the jacket portion of the neck may become 40 to 50 cells in height (Fig. 73*I–K*).

Coincident with formation of the jacket initials there is a transverse division of the axial cell into a **primary cover cell** and a **central cell** (Fig.

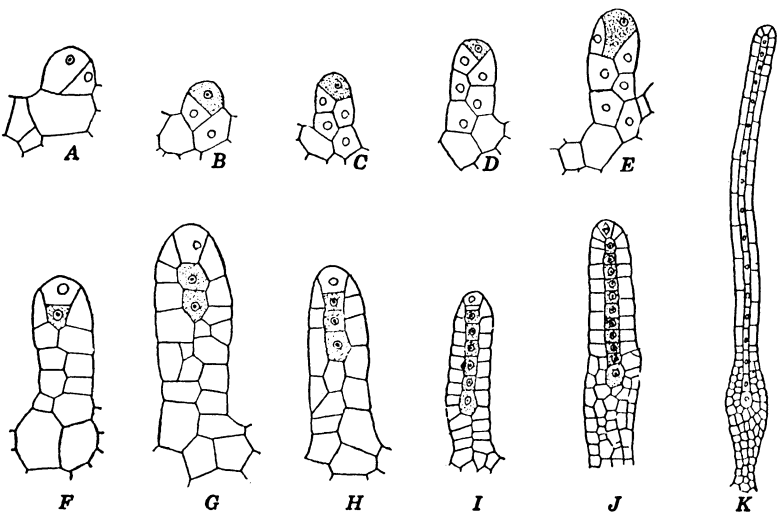

FIG. 73. *Cyathophorum bulbosum* (Hedw.) C.M. Stages in development of archegonium. (*After Burr*, 1939.) (*A–H*, × 350; *I–J*, × 175; *K*, × 85.)

73*E*). The central cell soon divides transversely into a **primary canal cell** and a **venter cell** (Fig. 73*G*). In genera where archegonial development has been studied in greatest detail[1] the neck of an archegonium has a double origin. The upper portion of it is derived from segments cut off from the primary cover cell. Segments cut off laterally from the primary cover cell contribute to the jacket layer of the neck; those cut off posterior to it contribute to the row of **neck canal cells.** The median and lower portion of the neck have the neck canal cells produced by the primary canal cell, and the jacket portion encircling them produced by the jacket initials. During late stages in development of an archegonium there is the usual division of the venter cell into a **venter canal cell** and **egg.** This is followed by the usual disintegration of the neck canal cells and the venter canal cell.

[1] Bryan, 1917; Burr, 1939; Holferty, 1904.

Abnormal archegonia are of frequent occurrence among Eubrya, and it is not uncommon to find archegonia in which cells within the neck, venter, or even the stalk divide and redivide to form a mass resembling androgonial cells. The phylogenetic significance of this has already been noted (see page 8).

Fertilization is effected through the agency of water. All that is necessary in paroicous and synoicous mosses is a connecting film of water between antheridia and archegonia. Among autoicous and heterothallic mosses there is generally a water transport of antherozoids to the vicinity of archegonia. This may be accomplished by raindrops spattering from heads containing antheridia to those with archegonia, or by antherozoid-containing water trickling down to archegonial branches. In the case of a moss growing on a vertical rocky surface it has been shown[1] that antherozoids were transported 2 to 3 feet. In any case entrance of antherozoids into an archegonium is in response to chemical stimuli.[2] Karyogamy follows soon after gametic union and in the case of *Funaria*[3] this may be completed within 10 hours.

The Embryo. Development of a sporophyte begins with an enlargement of the zygote and a transverse division of it. The epibasal daughter cell, by two successive diagonal divisions, differentiates an apical cell with two cutting faces. The hypobasal daughter cell gives rise to an apical cell in a similar manner. Young embryos of Eubrya differ from those of almost all other Bryophyta in this formation of two growing points. The upper apical cell alternately cuts off many segments right and left. These ultimately give rise to the capsule and major portion of the seta. Segments from the lower apical cell ultimately produce the foot and lower portion of the seta.

A considerable number of genera have been shown[4] to contain chloroplasts from the time when an embryo consists of but a few cells until it is mature. The presence of starch in these chloroplasts shows that photosynthesis begins early in development of a sporophyte and continues throughout further development. However, it is impossible to estimate the extent to which a sporophyte is independent of the gametophyte with respect to the necessary photosynthates.

The young embryo is long and slender. Its lower end burrows through the stalk of the archegonium and into the apex of the gametophore. Early growth of an embryo is accompanied by an enlargement of the surrounding archegonium, now known as the **calyptra.** Later on, more rapid growth and elongation of the embryonic sporophyte cause a transverse rupture of the calyptra, and the severed upper portion of the calyptra remains perched upon the sporophyte apex until its capsule is nearly mature.

[1] Burr, 1939. [2] Åkerman, 1915. [3] Beardsley, 1931.
[4] Bold, 1940.

Eubrya, unlike other mosses, do not have the apex of a gametophore developing into a pseudopodium. Sporophytes of most genera resemble those of Jungermanniales in forming a long seta which elevates the capsule above enveloping leaves of the gametophore. Elongation of the seta is gradual in Eubrya, instead of sudden and when the capsule is nearly mature as in Jungermanniales. Setae of Eubrya generally have a well-defined central strand. It is generally assumed that the chief function of the strand is conduction of food materials to the developing capsule, but

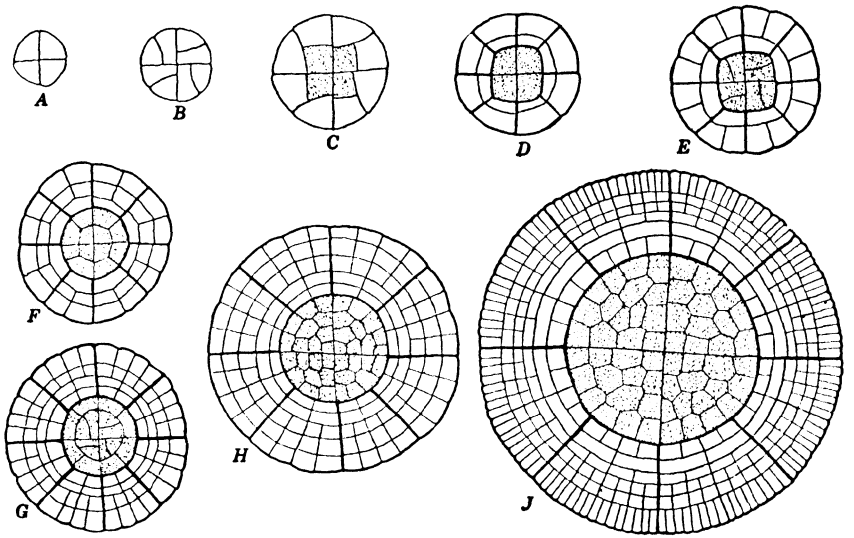

FIG. 74. *Funaria hygrometrica* Hedw. Diagrams showing progressive development at successive levels below the apical cell of a capsule. The endothecium and its derivatives are shaded; portions derived from each of the amphithecial cells are outlined with a heavy line. (× 300.)

there has been no experimental demonstration of this. Possibly the central strand of a seta is similar to the central strand of a leafy gametophore in that it functions chiefly as a mechanical tissue.

Development of the Capsule. The capsule of a sporophyte is derived from segments alternately cut off right and left by the apical cell at the apex of an embryo. The first division in a segment is vertical. A transverse section of a sporophyte apex at this stage of development shows four quadrately arranged cells because two vertically divided segments are apposed to each other (Fig. 74*A*). In most genera this is followed by a vertical division of each of the four cells.[1] Since the plane of division is also vertical and perpendicular to an internal wall, one daughter cell in each quadrant is approximately triangular when seen in transverse section, and

[1] Blomquist and Robertson, 1941; Burr, 1939; Evans and Hooker, 1915; Wenderoth, 1931; Wijk, 1929.

the other is approximately rectangular (Fig. 74*B*). The eight cells thus formed may or may not be so arranged with respect to one another that there is a regular alternation of triangular and rectangular cells. Periclinal division of the four rectangular cells differentiates a symmetrical quadrant of **endothecial cells** surrounded by an encircling layer of eight **amphithecial cells** (Fig. 74*C*).

In genera where ontogeny of the capsule has been followed in detail,[1] cell divisions in the amphithecium and its derivatives are according to a very definite pattern. The amphithecium divides periclinally to form two concentric layers eight cells in perimeter (Fig. 74*D*), the inner of which will be referred to as the **first ring.** Cells of the layer external to the first

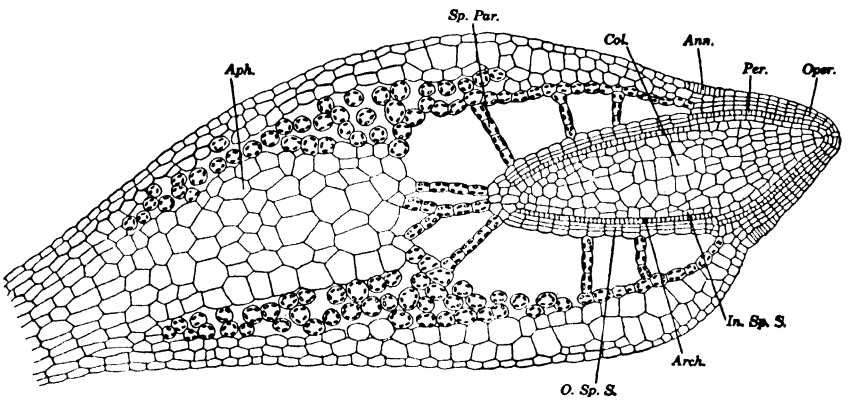

FIG. 75. Longitudinal section of an immature capsule of a sporophyte of *Funaria hygrometrica* Hedw. (*Ann.*, annulus; *Aph.*, apophysis; *Arch*, archesporium; *Col.*, columella; *In. Sp. S*, inner spore sac; *O. Sp. S.*, outer spore sac; *Oper*, operculum; *Per.*, peristome; *Sp. Par.*, spongy parenchyma.) (× 80.)

ring divide anticlinally and then all daughter cells divide periclinally (Fig. 74*E–F*). Of these two concentric layers 16 cells in perimeter, the inner will be referred to as the **second ring.** In turn, cells of the layer external to the second ring divide anticlinally and periclinally to produce two concentric layers 32 cells in perimeter, the inner of which will be referred to as the **third ring.** Similarly, the layer external to the third ring divides periclinally into two concentric layers, the inner the **fourth ring** and the outer the **fifth ring.**

The four quadrately arranged cells of the endothecium divide in a sequence similar to that which differentiates amphithecium and endothecium (compare Figs. 74*B* and 74*E*). However, subsequent divisions in the ring of eight cells corresponding to the amphithecium are in an irregular instead of a regular sequence.

[1] Blomquist and Robertson, 1941; Burr, 1939; Evans and Hooker, 1913; Wenderoth, 1931.

The great majority of Eubrya have the upper part of a capsule maturing into **operculum** and **peristome.** Since maturation in opercular and fertile portions of capsules of operculate mosses is different, development in the two regions will be discussed separately.

The archesporium of a capsule is endothecial in origin and, with the possible exception of *Archidium*,[1] is formed from the outermost layer of cells derived from the endothecium. Some genera, as *Polytrichum*, have an archesporium extending to the base of the capsule. Other genera, as *Funaria* (Fig. 75), do not differentiate an archesporium in the lower portion of a capsule. In such cases the lower portion of a capsule is sterile.

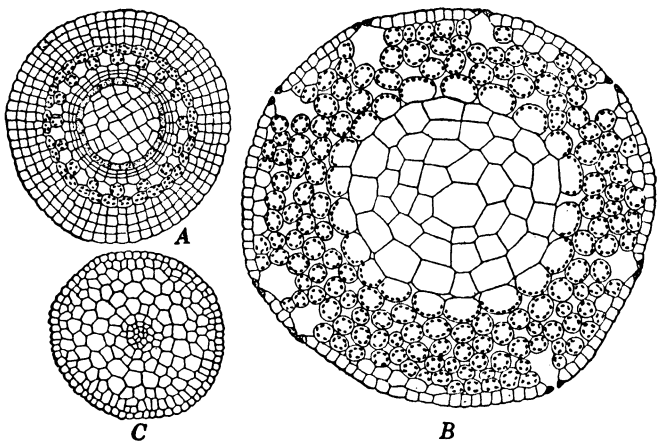

FIG. 76. Transverse sections of sporophytes of *Funaria hygrometrica* Hedw. *A*, through fertile portion of a young capsule. *B–C*, through the apophysis and stipe of a somewhat older capsule. (× 140.)

The archesporium usually develops into a sporogenous layer two cells in thickness and one in which all cells function as sporocytes. Endothecial derivatives internal to the archesporium develop into the **columella.** Columella cells adjoining the sporogenous tissue remain small and mature into the **inner spore sac.** The remainder of a columella may be composed of large colorless cells (*Funaria*) or differentiated into photosynthetic and colorless cells (*Polytrichum*).

The fertile portion of a capsule of *Funaria* will be used to illustrate the tissues matured from the first to fifth rings derived from the amphithecium. In *Funaria* cells of the first ring divide anticlinally to form a layer 32 cells in perimeter (Fig. 74*G–I*). Then all cells divide periclinally to form a layer four cells in thickness. This tissue, the **outer spore sac,** is one whose cells are without chloroplasts (Figs. 75, 76*A*). The second ring becomes 16 cells in perimeter by dividing anticlinally (Fig. 74*H*). Then the cells elon-

[1] Leitgeb, 1880.

gate radially, develop chloroplasts, and become laterally separated by intercellular spaces (Fig. 76*A*). Eventually each cell divides transversely to form a filament of three or four cells (Fig. 75). The third ring becomes 32 cells in perimeter but remains one cell in thickness. Its cells contain chloroplasts when mature (Figs. 75, 76*A*). The fourth ring becomes two cells in diameter. Its cells are relatively large and without chloroplasts when mature. Cells of the fifth ring divide anticlinally and then mature into an epidermis. Mature epidermal cells have greatly thickened walls,

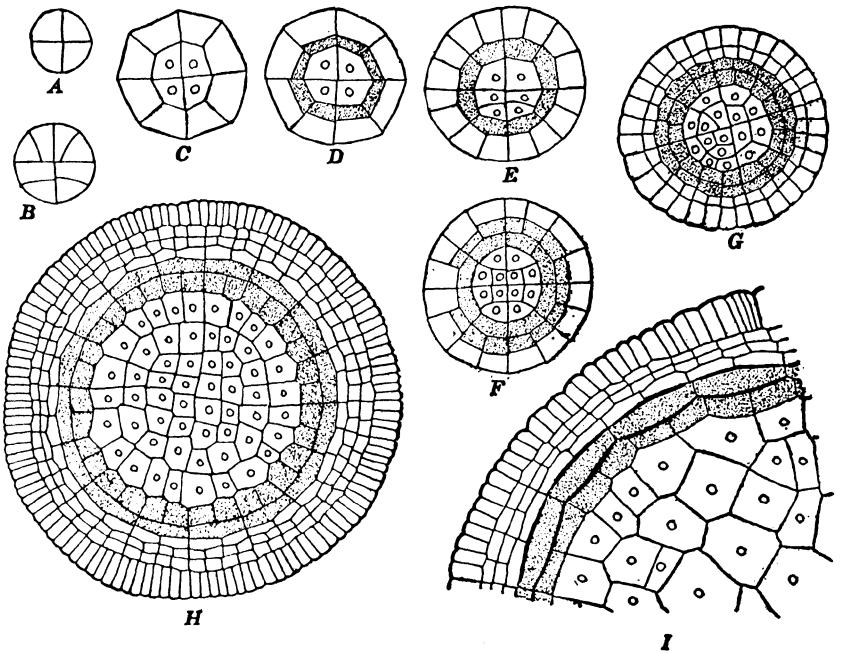

FIG. 77. *Funaria hygrometrica* Hedw. Transverse sections through opercular portion of capsule at successively lower levels. Nuclei are drawn in cells of the columella; cells of the endostome and exostome are shaded. (× 325.)

and here and there in the epidermis are pairs of guard cells surrounding a stoma.

Eubrya with the upper part of a capsule developing into **operculum** and **peristome** are **stegocarpous** mosses. The number of segments (**teeth**) comprising the peristome is always four or a multiple thereof and may be 4, 8, 16, 32, or 64. Teeth may be composed of entire cells, or composed of thickened portions of cell walls. In the latter type of peristome there may be a single set of teeth, or two sets of teeth, one external to the other.

The most detailed studies on development of peristome and operculum have been on genera in which the teeth are not composed of entire cells.[1]

[1] Blomquist and Robertson, 1941; Evans and Hooker, 1913.

These show that the peristome is formed from the first and second rings derived from the amphithecium. In *Funaria* the first ring becomes 32 cells in perimeter and constitutes the **inner peristomial layer.** The second ring becomes 16 cells in perimeter and constitutes the **outer peristomial layer.** Cells in the two layers are so oriented with respect to one another that one outer peristomial cell lies external to two inner peristomial cells (Fig. 77*H–I*). In maturation of a peristome there is a deposition of additional wall material on periclinal walls of peristomial cells. In *Funaria* a thickening of outer periclinal walls of the outer peristomial layer, and a thickening of periclinal walls common to the two peristomial layers results in a

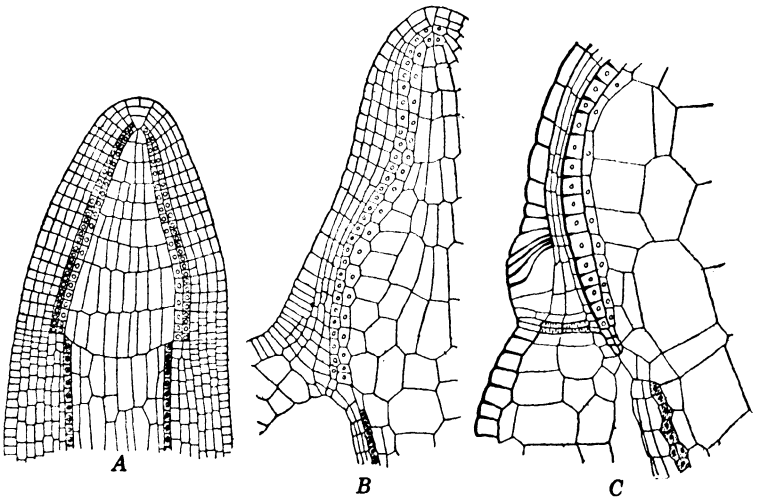

FIG. 78. *Funaria hygrometrica* Hedw. Longitudinal sections through opercular portion of capsule showing successive stages in development of peristome. (× 215.)

peristome with a double set of teeth. (Genera with the mature peristome consisting of a single set of teeth have thickening of periclinal walls restricted to common walls separating the two peristomial layers.) There is no appreciable thickening of anticlinal walls of peristome cells. This makes possible a vertical splitting of the peristome along the unthickened radial (anticlinal) walls. The number of teeth formed is dependent upon the number of cells in the outer peristomial layer and accordingly as it is 16 or 32 cells in perimeter it splits into 16 or 32 teeth. Genera with peristome teeth composed of entire cells may have lateral adhesions between the cells and so a formation of four or eight teeth.

In the portion external to the peristome the third to fifth rings derived from the amphithecium give rise to the operculum. In *Funaria* the third and fourth rings jointly develop into a thin-walled tissue three cells in thickness (Figs. 77*H–I*, 78*C*). Cells of the fifth ring mature into the epi-

dermis of the operculum. Epidermal cells at the base of an operculum enlarge radially to form an **annulus** whose lowermost cells are thin-walled at maturity (Fig. 78*C*). Other epidermal cells are thick-walled. During final ripening of a capsule there is a drying out and shriveling of thin-walled operculum cells below the epidermis, and in the thin-walled cells at the base of the annulus. This results in a very loose adhesion between operculum and underlying tissues. Shedding of the operculum has been thought to be due to a simple abscission, but it is more probable that upward hygroscopic movement of the peristome assists in the abscission. Shedding of the operculum does not result in an exposure of the spores because the peristome teeth still cover the mouth of the spore sac. Teeth of a peristome exhibit pronounced hygroscopic movements. In dry weather they bend outward and thus make possible a sifting out of spores from a capsule. In moist weather they bend down over the spore sac of a capsule. Thus, hygroscopic movement of teeth results in an open capsule at a time favorable for dispersal of spores by wind, and a closed one at a time unfavorable for spore dispersal. Although the foregoing principle of opening and closing applies to all stegocarpous mosses, there is considerable variation from genus to genus in the manner in which teeth bend.[1]

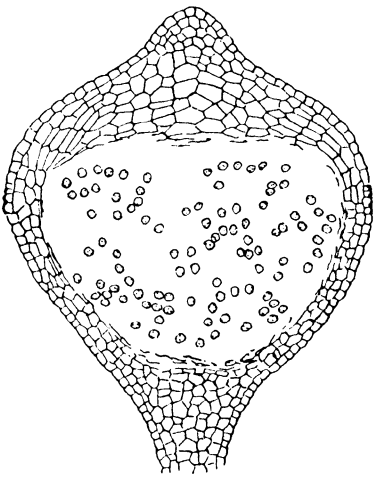

FIG. 79. Longitudinal section of capsule of *Physcomitrium sphaericum* (Ludw.) Bridw., a cleistocarpous moss in which the columella disintegrates. (*After Loeske*, 1929.) (× 50.)

There are some Eubrya where there is no formation of a peristome (Fig. 79). In these **cleistocarpous mosses** a capsule may open by splitting transversely, by splitting longitudinally, or by splitting irregularly. At one time the cleistocarpous genera were thought to be related to one another; but it is now generally believed that cleistocarpy has appeared in unrelated lines among Eubrya. The ontogeny of sporophytes of cleistocarpous mosses is essentially the same as in stegocarpous mosses.[2] In cleistocarpous mosses the columella may persist in the mature capsule, or it may be resorbed during spore development so that the center of the capsule is a spore-filled cavity. The extreme condition is found in *Archidium*. Here there is a differentiation of only a small number of sporocytes. Usually there are four or five, but the number may range anywhere from one to seven. The rather scanty evidence[2] seems to indicate that any cell derived

[1] Steinbrinck, 1897. [2] Leitgeb, 1880.

from the endothecium may become a sporocyte. In any case, there is a disintegration of all endothecial derivatives but the sporocytes and the central cavity of the globose sporophyte is filled with 4 to 28 spores of unusually large size.

Protonema. Germination of a spore usually does not take place until after it has been shed from the capsule, but in certain exceptional genera, as in certain exceptional Hepaticae, the spore develops into a multicellular structure before it is shed. Spores usually germinate immediately

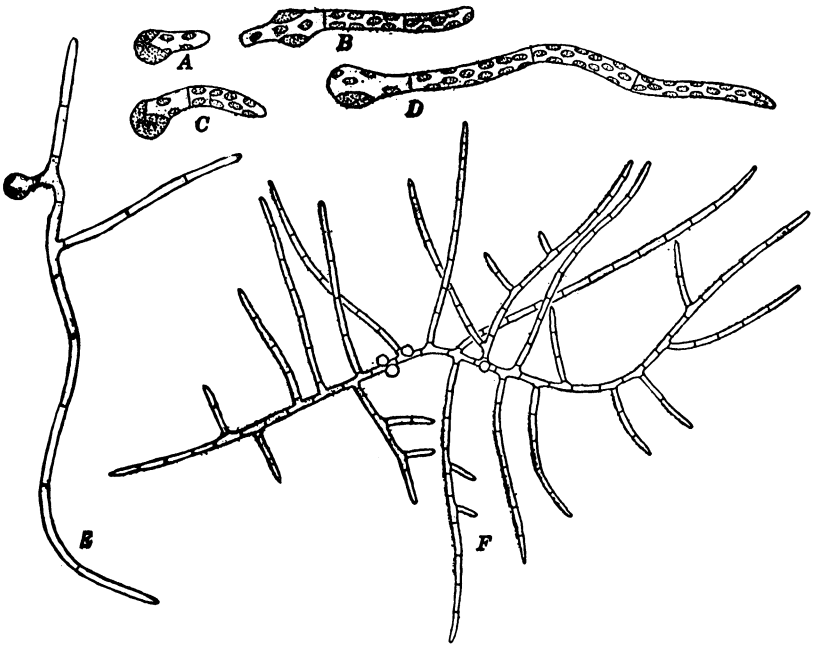

FIG. 80. *Splachnum ovatum* Hedw. Early stages in development of protonema from spores sown on nutrient agar. *A–D*, five days after sowing of spores. *E*, eight days after sowing. *F*, fourteen days after sowing and with initials of gametophores. (*A–D*, × 400; *E*, × 150; *F*, × 100.)

after shedding if conditions are favorable. The length of time they remain viable if conditions are unfavorable varies according to the species. In some species they remain viable but a year or two; in other species they are capable of germinating eight to sixteen years after shedding.[1]

A germinating spore increases somewhat in size, ruptures the outer spore wall layer (**exospore**), and then sends out one or two germ tubes in which the wall is continuous with the inner spore wall layer (**endospore**). A germ tube soon forms a cross wall near its point of emergence (Fig. 80). The cell cut off by this cross wall soon develops into a branched

[1] Malta, 1922; Meyer, 1941.

multicellular filament, the **protonema.** A protonema is differentiated into two kinds of branches, **chloronema**[1] or **chloronemal branches** which grow along the surface of the substratum or into the air for a short distance, and **rhizoids** or **rhizoidal branches** which penetrate the substratum. Chloronemal branches have colorless cell walls, cross walls at right angles to lateral walls, and contain numerous conspicuous chloroplasts. Rhizoidal branches have brown cell walls, diagonal cross walls, and either small chloroplasts or leucoplasts. Portions of rhizoidal branches growing exposed to light have colorless cell walls, cross walls at right angles to lateral walls, and contain conspicuous chloroplasts. Thus, the differences between chloronemal and rhizoidal branches are largely due to environmental conditions. There are a few genera in which, as in *Tetraphis*, the protonema is a flat plate much like that of *Sphagnum.*

When cultured in the laboratory the protonema is much branched and composed of a hundred or more cells before certain of the oldest cells produce erect, globose to club-shaped outgrowths—the **gametophore initials** (Fig. 80*F*). A gametophore initial may or may not form a cross wall separating its protoplast from that of the parent cell (Fig. 81*A–F*). In older portions of a protonema the gametophore initials are usually formed on the lowermost cell of a lateral branch.[2] Gametophore initials of *Funaria* are reported[3] as being formed only on a special profusely branched portion (the **caulonema**) of a protonema, but this is not true for such genera as *Pottia* and *Splachnum.* Early stages in development of a gametophore from an initial cell are more easily demonstrated in species with elongate club-shaped initials, as *Splachnum*, than they are in *Funaria* and other genera with globose initials. In *Splachnum* there is first a diagonal division at the apex of the gametophore initial and this is followed by two additional diagonal divisions that differentiate an apical cell with three cutting faces (Fig. 81*A–B*). The first derivatives from the apical cell may contribute only to the base of the leafy gametophore or there may be a very early differentiation of the first leaf. Rhizoids may grow out from the base of a young gametophore before formation of the first leaf (*Funaria);* or, as in *Splachnum*, there may be no formation of rhizoids until three or four leaves have been formed (Fig. 81*F–G*).

In single spore cultures grown on nutrient agar, protonemata of *Splachnum* became 5 to 6 cm. in diameter in 10 weeks, and those of *Pottia* became about 10 cm. in diameter in the same time. In these cultures, the protonemata of *Splachnum* bore 200 to 250 gametophores spaced 1 to 2 mm. from one another, whereas those of *Pottia* bore 35 to 50 gametophores spaced 5 to 10 mm. from one another. It is very probable that the extensive protonematal mat one often sees colonizing bare soil, such as a roadside embankment, is due to development from a large number of spores

[1] Correns, 1899. [2] Müller, 1874; Sironval, 1947. [3] Sironval, 1947.

instead of due to extensive growth of protonemata produced by a few spores. Most genera have a disappearance of the protonemata after gametophores produced by them have developed to the stage where they have rhizoids and several leaves. Certain annual genera have a persistence of the protonema throughout the entire life of the gametophytic generation. In some of these genera, as in *Ephemerum* (Fig. 71*D*, page 115), the protonema is the chief photosynthetic portion of the gametophyte.

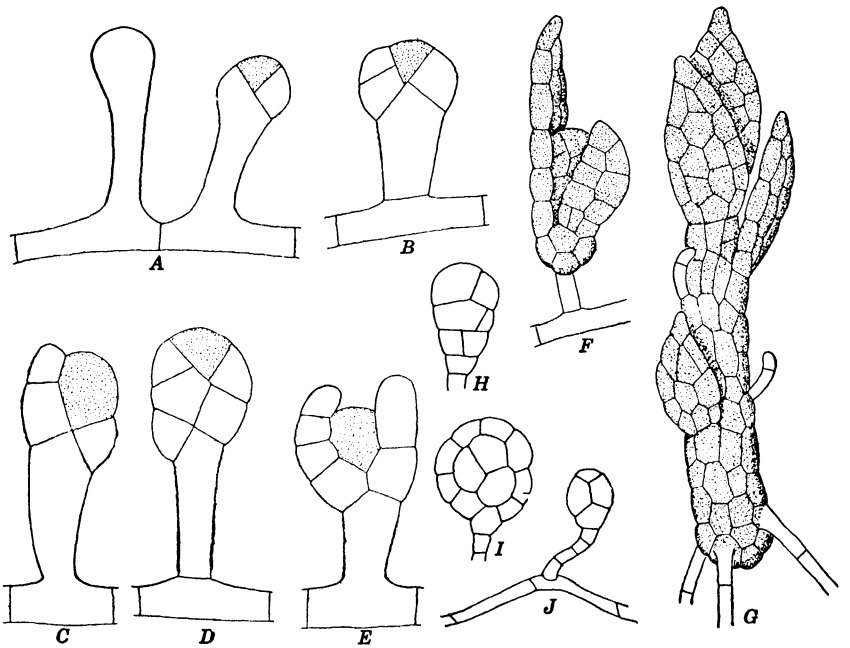

FIG. 81. *A–G*, *Splachnum ovatum* Hedw. *A–E*, early stages in development of gametophores (the apical cell shaded). *F*, gametophore with the first two leaves. *G*, gametophore with the first four leaves. *H–J*, gemmae (propagula) on rhizoids of *Barbula convoluta* Hedw. (*A–E*, × 360; *F*, × 200; *G*, × 135; *H–J*, × 90.)

Cells of rhizoids borne by a leafy gametophore may produce outgrowths resembling gametophore initials. These divide transversely into a stalk cell and a terminal cell. The stalk cell develops into a stalk two to four cells in length; the terminal cell divides to form an apical cell which gives rise to a globose mass of 20 to 30 cells without chloroplasts. The **gemmae** or **propagula** (Fig. 81*H–J*) thus formed do not develop further and remain dormant as long as they continue to be attached to the rhizoid. Gemmae becoming detached from a rhizoid may have the apical cell resuming activity and the segments cut off from it develop into a leafy gametophore.

Bibliography

Åkerman, Å. **1915.** *Bot. Notiser* **1915**: 205–209. [Chemotaxis, antherozoids.]

Allen, C. E. **1912.** *Arch. Zellforschung.* **8**: 121–188. 4 pl. [Development of antheridium.]
1917. *Ann. Bot.* **31**: 269–291. 2 pl. [Spermatogenesis.]

Beardsley, Martha L. **1931.** *Ann. Missouri Bot. Gard.* **18**: 509–540. 5 pl. [*Funaria.*]

Billings, W. D., and W. B. Drew. **1938.** *Amer. Midland Nat.* **20**: 302–330. 12 figs. [Succession.]

Blomquist, H. L., and Lora L. Robertson. **1941.** *Bull. Torrey Bot. Club* **68**: 569–584. 28 figs. [Development of peristome.]

Bold, H. C. **1940.** *Amer. Jour. Bot.* **27**: 318–322. 14 figs. [Nutrition of sporophyte.]
1948. *Bryologist* **51**: 55–63. 17 figs. [Protonema, *Sphagnum.*]

Bowen, Esther J. **1933.** *Ann. Bot.* **47**: 401–422. 20 figs. [Conduction of water.]
1933A. *Ibid.* **47**: 635–661. 41 figs. [Conduction of water.]
1933B. *Ibid.* **47**: 889–912. 23 figs. [Conduction of water.]

Brotherus, V. F. **1924–1925.** Bryales. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. 2 Aufl. Bd. 10. Pp. 143–478. 306 figs. Bd. 11. 1–542. 376 figs.

Brown, Mabel M. **1919.** *Amer. Jour. Bot.* **6**: 387–400. 1 pl. [Gametophyte, *Funaria.*]

Bryan, G. S. **1915.** *Bot. Gaz.* **59**: 40–56. 4 pl. [Archegonium, *Sphagnum.*]
1917. *Ibid.* **64**: 1–20. 8 pl. 1 fig. [Development of archegonium.]
1920. *Amer. Jour. Bot.* **7**: 296–303. 26 figs. [Embryogeny, *Sphagnum.*]
1920A. *Ibid.* **7**: 223–230. 2 pl. [Archegonium, *Sphagnum.*]
1927. *Bot. Gaz.* **84**: 89–101. 20 figs. [Abnormal archegonia.]

Burr, L. L. **1939.** *Trans. Roy. Soc. New Zealand* **68**: 437–456. 8 pl. 2 figs. [Morphology of *Cyathophorum.*]

Cain, S. A., and W. T. Penfound. **1938.** *Amer. Midland Nat.* **19**: 390–416. [Succession.]

Campbell, D. H. **1895.** The structure and development of mosses and ferns. London. 544 pp. 266 figs.
1918. *Ibid.* 3d ed. New York. 708 pp. 322 figs.

Correns, C. **1899.** Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. Jena. 472 pp. 187 figs.

Dening, K. **1935.** *Flora* N.F. **30**: 57–86. 3 figs. [Sexual dimorphism.]

Dixon, H. N. **1932.** Classification of mosses. In F. Verdoorn, Manual of Bryology. Pp. 397–412.

Ernst-Schwarzenbach, Marthe. **1939.** *Arch. Julius Klaus Stift. f. Vererbungsforsch.* **14**: 361–474. 4 pl. 34 figs. [Sexual dimorphism.]
1944. *Rev. Bryol. et Lichenol.* **14**: 105–113. 7 figs. [Sexual dimorphism.]

Evans, A. W., and H. D. Hooker. **1913.** *Bull. Torrey Bot. Club* **40**: 97–109. 26 figs. [Development of peristome.]

Fleischer, M. **1902–1904.** Die Musci der Flora Buitenzorg. Bd. 2. Leiden. 262 pp. 50 figs.
1920. *Ber. Deutsch. Bot. Ges.* **38**: 84–92. 1 pl. 1 fig. [Sexual dimorphism.]

Goebel, K. **1892.** *Flora* **76**: 92–104. 2 pl. [Sexual dimorphism.]
1898. *Ann. Jard. Bot. Buitenzorg.* **2.** Suppl. 65–72. [Dehiscence of antheridium.]

Holferty, G. M. **1904.** *Bot. Gaz.* **37**: 106–126. 2 pl. [Development of archegonium.]

Janzen, P. **1929.** Die Entwicklung und Biologie von Funaria hygrometrica. In L. Loeske, Die Laubmoose Europas. II. Funariaceae. Berlin. Pp. 72–111. 25 figs.

Kienitz-Gerloff, F. **1878.** *Bot. Zeitg.* **36**: 33–64. 3 pl. [Development of embryo.]

Kühn, E. **1870.** *Schenck u. Leurssen's Mitt. a. d. Gesamtgebeite d. Bot.* **1**: 1–56. 10 pl. [*Andreaea.*]

Leitgeb, H. **1880.** *Sitzungsber. Akad. Wiss. Wien* (Math.-Nat. Kl.). **80**[1]: 447–460. 1 pl. [Sporophyte of *Archidium.*]

Loeske, L. **1929.** Die Laubmoose Europas. II. Funariaceae. Berlin. 120 pp. 69 figs.
Lorch, W. **1931.** Anatomie der Laubmoose. In K. Linsbauer, Handbuch der Pflanzenanatomie **8**[1]: 1–358. 230 figs.
Mägdefrau, K. **1935.** *Zeitschr. Bot.* **29**: 337–375. 2 figs. [Water-conducting tissues.]
Malta, N. **1922.** *Acta Univ. Latviensis* **1**: 125–129. [Longevity of spores.]
Marchal, É., and É. Marchal. **1911.** *Bull. Cl. Sci. Acad. Roy. Belgique* **1911**: 750–782. 1 pl. [Apospory.]
Melin, E. **1915.** *Svensk Bot. Tidskr.* **9**: 261–293. 1 pl. 2 figs. [Antheridium, *Sphagnum*.] **1916.** *Ibid.* **10**: 289–311. 6 figs. [Archegonium, *Sphagnum*.]
Meyer, S. L. **1941.** *Bryologist* **44**: 69–75. [Longevity of spores.]
Mühldorf, A. **1930.** *Beih. Bot. Centralbl.* **47**: 169–191. 1 pl. [Antherozoids, *Sphagnum*.]
Müller, H. **1874.** *Arb. Bot. Inst. Wurzburg* **1**: 475–497. 9 figs. [Protonemata, Eubrya.]
Nawaschin, S. **1897.** *Flora* **83**: 151–159. 1 pl. [Spore liberation, *Sphagnum*.]
Phillips, E. A. **1951.** *Ecol. Monographs* **21**: 301–316. [Succession.]
Pottier, J. **1921.** *Ann. Sci. Nat. Bot.* 10 ser. **3**: 1–144. 32 pl. [Leaf, *Andreaea*.]
Rhuland, W. **1924.** Musci. Allgemeiner Teil. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. 2 Aufl. Bd. 10. 1–100. 90 figs.
Sachs, J. **1874.** Lehrbuch der Botanik. Leipzig. 928 pp.
Schaffner, J. H. **1938.** *Bryologist* **41**: 57–63. [Classification.]
Schimper, W. P. (editor). **1836-1855.** Bryologia Europa. Stuttgart. Vol. 1. 179 pp. 108 pl. Vol. 2. 138 pp. 87 pl. Vol. 3. 243 pp. 111 pl. Vol. 4. 250 pp. 122 pl. Vol. 5. 235 pp. 106 pl. Vol. 6. 150 pp. 105 pl.
Sharp, A. J. **1939.** *Amer. Midland Nat.* **21**: 267–354. 36 figs. [Ecology.]
Sironval, C. **1947.** *Bull. Soc. Roy. Bot. Belgique* **79**: 48–72. 24 figs. [Protonema, Eubrya.]
Steere, W. C. **1946.** *Amer. Midland Nat.* **36**: 298–324. 2 pl. [Fossil Musci.]
Steinbrinck, C. **1897.** *Flora* **84**: 131–158. 13 figs. [Peristome.]
Tansley, A. G., and E. Chick. **1901.** *Ann. Bot.* **15**: 1–38. 2 pl. [Water-conducting tissues.]
Waldner, M. **1887.** Die Entwicklung der Sporogone von Andreaea und Sphagnum. Leipzig. 25 pp. 4 pl.
Wenderoth, H. **1931.** *Planta* **14**: 344–385. 1 pl. 64 figs. [Development of peristome.]
Wettstein, F. von. **1923.** *Biol. Centralbl.* **43**: 71–83. [Apospory.]
Wijk, R. van der. **1929.** *Recueil Trav. Bot. Néerl.* **26**: 289–394. 43 figs. [Development of peristome.]

CHAPTER 6

PTERIDOPHYTES—INTRODUCTION

Pteridophytes have certain combinations of major characters not found either in bryophytes or in seed plants. They differ from them in having both the gametophytes and the sporophyte independent plants at maturity. On the basis of such sporophytic features as sporangial structure, manner in which sporangia are borne, and vegetative structure, the pteridophytes fall into four distinct groups (psilophytes, lycopods, horsetails, ferns). The question of what rank should be accorded these four groups has already been discussed (see page 2).

Origin of Pteridophytes. The origin of pteridophytes is a question that has been debated at length. Pteridophytes are known from as far back as the Silurian, or some 380 million years ago. During the Silurian and the immediately succeeding Lower Devonian there were a considerable number of psilophytes of much simpler construction than any other known type of pteridophyte. However, these do not bridge the gap between pteridophytes and plants lower in the evolutionary scale, so that theories concerning the origin of pteridophytes must be based upon comparative morphology of living and fossil forms. These theories fall into two general categories, those which postulate a direct origin from algae, and those which consider pteridophytes directly or indirectly related to bryophytes.

Proponents of a direct origin from algae take the stand that similarities between bryophytes and pteridophytes are due to a parallel evolution and not to a phylogenetic connection between the two. Some advocates[1] of a direct algal origin do not attempt to relate pteridophytes to any particular group of algae. Others[2] postulate an origin of pteridophytes by complex algae growing near the upper limits of the tide levels "transmigrating" from the ocean. Such an origin would imply that they came from brown algae (Phaerophyta) since these are the only present-day algae with motile reproductive cells that grow high in the intertidal zone. An origin has also been sought in the green algae (Chlorophyta). These green algae have usually been thought[3] to be of a filamentous chaetophoraceous type but it has also been suggested[4] that the ancestral green alga was an erect

[1] Eames, 1936; Scott, 1900. [2] Arnold, 1947; Church, 1919.
[3] Bohlin, 1901; Fritsch, 1916; Lotsy, 1909. [4] Fritsch, 1945.

parenchymatous form with an isomorphic life cycle in which there was an alternation of two vegetatively similar generations.

Bryophytes and pteridophytes are alike in so many features that there is good reason for thinking that there is a phylogenetic relationship between the two. These features include general similarity in vegetative structure of gametophytes of thallose bryophytes and pteridophytes, similarity in ontogeny and mature structure of antheridia, similarity in ontogeny and mature structure of archegonia, encapsulation of embryo in the archegonium, partial parasitism of mature sporophyte or embryo upon the gametophyte, and heteromorphic life cycle in which there is an alternation of two vegetatively unlike generations.

Some[1] of those who believe that there is a phylogenetic connection between bryophytes and pteridophytes think that the two are divergent evolutionary lines from hypothetical land plants of a very primitive archegoniate type.

Others think that pteridophytes have arisen from true bryophytes. Attempts to derive them from specific bryophytes have centered around the anthocerotes. The theory that pteridophytes have arisen from an anthocerotean type of bryophyte is based upon the idea that[2]

> The unlimited growth of the sporophyte . . . in connection with the highly developed assimilative tissue, makes the sporophyte of this plant the nearest approach to the entirely independent sporophyte of the ferns. Were the foot of the sporophyte in *Anthoceros* prolonged into a root penetrating the earth, it would become quite independent of the gametophyte, and were a special assimilative organ or leaf developed, a condition directly comparable to the sporophyte of the lower Pteridophytes or ferns would result.

The theory of an anthocerotean origin of pteridophytes received but little support when first promulgated by Campbell.[3] Opponents of the theory held that it left too many gaps between the anthocerotean type of sporophyte and the root-bearing, free-living sporophyte typical of all pteridophytes known at that time. The subsequent discovery of psilophytes in which the sporophyte was a rootless, leafless, dichotomously branched shoot invalidated much of this objection. If an anthocerotean type of sporophyte had a shifting of the meristematic region from base to apex this would make possible an initiation of dichotomous branching by the meristem and a restriction of spore formation to branch apices. Such a plant would resemble very closely the sporophyte of certain Psilophytales (Fig. 82). Such sporophytes might have the columella metamorphosing into a conductive strand (central cylinder). When growing in unusually favorable habitats, *Anthoceros* may show the beginnings of an

[1] Bower, 1935; Lignier, 1903; Zimmermann, 1930, 1938.
[2] Campbell, 1899, p 120. [3] Campbell, 1895.

approach to the condition described above. Sporophytes have been found[1] in which there was a restriction of spore formation to the distal end and in which the columella was differentiated into a conducting tissue in the lower portion.

Discussion of the anthocerotean origin of pteridophytes has centered around the sporophytic generation and has overlooked the fact that sex organs of pteridophytes have much in common with those of anthocerotes. In Anthocerotae, as in pteridophytes, the sex organs are embedded in the gametophyte. Archegonia of Anthocerotae are more reduced than those of

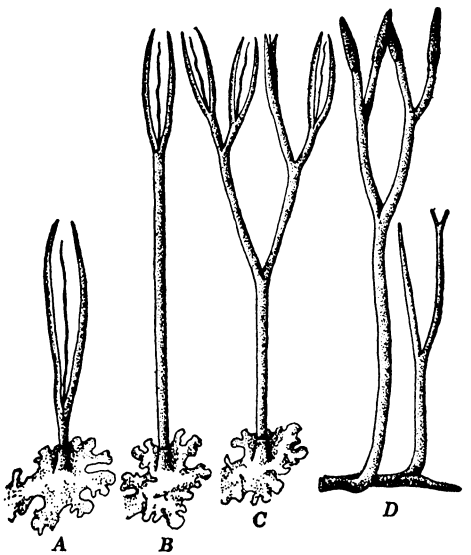

FIG. 82. Diagrams showing hypothetical sequence in the evolution of a semiparasitic anthocerotean type of sporophyte into a free-living psilophytan type of sporophyte.

Hepaticae in that they have no stalk. This is due to an obliteration of division of an archegonial initial into primary archegonial cell and primary stalk cell (see page 90). Direct functioning of the archegonial initial as the primary archegonial cell results in an embedded archegonium, but one which is surrounded by a jacket layer because the initial divides into an axial cell and three jacket initials (Fig. 83*B*). Evolution of the pteridophytic archegonium has been accompanied by a further reduction in the early ontogeny. Here, the archegonial initial functions directly as the axial cell and does not form jacket initials (Fig. 83*C*). Thus, the entire pteridophytic archegonium is homologous with the axial row and cover cells of the anthocerotean archegonium (Fig. 83*B–C*).

[1] Campbell, 1924.

The primitive type of antheridium among living pteridophytes, the so-called eusporangiate type, is found in *Lycopodium*, *Equisetum*, and the eusporangiate ferns. It consists of a large number of fertile cells, which lie embedded in the gametophyte, and a sterile layer external to the fertile cells. In anthocerotes, a superficial cell of the gametophyte divides periclinally into two daughter cells, the inner daughter cell developing into an antheridium, the outer developing into the layer roofing over the antheridial chamber. There seems to be some justification for thinking that the

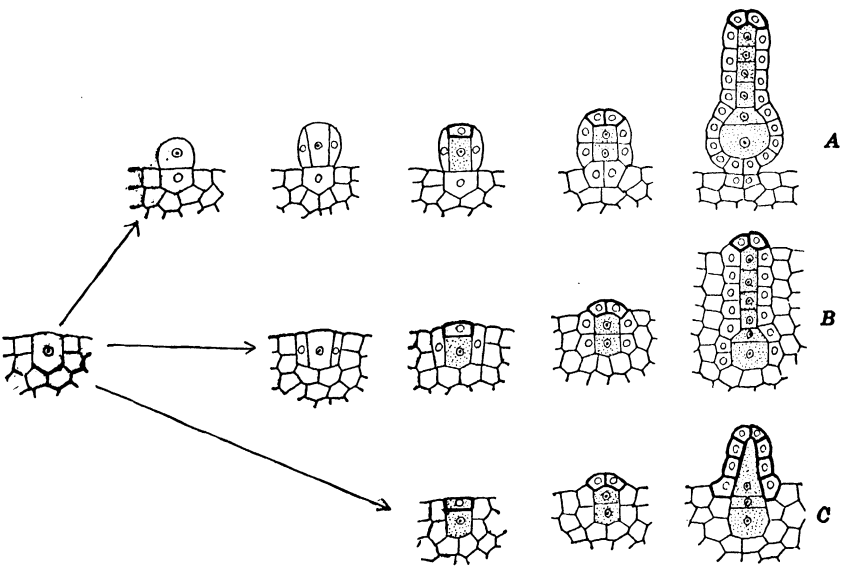

FIG. 83. Diagram showing homologous stages in development of archegonia of (*A*) Hepaticae, (*B*) Anthocerotae, and (*C*) pteridophytes. Homologous stages stand one above the other. The central cell and its derivatives are shaded; the primary cover cell and its derivatives are outlined with a heavy line; the basal cell, jacket initials, and their derivatives have their nuclei drawn in outline.

fertile portion of the eusporangiate type of antheridium corresponds to the entire anthocerotean antheridium, and that its so-called jacket layer is homologous with the cover of the archegonial chamber of anthocerotes (Fig. 84).

We know nothing concerning the embryology of the most primitive pteridophytes, the Psilophytales, since they are all fossil; but it is probably more than a mere coincidence that embryos of living Psilophyta, the Psilotales, show a remarkable superficial resemblance to those of anthocerotes (compare Figs. 56*H* and 109*B*).

Evolution of the Sporophyte among Pteridophytes. Until early in the present century there was an almost universal belief that evolution of

roots preceded,[1] or followed very closely upon,[2] establishment of the independent, self-sustaining sporophyte characteristics of pteridophytes. Because of this, attention centered around the nature of the shoot in primitive pteridophytes. There were three general theories concerning its nature:* (1) that it consisted solely of leaves, or the prototypes of leaves, and that the leaf-bearing axis appeared later in evolution of the shoot; (2) that appendages of the axis (leaves and sporangiophores) were evolved from superficial areas on the axis; and (3) that it is wholly axial in nature and that leaves and branches were evolved by a modification of branches. The great extension of our knowledge concerning psilophytes during the decade 1920–1930 showed that many of these primitive pteridophytes

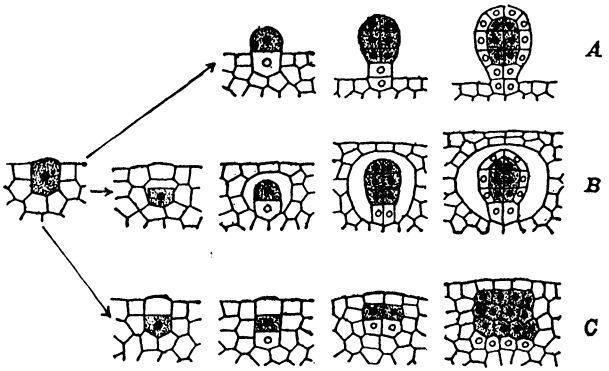

FIG. 84. Diagram showing the homologies in development of antheridia of (*A*) Marchantiales and (*B*) Anthocerotae, and (*C*) their homologies with the eusporangiate type of antheridium in pteridophytes. Homologous stages stand one above the other.

were rootless, leafless, free-living sporophytes consisting only of a dichotomously branched axis. Demonstration of the stem-like nature of these most primitive of pteridophytes invalidates theories that evolution of leaves preceded evolution of the axis.

The idea that the shoot is wholly axial in nature was first suggested by Bower,[3] but he did not attempt to visualize the structure of the primitive shoot. Later, Lignier[4] postulated that the primitive pteridophytic shoot was dichotomously branched, without leaves, and that a change of sympodial branching resulted in certain branches becoming dominant and constituting an axis, whereas others were subordinated and constituted the beginnings of leaves. Shortly after knowledge concerning primitive psilophytes began to accumulate, Zimmermann[5] coordinated these ideas in his **telome theory.** This theory holds that the primitive shoot was up-

[1] Campbell, 1895. [2] Bower, 1908.

* See Bower (1908), especially Chap. XI, for an extended discussion of these theories.

[3] Bower, 1884. [4] Lignier, 1903, 1908. [5] Zimmermann, 1930, 1938.

right, dichotomously branched, leafless, and similar to that of *Rhynia* (Fig. 96, page 161). He calls the ultimate dichotomies the **telomes** and calls the internodes below the telomes **mesomes.** Telomes and mesomes jointly constitute a **telome truss** ("Telomestände"). A telome truss may terminate in sterile telomes, or it may be fertile and with the telomes terminating in sporangia.

Before discussing the question of whether appendages of the axis (leaves and sporangiophores) arose as superficial outgrowths of the axis, or arose by modification of branches of the axis, it should be pointed out that foliage leaves are of two distinct types, microphyllous and macrophyllous. **Microphyllous leaves,** even when of large size, have a single

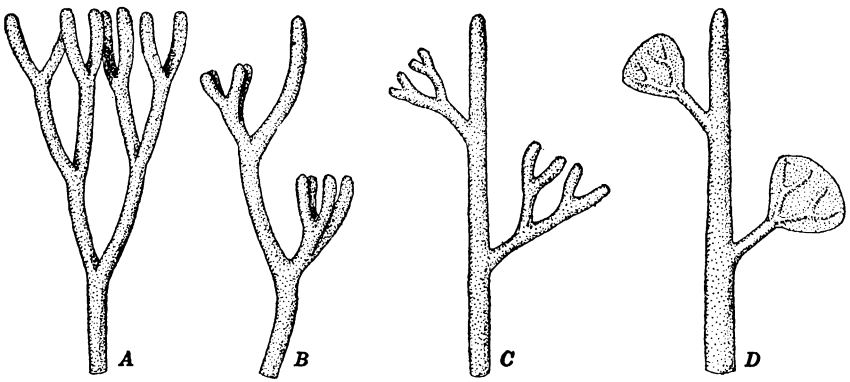

FIG. 85. Diagrams showing origin of macrophyllous leaves according to the telome theory.

unbranched vein running from base to apex.* **Macrophyllous leaves** always have a blade with a much-branched system of veins in which the venation may be open or closed.

According to the telome theory the first step in evolution of a macrophyllous leaf (a **cladode**) was a change from dichotomous to sympodial branching in an erect leafless shoot. This resulted in an axis bearing a succession of telome trusses (Fig. 85*B*). Orientation of members of a truss so that they were in one plane and a fusion of those members lateral to one another resulted in a leaf composed of a petiole and a blade with a dichotomously branched, freely ending vein system (Fig. 85*C–D*). Evidence supporting this cladode interpretation of the macrophyllous leaf is seen in the open ventation of many primitive fossil ferns. Further evidence is seen in the ontogeny of living ferns whose adult leaves have a netted venation and whose first-formed (juvenile) leaves have an open dichotomous venation.

* Certain fossil lycopods are an exception because they have two veins.

There are two theories concerning the origin of the lycopodian microphyllous leaf with its single vein. Adherents of the telome theory think that it arose in an upright, dichotomously branched, leafless shoot in which there was an "overtopping" as a result of a shift to sympodial branching. At each node there was a single telome, or possibly a telome truss that later became reduced to a single telome. Flattening of the telome at each node and a persistence of its single vascular strand resulted in the sessile lycopodian leaf with a single unbranched axial vein (Fig. 86*A–E*). According to the **enation theory** of Bower, lycopodian leaves are entirely new structures that appeared on a previously untenanted surface.[1] It is held that outgrowths (**enations**) of a more or less spine-like nature

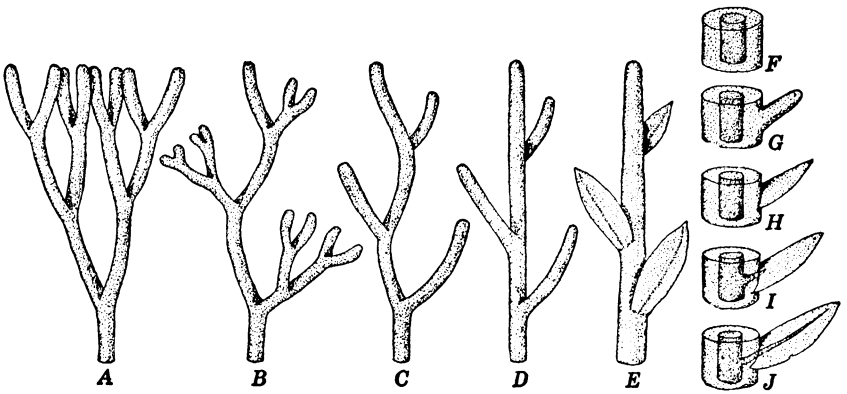

FIG. 86. Diagrams showing origin of microphyllous leaves. *A–E*, according to the telome theory. *F–J*, according to the enation theory.

appeared on the smooth surface of a leafless shoot, and that in the course of time these became flattened and leaf-like (Fig. 86*F–H*). At first these enations were without vascular connection with the central vascular strand of the shoot. Later, there was an appearance of a vascular strand that ran to the base of the leaf, and still later there was an evolution of a vascular strand (vein) that ran to the leaf tip (Fig. 86*I–J*). *Psilophyton* (Fig. 98, page 163) has been cited[2] as showing the first step in such a series, *Thurstophyton* as exemplifying the second step, *Asteroxylon* (Fig. 101, page 166) as a type where the vascular supply extends only to the leaf base, and *Arthrostigma* as a type where the vein extends only part way to the leaf apex.

The origin of the whorled arrangement of leaves in the equisetaceous series is obscure. *Sphenophyllum* and related forms had sessile wedge-shaped leaves with a dichotomously branched venation (Fig. 147*B–D*,

[1] Arber, 1921; Bower, 1908, 1935; Hirmer, 1927; Kräusel, 1932; Lang, 1931; Seward, 1933.

[2] Bower, 1935; Lang, 1931.

page 243). Such leaves seem to be of a cladode nature. The single-veined sterile leaf found in so many members of the equisetaceous series may be a reductional form of a sterile cladode leaf.

Evolution of Sporophylls. Leaves of a fern or a lycopod may be of two kinds: **foliage leaves** which are exclusively photosynthetic organs, and **sporophylls** whose primary function is the production of sporangia and spores. Leaves of almost all present-day ferns have sporophylls that also serve as the photosynthetic organ of the sporophyte. Sporophylls of a fern regularly bear numerous sporangia that, according to the genus, are

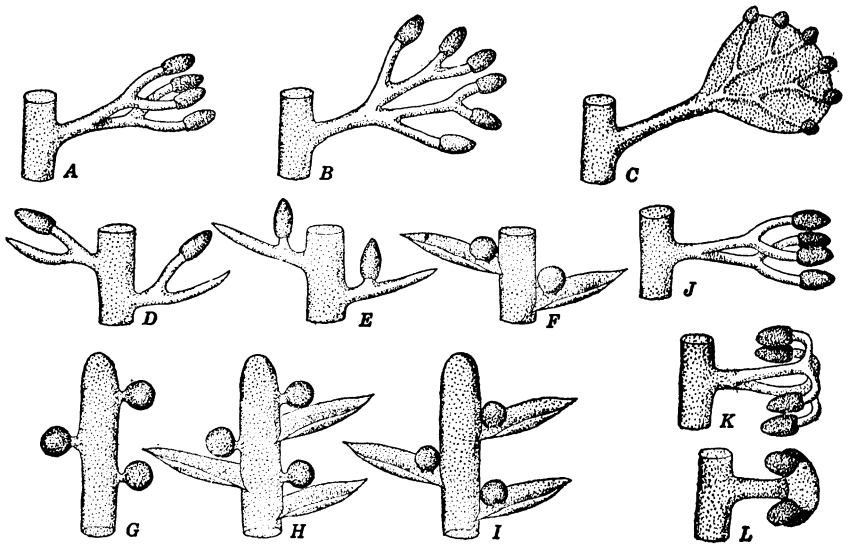

FIG. 87. *A–C*, Diagrams showing the origin of fertile leaves of ferns. *D–I*, diagrams showing the origin of sporophylls of lycopods. *D–F*, according to the telome theory. *G–I*, according to the enation theory. *J–L*, diagrams showing the origin of equisetaceous sporangiophores.

restricted to the blade margin or borne on the abaxial face. Genera with a restriction of sporangia to the blade margin are considered the more primitive of the two. There is a widespread interpretation of the filicinean leaf according to the telome theory and it is thought to have arisen by lateral fusion of members of a fertile telome truss (Fig. 87*A–C*).

Fertile leaves (sporophylls) of lycopods always have but one sporangium and this borne adaxially near the base. Adherents of the telome theory hold that such sporophylls arose by modification of a telome truss with two telomes, the upper fertile and the lower sterile. Flattening of the sterile telome and obliteration of the basal sterile portion of the fertile telome produced the lycopodian sporophyll (Fig. 87*D–F*). Adherents of the enation theory hold that lycopodian sporophylls were evolved on a leafless shoot bearing no other appendages other than numerous lateral sporan-

gia. After a leaf had been evolved by enation below each sporangium, the interval between sporangium and subtending leaf was shortened until the sporangium became sessile on the leaf (Fig. 87*G–I*.) Thus, the lycopodian sporophyll is interpreted as a composite structure composed of two essentially independent appendages. The fertile portion of *Zosterophyllum* (Fig. 100, page 165) has been cited[1] as exemplifying the prototype in the origin of lycopodial sporophylls by enation, but with no implication that *Zosterophyllum* is related to early lycopods.

The fertile appendages of equisetaceous pteridophytes have been thought to be leaf-like in nature and therefore called sporophylls. The designation of them as **sporangiophores**[2] is a better term since it is noncommittal as to whether or not it is leaf-like in nature. Such sporangiophores probably arose by a recurving of the tips of fertile dichotomously branched appendages, followed by a fusion of the bent arms (Fig. 87*J–L*). The recurved appendages of *Calamophyton* (Fig. 146, page 241) give support for such an interpretation. Some fossil members of the equisetaceous series had each sporangiophore subtended by a sterile leaf and one that is generally called a **bract.** The bracts were free from or united with the sporangiophores. However, when the two were fused with each other there was usually a separate vascular supply to bract and sporangiophore (Fig. 153*A*, page 250). Accordingly as one holds to the telome theory or to the enation theory, the bract arose by modification of a sterile arm of a telome truss, or arose as an enation.

Vascular Elements of Pteridophytes. The free-living, relatively large, sporophyte characteristic of pteridophytes was made possible by an evolution of adequate tissues for the upward and downward conduction of materials. All pteridophytes have two general types of conducting tissue, the xylem and the phloem. The chief function of the former is the upward conduction of water, and that of the latter is the upward and downward conduction of foods. Together they constitute the chief elements in the vascular system of the sporophyte. The origin of the vascular system is wholly unknown. If one believes in the anthocerotean origin of pteridophytes, there is a temptation to homologize the columella of an anthocerotean sporophyte with the vascular cylinder of a primitive pteridophyte.

The **tracheid** is the fundamental element of the xylem and is matured from a single embryonic cell. An embryonic cell destined to mature into a tracheid elongates greatly and deposits additional wall material upon limited portions of the inner face of the cell wall (Fig. 88*A–C*). Sooner or later there is a disappearance of the cytoplasm and nucleus. A mature tracheid, therefore, is an elongate dead cell consisting only of a cell wall. The first tracheids to mature in the xylem have the additional wall material deposited in transverse rings. Because of this they are called **annular**

[1] Bower, 1935. [2] Scott, 1900.

tracheids. Instead of being deposited in transverse rings, the additional wall material may be deposited in a continuous spiral. The result of this is a **spiral tracheid** (Fig. 88*D*). These two types of tracheid are not always distinct from each other and sometimes a tracheid has annular thickenings in one end of the lateral wall and a spiral thickening at the opposite end. Both types of tracheid are matured in regions of root, stem, or leaf

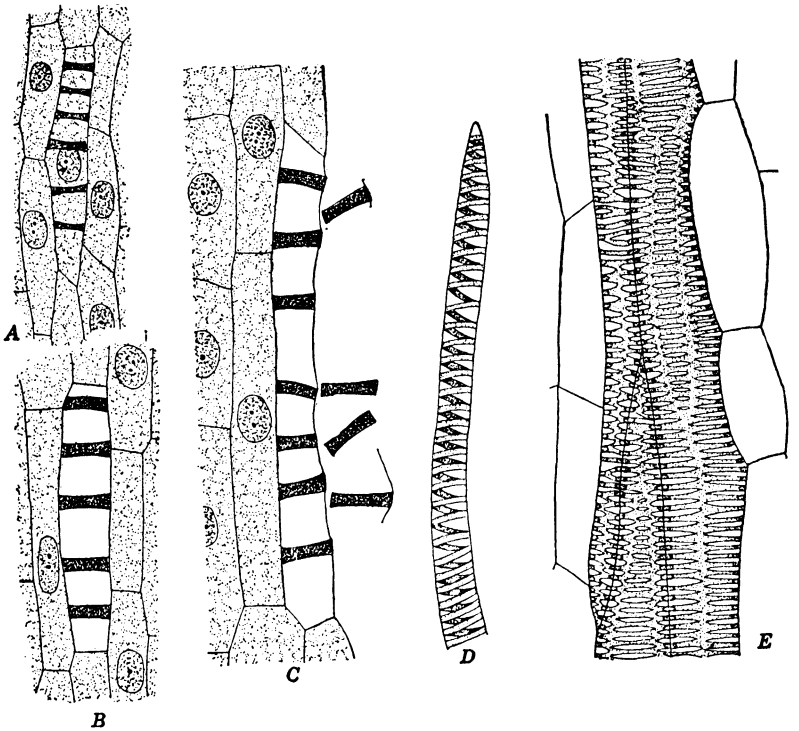

FIG. 88. *A–C*, stages in development of annular tracheids of *Equisetum telmateia* Ehrb. *D*, spiral tracheid of *Azolla filiculoides* L. *E*, scalariform tracheid of *Marsilea vestita* Hook. and Grev. (× 650.)

that are still elongating. In all cases there is considerable passive longitudinal stretching of these tracheids after they are mature and after their protoplasts have disappeared. As a result, the rings or successive spirals that were close together when first formed eventually come to lie some distance from one another. The portion of the xylem containing these tracheids which may be elongated after maturation is called the **protoxylem.** This name is based upon the fact that it is always the first-matured portion of the xylem. The portion of the xylem matured after elongation has ceased is the **metaxylem.** The xylem may consist wholly of protoxylem or, as in certain slowly growing organs, wholly of metaxylem.

Generally, however, both proto- and metaxylem are present in the vascular tissue of a root, leaf, or stem. Tracheids of the protoxylem are smaller in diameter than those of the metaxylem. This is quite evident when an organ is seen in transverse section, but the real determination of the protoxylem portion of any vascular strand rests upon the demonstration of annular and spiral tracheids from a study of longitudinal sections.

Tracheids of the metaxylem are structurally incapable of a longitudinal stretching after they are mature. The earliest tracheids matured in the metaxylem are the **scalariform tracheids** (Fig. 88*E*). These may be looked upon as spiral tracheids in which there are vertical bands of additional wall material connecting successive spirals one with another. There is the same lack of a hard and fast distinction between spiral and scalariform tracheids that there is between annular and spiral ones. This means that there may be no sharp line of demarcation between the first-matured (protoxylem) and later-matured (metaxylem) portions of the xylem. The type of tracheid most characteristic of older portions of the metaxylem is the **pitted tracheid,** in which there is a deposition of additional wall material on all but limited portions of the tracheid wall. The thin areas (pits) are usually transversely elongate, but in some cases they are circular. Pits of the Ophioglossaceae are unusual in that they are of the bordered type[1] usually found in seed plants.

If a **vessel** is defined as a vertical series of water-conducting elements with open perforations in the end walls, one may say that there are vessels in the pteridophytes. Unlike the angiosperms, the vessels of pteridophytes are of about the same diameter as tracheids. There are two types of vessel among the pteridophytes. Several members of the lycopodian series have vessels in which there has been a complete obliteration of cross walls between successive units.[2] Among the ferns, vessels have been found only in *Pteridium aquilinum* (L.) Kuhn. and the root of *Nephrodium filix-mas* Rich.[3] Here there are no cross walls (closing membranes) in pits on the end walls between successive vertical elements. Pits on the side walls have been described as being perforated,[4] but this has been denied.[5]

In addition to containing tracheids and vessels, the xylem may contain parenchyma. In some cases the parenchyma lies in a belt between the phloem and tracheids; in other cases, as in *Lycopodium cernuum* L., there is an intermingling of parenchymatous and water-conducting elements.

The phloem of pteridophytes is composed of **sieve tubes** and **phloem parenchyma.** A sieve tube consists of a series of elongate living cells in which the protoplasts are connected to one another through perforations

[1] Loughridge, 1932. [2] Duerden, 1933, 1934; Harvey-Gibson, 1894.
[3] Bancroft, 1911. [4] Gwynne-Vaughan. 1908. [5] Bancroft, 1911; Wright, 1920.

in the walls (Fig. 89). These perforations are of larger diameter than are the perforations (**plasmadesmen**) in walls of embryonic cells. The walls of each cell (**sieve-tube segment**) in a sieve tube are relatively thin and have the perforations in restricted areas, known as **sieve plates.** Sieve plates occur throughout the length of sieve-tube segments wherever they are in lateral contact with other segments. There may also be connections between the sieve tubes and the abutting phloem parenchyma cells.[1] Sometimes a distinction is made between **protophloem** and **metaphloem,** but, unlike the xylem, there are no pronounced morphological differences between the first-formed and later-formed elements in the phloem. A sieve tube remains functional until pads of callus are deposited on the sieve plates. Old sieve tubes of certain ferns regularly have callus pads; those of other ferns have no callus pads.[2] In some ferns, as *Pteridium aquilinum* L., callus pads may be formed and then resorbed.[1] If there is

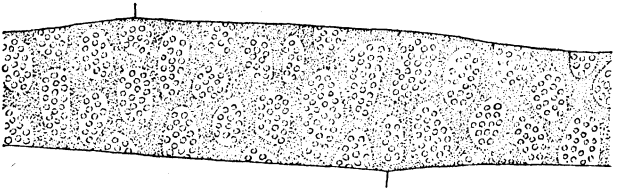

FIG. 89. Portion of a sieve tube of *Pteridium aquilinum* (L.) Kuhn. (× 650.)

no permanent formation of callus, a sieve tube may remain functional for years.

Secondary thickening of the vascular tissue by means of a cambium is of very rare occurrence among living pteridophytes, but it was quite common among equisetaceous and lycopodian plants that existed during the Carboniferous. *Botrychium* (page 283) and *Isoetes* (page 223) are the only living pteridophytes in which all stems regularly have a secondary thickening. In *Botrychium,* as in seed plants, the secondary xylem lies internal to and the secondary phloem external to the cambium. Tracheids of the secondary xylem are similar to those of seed plants in that they have bordered pits.[3] Secondary xylem and phloem in stems of *Isoetes* both lie internal to the cambium. Occasional individuals of one or two other living Pteridophyta, as *Ophioglossum* (page 283),[4] may produce a very limited amount of secondary tissue.

Evolution of the Vascular System. The older plant anatomists held that the vascular bundle is the fundamental unit in the vascular system of pteridophytes and higher plants. In 1886 Van Tieghem and Douliot[5] proposed an entirely different interpretation of the body of a vascular plant. They held that the fundamental parts of a shoot are the cortex and

[1] Hume, 1912. [2] Boodle, 1901. [3] Wright, 1920.
[4] Boodle, 1899. [5] Van Tieghem and Douliot, 1886.

a central cylinder, which they called the **stele,** and that the two are delimited from each other by the **endodermis.** They recognized three types of stelar construction and thought that shoots with a single stele (**monosteles**) were rarer than those containing more than one stele (**polysteles**).

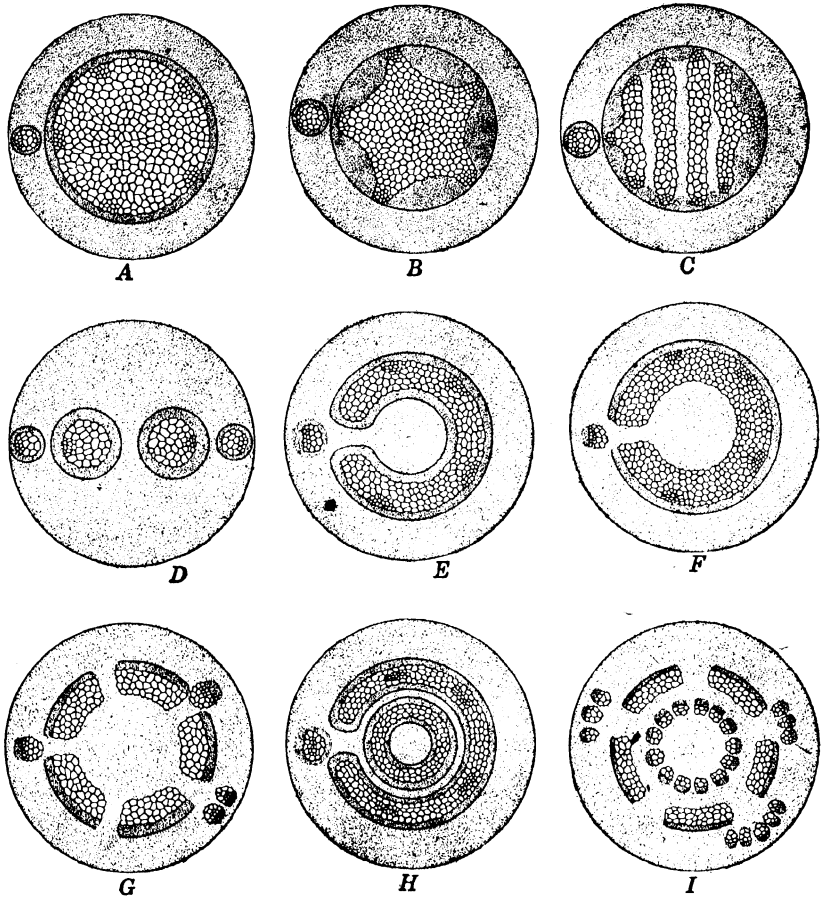

FIG. 90. Diagrams of various types of stele. *A–D*, protosteles. *A*, haplostele, *B*, actinostele. *C*, plectostele. *D*, polystele. *E–I*, siphonosteles. *E*, amphiphloic solenostele. *F*, ectophloic solenostele. *G*, dictyostele. *H*, polycyclic solenostele. *I*, polycyclic dictyostele.

We now know that practically all shoots are monostelic and that a polystelic condition (Fig. 90*D*) is of rare occurrence.

Jeffrey was the first to interpret the stelar theory from the phylogenetic standpoint.[1] He held that the primitive type of stelar construction is that in which the vascular tissue is a solid mass and one in which a central core

[1] Jeffrey, 1898.

of xylem is completely ensheathed by a layer of phloem. There has been a very general acceptance of this concept and of the name (**protostele**) that he proposed for this type of stele. Protosteles with a smooth core of xylem are generally considered more primitive than those in which the xylem core has radiating ribs. The former type of protostele has been called[1] a **haplostele** (Fig. 90*A*), the latter an **actinostele** (Figs. 90*B*, 113*A*). The most advanced type of actinostele is that in which the xylem is divided into a number of separate plates that lie parallel to, or radiate to, one another. Such actinosteles have been called **plectosteles**[2] (Fig. 90*C*).

Evolutionary changes among protosteles have involved shifts in the relative position of the protoxylem and metaxylem. The significance of the relative position of the xylem elements was recognized by paleobotanists before shoots were interpreted according to the stelar theory. Vascular strands with the protoxylem developing at the outer face were called[3] **exarch**; those with protoxylem at the middle of the metaxylem were called **mesarch**; and those with protoxylem at the inner face, **endarch**. There was an early incorporation of this concept in the stelar theory,[4] with an interpretation of the exarch condition as more primitive than the mesarch and the latter as more primitive than the endarch.

The vascular connection between the stele and the base of a leaf is called the **leaf supply.** The leaf supply in the cortex of protostelic stems always consists of but one vascular strand or **leaf trace.** Stems with a more elaborate type of stelar construction may have more than one leaf trace connecting with each leaf. A leaf trace is often described as departing from the stele and running through the cortex. This is somewhat misleading since it infers that a trace is an outgrowth from the stele that has pushed through the cortex. Actually, of course, a trace is a vascular strand matured from embryonic cortical cells. **Branch traces** are similar to leaf traces, except that they connect with branches, not leaves. Leaf traces of protostelic stems are often similar in structure to the steles from which they depart.

Protosteles are generally encircled by an **endodermis,** a layer one cell in thickness. An endodermis may be recognized by means of the peculiar thickenings (**Casparian strips**) on radial walls of its cells (Fig. 155*B*). Sometimes, also, endodermal cells have suberin lamellae on the inner tangential or on all walls. Sometimes endodermal cells may also be recognized because of their brownish color and their tannin-filled content. It has been held[5] that the endodermis is always differentiated in the innermost layer of the cortex. Hence it affords a criterion for distinguishing between tissues of cortical and of stelar origin. This generalization is open to question since the endodermis may be differentiated from cells of the

[1] Brebner, 1902. [2] Zimmermann, 1930. [3] Scott, 1900.
[4] Wordsell, 1902. [5] Jeffrey, 1917.

stele (*Selanginella*)[1] or from a layer that contributes to both the cortex and the stele (*Schizaea*).[2] Furthermore, there is considerable evidence showing that the primary function of an endodermis is physiological and that it serves as a barrier regulating lateral flow of water and dissolved substances between stele and cortex.[3] Thus, the development or nondevelopment of an endodermis external to the vascular cylinder may rest upon physiological causes rather than the specific nature of the innermost cortical cells.

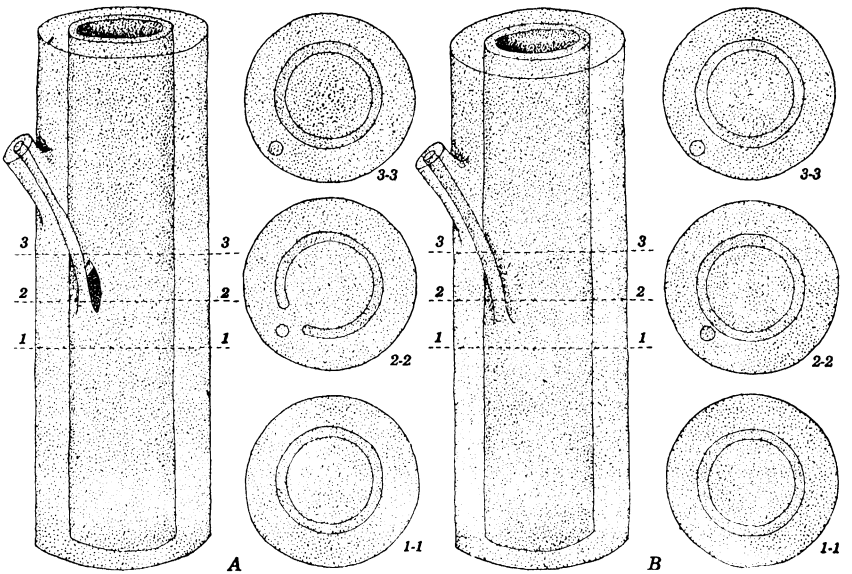

FIG. 91. *A*, stereodiagram of node, leaf base, and portions of adjoining internodes of pteropsidan solenostele; and diagrams of cross sections at levels 1–1, 2–2, 3–3. *B*, the same of a lycopsidan solenostele.

There is a general acceptance of the theory[4] that the stele with a tubular vascular region and a parenchymatous central region was evolved from a protostele. In the vascular portion of such **siphonosteles**[4] there are parenchymatous areas (**gaps**) immediately above the branch traces only or immediately above each leaf and branch trace (Fig. 91*A*). There are never any gaps above departing roots.

The method by which a protostele evolved into a siphonostele has been a subject of acrimonious debate. According to one theory,[5] the parenchymatous tissue internal to the phloem and xylem is cortical in origin. Adherents of this theory hold that the presence of an endodermis at the

[1] Barclay, 1931. [2] Bartoo, 1930.
[3] Priestley and North, 1922; Priestley and Radcliffe, 1924.
[4] Jeffrey, 1898. [5] Jeffrey, 1902, 1910, 1917.

inner face of the vascular tissue proves that the parenchymatous cells encircled by this endodermis are cortical in origin. They hold that siphonosteles with an internal endodermis are more primitive than those without an inner endodermis. Siphonosteles of the latter type are thought to have arisen by an obliteration of the inner endodermis during the course of evolution. The chief basis of this theory is the specific nature of the endodermis. However, as already noted, this is open to question. Thus, instead of representing an invasion of cortical tissue, the inner endodermis may merely represent the differentiation of a physiological barrier between vascular tissue and the pith. It is also extremely difficult to interpret certain types of siphonostele on the basis of an invasion of cortical tissue. For example, it is practically impossible to visualize the type of cortical invasion that would produce polycyclic siphonosteles (Fig. 90*H*).

According to another theory, a siphonostele was evolved from a protostele by a metamorphosis of the inner vascular elements into parenchyma.[1] The chief argument in favor of the intraxylic origin of the pith, and one unanswered by proponents of the invasion theory, is the repeatedly described occurrence of siphonosteles[2] in which tracheids are intermingled with the parenchymatous cells of the pith (Fig. 198). The "mixed pith" just described is found only in relatively primitive fossil and living ferns. Steles in which there is a regular occurrence of a mixed pith may be looked upon as transitional types between true protosteles and true siphonosteles.

A siphonostele may be **amphiphloic**[3] with phloem both external and internal to the xylem (Fig. 90*E*), or it may be **ectophloic**[3] with phloem restricted to the external face of the xylem (Fig. 90*F*). Adherents of the intrusion theory of the origin of pith think that the internal phloem also arose by intrusion. Thus an amphiphloic siphonostele is more primitive than an ectophloic one. Some adherents of the intraxylic origin of the pith hold[4] that the internal phloem is intraxylic in origin.

Whatever its origin, the evolution of siphonostele has been accompanied by an appearance of parenchymatous areas (gaps) in the vascular cylinder. Steles with gaps fall into two categories;[5] those in which there are gaps axillary to both the leaf and branch traces and those in which there are gaps axillary to branches only (Fig. 91). Steles with leaf gaps always have macrophyllous leaves; those without leaf gaps always have microphyllous leaves.[5] According to the presence or absence of leaf gaps, the vascular plants are divided into two groups, the Pteropsida and the Lycopsida.[5] The Pteropsida include the ferns, gymnosperms, and angio-

[1] Boodle, 1901; Gwynne-Vaughan, 1903.
[2] Bower, 1911; Gwynne-Vaughan, 1914; Petry, 1914; Thompson, 1920.
[3] Jeffrey, 1898. [4] Thompson, 1920. [5] Jeffrey, 1902.

sperms; the Lycopsida include the lycopods, horsetails, and the psilotaceous series. Among the simpler siphonostelic Pteropsida and almost always among the siphonostelic Lycopsida, successive gaps in the stele are a considerable distance above one another (Fig. 90*E*). Such siphonosteles without an overlapping of gaps are **solenosteles.**[1] In the more advanced siphonostelic Pteropsida, successive gaps may overlap one another (Figs. 90*G*). Siphonosteles with overlapping gaps are **dictyosteles,**[2] and the intervening portion of the vascular tissue lateral to two overlapping gaps is a **meristele.**[2] When there are numerous meristeles, the dictyostele looks like a cylindrical meshwork. The meristeles of such a dictyostele correspond to the vascular bundles of the older plant anatomists. A dictyostelic condition may be due in part to openings in the vascular cylinder that are not gaps. Lacunae in the vascular cylinder that are not gap-like in nature are called **perforations.**[3] These are sometimes present in solenosteles,[4] but they are of much more frequent occurrence in dictyosteles. Primitive siphonosteles have but one undivided leaf trace departing at each node. More advanced siphonosteles have the distal end of the trace divided into more than one strand (Fig. 90*G*) or have a leaf supply consisting of more than one trace (Fig. 90*I*).

The polycyclic condition[5] is the most complex type of stelar organization found among pteridophytes. Polycyclic steles are always siphonostelic and have an internal vascular system connected with an outer siphonostele. This internal connection is always at a node, and in most cases the vascular supply to the leaf departs from both the inner and outer portions of a polycyclic stele. Typical polycyclic steles have two or more concentric cylinders of vascular tissue. In some cases the outer cylinder is a solenostele (Figs. 90*H*, 208); in others it is a dictyostele (Figs. 90*I*, 228*A*). The vascular system internal to the outer siphonostele may be protostelic or siphonostelic.

The data that have accumulated tend to confirm the modified stelar theory as postulated in the years immediately following 1900. During the decade 1920–1930 there was a discovery of a group of fossil pteridophytes, the Psilophytales, of a much more primitive type than was known when the stelar theory was developed in its present form. Without exception, these Psilophytales had a type of vascular organization that the stelar theory postulated as the most primitive, that is, the protostelic central cylinder. Study of the anatomy of sporophytes of living pteridophytes has also shown that steles of many stems recapitulate the stelar theory during their ontogeny. Many species have stems that are protostelic in the first-formed portion and siphonostelic in later-formed portions. *Matonia pectinata* R. Br. affords the best example of this recapitulation. Here, as de-

[1] Brebner, 1902; Gwynne-Vaughan, 1901. [2] Brebner, 1902.
[3] Bower, 1923. [4] Gwynne-Vaughan, 1903. [5] Tansley, 1907–1908.

velopment progresses, there is a transition from protostely to solenostely, and then a transition to a polycyclic condition in which the internal vascular tissue is at first protostelic and then siphonostelic.

At one time it was hoped that stelar organization would be a helpful feature in showing phylogenetic relationships among the ferns but this hope has not been realized. This is due to the fact that an evolution from protostely to siphonostely and an evolution from siphonostely to dictyostely has taken place in several independent lines and at different rates. These evolutionary changes in the stelar organization may be found within the limits of a single family or even a single genus. For example, certain species of *Gleichenia* (see page 320) are protostelic and others are solenostelic.

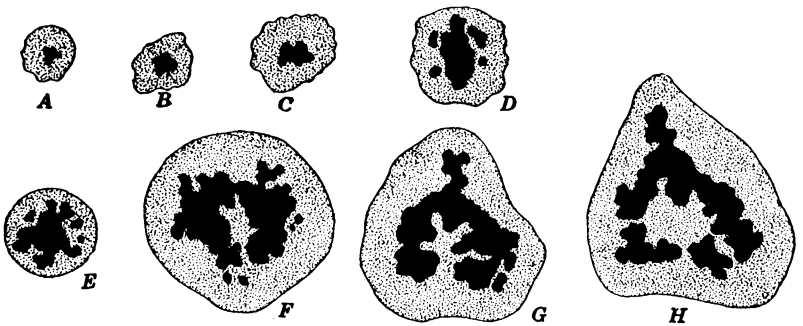

FIG. 92. *Psilotum triquetrum* Sw. Sections of stem at successive levels from base to apex showing the increased complexity of the xylem column which accompanies an increase in diameter of the stem. (*After Wardlaw*, 1924.) (× 46.)

Bower and his students are the chief ones who have attempted to analyze the factors causing a change from the primitive protostelic condition. They find[1] that fluted protosteles (actinosteles) and various types of siphonosteles are usually larger in diameter and with a proportionally greater surface than are haplosteles. This comes out most strikingly when first-formed portions of a stem have a smooth protostele (haplostele) and later-formed portions have a fluted protostele (actinostele) or a more advanced type of vascular organization.[2] The same holds for roots.[3] These stems and roots show that stelar construction in regions of larger diameter is not a magnified image of stelar construction in regions of smaller diameter (Fig. 92). Increase in stelar complexity with an increase in diameter has been considered[4] an attempt to maintain physiological interrelationships within a stem or root. The proportion of surface to volume is relatively high in the xylem of a haplostele of small diameter. If the diameter of such a haplostele were to be increased, the surface would increase as the square of the radius and the volume as the cube of the radius. Thus,

[1] Bower, 1920, 1923, 1923*A*; Wardlaw, 1924, 1925, 1928. [2] Wardlaw, 1924, 1925.
[3] Wardlaw, 1928. [4] Bower, 1920, 1923; Wardlaw, 1924, 1925.

quadrupling the diameter of a haplostele would result in one with a markedly different proportion of surface to volume. This would affect both the surface relations of xylem and phloem, and the relationships between the vascular system of shoot and its appendages. On the other hand, as actual computations show,[1] if increase in diameter of stem or root is accompanied by a change in complexity of outline of the vascular system, there is an approximate maintenance of the original proportions between surface and volume of the vascular tissues. Increase in stelar complexity with increase in size also affords certain structural advantages since, in proportion to its volume, a tabular or a radiate mass of xylem is a more efficient mechanical support than a solid cylindrical mass.

Gametophytes of Pteridophytes. Except for a few heterosporous lycopods, nothing is known concerning the gametophyte generation of the fossil pteridophytes. Hence all inferences concerning the structure of the primitive pteridophytic gametophyte must be based upon data derived from a comparison of those of living homosporous genera. A majority of these have green, dorsiventrally differentiated, thallose gametophytes with sex organs restricted to the ventral surface. In some cases (as in the Psilotales, the Ophioglossales, and certain species of *Lycopodium*) the gametophyte is devoid of chlorophyll, subterranean in habit, and nourished through the agency of a mycorhizal fungus. These gametophytes are almost always interpreted as being derived from a thallose green type. The filamentous green prothallus found in a few ferns, as *Schizaea* (Fig. 201), is also considered a derived rather than a primitive type.

Gametophytes of *Equisetum* and of the more primitive living ferns seem to show that the primitive pteridophytic gametophyte was thallose, more or less elongate, and more than one cell in thickness except along the lateral margins. Such a gametophyte may be compared with those of the Anthocerotae and of the thallose Jungermanniales. It is uncertain whether the sex organs were borne on the dorsal or the ventral side of the primitive gametophyte. They are regularly dorsal in *Equisetum*. Most ferns have sex organs on the ventral side only, but occasional individuals may have a few antheridia on the dorsal side. Thus, there is a certain amount of justification for assuming that the sex organs were dorsal in position and that there has been a shifting of them to a ventral position during evolution of the filicinean series. The structure of the archegonium is so standardized throughout the pteridophytes that one is justified in believing that those on archaic gametophytes differed but little from those on present-day ones. The theory[2] that the primitive gametophyte had an embedded antheridium is widely accepted. A hypothesis deriving this embedded antheridium from that of Anthocerotae has been given on page 134.

[1] Wardlaw, 1924. [2] Campbell, 1894.

Gametophytes of many homosporous ferns show certain changes from the theoretical primitive type. As far as vegetative structure is concerned, there is a marked tendency toward a thallus one cell in thickness, except immediately posterior to the growing point. This is accomplished by a restriction of growth in length but not in breadth. The result is the heart-shaped thallus typical of so many fern gametophytes. Sometimes, as in *Schizaea* and the Hymenophyllaceae, changes in the gametophyte have been retrogressive and to a filamentous or a strap-shaped type of plant body. The simpler ferns have embedded antheridia; more advanced ferns have emergent antheridia that project beyond the surface of a gametophyte. Emergent antheridia show evolutionary changes in the structure of the jacket layer. In the primitive type of emergent antheridium there is an indefinite number (10 to 20) of irregularly arranged jacket cells; in advanced antheridia there are 3 (sometimes 4) regularly arranged jacket cells.

Evolution of heterospory in the sporophytic generation involved marked changes in the succeeding gametophytic generation. Heterospory has been independently evolved in the lycopodian, the equisetaceous, and the filicinean series of pteridophytes. Sometimes, as among the giant horsetails, the heterospory is not pronounced. Generally, as in the ferns and the lycopods, the macrospores are many times larger than the microspores. Gametophytes of heterosporous genera differ markedly from those of homosporous genera. Unfortunately there are no living genera of an intermediate type showing steps in this modification of the gametophyte. All heterosporous genera show a very great reduction in the male gametophyte developed from the microspore. In some cases, as *Isoetes* (page 230), it is quite evident that there has been a reduction to a single vegetative cell and a single antheridium. Microgametophytes of other genera also have but one vegetative cell, but there is a possibility that they may have more than one antheridium. Female gametophytes developed from macrospores generally have more than one archegonium and many vegetative cells. Reduction of the female gametophyte has been the most extensive in *Marsilea* (page 369). Here there is but one archegonium and only a few vegetative cells.

Life Cycle of Pteridophytes. The typical life cycle of a pteridophyte consists of an alternate succession of sporophytic and gametophytic generations. However, the alternate succession may be accompanied by a vegetative multiplication of either generation. When there is an alternation of the two generations, the sporophyte generally results from a union of gametes produced by the gametophyte, and the gametophyte results from a spore produced by the sporophyte. In such an alternation, the number of chromosomes is doubled at the time of gametic union and halved at the time of spore formation.

More than half a century ago there was the discovery that a gametophyte might give rise to a sporophyte without gametic union[1] and that a sporophyte might give rise to a gametophyte without a production of spores.[2] The first-named phenomenon has been called **apogamy,**[3] the second, **apospory.**[4] Apogamy and apospory are now known to be very widespread among ferns, and frequently a plant is both apogamous and aposporous.[5] Apogamy is also known for one of the lycopods (*Selaginella*).

Aposporously produced gametophytes grow directly out of the leaf of a sporophyte (Fig. 93). They usually develop along the margins or at the apex of a blade, but it has also been found that they may grow out of

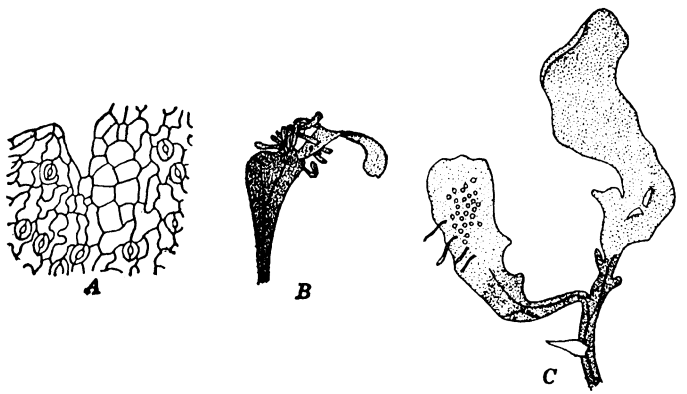

FIG. 93. Aposporous development of gametophytes from leaf apex of a sporophyte. *A*, primordium of gametophyte. *B–C*, developing and mature gametophytes. (*After Steil*, 1919*A*.) (*A* × 160; *B–C*, × 15.)

sporangia in a sorus. Apospory may be induced in certain species that are not normally aposporous. This is usually done by cutting a leaf from a young sporophyte and maintaining the severed leaf under conditions favorable for the formation of regenerative outgrowths.[6] Sometimes aposporous gametophytes show certain sporophytic characters. Not infrequently, tracheids, a purely sporophytic element, are present in gametophytic tissue back of the apical notch. Very rarely an aposporous gametophyte may have such sporophytic characters as stomata[7] or sporangia.[8]

Many aposporously produced gametophytes bear antheridia and archegonia that are of normal structure and with functional gametes. In such gametophytes chromosome counts show that the chromosome number is $2n$ in the gametophyte and that the sporophyte resulting from union of their gametes has $4n$ chromosomes.[9] Such tetraploid sporophytes have

[1] Farlow, 1874. [2] Druery, 1885. [3] DeBary, 1878. [4] Bower, 1885.
[5] Steil, 1939. [6] Lawton, 1932. [7] Goebel, 1908.
[8] Lang, 1898; Lawton, 1932; Pace, 1910. [9] Heilbronn, 1932; Lawton, 1932.

been induced to form tetraploid aposporous gametophytes. Ferns in which the aposporously induced gametophyte has the diploid number of chromosomes may also be cross-fertile with haploid gametophytes and so produce a sporophyte with a triploid ($3n$) number of chromosomes.[1]

When apogamy occurs, the sporophyte may be derived from a single cell of the gametophyte. This cell may be[2] a vegetative one (Fig. 94*A–D*); it may be[3] one adjacent to or a component of the archegonium (Fig. 94*E–F*); or it may be[4] the egg of the archegonium (Fig. 94*G*). Apogamous development of an egg into a sporophyte is generally called **parthenogenesis.** The discovery of embryos beneath intact canal and venter canal cells of

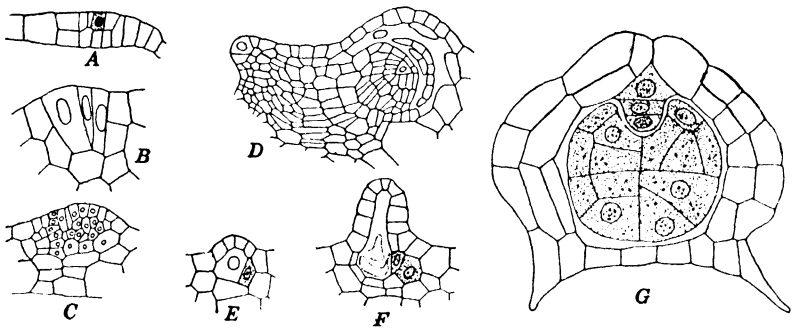

FIG. 94. Apogamous production of sporophytes. *A–D*, stages in apogamous production of a sporophyte from a vegetative cell of the gametophyte of *Nephrodium molle* Desv. *E–F*, from a vegetative cell adjoining the archegonium of *Cyathea tussacii* Desv. *G*, by parthenogenetic germination of egg of *Marsilea drummondii* A. Br. (*A–D, after Yamanouchi*, 1908; *E–F, after Stokey*, 1918; *G, after Strasburger*, 1907.)

unopened archegonia of *Marsilea* demonstrates parthenogenesis beyond all doubt (Fig. 94*G*). There are also apogamously produced sporophytes that are not referable to a single cell of the gametophyte. Here[5] the sporophyte is first recognizable as a small meristematic mass of cells, usually located on the ventral side of the gametophyte and posterior to the apical notch. A gametophyte has also been described[6] as giving rise to a new sporophyte by a process that is neither apogamy nor a true gametic union. In *Lastrea pseudo-mas* var. *polydactyla* Wills a nucleus from a gametic cell was thought to migrate into an adjoining cell and there fuse with its nucleus. The cell with the fused nucleus then developed into a sporophyte with a diploid number of chromosomes. This gamete-like fusion in vegetative cells has not been found in any other fern, and a reinvestigation of the species in which it was found holds[7] that the putative nuclear migrations are artifacts.

[1] Lawton, 1932; Manton, 1932. [2] Yamanouchi, 1908. [3] Stokey, 1918.
[4] Strasburger, 1907. [5] Allen, 1911; Duncan, 1941; Steil, 1919, 1933.
[6] Farmer and Digby, 1907. [7] Döpp, 1939.

Apogamy is found both in aposporously produced gametophytes and in those developing from spores. When an aposporously formed gametophyte gives rise to a sporophyte by apogamy both generations have the diploid number of chromosomes.[1] In gametophytes developing from spores, apogamy may be obligate because there are no sex organs, or because one or both kinds of sex organs are abortive. Several species with such gametophytes have been found[2] to have an incomplete mitosis in the penultimate generation of sporogenous cells in a sporangium. This results in half the usual number of sporocytes and a chromosome number of $4n$ in their nuclei. Meiotic division of sporocytes with these "restitution" nuclei produces spores with $2n$ chromosomes, and in the life cycle both the gametophyte and the apogamously produced sporophyte have the diploid number of chromosomes.

Apogamy may also be induced in gametophytes developed from spores with n chromosomes and in which sporophytes produced by gametic union have $2n$ chromosomes. Cultures of such gametophytes under appropriate conditions result in apogamy.[3] A haploid gametophyte that has been producing normal sex organs with functional gametes may, after being cultured for one to four years, become apogamous.[4] Counts of chromosomes in one species where apogamy was induced in a gametophyte with n chromosomes show that both gametophyte and sporophyte have the haploid number of chromosomes.[3]

Evolution among Pteridophytes. Pteridophytes have been traced with certainty back to the Silurian. Almost all the earliest known pteridophytes belong to the Psilophytales, a series that was widespread during the Devonian and that, as far as the fossil record shows, became extinct toward the end of that period. In addition to being the oldest, the Psilophytales are also the most primitive of known pteridophytes. Their rootless sporophyte consisted only of leafless branches, or of branches bearing small leaves without veins. Their sporangia resembled those of bryophytes and were borne singly at the tips of branches.

There was an early appearance of three divergent evolutionary lines from the Psilophytales and primitive members of all three series (lycopods, horsetails, ferns) are known from at least as far back as the Middle Devonian (Fig. 95). The lycopodian series is characterized by microphyllous sporophytes in which the vascular system is without leaf gaps. Fertile portions of the sporophyte have sporophylls with a single sporangium that is borne adaxially and near the base of the sporophyll. The theories as to how a psilophyte type of sporophyte gave rise to one of the lycopod type have been discussed on page 137. Whatever its origin, phylogenetic progress within the lycopodian series was at a rapid rate, and there was an

[1] Lawton, 1932. [2] Döpp, 1932, 1939; Patterson, 1942; Steil, 1919; Studer, 1950.
[3] Duncan, 1941. [4] Stokey, 1945, 1948.

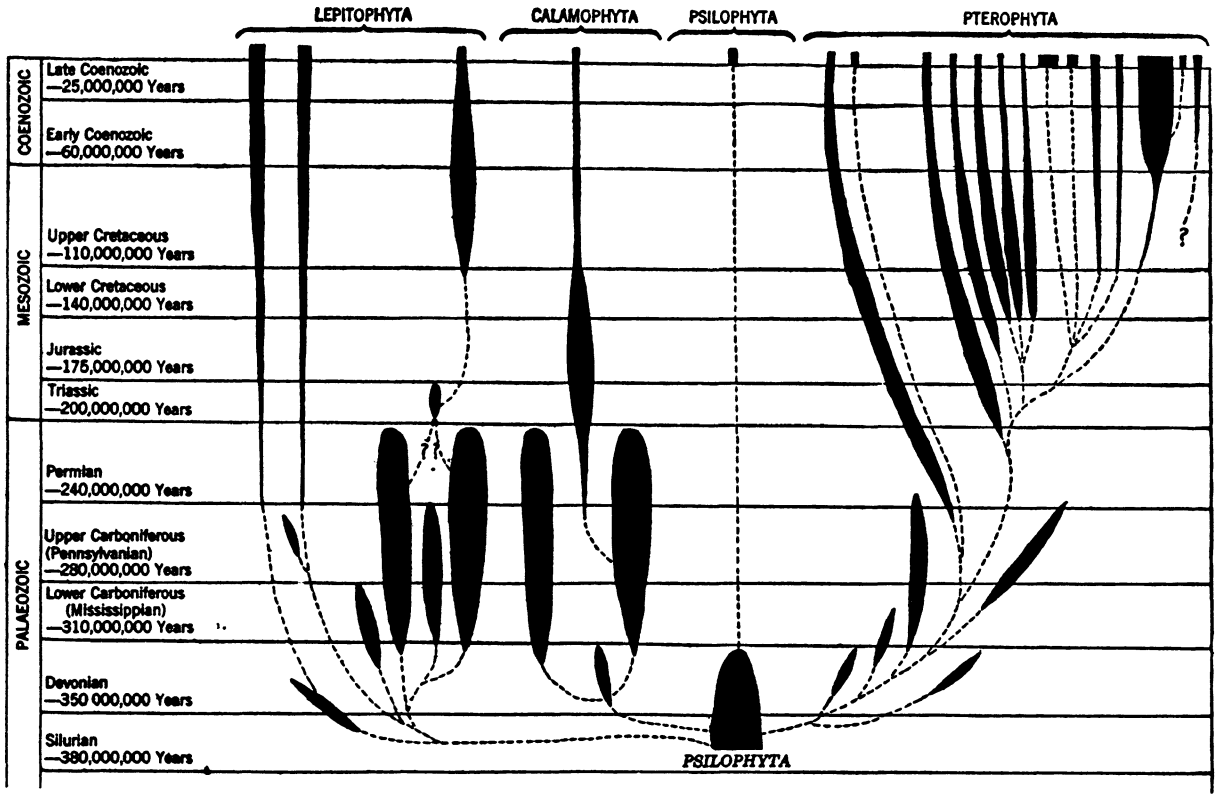

FIG. 95. Diagram showing the geological range and the suggested interrelationships among pteridophytes. For further details see Figs. 110, 145, and 162.

early evolution of a sporophyte of tree-like proportions in which there was a true secondary thickening of the vascular system. These "giant lycopods," which were an important element in the flora of the Carboniferous, disappeared during the Permian. Extinction of the giant lycopods during the Permian, together with extinction of the giant horsetails and many ferns of the Carboniferous, is contemporaneous with appearance of the extensive Permian ice sheet. It is thought that many of the pteridophytes evolved during the equable moist climate of the Carboniferous did not have sufficient hardiness to withstand the rigorous climate that prevailed during the glacial period of the Permian. In the flora of today there are four genera belonging to the lycopodian series. Three of them (*Lycopodium, Selaginella,* and *Phylloglossum*) are obviously related to the Carboniferous lycopods; the relationship of the fourth genus (*Isoetes*) is less pronounced. At one time *Lycopodium* and *Selaginella* were thought to be degenerate relicts of the giant lycopods, but they are now considered direct descendants of herbaceous lycopods that existed during the Carboniferous.

Evolution of the equisetaceous series from a psilophyte type included evolution of a sporophyte with leaves borne in transverse whorls along the stem; and evolution of a distinctive type of fertile appendage, the sporangiophore. A possible method of evolution of the sporangiophore has been discussed on page 138. Evolution of horsetails was at the same rapid rate as in lycopods and by the beginning of the Carboniferous some members of the series were of tree-like proportions and with a secondary thickening of stem and branches. Sporangial evolution was not so great as in the lycopods and no member of the series progressed beyond an incipient heterospory. Extinction of the "giant horsetails" was contemporaneous with that of the giant lycopods. *Equisetum* is the only genus in the flora of today, and it is probably a degenerate relict of the giant horsetails.

The filicinean series, the third evolutionary line from the Psilophytales, differs from the two foregoing series in having leaves bearing more than one sporangium and in having leaf gaps in the vascular cylinder. The method by which a psilophyte gave rise to macrophyllous leaves of the filicinean type has been discussed on page 136. The earliest known members of the series are from the Middle Devonian and they are of an intermediate type between ferns and psilophytes since their vegetative portions are fern-like and their sporangia resemble those of Psilophytales. Many ferns are known from the Carboniferous but because of their relatively small size they did not, as in the present-day flora of certain areas, constitute a conspicuous element in the landscape. Most of the Carboniferous ferns were quite different from those living today; and, similar to Carboniferous lycopods and horsetails, they became extinct during the unfavorable climate of the Upper Permian (Fig. 95). However, the Carbon-

iferous also included ferns directly related to certain present-day ferns. Some of the ferns of the flora of today arose during the Triassic and Jurassic periods immediately following the Permian. Certain of these families, as the Matoniaceae and Dipteridaceae, now include only a few vestigial species of limited geographical distribution. Other families in the flora of today, as the Cyatheaceae and Polypodiaceae, which are known from as far back as the Jurassic, have survived in wide variety. Still other families of present-day ferns are without any known fossil members (Fig. 162, page 266).

Bibliography

Allen, Ruth F. **1911.** *Trans. Wis. Acad.* **17**: 1–56. 6 pl. [Apogamy.]

Arber, E. A. N. **1921.** Devonian floras. Cambridge. 100 pp. 47 figs.

Arnold, C. A. **1947.** An introduction to paleobotany. New York. 433 pp. 187 figs.

Bancroft, Nellie. **1911.** *Ann. Bot.* **25**: 745–759. 1 pl. 3 figs. [Vessels.]

Barclay, B. D. **1931.** *Bot. Gaz.* **91**: 452–461. 19 figs. [Ontogeny of endodermis.]

Bartoo, D. R. **1930.** *Ibid.* **89**: 137–153. 27 figs. [Ontogeny of endodermis.]

Bessey, C. E. **1907.** A synopsis of plant phyla. *Univ. Nebr. Studies* **7**, No. 4: 1–99.

Bliss, Mary C. **1939.** *Amer. Jour. Bot.* **26**: 620–624. 16 figs. [Tracheal elements.]

Bohlin, K. **1901.** Utkast till de gröna algernas och arkegoniaternas fylogeni. Upsala. 43 pp.

Boodle, L. A. **1899.** *Ann. Bot.* **13**: 377–394. 1 pl. [Secondary thickening.]

1901. *Ibid.* **15**: 359–421. 3 pl. [Sieve tubes, origin of pith.]

Bower, F. O. **1884.** *Phil. Trans. Roy. Soc. London* **175**, Part 2: 565–615. 4 pl. [Phylogeny of peteridophytes.]

1885. *Jour. Linn. Soc. Bot. London* **21**: 360–368. 2 pl. 6 figs. [Apospory.]

1908. The origin of a land flora. London. 727 pp. 361 figs.

1911. *Ann. Bot.* **25**: 537–553. 2 pl. [Origin of pith.]

1920. *Proc. Roy. Soc. Edinburgh* **41**: 1–25. 19 figs. [Size and stelar morphology.]

1923. The ferns. Vol. 1. Cambridge. 359 pp. 309 figs.

1923A. *Proc. Roy. Soc. Edinburgh* **43**: 117–126. [Size and stelar morphology.]

1935. Primitive land plants. London. 658 pp. 449 figs.

Brebner, G. **1902.** *Ann. Bot.* **16**: 517–552. 2 pl. 2 figs. [Stelar theory.]

Campbell, D. H. **1894.** *Ann. Bot.* **8**: 1–20. 2 pl. [Primitive gametophytes.]

1895. The structure and development of mosses and ferns. 1st ed. London. 544 pp. 266 figs.

1899. Lectures on the evolution of plants. New York. 319 pp. 60 figs.

1917. *Proc. Nation. Acad. Sci.* (U.S.) **3**: 494–496. [Self-sustaining sporophytes of Bryophyta.]

1924. *Ann. Bot.* **38**: 473–483. 8 figs. [Self-sustaining sporophytes of Bryophyta.]

Church, A. H. **1919.** Thalassiophyta and the subaerial transmigration. Oxford. 95 pp.

DeBary, A. **1878.** *Bot. Zeitg.* **36**: 449–487. 1 pl. [Apogamy.]

Döpp, W. **1932.** *Planta* **17**: 86–152. 10 pl. 2 figs. [Apogamy.]

1939. *Ibid.* **29**: 481–533. 45 figs. [Apogamy.]

Druery, C. T. **1885.** *Jour. Linn. Soc. Bot. London* **21**: 354–357. [Discovery of apospory.]

Duerden, H. **1933.** *Ann. Bot.* **47**: 187–195. 1 pl. [Vessels.]

1934. *Ibid.* **48**: 459–465. 1 pl. [Vessels.]

Duncan, R. E. **1941.** *Amer. Jour. Bot.* **28**: 921–931. 37 figs. [Apogamy.]

Eames, A. J. **1936.** Morphology of vascular plants. Lower groups. New York. 433 pp. 213 figs.

Farlow, W. G. **1874.** *Quart. Jour. Microsc. Soc.* N.S. **14**: 266–272. 2 pl. [Discovery of apogamy.]
Farmer, J. B., and L. Digby. **1907.** *Ann. Bot.* **21**: 161–199. 5 pl. [Apospory and apogamy.]
Fritsch, F. E. **1916.** *New Phytol.* **15**: 233–250. 2 figs. [Origin of pteridophytes.]
1945. *Ann. Bot.* N.S. **9**: 1–29. 22 figs. [Origin of pteridophytes.]
Goebel, K. **1908.** Einleitung in die experimentelle Morphologie der Pflanzen. Leipzig. 260 pp. 135 figs.
Gwynne-Vaughan, D. T. **1901.** *Ann. Bot.* **15**: 71–98. 1 pl. [Stelar theory.]
1903. *Ibid.* **17**: 689–742. 3 pl. [Stelar theory.]
1908. *Ibid.* **22**: 517–523. 1 pl. [Vessels.]
1914. *Ibid.* **28**: 351–354. 1 pl. [Origin of pith.]
Harvey-Gibson, R. J. **1894.** *Ibid.* **8**: 133–206. 4 pl. [Vessels.]
Heilbronn, A. **1932.** *Ber. Deutsch. Bot. Ges.* **50**: 289–299. 6 figs. [Apospory.]
Hirmer, M. **1927.** Handbuch der Paläobotanik. Bd. 1. Munich. 708 pp. 817 figs.
Hofmeister, W. **1851.** Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farrn, Equisetaceen, Rhizocarpeen, und Lycopodiaceen) und der Samenbildung der Coniferen. Leipzig. 179 pp. 33 pl.
Hume, E. M. Margaret. **1912.** *Ann. Bot.* **26**: 573–587. 2 pl. [Sieve tubes.]
Jeffrey, E. C. **1898.** *British Assn. Adv. Sci. Rept.* 67th Meeting, Toronto. **1897**: 869–870. [Stelar theory.]
1902. *Phil. Trans. Roy. Soc. London B* **195**: 119–146. 6 pl. [Stelar theory.]
1910. *Bot. Gaz.* **50**: 401–414. 1 pl. [Stelar theory.]
1917. The anatomy of woody plants. Chicago. 478 pp. 306 figs.
Kräusel, R. **1932.** *Ber. Deutsch. Bot. Ges.* **50**: 5–12. [Phylogeny.]
Lang, W. **1898.** *Phil. Trans. Roy. Soc. London B* **190**: 189–238. 5 pl. [Sporangia on gametophytes.]
1931. *Ibid.* **219**: 421–442. 2 pl. [*Psilophyton.*]
Lang, W. H., and Isabel C. Cookson. **1935.** *Ibid.* **224**: 421–449. 4 pl. [Silurian peteridophytes.]
Lawton, Elva. **1932.** *Amer. Jour. Bot.* **19**: 303–333. 22 figs. [Apospory.]
Lignier, O. **1903.** *Bull. Soc. Linn. Normandie* 5 ser. **7**: 93–137. 8 figs. [Evolution of sporophyte.]
1908. *Compt. Rend. Assoc. Franc. Adv. Sci.* **1908**: 530–542. [Evolution of sporophyte.]
Lotsy, J. P. **1909.** Vorträge über botanische Stammesgeschichte. Bd. 2. Jena. 901 pp. 553 figs.
Loughridge, G. A. **1932.** *Bot. Gaz.* **93**: 188–196. 24 figs. [Tracheids.]
Manton, Irene. **1932.** *Jour. Genetics* **25**: 423–430. 4 figs. [Apospory.]
Pace, Lula. **1910.** *Bot. Gaz.* **50**: 49–58. 11 figs. [Sporangia on gametophytes.]
Patterson, Sister Mary Thomasine. **1942.** *Bot. Gaz.* **104**: 107–114. 9 figs. [Apogamy.]
Petry, L. C. **1914.** *Ibid.* **57**: 169–192. 16 figs. [Origin of pith.]
Priestley, J. H., and Edith E. North. **1922.** *New Phytol.* **21**: 113–139. 5 figs. [Endodermis.]
Priestley, J. H., and Francis M. Radcliffe. **1924.** *Ibid.* **23**: 161–193. 12 figs. [Endodermis.]
Schenck, H. **1908.** *Bot. Jahrb.* **42**: 1–37. 25 figs. [Origin of pteridophytes.]
Scott, D. H. **1900.** Studies in fossil botany. 1st ed. London. 533 pp. 151 figs.
1909. *Ibid.* 2d ed. Vol. 2. London. 321 pp. 95 figs.
1923. *Ibid.* 3d ed. Vol. 2. 446 pp. 136 figs.
Seward, A. C. **1933.** Plant life through the ages. 2d ed. Cambridge. 603 pp.
Steil, W. N. **1919.** *Ann. Bot.* **33**: 109–132. 3 pl. [Apogamy.]
1919A. *Bot. Gaz.* **67**: 469–482. 2 pl. 4 figs. [Apospory.]

1933. *Ibid.* **95**: 164–167. 6 figs. [Apogamy.]
1939. *Bot. Rev.* **5**: 433–453. [Apogamy and apospory.]
Stokey, Alma G. **1918.** *Bot. Gaz.* **65**: 97–102. 10 figs. [Apogamy.]
1945. *Ibid.* **106**: 402–411. 53 figs. [Apogamy.]
1948. *Ibid.* **109**: 363–380. 90 figs. [Apogamy.]
Strasburger, E. **1907.** *Flora* **97**: 123–191. 6 pl. [Apogamy.]
Studer, Sister Mary Mira. **1950.** *Trans. Amer. Microsc. Soc.* **69**: 222–235. 3 pl. [Apogamy.]
Tansley, A. G. **1907–1908.** *New Phytol.* **6**: 25–35, 53–68, 109–120, 135–155, 187–203, 219–238, 253–269. 75 figs. **7**: 1–16, 29–40. 5 figs. [Stelar theory.]
Thompson. J. McL. **1920.** *Trans. Roy. Soc. Edinburgh* **52**: 715–735. 4 pl. 9 figs. [Stelar theory.]
Van Tieghem, P., and H. Douliot. **1886.** *Ann. Sci. Nat. Bot.* 7 ser. **3**: 275–322. 3 pl. [Stelar theory.]
Wardlaw, C. W. **1924.** *Trans. Roy. Soc. Edinburgh* **53**: 503–532. 18 figs. [Size and stelar morphology.]
1925. *Ibid.* **54**: 281–308. 17 figs. [Size and stelar morphology.]
1928. *Ibid.* **56**: 19–56. 22 figs. [Size and stelar morphology.]
Wordsell, W. C. **1902.** *Bot. Gaz.* **34**: 216–223. 7 figs. [Stelar theory.]
Wright, Gertrude. **1920.** *Ibid.* **69**: 237–247. 2 pl. 6 figs. [Vessels.]
Yamanouchi, S. **1908.** *Ibid.* **45**: 289–318. 2 pl. 3 figs. [Apogamy.]
Zimmermann, W. **1930.** Die Phylogenie der Pflanzen. Jena. 452 pp 250 figs.
1938. Phylogenie. In F. Verdoorn, Manual of Pteridology. The Hague. Pp. 558–618. 20 figs.

CHAPTER 7

PSILOPHYTA

The Psilophyta have sporophytes differing from those of all other vascular plants in being rootless. The sporophyte is generally differentiated into a rhizoid-bearing subterranean portion and an aerial portion. The aerial portion is sparingly to profusely branched, and with a protostelic vascular strand. In most genera the aerial branches are leafless, but in a few genera they are closely beset with small, simple, veinless leaves. Sporangia are almost always terminal in position and borne singly at the tips of elongate or very much shortened branches. The gametophyte (known only from the two living genera) is subterranean and colorless. All members of the division are grouped in a single class, the Psilophytinae.

For over half a century paleobotanists considered *Psilophyton* (Fig. 98) a genus of questionable validity.* This was not due to an incomplete description of *Psilophyton*[1] but because it was so unlike any other known vascular plant, living or fossil. The significance of this peculiar plant became apparent upon the discovery[2] of well-preserved remains of other plants of a similar nature. Some 25 genera of these pteridophytes are now known and all are referable to a single order, the *Psilophytales*. The time range of the Psilophytales is from the Middle Silurian to the Upper Devonian and they are known in greatest abundance from the Lower and Middle Devonian. The occurrence of fossil remains of Psilophytales in such widely scattered regions as eastern Canada, Wyoming, Scotland, western Europe, and Australia shows that they must have been widespread during the time they lived.

The simplicity of structure of Psilophytales is widely believed to be due to their primitive nature and not to a reduction from a more elaborate organization. One of the most striking primitive features is the single sporangium terminating a branch tip and quite obviously a part of the branch. Other primitive vegetative features include a lack of roots, a

* The changed attitude toward *Psilophyton* before and after Kidston and Lang's discovery of the Rhynic flora in 1917 is well illustrated by the treatment of the genus in treatises on paleobotany by Scott (1900, 1920) and by Seward (1910, 1933).

[1] Dawson, 1859. [2] Kidston and Lang, 1917.

quite general lack of leaves, a protostelic vascular system, and a dichotomous branching throughout the entire plant or terminal portions of it. It is also widely believed that the psilophytan complex is the ancestral stock that gave rise to other vascular cryptogams but, as shown in the preceding chapter, there is diversity of opinion concerning the manner in which psilophytes did this.

The systematic position of two living genera of pteridophytes (*Tmesipteris* and *Psilotum*) was a troublesome question until it was realized[1] that they have affinities with the Psilophytales. The current practice is to segregate *Psilotum* and *Tmesipteris* in a separate order, the Psilotales, and to place this order and the Psilophytales in a taxon distinct from other major taxa of pteridophytes.

ORDER 1. PSILOPHYTALES

The Psilophytales had a rootless, dichotomously branched sporophyte that was generally differentiated into a subterranean and an aerial portion. The aerial portion was leafless or with small leaves. Most genera had sporangia borne singly at the tips of branches, but certain genera had them borne in a cluster at the tip of a branch.

All genera are fossil and the known fossil record indicates that the Psilophytales became extinct during the Upper Devonian. The reasons for this are obscure, although it might be argued that their sudden disappearance from the land flora was due to their being crowded out by other vascular plants better suited to land conditions of that time.

The order has been divided[2] into nine families but some of these families are founded upon very imperfectly known genera. Differences between genera in which there is an adequate knowledge of vegetative and reproductive structures justify the recognition of five families.

FAMILY 1. RHYNIACEAE

Members of this family had a sporophyte that was small and differentiated into subterranean and aerial portions. The subterranean portion was rhizome- or corm-like and with numerous unicellular rhizoids. The aerial portion was leafless and with dichotomously forked cylindrical branches. The sporangia, which were indehiscent and had a jacket layer several cells in thickness, were borne terminally and singly on the branch apices. There are some half dozen genera in the family.

Rhynia, the type genus, is known only from a single Middle Devonian deposit in Scotland. However, the numerous specimens of the two species that have been found at this station[3] are so excellently preserved that they give considerable information concerning the form and

[1] Kidston and Lang, 1920. [2] Kräusel, 1938.
[3] Kidston and Lang, 1917, 1920*A*, 1921.

structure of this very primitive vascular plant. *Rhynia* was a rootless vascular plant (with a maximum height of about 20 cm.) that grew in swampy marshes comparable to the peat marshes of today.[1] The plant body consisted of a horizontal rhizome whose branches turned gradually or abruptly upward and became leafless aerial shoots (Fig. 96). Rhizoids were borne in patches on the underside of the rhizome. The aerial branches were dichotomously forked, cylindrical, and tapered gradually. Elongate sporangia, resembling those of certain Hepaticae, were borne at the tips of the ultimate dichotomies of the aerial branches.

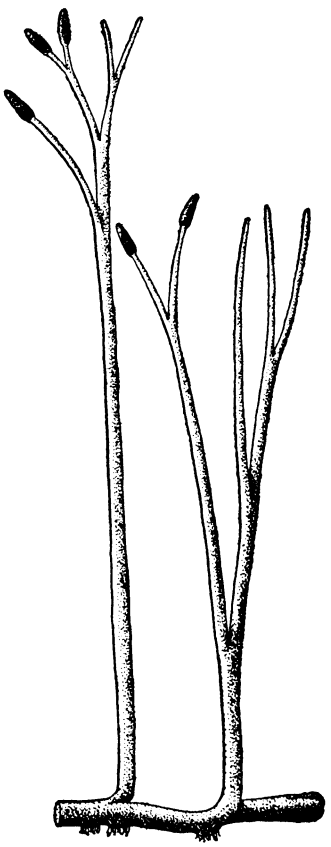

FIG. 96. Reconstruction of *Rhynia major* Kidston and Lang. (*Based upon Kidston and Lang*, 1921.)

Both the subterranean and the aerial portions of the plant were internally differentiated into epidermis, cortex, and stele, but there was no endodermal layer separating the latter two. The stele was protostelic and with a cylindrical mass of xylem completely ensheathed by a phloem layer several cells in thickness (Fig. 97*A*). The xylem contained tracheids only. The preservation of tracheids is imperfect in most specimens but in certain cases they show an annular thickening on their walls.[2] Some specimens have all tracheids of the same diameter; other specimens have the peripheral tracheids greater in diameter than those at the center of the xylem.[3] The phloem layer was generally four to five cells in thickness and composed of elongate thin-walled cells with diagonal end walls. The cortex, which had a diameter about tenfold that of the stele, was differentiated into an inner and an outer portion. The inner cortex was much thicker than the outer and consisted of spherical cells separated from one another by fairly large intercellular spaces. It is thought that this was the chief photosynthetic tissue of the plant. The outer cortex, which was one to four cells in thickness, was composed of large angular cells without conspicuous intercellular spaces except immediately internal to the stomata.

[1] Kidston and Lang, 1921*A*.
[2] Kidston and Lang, 1917.
[3] Kidston and Lang, 1920.

The epidermal layer was one cell in thickness and with a conspicuous cuticle on the free face. As seen in surface view, the epidermal cells were broadly fusiform and in more or less regular transverse series. Here and there in the epidermis of aerial branches were pairs of guard cells surrounding a stoma.

Numerous detached sporangia of *Rhynia* have been found, but it is not known whether these were borne on all or only on certain of the aerial branches. The sporangia were always borne singly and at the terminus

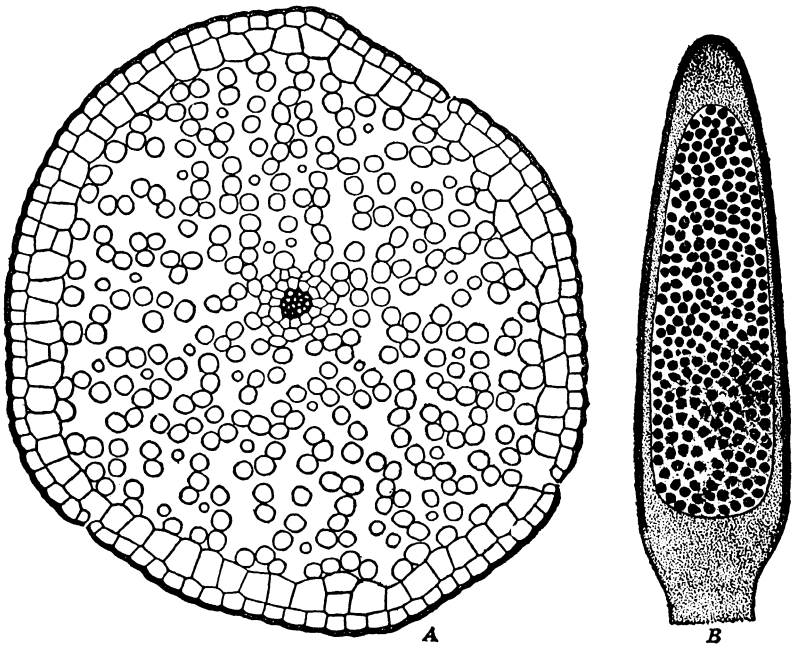

FIG. 97. *Rhynia gwynne-vaughani* Kidston and Lang. *A*, semidiagrammatic transverse section of an aerial branch. *B*, longitudinal section of a capsule. (*A*, × 60; *B*, × 6.)

of a branch. They were cylindrical and with a diameter somewhat greater than that of the subtending branch tip (Fig. 97*B*). A sporangium had a jacket layer several cells in thickness in which the cells of the outermost layer were thick-walled and had a heavy cuticle. The sporangia were indehiscent, and liberation of spores seems to have taken place by a decay of the jacket layer. The sporangial cavity, which was without a columella, contained many spores, all of which were of the same size. In some specimens the spores within the sporangium are united in tetrads; in other specimens they lie free from one another.

If the sporangia and fragments of the subtending branch were the only known portions of the plant body, one would unquestionably assign *Rhynia* to the Bryophyta. The resemblance of these sporangia to those of Bryophyta is even more marked in *Hornea*, a genus belonging to the

Rhyniaceae and discovered in the deposits containing *Rhynia*. Sporangia of *Hornea*[1] resemble those of *Rhynia* in general appearance but differ in that they contain a well-defined columella that extends nearly to the apex of the sporangial cavity.

FAMILY 2. PSILOPHYTACEAE

Sporophytes of Psilophytaceae were much like those of Rhyniaceae except that major aerial branches bore small spine-like outgrowths. Three genera are referred to the family.

Psilophyton, the type genus, has been found in Lower Devonian deposits at widely scattered stations in both the Eastern and Western Hemispheres.[2] It appears to have been gregarious in habit and to have grown in swampy ground. The sporophyte had a rootless rhizome with numerous rhizoids. The rhizome bore erect branches in which the dichotomous forking was sympodial and with one arm of each dichotomy overtopping the other (Fig. 98). Growing tips of erect branches sometimes had the spiral uncoiling (circinate vernation) found in growing tips of fern leaves. Spiny outgrowths were present on the major branches[3] and a careful anatomical study[4] of them shows that the outgrowths were neither leaf-like nor branch-like, and probably were glandular in nature.

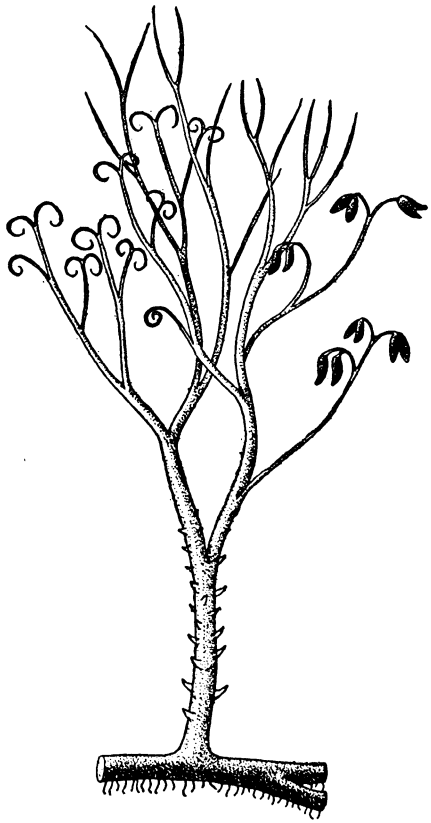

FIG. 98. Reconstruction of *Psilophyton princeps* Dawson. (*Based upon Dawson*, 1859, 1888.)

At the center of a branch was a central cylinder composed of annular tracheids. External to this was a cortex, parenchymatous in the inner portion and with elongate thick-walled cells in the outer portion. The presence of stomata in the epidermal layer suggests that, as in *Rhynia*, the outermost portion of the cortex was a photosynthetic tissue.

[1] Kidston and Lang, 1920. [2] Dorf, 1933.
[3] Dawson, 1859; Dorf, 1933. [4] Lang, 1931.

Sporangia were borne at the tips of branches, and frequently in pairs because of a forking of the branch just below the sporangial region. Sporangia were considerably broader than the subtending branch, were obovoid, and with a blunt or an acute apex. The jacket portion of a sporangium was several cells in thickness. Spores within a sporangium were somewhat variable in size[1] but this is not to be taken as an incipient heterospory.

FAMILY 3. PSEUDOSPOROCHNACEAE

The Pseudosporochnaceae had a relatively large sporophyte with a conspicuous rootless main trunk terminating in several dichotomously forked main branches. These, in turn, bore many leafless branchlets, the ultimate dichotomies of which terminated in sporangia.

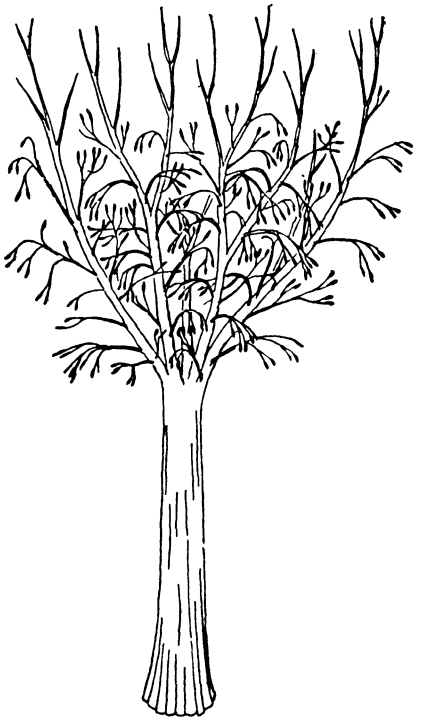

FIG. 99. Reconstruction of *Pseudosporochnus krejcii* Potonié and Bernard. (*After Krausel and Weyland*, 1933.)

The single genus of the family, *Pseudosporochnus*, is known from the Middle Devonian of Scotland, Bohemia, and the eastern part of the United States.[2] Reconstructions based on fragments seem to show that it was tree-like in habit and some 3 meters tall when conditions for development were favorable.

The tree-like sporophyte had a conspicuous, longitudinally fluted trunk with a bulbous base that was without roots or root-like branches (Fig. 99). The trunk was unbranched for a considerable distance upward and then forked rather abruptly into several large branches. It is uncertain[2] whether the trunk and its main branches were woody and with secondary thickening, or were herbaceous in nature. Each of the main branches was leafless and with a repeated dichotomous branching. The ultimate branchlets were of a hair-like fineness and many of them were swollen at their tips. These swellings have been considered leaves, but maceration of them shows that they were sporangia containing spores 4 to 7 μ in diameter.[2]

[1] Lang, 1931. [2] Kräusel and Weyland, 1933.

FAMILY 4. ZOSTEROPHYLLACEAE

Members of this family had branched, rootless, leafless sporophytes. The family differs from others of the order in having the sporangia borne laterally and in a spike-like cluster on the terminal portion of erect branches. There are three genera, of which *Zosterophyllum* is the most completely known.

Zosterophyllum (Fig. 100) has been found in Middle Silurian, Lower Devonian, and Middle Devonian deposits; and in such widely separated places as Scotland and Australia. Of the four species three are thought[1] to have been terrestrial; and the fourth is thought[2] to have grown submerged, but with the fertile portions projecting above water. In the presumedly terrestrial *Z. myretonianum* Penh. there was a rhizomatous portion from which arose a tuft of erect axes with a sparse dichotomous or lateral branching. Successive branches of the rhizomatous portion were close to one another, and with one arm of a dichotomy growing upward and the other growing horizontally or downward. Branches of the sporophyte had a central core of xylem composed of tracheids with annular thickenings close to one another.[3] Nothing is known concerning structure of the cortex, but there was an epidermis with a thick cuticle. Stomata have not been clearly demonstrated but there are indications that they were present.[3] Sporangia were borne laterally toward the free ends of upright branches. In some species the sporangia were borne in a radial spiral succession; in other species they were borne in vertical rows.[4] Each sporangium was subtended by a stalk with a vascular strand connected to the axis bearing the sporangium. A sporangium was kidney-shaped and certain species have been shown[5] to have had a definite line of dehiscence.

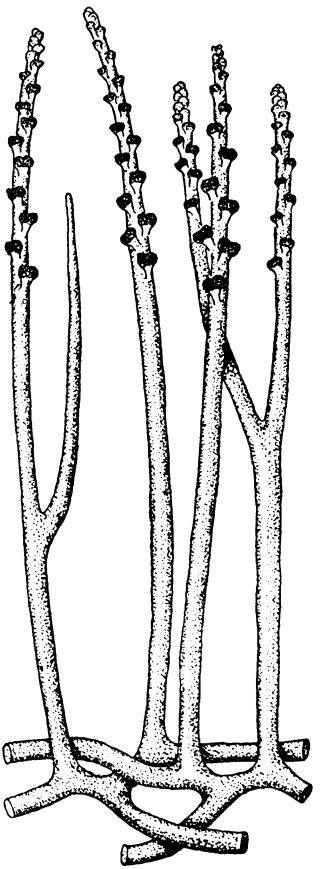

FIG. 100. Reconstruction of *Zosterophyllum myretonianum* Penh. (*Based upon Lang*, 1927.)

[1] Croft and Lang, 1942; Lang, 1927; Lang and Cookson, 1935.
[2] Krausel and Weyland, 1935. [3] Lang, 1927. [4] Croft and Lang, 1942.
[5] Croft and Lang, 1942; Lang and Cookson, 1935.

FAMILY 5. ASTEROXYLACEAE

The Asteroxylaceae had a plant body with a prostrate rhizome bearing two kinds of branches, one leafless and subterranean, the other erect and having many small leaves. The sporangia were dehiscent and had a jacket layer several cells in thickness. It is very probable that they were borne at the tips of leafless branchlets.

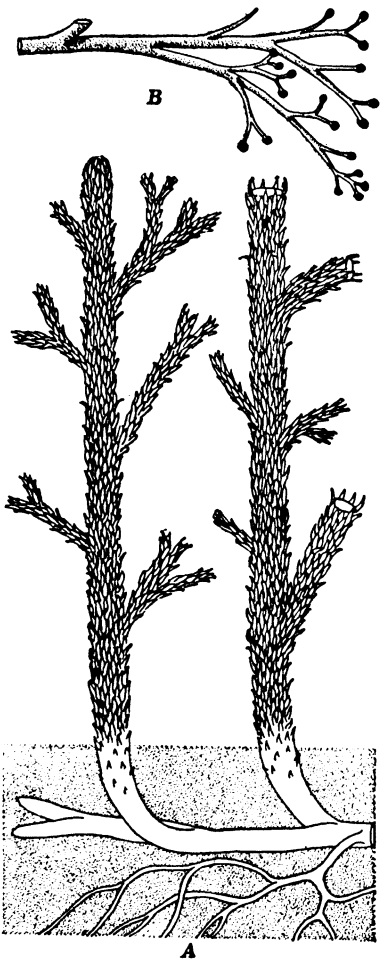

FIG. 101. Reconstruction of *Asteroxylon mackiei* Kidston and Lang. *A*, rhizome and vegetative branches. *B*, a fertile branch. (*Based upon Kidston and Lang*, 1921.)

The Asteroxylaceae, with the single genus *Asteroxylon*, differ so markedly from other Psilophytales that they might well be placed in a separate order. There are two species of *Asteroxylon: A. mackiei* Kidston and Lang, found in Middle Devonian deposits at Rhynie, Scotland;[1] and *A. elberfeldense* Kräusel and Weyland, found in Middle Devonian deposits near Elberfeld, Germany.[2] Although differing somewhat in appearance the two obviously belong to the same genus.

Asteroxylon had a horizontal, subterranean, leafless, dichotomously branched rhizome. The tips of certain dichotomies of the rhizome grew upward toward the air and developed into branched aerial shoots that were closely beset with small leaves (Fig. 101*A*). Tips of other dichotomies developed into slender, leafless, repeatedly forked, subterranean branches that resemble the rhizophores of the Lycopodinae (page 196). These branches probably functioned in a root-like manner. According to the species, the leafy shoots had a pronounced or an obscure dichotomous branching. One species had the branch tips clothed with leaves;[2] the other had naked, circinately vernate, branch apices. Although it is known that the sporangia were borne at the tips of leafless aerial branches, it is uncertain

[1] Kidston and Lang, 1920*A*, 1921

[2] Kräusel and Weyland, 1926.

whether these dichotomously forked branches (Fig. 101*B*) were borne terminally or laterally on the leafy shoots.

The rhizome portion of the plant body was cylindrical and had a structure similar to that of *Rhynia* when seen in cross section. The leafy branches had a more complex internal organization. Similar to the rhizome, they were internally differentiated into central cylinder and cortex (Fig. 102). The central cylinder was a mesarch actinostele. The xylem was 4- to 10-rayed and had a small mass of protoxylem a short distance inward from the outer face of each ray. Except for occasional annular

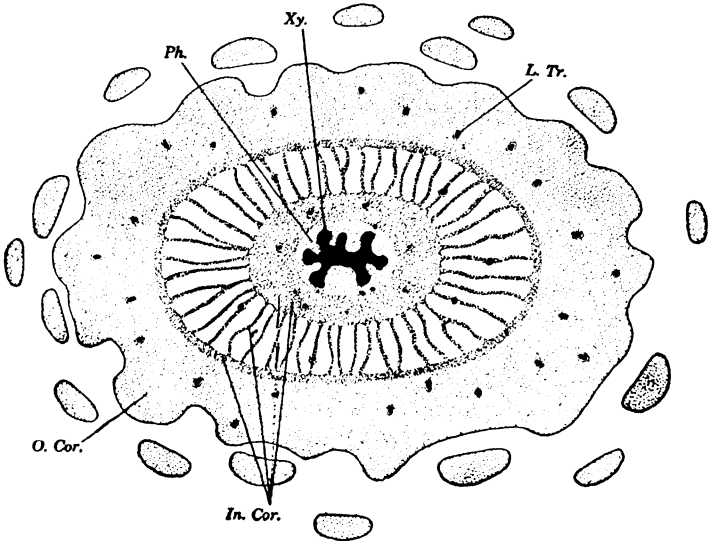

FIG. 102. Transverse section of a leafy shoot of *Asteroxylon mackiei* Kidston and Lang. (*In. Cor.*, inner cortex; *L. Tr.*, leaf traces; *O. Cor.*, outer cortex; *Ph.*, phloem, *Xy.*, xylem.) (× 6.)

tracheids in the protoxylem, the entire xylem mass was composed of spiral tracheids. The xylem was encircled by a layer of phloem that was thin external to the xylem ways and thick between them. It is thought[1] that the phloem was composed of long, thin-walled, tubular cells with pointed or with transverse end walls. Small leaf traces were given off from the arms of the xylem. A leaf trace extended diagonally upward through the phloem to the base of a veinless leaf. Leaf traces were concentric in organization and had a layer of phloem completely ensheathing an endarch cylinder of xylem. Aerial shoots had their cortices differentiated into an outer and an inner portion. The outer cortex, except for the leaf traces, was a more or less homogeneous parenchymatous tissue. The inner

[1] Kidston and Lang, 1920*A*.

cortex consisted of three concentric regions: an outer layer of tangentially compressed cells, a middle radially septate layer with conspicuous radially elongate intercellular spaces, and a broad homogeneous inner layer. The epidermal layer of the shoot was one cell in thickness and contained stomata.

Fragments of slender, leafless, dichotomously forked branches with sporangia at their tips have been found intermingled with *Asteroxylon*.[1] These are generally considered the fruiting portion of the plant, but their connection with leafy shoots has not been established beyond all doubt. The sporangia were pear-shaped with the narrow end attached to the branch tip. The sporangia had a jacket several cells in thickness, in which the epidermal cells over the sporangial apex had thickened radial and inner tangential walls. The apical dehiscence of mature sporangia seems to have been due to hygroscopic changes in these annulus-like cells. The sporangial cavity was without a columella and contained a considerable number of spores. These were developed in tetrads and were about 65μ in diameter when mature.

ORDER 2. PSILOTALES

The Psilotales have a rootless, dichotomously branched sporophyte that is generally differentiated into a rhizome and an aerial shoot. The aerial shoots may be leafless or may bear many small leaves. The sporangia are borne in diads or triads and directly upon the stem or at the bases of leaves. The gametophytes are subterranean and without chlorophyll. The antheridia lie partially embedded in the gametophyte.

This order contains but two rather closely related genera, *Psilotum* and *Tmesipteris*, both of which are known only in the living condition. They are placed in a single family, the Psilotaceae. *Tmesipteris*, found in Australia, New Zealand, and certain smaller Pacific Ocean Islands, is generally regarded as having but one species, *T. tannensis* Bernh. (Fig. 103*C*). Several species have been described for *Psilotum*, but these are usually reduced to two, *P. triquetrum* Sw. (Fig. 103*A*) and *P. flaccidum* Wall. The two species of *Psilotum* are widespread in tropical and subtropical regions of both hemispheres, but *P. triquetrum* is the commoner of the two. Both genera are usually epiphytic in habit and grow upon tree ferns, but all species may also be terrestrial and grow in soil or in the crevices of rocks.

Both genera have rootless brown rhizomes with a repeated dichotomous branching in which the tip of any dichotomy may develop into a green aerial shoot. The rhizome generally contains a mycorhizal fungus.

Aerial shoots of epiphytic individuals are usually pendant; those of terrestrial individuals are frequently erect. The aerial shoots are quite

[1] Kidston and Lang, 1920*A*.

different in the two genera. In *Tmesipteris* the shoot is generally unbranched and only rarely has a single dichotomy. Near its attachment to the rhizome, the shoot has minute, scale-like leaves; farther up a shoot the leaves are progressively larger and more broadly lanceolate. Most of the leaves toward the distal end of a shoot are bifurcate and have a pair of sporangia in their axils (Fig. 103*D–E*). This fertile portion of the plant

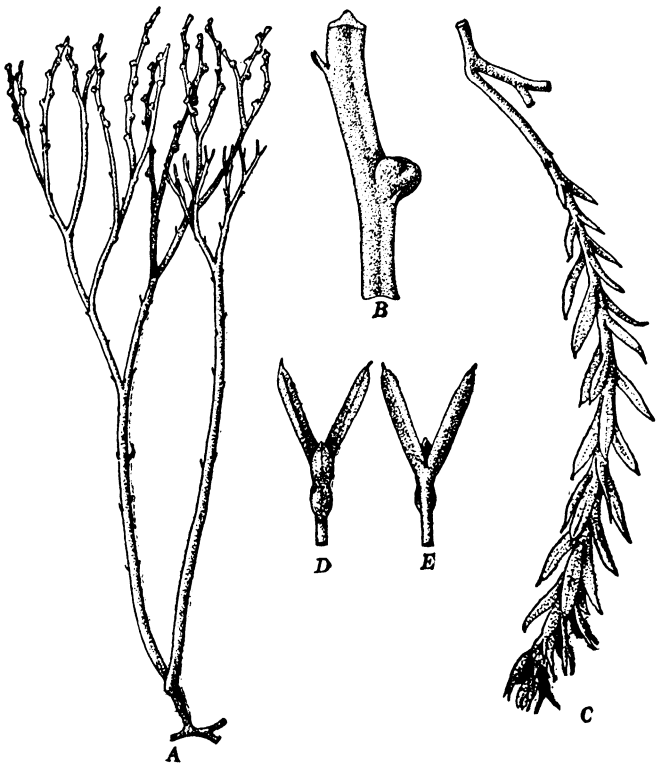

FIG. 103. *A–B*, *Psilotum triquetrum* Sw. *A*, portion of a shoot. *B*, portion of a shoot with a sporangiophore in the axil of a leaf. *C–E*, *Tmesipteris tannensis* Bernh. *C*, portion of a pendant shoot. *D–E*, ventral and dorsal view of leaf and sporangiophore. (*A*, × ½; *B*, × 4; *C*, × ⅘; *D–E*, × 2½.)

is sometimes called a "strobilus," but it is a very lax structure as compared with strobili of lycopods. The aerial shoot of *Psilotum* regularly has several dichotomous branchings. The basal portion of the shoot is cylindrical; the distal green portion may be radially symmetrical and longitudinally ribbed (*P. triquetrum*), or it may be markedly flattened (*P. flaccidum*). Leaves on aerial branches of *Psilotum* are small, scale-like, and more or less irregular in distribution. The sporangia are borne in triads on very short stalks and in the axils of minute bifid leaves. Most

of them lie toward the apices of aerial branches, but occasional ones may be relatively low on a branch. (Fig. 103 *A–B*).

Apices of rhizomes and aerial branches in both genera have a single apical cell with three cutting faces.[1] Mature portions of rhizomes of both genera are actinostelic and have a relatively simple cortex surrounding the stele.

Aerial branches of *Psilotum*[2] are also actinostelic. In these branches the boundaries between stele and cortex are sharply delimited by an endodermal layer with distinct Casparian strips in the radial walls (Fig. 104). The xylem is actinostelic, generally with six rays. It is exarch in arrangement and has a few protoxylem elements at the tip of each ray. The center

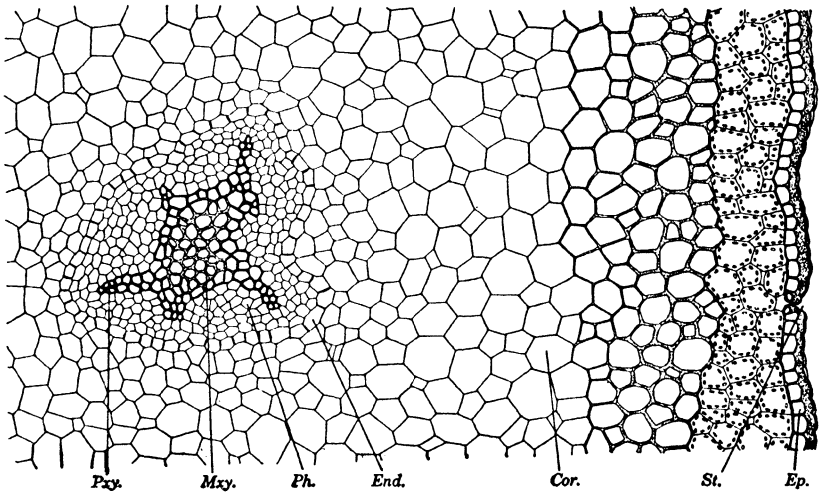

FIG. 104. Transverse section of stele and part of cortex of *Psilotum triquetrum* Sw. (*Cor.*, cortex; *End.*, endodermis; *Ep.*, epidermis; *Mxy.*, metaxylem, *Ph.*, phloem; *Pxy.*, protoxylem; *St.*, stoma.) (× 80.)

of the xylem mass is composed of thick-walled sclerenchyma fibers with simple pits in their walls.[3] The thin-walled elements between endodermis and xylem are vertically elongate cells. This tissue is usually called the phloem, but typical sieve tubes have not been demonstrated in it.[3] In some cases there are a few secondary xylem elements between the phloem and the primary xylem.[4] The cortex in aerial branches of *P. triquetrum* is thin-walled and without intercellular spaces for a considerable distance external to the endodermis; outward from this the cells have thicker and thicker walls. The sclerenchymatous portion of the cortex is abruptly succeeded by thin-walled cells with numerous chloroplasts. This photosynthetic portion of the branch is two to five cells in breadth and composed

[1] Ford, 1904; Holloway, 1918. [2] Ford, 1904; Stiles, 1910.
[3] Ford, 1904. [4] Boodle, 1904; Stiles, 1910.

of vertically elongate cells with small intercellular spaces between the vertical walls. The epidermis is one cell in thickness and heavily cutinized. Stomata are found chiefly in the grooves between longitudinal ridges of the stem.

Aerial branches of *Tmesipteris* have no well-defined endodermal layer.[1] The vascular cylinder is solenostelic and has a small mass of thin-walled parenchyma (**pith**) internal to the tracheids (Fig. 105). Vigorously growing branches have the xylem in a definite cylinder and five small groups of

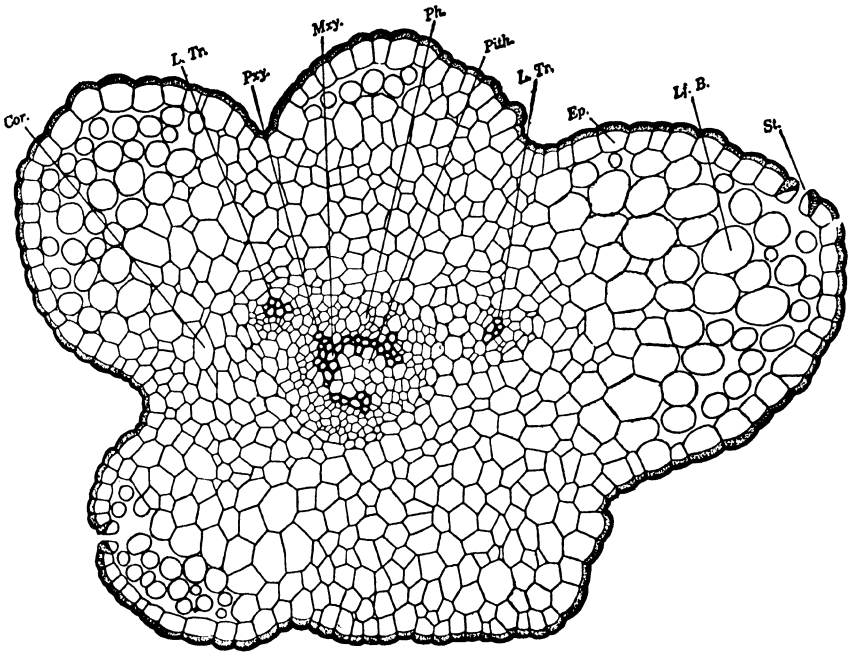

FIG. 105. Transverse section of shoot of *Tmesipteris tannensis* Bernh. (*Cor.*, cortex; *Ep.*, epidermis; *L. Tr.*, leaf trace; *Lf. B.*, leaf base; *Mxy.*, metaxylem; *Ph.*, phloem; *Pxy.*, protoxylem; *St.*, stoma.) (× 80.)

mesarch protoxylem in the cylinder. The xylem of the stele becomes inconspicuous toward the apices of branches and consists largely of traces departing to the leaves. The major portion of the phloem is composed of sieve tubes with sieve plates on their lateral walls. These sieve tubes are atypical in that they have lignified walls. Leaf traces have their xylem mesarch in arrangement and ensheathed by a layer of phloem after the leaves have departed from the stele. The cortex is composed of angular cells without intercellular spaces, and the epidermis is one cell in thickness, heavily cutinized, and without stomata. Outer portions of branches

[1] Sykes, 1908.

that belong more to the leaf base than to the cortex have stomata in the epidermal layer and conspicuous intercellular spaces in the subepidermal tissue.

Leaves of *Tmesipteris* have a single vascular bundle that is continuous with a leaf trace from the stem. As seen in cross section, a leaf bundle has four or five scalariform tracheids surrounding one or two protoxylem elements. The xylem is surrounded by phloem and this, in turn, is ensheathed by a poorly defined endodermal layer.[1] All mesophyll cells in the flattened blade are angular in outline and have small intercellular spaces between them. The epidermal layer has its stomata somewhat sunken below the surface of the blade. One form of *T. tannensis* has stomata on both faces of the blade; the other form has them only on the adaxial face. Leaves of *Psilotum* are always small and simple in structure. The surface layer of the leaf is a cutinized epidermis without stomata. The interior of the leaf consists entirely of parenchyma similar in appearance to the photosynthetic tissue of the branch.[2] The leaves are without a vein, but in *P. flaccidum* there is a leaf trace which terminates just below the leaf base.

Sporangia of *Tmesipteris* are borne in pairs at the base of a large bifid leaf-like appendage (Fig. 103*D–E*); those of *Psilotum* are borne in triads on minute appendages subtended by a bract (Fig. 103*B*). Because the sporangia are fused with one another the group is sometimes called a **synangium,** but the application of this term to fused sporangia of Psilotales is misleading because the structure is not homologous with the synangium of marattiaceous ferns. The so-called synangium of Psilotales is generally interpreted[3] as a sporangiophore fused with a subtending bract. Stages in early ontogeny show that there are separate sporangia and not one septate sporangium. The regular occurrence of a vascular supply in the short pedicel subtending the two (or the three) sporangia, and the occasional occurrence of fructifications with elongate pedicels seem to show that the pedicels are homologous with those of equisetaceous sporangiophores (see page 237). Additional evidence for the sporangiophoric nature is seen in aberrant fructifications where a repeatedly forked "sporophyll" bears two or three "synangia" and where the "synangium" is replaced by a leaf-like lobe.

There are evident homologies between fructifications of Psilotales and fertile portions of those sporophytes of Psilophytales where one arm of a branch is fertile and the other sterile. A condensation of the fertile arm to a condition where there are very short dichotomies terminating in sporangia would result in the psilotan sporangiophore; and flattening and shortening of the sterile arm would result in the bract (or pair of bracts) subtending the psilotan sporangiophore.

[1] Sykes, 1908. [2] Ford, 1904.

[3] Bower, 1935; Eames, 1936; Scott, 1900; Sykes, 1908; Thomas, 1902.

In very early stages of development of *Tmesipteris* it is impossible to tell whether a meristematic lateral outgrowth just back of the stem apex will develop into a fructification or into a leaf. In the case of *Psilotum* the bract subtending the sporangiophore is well along toward maturity before the sporangiophore begins to develop. A sporangiophore of *Psilotum* is first recognizable as a small meristematic hump on the adaxial face of a bract and near its base. Growth of a sporangiophore is said[1] to be due to an apical cell with three cutting faces, but this cell, if present, is not generally recognizable. The sporangia are differentiated early in the ontogeny of a sporangiophore. Judging from very early stages in sporangial

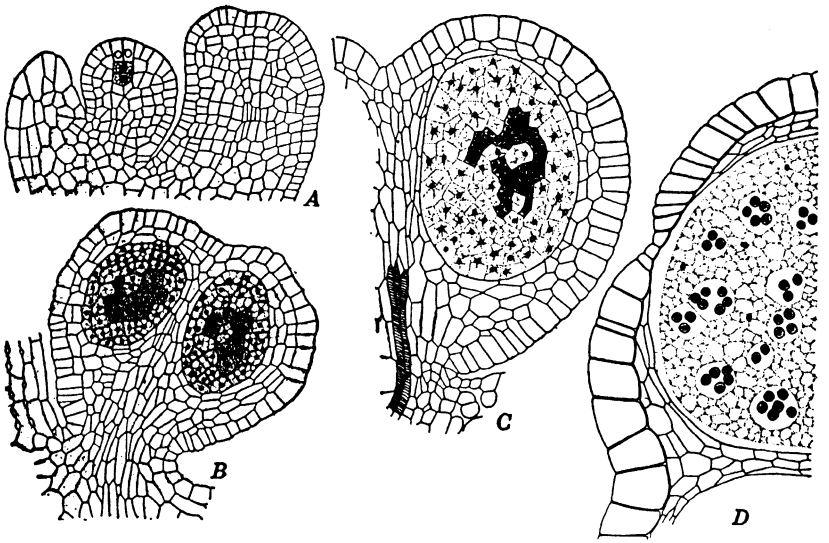

FIG. 106. *Psilotum triquetrum* Sw. *A*, vertical section of a stem apex bearing a young leaf and a sporangiophore. *B–C*, vertical sections of sporangiophores at later stages of development. *D*, transverse section of a portion of an older sporangiophore and through the line of dehiscence of a sporangium. (× 50.)

development (Fig. 106*A*), each of the three sporangia is developed from a single epidermal cell of the sporangiophore. Irrespective of whether formed from one or more than one cell, the first plane of division is periclinal. The outer daughter cell is the **jacket initial**; the inner cell is the **archesporial (primary sporogenous) cell.** Repeated periclinal and anticlinal division of the jacket initial results in a jacket layer four to five cells in thickness (Fig. 106*B–D*). Division and redivision of the archesporial cell produce a large number of sporogenous cells. Unlike most other Pteridophyta, neither the outermost sporogenous cells nor the innermost jacket cells develop into a tapetum. As the sporangium approaches maturity, irregular groups of cells in the sporogenous tissue become

[1] Bower, 1894.

densely filled with cytoplasm, divide repeatedly, and ultimately give rise to the spore mother cells (Fig. 106*B–C*). The remaining sporogenous cells, whose protoplasts are watery, divide slowly and disintegrate into a plasmodial mass as the spores are being formed (Fig. 106*C–D*). Spore formation is accompanied by a thickening of cell walls in the epidermal layer of the jacket except in a small vertical row. This row, running from base to apex of the sporangium, is the future line of longitudinal dehiscence of the sporangium (Fig. 106*D*).

Gametophytes of Psilotales are subterranean in habit, devoid of chlorophyll, and saprophytic in nutrition through the agency of symbiotic phycomycetous fungi in their cells. This mycorhizal mode of nutrition is

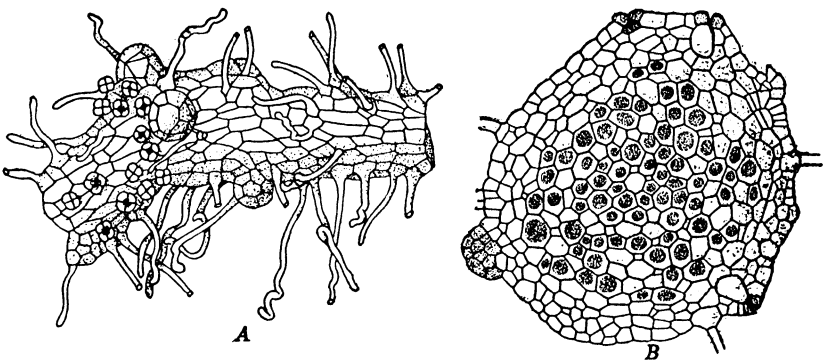

FIG. 107. *Tmesipteris tannensis* Bernh. *A*, surface view of a gametophyte. *B*, transverse section of a gametophyte. (*A*, *after Lawson*, 1917*A*; *B*, *after Holloway*, 1918.)

not peculiar to the order since it is also found in *Lycopodium* and in certain eusporangiate ferns. The gametophytes are irregularly cylindrical in shape with one or two irregular dichotomous branchings (Fig. 107*A*). The entire surface of the thallus is covered with long unicellular rhizoids. Each branch is meristematic. In *Tmesipteris*[1] the meristematic region has a single apical cell but this has not been observed[2] in *Psilotum*. In mature portions of a gametophyte the epidermis and a subepidermal layer two to four cells in thickness are composed of relatively small cells free from fungi and rich in starch. The remaining internal cells are larger and densely packed with the mycorhizal fungus. Gametophytes of *Psilotum* have been found[2] with a strand composed of annular and scalariform tracheids extending back from the growing apex. A similar development of tracheids has been observed in certain ferns and it has been held that[3] "One of the best evidences of apogamy in ferns is the appearance of tracheids just back of the apical notch of the prothallium." Gametophytes of Psilotales are homothallic, with sexual organs scattered over the entire

[1] Holloway, 1918. [2] Holloway, 1939. [3] Steil, 1939.

surface, and with archegonia more numerous than antheridia, or vice versa.[1]

The antheridial initial is a superficial cell of the gametophyte.[1] It divides periclinally into an outer cell, the **jacket initial,** and an inner cell, the **primary androgonial cell** (Fig. 108*A*). Division and redivision of the primary androgonial cells result in a considerable number of androgonial cells, the last cell generation of which are **androcytes** (Fig. 108*C–E*). The androcytes metamorphose into spirally coiled multiflagellate antherozoids.[2] Development of the androgonial tissue is accompanied by an anticlinal division and redivision of the jacket initial to form a **jacket layer**

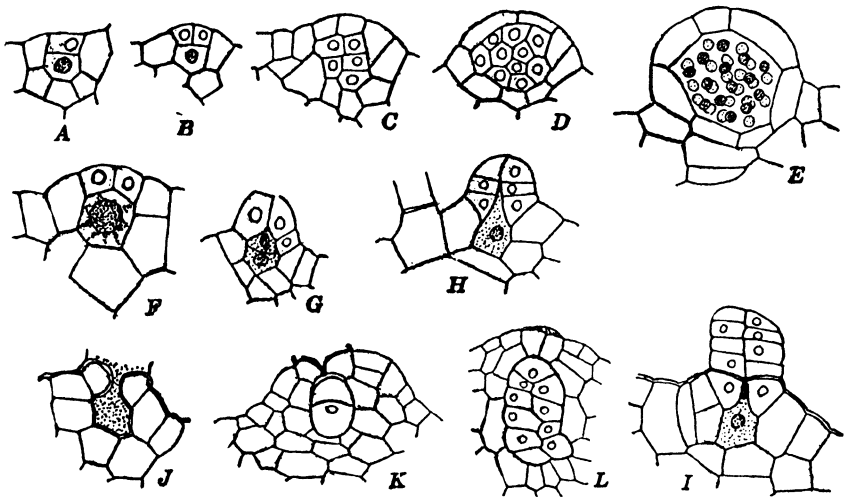

FIG. 108. *Tmesipteris tannensis* Bernh. *A–E*, vertical sections of antheridia at various stages of development. *F–J*, vertical sections of archegonia at various stages of development. *K–L*, vertical sections of young embryos within archegonia. (*A–J*, *after Holloway*, 1918; *K–L*, *after Holloway*, 1921.) (*A–J*, × 115; *K–L*, × 75.)

one cell in thickness that lies external to the outer face of the androgonial tissue (Fig. 108*B–E*). At the center of a mature jacket layer is a triangular **opercular cell** whose eventual disintegration provides an opening for the escape of antherozoids. Mature antheridia of Psilotales project in a dome-like manner above the gametophyte. They appear to be of an emergent type, but in reality they are the same embedded type as those of *Lycopodium*, *Equisetum*, and the eusporangiate ferns.

The archegonial initial is also a superficial cell of the gametophyte. The first division of this initial is periclinal and into a **primary cover cell** and a **central cell.** By two successive anticlinal divisions the primary cover cell gives rise to four quadrately arranged **neck initials** (Fig. 108*F*). Peri-

[1] Holloway, 1918, 1921, 1939; Lawson, 1917, 1917*A*.

[2] Darnell-Smith, 1917; Lawson, 1917, 1917*A*.

clinal division of each of the neck initials results in an archegonial neck four to five cells in height (Fig. 108*G–I*). Development of neck initials into a neck is accompanied by a periclinal division of the central cell into a **primary canal cell** and a **primary venter cell** (Fig. 108*G*). The primary canal cell elongates vertically as the neck develops, but it is uncertain[1] whether or not it divides into two canal cells. The behavior of the primary venter cell is also in doubt. The scanty data at hand seem to show that it functions directly as the egg and does not undergo the usual division into venter canal cell and egg. As archegonia approach maturity there is a cutinization of cell walls in the lowermost tier of neck cells (Fig. 108*I*) and a sloughing off of all neck cells above them. Sloughing off of the upper portion of the neck, together with disintegration of the canal cell (or cells), leaves a passageway for entrance of antherozoids into the venter of the archegonium (Fig. 108*J*).

Development of the sporophyte[2] begins with a division of the zygote in a plane at right angles to the long axis of the archegonium (Fig. 108*K*). The hypobasal daughter cell develops into the **foot** of the embryo. This portion of the embryo is sharply distinguishable through all developmental stages until the young sporophyte becomes an independent plant. The epibasal daughter cell of the zygote develops into the shoot portion of the sporophyte. Unlike other pteridophytes, there is no formation of either a primary root, a primary leaf, or a suspensor during embryonal stages.

The first division in development of the epibasal cell into a foot is in a plane perpendicular to the preceding plane of division. Subsequent divisions in the two halves of the foot are in an irregular sequence (Figs. 108*L*, 109*A–C*). As development of the foot continues it becomes a cylinder with a length about equal to the breadth. Superficial cells on free faces of the foot elongate into short haustoria that burrow into abutting gametophytic tissue. The *Anthoceros*-like foot functions as an absorptive organ until the shoot portion of the embryo becomes a self-sustaining plant.

Development of the shoot from the epibasal daughter cell of the zygote begins with a vertical division. The two daughter cells thus formed divide transversely. Subsequent divisions are in a more or less irregular sequence (Figs. 108*K*, 109*A–C*). The shoot portion of a young embryo is hemispherical in shape and vertically differentiable into two halves, derived, respectively, from the first two cells of the shoot. There is an early differentiation of an apical cell in one or in both halves of the young shoot. In either case the apical cell lies midway between base and apex of the half in which it is formed. Further development of the shoot is due in large part to activity of the apical cell or cells. If one of these is present the shoot tends to elongate vertically; if two are present it has two horizontal branches that grow in opposite directions. Early stages in embryonal

[1] Holloway, 1918, 1939; Lawson, 1917*A*. [2] Holloway, 1918, 1921, 1939.

development are accompanied by growth of adjacent gametophytic tissue into a calyptra-like structure that overarches the upper portion of the embryo (Fig. 109*A–C*). After the apical cell begins to function, the developing shoot grows through the calyptra and projects beyond the gametophyte. The protruding portion of the sporophyte soon develops rhizoids here and there on its surface and becomes infected with a mycorhizal fungus. A developing shoot is capable of nourishing itself after it has a mycorhizal fungus, and it may become an independent plant (the young rhizome) any time after infection takes place (Fig. 109*D–F*). Separation from the gametophyte is due to an abscission layer formed in the region where shoot and foot adjoin each other. When abscission does take place,

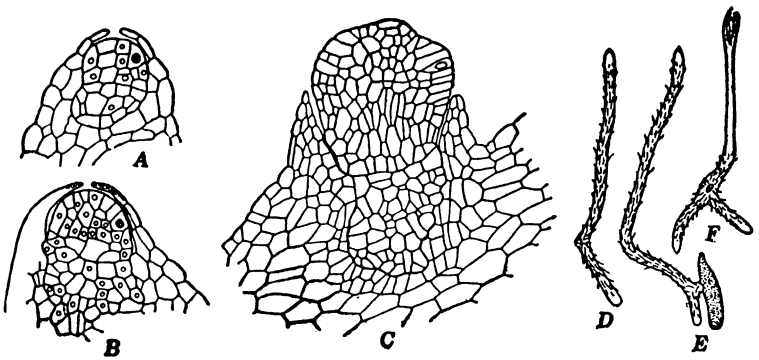

FIG. 109. *Tmesipteris tannensis* Bernh. *A–C*, stages in development of embryo. *D–F*, young sporophytes after emergence from gametophyte. (*After Holloway*, 1921.) (*A–C*, × 50; *D–E*, × 3; *F*, × 1½.)

the foot usually remains embedded in the gametophyte. The young rhizome thus separated from the gametophyte has an embryonic stele a short distance back from the growing point, and posterior to this is a mature stele with xylem and phloem. Young rhizomes growing through the soil frequently have lateral branches. Sometimes these are due to a dichotomy, but more often they are due to a formation of adventitious branch apices in older portions of the rhizome. The original branch, or certain of the adventitious branches, eventually grow above the soil and develop into typical aerial shoots.

Bibliography

Arnold, C. A. **1947.** An introduction to paleobotany. New York. 433 pp. 187 figs.

Boodle, L. A. **1904.** *Ann. Bot.* **18**: 505–517. 1 pl. 7 figs. [Secondary zylem, *Psilotum*.]

Bower, F. O. **1894.** *Phil. Trans. Roy. Soc. London B* **185**: 473–572. 11 pl. [Sporangia, *Psilotum*, *Tmesipteris*.]

1935. Primitive land plants. London. 658 pp. 449 figs.

Croft, W. N., and W. H. Lang. **1942.** *Phil. Trans. Roy. Soc. London B* **231**: 131–163. 3 pl. 8 figs. [*Zosterophyllum*.]

Darnell-Smith, G. P. **1917.** *Trans. Roy. Soc. Edinburgh* **52**: 79–91. 2 pl. [Gametophyte, *Psilotum.*]

Dawson, J. W. **1859.** *Quart. Jour. Geol. Soc.* **15**: 477–488. 6 figs. [*Psilophyton.*]

1888. The geological history of plants. New York. 290 pp. 79 figs.

Dorf, E. **1933.** *Bot. Gaz.* **95**: 240–257. 2 pl. [Psilophytales.]

Eames, A. J. **1936.** Morphology of vascular plants. Lower groups (Psilophytales to Filicales). New York. 433 pp. 215 figs.

Ford, Sibille O. **1904.** *Ann. Bot.* **18**: 589–605. 1 pl. [Anatomy of *Psilotum.*]

Holloway, J. E. **1918.** *Trans. New Zealand Inst.* **50**: 1–44. 3 pl. 92 figs. [Gametophyte, *Tmesipteris.*]

1921. *Ibid.* **53**: 386–422. 1 pl. 95 figs. [Gametophyte, *Tmesipteris.*]

1939. *Ann. Bot.* N.S. **3**: 313–336. 2 pl. 67 figs. [Gametophyte, *Psilotum.*]

Kidston, R., and W. H. Lang. **1917.** *Trans. Roy. Soc. Edinburgh* **51**: 761–784. 10 pl. [*Rhynia.*]

1920. *Ibid.* **52**: 603–627. 10 pl. [*Rhynia.*]

1920A. *Ibid.* **52**: 643–680. 17 pl. [*Asteroxylon.*]

1921. *Ibid.* **52**: 831–854. 5 pl. [*Asteroxylon, Rhynia.*]

1921A. *Ibid.* **52**: 855–902. 10 pl. 1 fig. [*Asteroxylon, Rhynia.*]

Kräusel, R. **1938.** Psilophytinae. In F. Verdoorn, Manual of Pteridology. The Hague. Pp. 496–499.

Kräusel, R., and H. Weyland. **1923.** *Senckenbergiana* **5**: 154–184. 4 pl. [Psilophytales.]

1926. *Abhandl. Senckenbergischen Naturf. ges. Frankfurt a/M.* **40**: 115–155. 15 pl. 46 figs. [*Asteroxylon.*]

1929. *Ibid.* **41**: 319–359. 15 pl. 34 figs. [Psilophytales.]

1933. *Palaeontographica* **78,** Abt. *B*: 1–46, 7 pl. 39 figs. [*Pseudosporochnus.*]

1935. *Ibid.* **80**, Abt. *B*: 171–190. 4 pl. 11 figs. [*Zosterophyllum.*]

Lang, W. H. **1927.** *Trans. Roy. Soc. Edinburgh* **55**: 443–455. 2 pl. [*Zosterophyllum.*]

1931. *Phil. Trans. Roy. Soc. London B* **219**: 421–442. 2 pl. [*Psilophyton.*]

Lang, W. H., and Isabel C. Cookson. **1930.** *Ibid.* **219**: 133–163. 3 pl. [*Zosterophyllum.*]

1935. *Ibid.* **224**: 421–449. 4 pl. [*Zosterophyllum.*]

Lawson, A. A. **1917.** *Trans. Roy. Soc. Edinburgh* **51**: 785–794, 3 pl. [Gametophyte, *Tmesipteris.*]

1917A. *Ibid.* **52**: 93–113. 5 pl. [Gametophyte, *Psilotum, Tmesipteris.*]

Scott, D. H. **1900.** Studies in fossil botany. 1st ed. London. 533 pp. 151 figs.

1920. *Ibid.* 3d ed. Vol. 1. London. 434 pp. 189 figs.

Seward, A. C. **1910.** Fossil plants. Vol. 2. Cambridge. 624 pp. 265 figs.

1933. Plant life through the ages. Cambridge. 603 pp. 140 figs.

Steil, W. N. **1939.** *Bot. Rev.* **5**: 433–453. [Apogamy and apospory.]

Stiles, W. **1910.** *Ann. Bot.* **24**: 373–387. 1 pl. [Anatomy, *Psilotum.*]

Sykes, M. G. **1908.** *Ibid.* **22**: 63–89. 2 pl. 13 figs. [Anatomy, *Tmesipteris.*]

Thomas, A. P. W. **1902.** *Proc. Roy. Soc. London* **69**: 343–350. [Relationships, Psilophytales.]

CHAPTER 8

LEPIDOPHYTA

Members of the division Lepidophyta, to which all lycopods are referred, have a sporophyte differentiated into stem, leaves, and roots. The leaves are microphyllous and with a single vein. They are generally spirally arranged but in certain cases they are in opposite pairs or in whorls. Steles of Lepidophyta may be protostelic, siphonostelic, or polystelic; but in no case are there leaf gaps above the leaves. Fertile leaves (sporophylls) produce but a single sporangium and this on the adaxial face and near the base of the sporophyll. Most Lepidophyta have the sporophylls borne in strobili.

There is a widespread belief that Lepidophyta have been derived from the Psilophytales, but the manner in which psilophytes evolved the leaves and sporophylls characteristic of Lepidophyta is a matter of dispute (see page 138). Evolution of the lycopodian series undoubtedly occurred early in the progressive evolution of vascular plants since one lycopod *Baragwathia*, (page 182) has been found in the Middle Silurian and contemporaneous with the oldest known psilophytes. Early in their history the Lepidophyta appear to have begun evolving in two independent lines, superficially distinguishable from each other by the presence or absence of a small laminate outgrowth, the **ligule,** near the base of each leaf and on the adaxial face. The evolutionary line in which leaves lack ligules (eligulate lycopods) has retained the simple herbaceous structure and homospory thought to be characteristic of the most primitive lycopods. Nowhere among the eligulate lycopods was there an evolution of heterospory or of the secondary thickening that made possible a sporophyte of tree-like proportions. The other evolutionary line, the ligulate lycopods, became heterosporous early in its phylogeny. Certain of them, the Selaginellales, retained the primitive herbaceous type of sporophyte. By the end of the Devonian, other ligulate lycopods had evolved a cambium producing secondary vascular tissues and so made possible the arborescent lepidodendrads that were so abundant during the Carboniferous. Evolution of a seed-like method of reproduction took place among the arborescent lycopods known as the lepidocarps. A somewhat similar seed-like

method of reproduction seems to have been evolved independently in the herbaceous line leading to the present-day genus *Selaginella*. Practically all the lepidodendrads and lepidocarps became extinct prior to or during the extensive glacial period(s?) of the Permian. *Isoetes*, a present-day genus, is probably a degenerate remnant of a post-Permian offshoot from the lepidodendrads (Fig. 110).

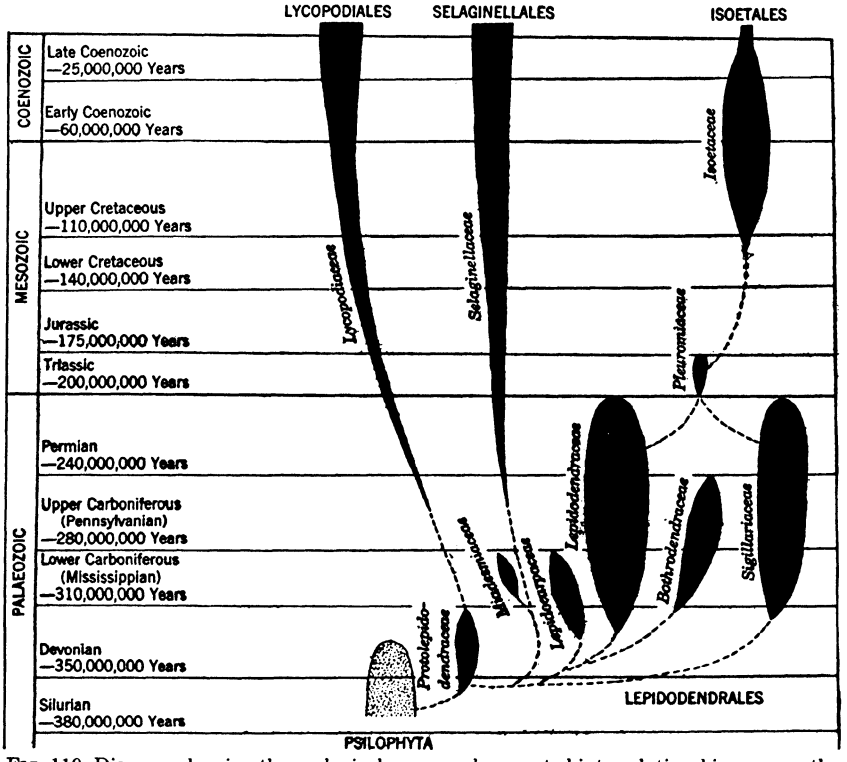

FIG. 110. Diagram showing the geological range and suggested interrelationships among the Lepidophyta.

The vascular organization of all genera referred to the division differs from that of other pteridophytes with leaves, roots, and stem in the lack of gaps above departing leaf traces. The discoverer of this feature holds[1] that the equisetaceous series has a similar lack of gaps but, as noted elsewhere (page 239), this is open to question. Lack of leaf gaps does not mean that lycopods have undissected vascular cylinders since they do have gaps above departing branches.

Most Lepidophyta have stems with a single stele, but those of *Sela-*

[1] Jeffrey, 1902, 1917.

ginella (Fig. 120) may be polystelic and contain two, three, four, or more parallel steles in the interval between two successive branches. From the standpoint of the stelar theory the Lepidophyta are remarkable for their lack of evolutionary progress in organization of the primary xylem, and throughout the division the protoxylem is almost always exarch. However, there is frequently an advance from a condition where the protoxylem completely encircles the metaxylem to a polyarch condition where there are a number of protoxylem ribs. Many members of the division have a protostelic vascular cylinder. This may be a simple haplostele, or it may be actinostelic and one with few or with many protoxylem ridges. Other lycopods have the center of the xylem composed of parenchyma rather than tracheids. Such cylinders are to be considered siphonosteles. In spite of the primitive organization of primary vascular tissues the stems of many genera are characterized by one advanced feature—the ability to form secondary vascular tissues by means of a cambium.

Although leaves of Lepidophyta are called microphyllous, this does not necessarily mean that leaves are of small size throughout the division, since those of certain fossil species were a half meter or more in length. Lepidophyta are microphyllous in the sense that their leaves have but one vein running upward from the leaf base without branching. In exceptional cases, as in certain sigillarians, the leaf had two parallel veins but genera with bifasicular leaves are immediately derived from ancestors with unifasicular leaves.

The division Lepidophyta contains but one class, the *Lycopodinae*. There is more or less general agreement concerning the limits of families within the Lycopodinae but, except for the Lycopodiales, this does not hold when it comes to grouping the families in orders. The Lepidocarpaceae and Miadesmiaceae have been placed together in a separate order, variously called the Lepidospermae[1] and Lepidocarpales,[2] because both have seed-like reproductive bodies. Differences in the seed-like bodies and the marked differences in vegetative structure show that the two families are not closely related and that the order is not a natural one. These two families are probably in a more logical position when referred to the Selaginellales and Lepidodendrales according to the herbaceous or arborescent nature of the sporophyte. Isoetaceae and Pleuromiaceae are generally recognized as being related. Some[3] think that differences between the two families warrant placing them in separate orders, whereas others[4] place the two in the same order. On pages to follow, the Lycopodinae are grouped into four orders (Lycopodiales, Selaginellales, Lepidodendrales, and Isoetales).

[1] Hirmer, 1927; Zimmermann, 1930. [2] G. M. Smith, 1938.
[3] Arnold, 1947; Eames, 1936; Zimmermann, 1930.
[4] G. M. Smith, 1938; von Wettstein, 1935.

ORDER 1. LYCOPODIALES

Lycopodiales differ from all other orders of Lycopodinae in being homosporous and in having leaves without ligules. The sporophyte is herbaceous and without a secondary thickening of stem or roots. Sporophylls may or may not be restricted to the terminal portion of branches and organized into definite strobili. Gametophytes, known only from the two living genera of the order, are wholly or partly subterranean. The antheridia are embedded in the gametophyte and their antherozoids are biflagellate.

There are two families, the Protolepidodendraceae and the Lycopodiaceae.

FAMILY 1. PROTOLEPIDODENDRACEAE

This somewhat artificial family includes a number of extinct genera known only from the Silurian and the Devonian. The sporophytes were mostly of small size. They were herbaceous and with the branches densely clothed with microphyllous leaves without ligules. Sporophylls were not localized in definite strobili and their sporangia were homosporous. There are about a half dozen genera in the family.

Baragwanthia, with the single species *B. longifolia* Lang and Cookson, is the oldest of all known lycopods It has been found at a single locality in Australia and from a deposit assigned to the Middle Silurian.[1] The maximum length of leafy shoots in carbonized compressions from this locality is 28 cm., and stems of most specimens are 1 to 2 cm. in diameter. The stem had a central cylinder composed of annular tracheids. The stems were densely clothed with spirally borne, linear, foliage leaves 1.0 to 0.5 mm. in breadth and with a length up to 4 cm. There were foliage leaves above and below fertile portions of a shoot. There are sporangia associated with the leaves in the fossil remains, but it is uncertain whether each sporangium was borne adaxially on a sporophyll or borne directly on the stem and between the leaves. Spores within sporangia were all of the same size.

Protolepidodendron has been found in Middle and Lower Devonian deposits in Germany, Bohemia, Scotland, and the eastern part of the United States.[2] Extensive and fairly well preserved material of the type species, *P. scharyanum* (Stur.) Krejci, show that it had a leafy, branched, prostrate axis.[3] The tips of certain branches of the axis bent upward and grew to a height of 20 to 30 cm. (Fig. 111*A*). These erect branches sometimes had one or two dichotomies. The prostrate axis and the tips of erect branches were densely clothed with small thorn-like leaves that were bi-

[1] Lang and Cookson, 1935. [2] Arnold, 1939; Kräusel and Weyland, 1929, 1932.
[3] Kräusel and Weyland, 1932.

furcate at their apices. The leaves were without ligules. Certain of the erect branches bore sporophylls here and there along their entire length. Sporophylls had much the same shape as sterile leaves and had bifurcate apices. Each sporophyll had a single sporangium that was borne adaxially and some distance from the sporophyll's base (Fig. 111*C*).

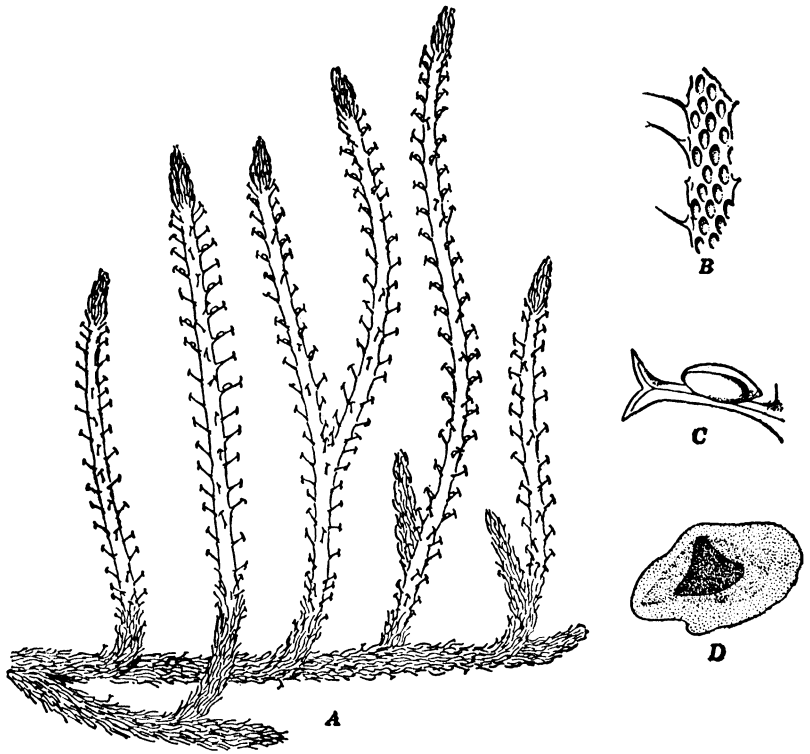

FIG. 111. *Protolepidodendron scharyanum* (Stur.) Krejci. *A*, reconstruction of the sporophyte. *B*, surface view of a fragment of a shoot. *C*, a fertile leaf. *D*, transverse section of a stem. (*A*, *C–D*, *after Kräusel and Weyland*, 1932; *B*, *after Kräusel and Weyland*, 1929.) (*A*, × ⅛; *B*, × ½; *C*, × 4; *D*, × 7½.)

The branches were protostelic and with a simple parenchymatous cortex external to the stele (Fig. 111*D*). The xylem of a stele was triradiate and had small protoxylem elements a short distance inward from the tip of each ray. Certain if not all of the metaxylem elements were of a scalariform type. Leaf traces departed from angles of the xylem mass, but it is not definitely known whether or not a leaf trace was continuous with the single vein of a leaf. The stem did not form secondary vascular tissues, but there is a possibility that it had a phellogen which formed a small amount of periderm.

FAMILY 2. LYCOPODIACEAE

The Lycopodiaceae have herbaceous sporophytes with the stem bearing many small microphyllous leaves without ligules. Sporophylls and foliage leaves may be similar or dissimilar in shape, and the sporophylls may or may not be borne in definite strobili. Members of this family are homosporous and in the two living genera the gametophytes are wholly or partly subterranean and often primarily nourished through the agency of a mycorhizal fungus.

Of the two living genera, one (*Lycopodium*) is world-wide in distribution and with some 180 species, the other (*Phylloglossum*) is monotypic and known only from Australia, Tasmania, and New Zealand. The fossil genus *Lycopodites*, which had a structure quite similar to that of *Lycopodium*, is known from as far back as the Upper Devonian.[1] This shows that the Lycopodiaceae are a very ancient group.

A majority of the species of *Lycopodium* are tropical, but certain of them are widely distributed in temperate regions. All species of *Lycopodium* have relatively small, herbaceous or shrubby sporophytes (Fig. 112). Some species are epiphytic and with erect or pendant sporophytes; others are terrestrial and the sporophyte may have an upright stem or one that grows horizontally above or below the surface of the soil. The stem and its branches are densely clothed with small leaves.

Lycopodium is divided into two subgenera that differ in general organization of the sporophyte. Species referred to the subgenus *Urostachya*[2] have branched or unbranched stems that are erect or pendant, but never creeping. If the stem is branched, the branching is always dichotomous and usually with successive dichotomies at right angles to one another. Species of this subgenus have no adventitious roots along the stem. Foliage leaves and sporophylls of most species in the subgenus are approximately the same size and both are green. There is, however, considerable variation in distribution of the two. In *L. selago* L. and related species there are alternate sterile and fertile zones throughout the length of stem and branches. Certain other species of the subgenus have the sporophylls restricted to the distal part of stem and branches. Although such portions of the plant are properly called strobili, there is considerable variation in the distinctiveness of the strobili. These are most distinctive in the group of species related to *L. phlegmaria* L. (Fig. 112*A*) where the strobili are dichotomously branched and where the sporophylls, although green and of the same shape, are much smaller than the foliage leaves.

Species of the subgenus *Rhopalostachya* typically have prostrate stems bearing upright branches. The branching in the first-formed portion of the sporophyte may be dichotomous; but in later-developed portions it is

[1] Hirmer, 1938. [2] Pritzel, 1900.

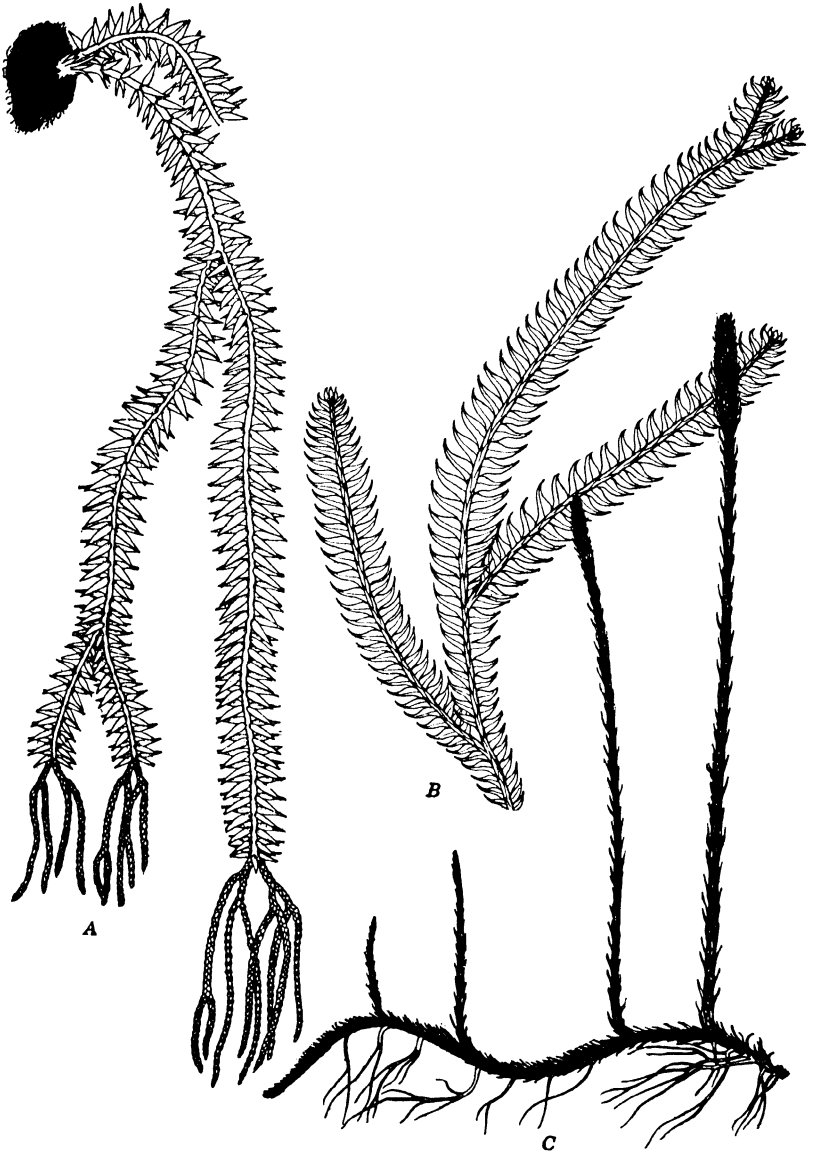

FIG. 112. *A*, *Lycopodium phlegmaria* L. *B*, *L. volubile*. L. *C*, *L. inundatum* L. (*A*, *C*, × ½; *B*, × 1½.)

always monopodial. The species with a creeping stem generally have their adventitious roots borne along the entire length of the prostrate portion. All members of the subgenus have the sporophylls in well-defined strobili, which may be simple or branched. The sporophylls differ from foliage leaves in that they are smaller in size, are paler in color, and have a dentate margin. Most species of the subgenus have all foliage leaves alike but a few species are like *Selaginella* in that the leaves are of two sizes and in definite vertical rows along the stem.

Vegetative propagation of the sporophyte is of frequent occurrence in *Lycopodium* and may result in stands of considerable extent that have been derived from one original individual.[1] Species with creeping stems have the apical growth, branching, and the progressive death of the older portions found in other pteridophytes with prostrate stems. In addition to this there are several other methods by which the plant multiplies. It has been shown[2] that new plants may result from (1) vegetative propagation of the gametophyte, (2) vegetative propagation of the juvenile (protocorm) stage of the sporophyte, (3) gemmae produced from cortical cells of the root, (4) tubers developed at the apices of roots, and (5) bulbils. The bulbils, which are found only in species belonging to the subgenus *Urostachys*, bear a superficial resemblance to the protocormous stage of young sporophytes (see page 195). Bulbils may be formed anywhere on the stems. Bulbils have been variously interpreted as modified lateral branches, as modified sporangia, and as modified leaves. The latter interpretation seems the most logical since a bulbil has the same position, the same dorsiventrality, and the same vascular supply as a leaf.[3]

The apex of a stem has a number of apical initials instead of a single apical cell as in stems of most other pteridophytes. When interpreted according to the tunica-corpus theory, the group of initials corresponds to the corpus found in stems of angiosperms and a tunica is lacking.[4] Internodes only one or two removed from the apical meristem have a well-defined differentiation of tissues maturing into epidermis, cortex, and stele.

The epidermis in mature portions of a stem is one cell in thickness and has stomata that appear to be similar in structure to those of the leaf. Stomata of leaves have been shown[5] to be identical in structure with those of certain angiosperms. The cortex varies greatly in relative thickness from species to species. In some species its radial thickness is several times that of the stele; in other species the two are approximately equal. There is also considerable variation in structure of the cortex. Some species have a cortex that remains soft and parenchymatous throughout the life of the sporophyte; other species have a sclerification of the inner or

[1] Holloway, 1916. [2] Holloway, 1917. [3] R. W. Smith, 1920.
[4] Härtel, 1938. [5] Copeland, 1902.

the outer portion of the cortex; still other species have a sclerification of the entire cortex in mature portions of the stem. At the inner face of the cortex there may be an endodermal layer which, at least in younger portions of the stem, has characteristically thickened radial walls. In view of statements that the endodermal layer of *Selaginella*[1] and of *Pteris*[2] is of stelar origin, it may be possible that the endodermis of *Lycopodium* belongs to the stele instead of to the cortex.

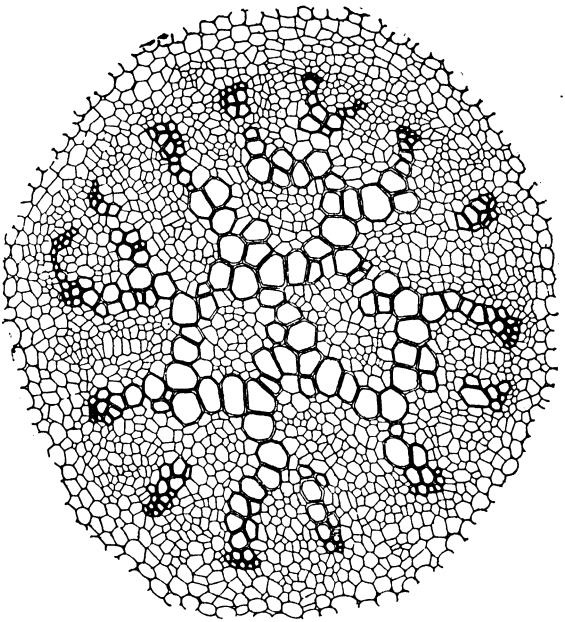

FIG. 113. *Lycopodium phlegmaria* L. Transverse section of vascular cylinder of stem. (× 110.)

Internal to the endodermis is a pericyclic layer which is usually three to six cells in thickness. There is great variation of organization of the vascular elements, even within the same species. The same species may vary greatly both from individual to individual and in different portions of the same individual. Study of stems of young sporophytes and of first-formed portions of mature sporophytes shows[3] that the vascular elements are organized into an exarch actinostele very similar in appearance to the actinosteles characteristic of roots of vascular plants. In some cases the actinostele has three or four protoxylem points; in other cases there may

[1] Barclay, 1931. [2] Chang, 1927.

[3] Chamberlain, 1917; Holloway, 1910; Jones, 1905; Spessard, 1928; Wardlaw, 1924; Wigglesworth, 1907.

be as many as a dozen protoxylem points. Later-formed portions of a stem may retain the actinostelic organization characteristic of the juvenile plant (Fig. 113). Species with this type of organization in the older portions of the stem are thought to be the most primitive of the genus as far as the vascular organization is concerned.[1] Other species may have a plectostelic organization of the vascular elements (Fig. 90*C*, page 143); or may have masses of xylem and phloem indiscriminately mixed with one another. Attempts have been made to correlate the actinostelic and plectostelic types with the growth habit of the plant. It has been held[2] that the plectostelic organization is found chiefly in horizontal portions of the plant and the actinostelic in erect portions, but so many exceptions have been shown[1] for the foregoing generalization that its validity is to be questioned. According to another interpretation the organization of the vascular elements is profoundly affected by the size of the stele (see page 148).

The root system of *Lycopodium* is largely adventitious; and according to the subgenus, adventitious roots are restricted to the basal portion of the stem or are formed along its entire length. Adventitious roots are formed chiefly from pericyclic tissue, but they may be formed both from it and from the endodermis.[3] A developing adventitious root does not grow straight out through the cortex but grows downward through it for a centimeter or more before emerging from the stem. As a result, transverse sections of stems frequently show several roots within the cortex. While growing through the cortex the roots are unbranched, but after emerging from the stem they may branch freely. The branching is always dichotomous and generally with successive dichotomies at right angles to one another.

Roots of *Lycopodium* have the differentiation into epidermis, cortex, and stele typical of other vascular plants. The epidermis gives rise to numerous root hairs, but these are somewhat peculiar in that they lie in pairs. The occurrence of root hairs in twos results from the fact that the hair initials are formed in pairs by the oblique or anticlinal division of a young epidermal cell.[4] The cortex is several cells in thickness and often becomes heavily sclerified in the outer half as the root grows older. In some cases the stele is **monarch** with the protoxylem in one mass; in other cases it is either **diarch** with two protoxylem masses, or **triarch** with three groups in protoxylem. Sometimes the same root is diarch in one portion and tetrarch in another.[3] Most roots are diarch (Fig. 114*B*) and have a **C**- or **U**-shaped mass of xylem so oriented that the opening of the **C** or the **U** faces away from the stem. The protoxylem lies at the tips of the curved xylem mass, and the intervening portion consists of metaxylem.

[1] J. B. Hill, 1914. [2] Holloway, 1910; Jones, 1905.
[3] Saxelby, 1908. [4] Stokey, 1907.

Diarch roots generally have but one mass of phloem, and this lies between the points of the C or the U.

Most species have small leaves and in only a few species do they attain a length of 2 to 3 cm. Leaves are generally lanceolate in outline and with a broad base. They may be spirally arranged or borne in whorls; and in the latter case they may be of two sizes and with the four-ranked arrangement found in many species of *Selaginella*. First-formed leaves on a stem may be very simple in structure and without a vein;[1] later-formed ones always

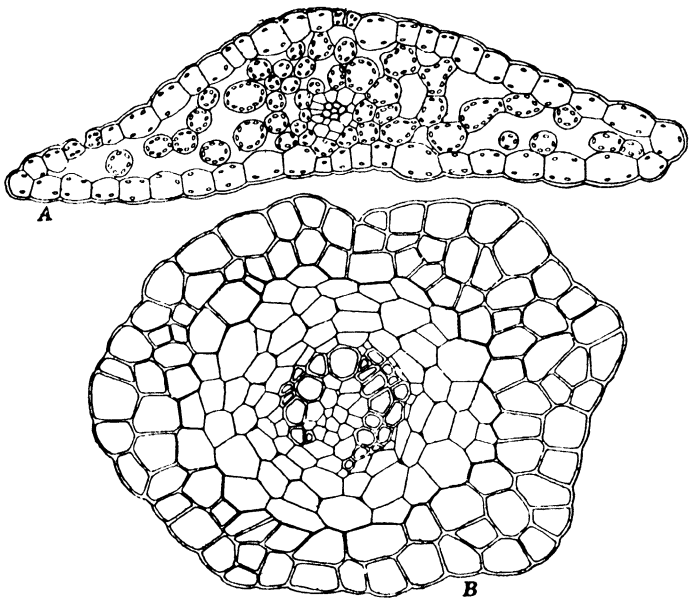

FIG. 114. *A*, transverse section of leaf of *Lycopodium volubile* L. *B*, transverse section of root of *L. serratum* Thbg. (*A*, × 160; *B*, × 215.)

have a single unbranched vein running from base to apex or only part way to the apex. The vein connects with a leaf trace extending through the cortex to the stele. As is the case with other Lepidophyta, there are no leaf gaps in the portion of the stele above the departing leaf traces.

Leaf primordia arise very close to the apical meristem. Opinion is divided as to whether a leaf develops from several adjoining embryonic epidermal cells[2] or from a single one of them.[3] Very young leaves consist of a homogeneous mass of embryonic cells. Later on, there is both a basipetalous and an acropetalous differentiation of an embryonic vein within the basal region. All the xylem elements in a mature vein are spirally thickened tracheids, and the first ones to mature lie near the center of the

[1] Wigglesworth, 1907. [2] Turner, 1924. [3] Härtel, 1938.

vein. A vein may be ensheathed by an endodermis, or an endodermis may be lacking. The intervening embryonic tissue between vein and epidermis matures into a parenchyma in which the cells may be angular in outline and without intercellular spaces, or rounded and with intercellular spaces (Fig. 114*A*). The epidermis of most species has stomata on both faces of a leaf, but in species with dimorphic leaves the stomata are frequently restricted to one face of a leaf.

Sporophylls of a majority of species are borne in definite strobili at the apices of stem and branches (Fig. 112*A*, *C*); but in a number of species,

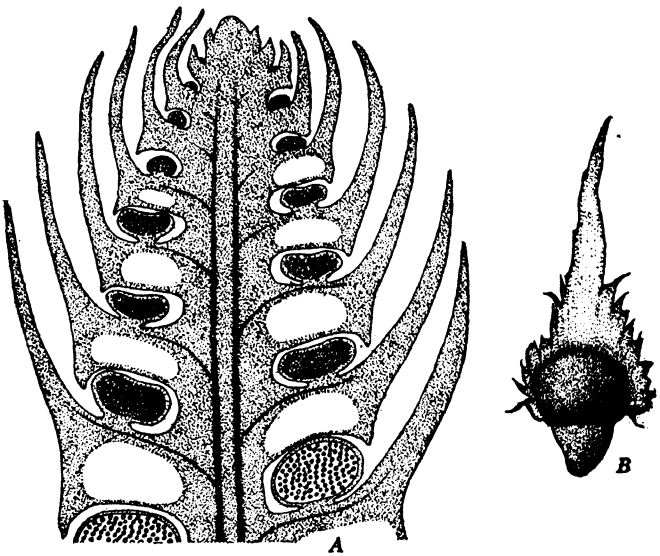

FIG. 115. *Lycopodium cernuum* L. *A*, vertical section of apical portion of a strobilus. *B*, dorsal view of a sporophyll and sporangium. (× 20.)

including *L. selago* L., they are borne in series alternating with series of foliage leaves. A sporophyll produces but one sporangium, and this adaxially and near the base of the sporophyll (Fig. 115). A mature sporangium is always kidney-shaped and, according to the species, with a long and slender or short and massive stalk.

Sporangia begin to develop at a time when the sporophyll is composed of embryonic cells. The first evidence of sporangial development is a periclinal division of a small group of epidermal cells on the adaxial side of a sporophyll and near its base.[1] Inner daughter cells formed by this periclinal division contribute to the stalk and the basal portion of a sporan-

[1] Bower, 1894.

gium; outer daughter cells give rise to the bulk of the sporangium. The first division of the outer cells is also periclinal and into an outer layer, the **jacket initials**; and an inner layer, the **archesporial cells.** The plate of archesporial cells, by periclinal and anticlinal division, develops into a rather massive **sporogenous tissue** (Fig. 116*B–D*). Practically all members of the last cell generation of the sporogenous tissue function as **spore mother cells** that become rounded, separate from one another, and float about in a viscous liquid as they divide into tetrads of spores in the well-known manner. The jacket initials external to the sporogenous tissue divide to form a jacket layer three or more cells in thickness (Fig. 122).

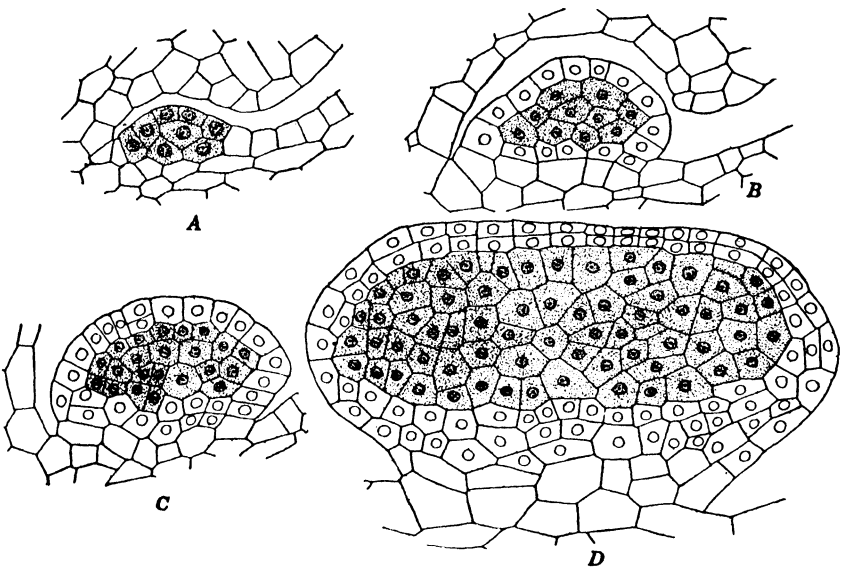

FIG. 116. *Lycopodium cernuum* L. Stages in development of sporangia. (× 325.)

Shortly before the spore-mother-cell stage of development, there is a differentiation of a nutritive tissue (**tapetum**) about the sporogenous tissue. This is formed in part from the innermost layer of jacket cells and in part from sporangial cells just beneath the sporogenous tissue. *Lycopodium*, unlike most other pteridophytes, has no disintegration of the tapetum during the formation of spores. As the sporangium approaches maturity, there is the differentiation of a narrow transverse strip of cells (the **stomium**) across the apical portion of the outermost jacket layer. The cell walls in the stomial portion thicken differently from those of other cells in the sporangial jacket. When strains and stresses are set up by a drying out of cells in the mature sporangium, there is a transverse rupture of the sporangium apex along the line of the stomium.

Spores of *Lycopodium* may begin germination within a few days after they are shed,[1] but several species are known[2] in which germination does not begin until after the spores are three to eight years old. Development of the gametophyte to the point where there are mature sexual organs takes from 8 months to 6 or 15 years. The rate of growth of gametophytes is more or less correlated with the proportion of photosynthetic tissue and is slowest in those species that have a colorless gametophyte nourished by a mycorhizal fungus.

The first cell division of a germinating spore takes place before the outer spore wall layer is ruptured and results in two hemispherical daughter cells of approximately equal size.[2] One of these daughter cells, the **basal cell,** undergoes no further division than the cutting off of a small, lens-shaped, rudimentary **rhizoidal cell.** The other daughter cell, by two successive divisions, produces an **apical cell** with two cutting faces. All the species with colorless gametophytes and most of those with chlorophyll may have an entrance of a symbiotic phycomycetous fungus into the basal cell at the time when the gametophyte is four- to five-celled (Fig. 117*A–B*). If there is no entrance of the fungus there is no further development of the gametophyte. Gametophytes developing beyond this early stage have the apical cell cutting off some half dozen segments and then becoming replaced by a group of meristematic cells. Segments cut off by the apical cell divide periclinally, and the outer cells thus formed become infected with the symbiotic fungus in the same manner as does the basal cell. The apical group of meristematic cells differentiated early in the ontogeny of a gametophyte produces the major portion of the adult gametophyte. There is great diversity in form and structure of mature gametophytes.[3] Certain species have wholly subterranean gametophytes that may be erect and conical or may be freely branched. Gametophytes of other species are only partly subterranean, and with the aerial portion branched and containing chloroplasts.

Sex organs of *Lycopodium* begin to develop just back of the apical meristem.[4] The initial cell of an antheridium is an epidermal cell that divides periclinally into an outer cell (the **jacket initial**) and an inner cell (the **primary androgonial initial**). The primary androgonial cell divides and redivides to form a large mass of **androgonial cells** that lie embedded within the gametophyte (Fig. 117*D–G*). Coincident with formation of the androgonial cells, the jacket initial divides and redivides anticlinally to form a **jacket layer,** one cell in thickness, which overlies the androgonial cells. At the center of the jacket layer is a triangular cell comparable to the **oper-**

[1] Treub, 1888. [2] Bruchmann, 1910.

[3] Bruchmann, 1898, 1910; Chamberlain, 1917; Haberlandt, 1918; Holloway, 1920; Spessard, 1922.

[4] Lang, 1899; Spessard, 1922.

cular cell in antheridia of eusporangiate ferns (see page 291), but differing from it in not cutting off so many daughter cells on each of the three sides. Metamorphosis of the last cell generation of androgonial cells, the **androcytes,** into antherozoids has not been followed in detail but it is thought to

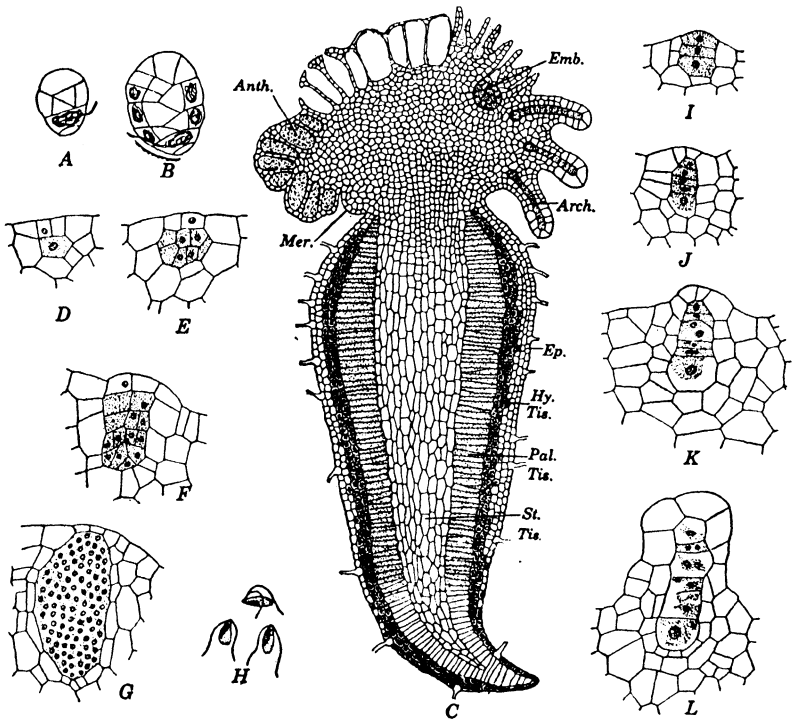

FIG. 117. *A–B*, early stages in development of gametophyte of *Lycopodium annotinum* L. *C*, vertical section of a mature gametophyte of *L. complanatum* L. *D–L*, *L. clavatum* L. *D–G*, stages in development of antheridia. *H*, antherozoids. *I–L*, stages in development of archegonia. (*Anth.*, antheridium; *Arch.*, archegonium; *Emb.*, embryo; *Ep.*, epidermis; *Hy. Tis.*, hyphal tissue; *Mer.*, meristem; *Pal. Tis.*, palisade tissue; *St. Tis.*, storage tissue.) (*A–B, after Bruchmann*, 1910; *C, H, after Bruchmann*, 1898; *D–G, I–L, after Lang*, 1899.) (*A–B*, × 235; *D–F*, × 265; *G, I–L*, × 185; *H*, × 275.)

take place as in other pteridophytes.[1] The antherozoids (Fig. 117*H*) are fusiform, broadly rounded at the posterior, and with two flagella at the anterior end.[2] Liberation of antherozoids is effected by a breaking down of the opercular cell.

The first division of an archegonial initial is periclinal and into a **primary cover cell** and a **central cell.**[3] The central cell divides periclinally into a **primary canal cell** and a **primary venter cell** (Fig. 117*I*). In some

[1] Lang, 1899. [2] Bruchmann, 1898.
[3] Bruchmann, 1910; Lang, 1899; Spessard, 1922.

species the primary canal cell divides transversely to form four **canal cells**; in other species six to eight, or even more, canal cells are formed (Fig. 117*J–L*). The primary venter cell eventually becomes broader than cells in the canal row. There has been no critical investigation to show whether this cell functions directly as the **egg** or whether it divides to form a venter canal cell and an egg. Meanwhile, by two successive anticlinal divisions at right angles to each other, the primary cover cell divides to form four **neck initials.** Transverse division of the neck initials results in a neck three to four cells in height and typically composed of four vertical rows of cells. The portion of the mature archegonium derived from the primary cover cell, together with the canal cells it ensheaths, projects vertically above the gametophyte. The remaining canal cells and the egg lie embedded within the prothallus. The cells lateral to the egg and lower portion of the canal row are not portions of the archegonium since they are formed by division and redivision of prothallial cells immediately adjacent to the archegonial initial. As is the case with archegonia of Bryophyta, all members of the axial row except the egg disintegrate shortly before the archegonium is mature. Opening of the apex of the archegonial neck seems to take place by a spreading apart and partial disintegration of the uppermost neck cells.

The first division of a zygote is always transverse.[1] The daughter cell next to the neck of the archegonium becomes a **suspensor** which pushes the other daughter cell, sometimes called the **embryonic cell,** more deeply into the gametophyte. The suspensor may remain one-celled, or it may become three-celled. The embryonic cell eventually develops into the mature sporophyte. Its first division is vertical, and this is followed by a vertical division of the two daughter cells thus formed (Fig. 118*A*). Transverse division of each of these cells results in an eight-celled embryo in which the cells are in two superimposed tiers of four cells each. The tier of cells adjoining the suspensor eventually develops into the **foot** of the young sporophyte; the distal tier develops into the remaining portions of the sporophyte. In some species it is impossible to trace the parts of the young sporophyte back to particular cells in the distal tier of four. It has been held[1] that the two cells facing the apical meristem of the gametophyte develop into the **stem** and the two facing away from the meristem develop into the **cotyledon** and the primary **root.** However, the young sporophyte is a many-celled structure before the cotyledon and the embryonic stem become evident (Fig. 118*B–D*). Differentiation of the primary root takes place even later and at one side of the region where cotyledon and foot adjoin each other. Until this time the embryo remains embedded within the gametophyte, growing downward and forward toward the meristem of the gametophyte. Eventually the growing stem and coty-

[1] Bruchmann, 1910.

ledon burst through the apical region of the gametophyte. Following this, the cotyledon and stem show a markedly negative geotropic response and start to grow upward into the air.

Sometimes the distal four cells of the eight-celled stage develop into a massive globose structure (the **protocorm**) which grows through the gametophyte, becomes green, and develops rhizoids on its lower surface. From the upper surface of the protocorm arise a few to many erect, conical outgrowths (**protophylls**) which are leaf-like in function and which have stomata in their epidermal layer (Fig. 118*E–F*). After having formed an indefinite number of protophylls, the protocorm then differentiates a meristematic region which develops into the stem of the adult plant. The

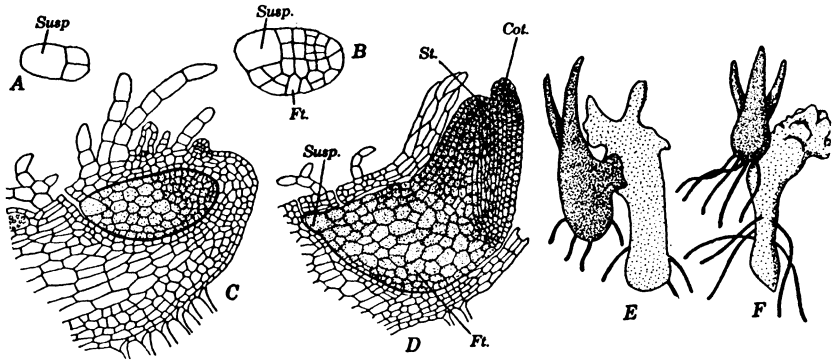

FIG. 118. *A–D*, stages in development of embryo of *Lycopodium phlegmaria* L. *E–F*, vertical sections of gametophytes and protocorms of *L. cernuum* L. (*Cot.*, cotyledon; *Ft.*, foot; *St.*, stem; *Susp.*, suspensor.) (*A–D*, *after Bruchmann*, 1910; *E*, *after Holloway*, 1920; *F*, *after Holloway*, 1916.)

protocorm has been variously interpreted. Some[1] consider it a structure of great antiquity and the phylogenetic percursor of the stem. Others[2] hold that it is a late phylogenetic specialization and represents a "gouty interlude" in the early ontogeny of the sporophyte.

ORDER 2. SELAGINELLALES

Members of this order have sporophytes with herbaceous stems that are usually without any indication of a secondary thickening. Foliage leaves are microphyllous, all alike or dimorphic, and each with a ligule. Roots are borne at the distal end of branches (**rhizophores**) of the stem. The sporophytes are heterosporous, with vegetative portions of all sporophylls alike, but with macro- and microsporangia different in size and shape. The sporophylls are always borne in strobili at the ends of branches. Macro- and microgametophytes are markedly different in size, and antherozoids produced by microgametophytes are biflagellate.

[1] Treub, 1890. [2] Bower, 1908; Holloway, 1910.

Of the two families here placed in the order, one, the Miadesmiaceae, is usually placed in the Lepidodendrales.

FAMILY 1. SELAGINELLACEAE

Members of this family have a sporophyte with a vegetative structure typical for the order, and have the macrogametophyte escaping from the macrosporangium at some stage in its development.

There are two genera: *Selaginella*, a genus with 600 or more living species; and *Selaginellites*, an extinct genus known from as far back as the Upper Carboniferous. To be placed with certainty in *Selaginellites* a fossil species must be shown to have been heterosporous and this is demonstrated by a finding of both kinds of spores or only the macrospores. About half a dozen species are known for Selaginellites; some with 16 to 24 macrospores in a macrosporangium, others with but 4 spores.[1] *Selaginellites* gives good reason for believing that, similar to Lycopodiales, the Selaginellales are a series of ancient origin.

Selaginella is world-wide in distribution, but most of the species are tropical and many of them grow in damp forests. Of the species growing in temperate regions, approximately 40 are found in the United States. Certain of these grow in damp shady habitats; others are xerophytic and grow on dry rocky cliffs or on soil that periodically becomes dry. These xerophytic species are able to withstand desiccation for months, the rosette-like system of branches coiling tightly together as the plant dries out and reexpanding when it is moistened.

The size of the sporophyte varies greatly from species to species. At one extreme are those in which it is not much larger than most mosses; at the other are those in which it is a slender vine attaining a length of 20 meters. There are two general types of sporophyte in the genus. In the 50 or more species referred to the subgenus *Homoeophyllum*[2] the stem is generally erect, with all leaves of the same size, spirally arranged, and more or less densely clothing the stem. The majority of species, all placed in the subgenus *Heterophyllum*, generally have prostrate stems with short erect branches. The dimorphism of the leaves is seen to best advantage on the prostrate axis (Fig. 119). In this markedly dorsiventral portion the leaves are borne in pairs and with the two of a pair markedly different in size. The smaller leaf of each pair is inserted on the dorsal side of the stem, the larger leaf inserted on the ventral side. Successive pairs of leaves are so oriented that large leaf alternates with large leaf, and small leaf with small leaf. The prostrate axis bears elongate, downwardly growing, colorless, leafless, cylindrical appendages—**rhizophores**—each of which typically develops a tuft of adventitious roots at the free end.

[1] Darrah, 1938; Halle, 1908; Seward, 1913. [2] Hieronymus, 1900.

The growing apex of a stem may consist of a meristematic tissue, as in *S. oregana* D.C. Eaton; but more frequently, as in *S. kraussiana* A. Br., there is a single well-defined apical cell. In the only species where the apical cell has been studied in detail (*S. wildenovii* Bak.) the first division in segments cut off by the apical cell is periclinal,[1] the outer daughter cell thus formed contributing to the epidermis and cortex, the inner daughter cell contributing to the stele, the outermost layer of which is the endodermis.

FIG. 119. *Selaginella kraussiana* A.Br. Portion of a sporophyte. (× 1½.)

Except for rhizomes of certain species, mature portions of the stem differ from those of other pteridophytes in having the vascular tissue set off from the cortex by radially elongate endodermal cells, the so-called **trabeculae,** with conspicuous intercellular spaces between them (Fig. 120*B*). The cortex generally consists of angular cells without intercellular spaces, but in a few cases[2] the cells are rounded and have small intercellular spaces. All cells of the cortex may be thin-walled, or those toward the exterior may be heavily sclerified. The epidermis is one cell in thickness and without stomata.

The organization of the stele ranges all the way from that of a simple protostele to that of a polycyclic siphonostele, perforated here and there by branch gaps. The stem may also be polystelic and have 2, 3, 4, or as

[1] Barclay, 1931. [2] Harvey-Gibson, 1894.

many as 16 separate steles running through the intervening region between two successive branchings of the stem.[1] *S. Kraussiana*, one of the polystelic species, is distelic in the intervals between successive branchings (Fig. 120*A*). Both the steles in this stem are protostelic in organization, and each has a single exarch mass of protoxylem. The protoxylem masses of the two are so oriented with respect to one another that they

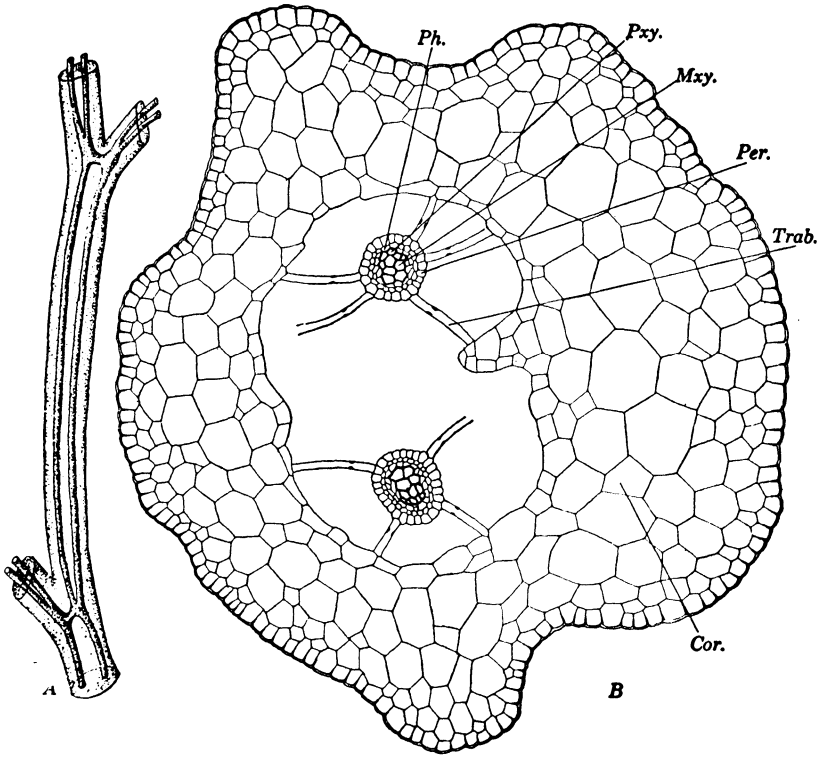

FIG. 120. *Selaginella kraussiana* A.Br. *A*, portion of a stem cleared to show the vascular tissues. *B*, transverse section of a stem. (*Cor.*, cortex; *Mxy.*, metaxylem; *Per.*, pericycle; *Ph.*, phloem; *Pxy.*, protoxylem; *Trab.*, trabeculae.) (*A*, × 15; *B*, × 160.)

face in opposite directions. The metaxylem of each bundle lies centripetal to the protoxylem. The xylem is ensheathed by a layer of parenchyma one to two cells in thickness. External to this is a single layer of sieve tubes except in the region radial to the protoxylem.[2] Parenchyma and sieve tubes are in turn surrounded by a pericylic layer one cell in thickness. The outermost layer in each stele is an endodermis, also one cell in thickness. When first formed, the endodermal cells abut laterally on one another; later on they become laterally separated and each elongates

[1] Wardlaw, 1925. [2] Harvey-Gibson, 1894.

greatly in the axis radial to the stele. The result is the characteristic mass of long radiating cells (trabeculae) bridging the wide space between the steles and the inner face of the cortex. In spite of their great radial elongation the trabecular cells still retain the transverse girdles (Casparian strips) characteristic of endodermal cells (Fig. 120*B*).

The morphological nature of the rhizophore has been debated at length. It has been held to be a root, a branch of the stem, and a structure falling in neither of these categories. The argument for its root-like nature is based largely upon its positive geotropism and the similarity of its anatomical organization to that of a root.[1] One of the strongest anatomical arguments in favor of its root-like nature is the fact that species with polystelic stems always have a monostelic rhizophore. The reasons for considering the rhizophore a portion of the stem seem more conclusive. These include its exogenous origin, its lack of a cap, its formation at definite places with respect to dichotomies of the stem,[2] and the experimental demonstration[3] that apices of decapitated rhizophores may develop into leafy shoots. Against the two foregoing interpretations is the suggestion that it is an organ *sui generis*[4] and neither a root nor a stem.

All roots borne by the adult plant are adventitious in origin. In a majority of the species these are formed only at the distal end of the rhizophores, but in a few species, as *S. wallichii* Spr., adventitious roots may develop anywhere along the stem.[5] Roots of *Selaginella* are delicate, sparingly branched, and with a small stele. Typically this is monarch in organization and has one phloem and one xylem mass.

Foliage leaves are small, simple, and symmetrical or asymmetrical in outline. According to the species, all foliage leaves are alike in size, or they are of two different sizes. In either case, there is always a small membranous outgrowth, the **ligule,** on the adaxial side of the leaf and near its base.

Leaf primordia are formed very close to the stem apex. In some cases the young primordium seems to be derived from a single epidermal cell near the growing point of the stem. During the course of development of the primordium, there is the differentiation of a single embryonic vascular bundle which extends without branching to the apex of the leaf. At the leaf base this connects with a single embryonic leaf trace which runs diagonally down through the cortex to the stele.

The vascular bundle of a mature leaf is very simple. In *S. kraussiana,* for example, the xylem near the base of the leaf consists of four to five tracheids, one of which is annular and the others spiral (Fig. 121*A*). All cells of the mesophyll between vein and epidermis contain chloro-

[1] Harvey-Gibson, 1902; Uphof, 1920. [2] Bruchmann, 1905. [3] Wordsell, 1910.
[4] Bower, 1908, 1935; Goebel, 1905. [5] Harvey-Gibson, 1902.

plasts. According to the species, each mesophyll cell contains a single large cup-shaped chloroplast or several chloroplasts. In either case there are several spindle-shaped, pyrenoid-like bodies at the center of the chloroplast.[1] Each of the pyrenoid-like bodies may be transformed into a rudimentary starch grain. The only other archegoniates with a similar chloroplast structure are *Isoetes* and the Anthocerotae. The mesophyll has conspicuous intercellular spaces. The entire tissue may be organized into a spongy parenchyma, or there may be the differentiation of a distinct palisade layer toward the morphologically upper side of the leaf. The epidermis, which is one cell in thickness, may have stomata on the

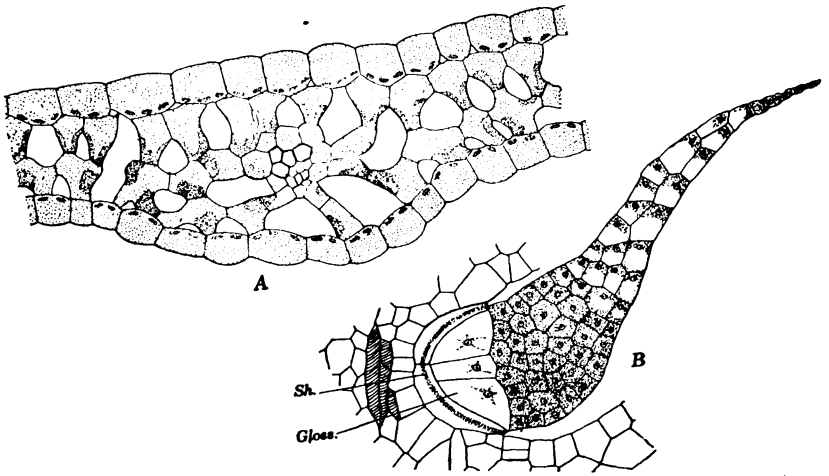

FIG. 121. *Selaginella kraussiana* A.Br. *A*, transverse section of a leaf. *B*, vertical section of a ligule passing through the sheath (*Sh.*) and glossopodium (*Gloss.*). (× 325.)

adaxial, on the abaxial, or on both surfaces. Stomata are largely restricted to portions of the epidermis external to the midrib.[2]

The ligule is a structure differentiated early in the ontogeny of a leaf and is one that matures early. It is formed from a transverse strip of the embryonic epidermis two to three cells tall and six to eight cells broad.[3] Periclinal division of each of these cells results in an inner layer, which ultimately becomes the sheath of the ligule, and an outer layer, which develops into the remainder of the ligule. A mature ligule is tongue- to fan-shaped and more than one cell in thickness, except at the apex (Fig. 121*B*). Its base consists of a cup-shaped **sheath** whose cells are tubular in shape and without protoplasts when mature. In *S. Kraussiana* the sheath cells have a Casparian strip similar to that of endodermal cells. Immediately adjoining the sheath is the **glossopodium,** a hemi-

[1] Ma, 1931. [2] Harvey-Gibson, 1897. [3] Harvey-Gibson, 1896.

spherical mass of thin-walled cells with greatly vacuolate protoplasts. The remaining cells of the ligule are more or less cubical and densely filled with protoplasm. The significance of the ligule is not apparent. It has been held that its precocious maturation results in a protective structure that prevents undue drying out of the stem apex and the young leaves, but this does not seem to hold in all cases since there are species whose ligules never overarch the growing apex.

The sporophylls of *Selaginella* are similar in structure to foliage leaves and each has a ligule at its base. A sporophyll bears a single stalked

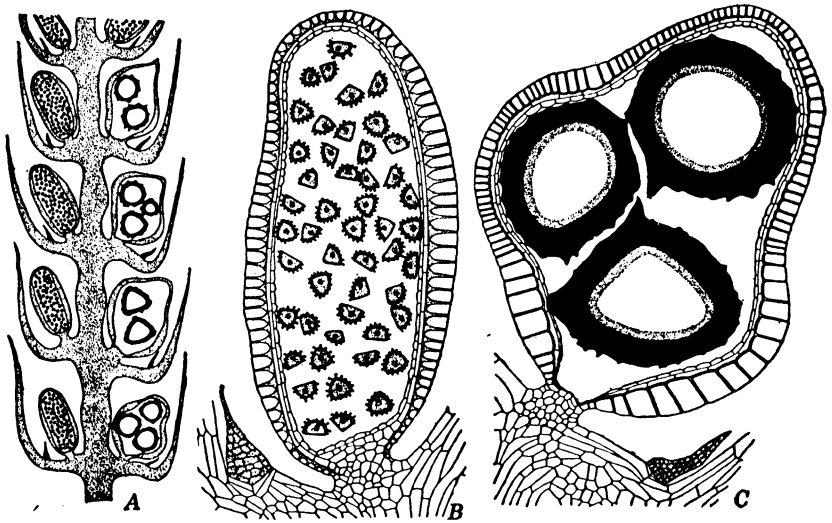

FIG. 122. *Selaginella oregana* D. C. Eaton. *A*, vertical section of a portion of a strobilus. *B*, vertical section of a microsporangium. *C*, vertical section of a macrosporangium. (*A*, × 14; *B*, × 105; *C*, × 80.)

sporangium that lies on the adaxial face and between the ligule and base of the sporophyll. The sporangia are of two distinct kinds, **macrosporangia** and **microsporangia,** so called because they contain, respectively, **macrospores** and **microspores.** According to the nature of their sporangia, the sporophylls are called **macrosporophylls** and **microsporophylls.** These are always in definite strobili. Strobili are always developed at the apices of branches, but the apex may continue vegetative growth after the sporophylls have been formed and thus produce a shoot with sporophylls and foliage leaves in alternate zones along the stem.[1] The sporophylls are always spirally arranged upon the strobilar axis, but the spiral is generally so condensed that the leaves appear to lie opposite each other in pairs and in four distinct vertical rows. Most species have macrosporo-

[1] Mitchell, 1910; Steel, 1923; Sykes and Stiles, 1910.

phylls and microsporophylls borne in the same strobilus, but there are certain species in which a strobilus has only macrosporophylls or only microsporophylls.[1] When the strobilus has both kinds of sporophylls, all those in the lower portion may be macrosporophylls and all in the upper portion microsporophylls, or there may be two vertical rows of each kind (Fig. 122).

Development of macro- and microsporangia is identical up to the sporocyte stage. There is considerable diversity of opinion as to whether the

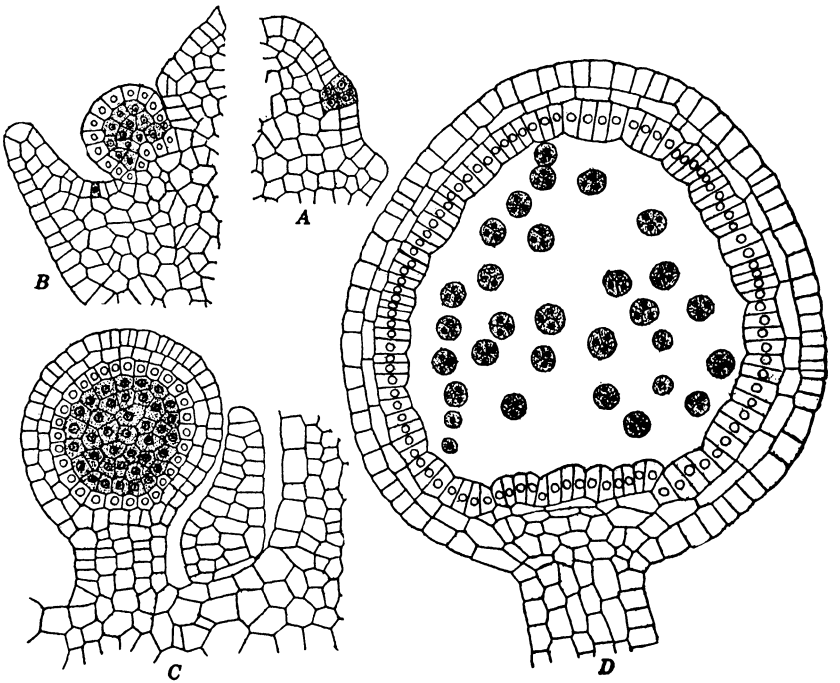

FIG. 123. *Selaginella kraussiana* A.Br. *A* apex of a strobilus with initials of a microsporangium. *B–D*, stages in development of microsporangia. (× 325.)

sporangium comes from a single initial cell or a transverse row of initials.[2] Some species have embryonic epidermal cells of the stem functioning as the sporangial initials; other species have cells at the leaf base developing into the sporangia. However, in both cases the end result is the same since the mature sporangium is a distinctly axillary structure at the base of the sporophyll. Irrespective of whether there is one or a group of initials, the first division is periclinal and into an outer **jacket initial** (or initials) and an inner **archesporial cell** (or cells) (Fig. 123*A*). Vertical and transverse division of the archesporial cell (or cells) results in a mass of sporogenous

[1] Mitchell, 1910. [2] Bower, 1894; Campbell, 1918; Lyon, 1901.

tissue (Fig. 123*B*). Development of the sporogenous tissue is accompanied by a development of the jacket initial (or initials) into a **jacket layer** two cells in thickness. Cells in the outer layer of the jacket eventually become thick-walled; those in the inner layer remain thin-walled. Even before the jacket has become two cells in thickness there is the differentiation of a conspicuous **tapetum** (Fig. 123*C–D*). Except for the portion immediately above the stalk all of this is derived from the outermost layer of sporogenous cells.

In microsporangia all sporogenous cells of the last cell generation in the sporogenous tissue are potential sporocytes, but 10 to 20 per cent of them may disintegrate. The functional sporocytes round up and become separated from one another during meiosis. Each of the four microspores formed by division of a sporocyte is broadly pyramidal with a rounded base (Fig. 122*B*). Its wall may be composed of two or of three layers.[1] These differences in wall structure are correlated with differences in the development of the microgametophyte. Unlike most other pteridophytes, the microspore begins to develop into a microgametophyte before it is shed from the sporangium. Liberation of these immature microgametophytes from the sporangium is due to a vertical apical dehiscence of the sporangial jacket into two valves caused by differential hygroscopic changed in the apical and lateral parts of the jacket. The sporangial jacket opens with a sudden jerk that ejects only a portion of the contained microgametophytes. Those not immediately liberated may be ejected by subsequent closings and openings of the jacket, or they may be dislodged from the opened sporangium by air currents.[2]

Developing macrosporangia produce a considerable number of sporocytes. Generally all but one of these eventually disintegrate, but the finding of 8, 12, and 24 macrospores in macrosporangia of exceptional individuals[3] shows that more than one sporocyte of a macrosporangium may be functional. Most macrosporangia with a single functional sporocyte have it dividing to form four small macrospores which increase equally in size as sporangial development continues. In certain species one or more of the four may regularly fail to enlarge, so that the mature sporangium typically contains one, two, or three functional macrospores.[4]

Adult macrosporangia are generally four-lobed, as seen in top view, and have a single macrospore in each of the four lobes. During maturation of the sporangial jacket most of the cells in the outer layer have a thickening of the radial and inner tangential walls (Fig. 122*C*). However, there is no thickening of walls in a vertical apical strip of cells. Drying out of the sporangial jacket initiates a hydroscopic movement of the thick-walled cells that splits the sporangium along the strip of

[1] Belajeff, 1885. [2] Duthie, 1923, 1924; Mitchell, 1910.
[3] Duerden, 1929. [4] Duerden, 1929; Mitchell, 1910.

thin-walled jacket cells. In some species breaking of the jacket into two valves may be so abrupt that all macrospores, or the macrogametophytes into which they have developed, are catapulted from the sporangium;[1] in other species there is no ejection of them when the sporangium opens.[2]

Development of microspores into microgametophytes begins before the microsporangium dehisces. In *S. Kraussiana*, as in all other species, the first cell division is markedly asymmetrical and into a small lens-shaped **prothallial cell** and a large **antheridial cell.** The antheridial cell then divides in a plane perpendicular to the prothallial cell and both of its daughter cells divide in a plane at right angles to the first plane of division (Fig. 124*C*). One daughter cell of each pair thus formed divides no further and becomes the first cell of the jacket layer of the antheridium. The other daughter cell of each pair divides by means of

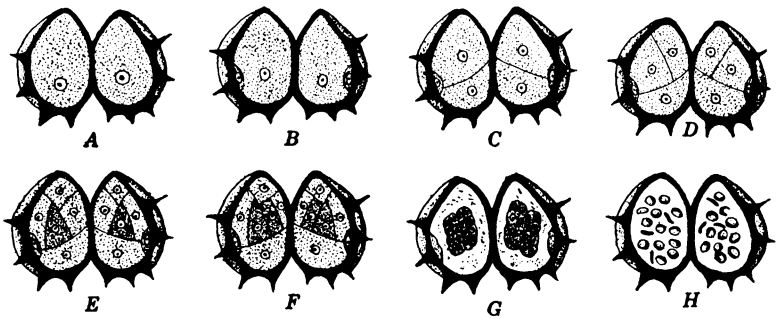

FIG. 124. *Selaginella kraussiana* A.Br. Stereodiagrams of stages in development of microgametophyte. The spores and microgametophytes are drawn as if they were split longitudinally and the two halves spread apart. (*Diagrams based upon Slagg*, 1932.)

a curving cell plate parallel to the prothallial cell (Fig. 124*D*). Of the two daughter cells thus formed, that nearest the prothallial cell divides periclinally into a **primary androgonial cell** and a **jacket cell** (Fig. 124*E*). Anticlinal division of its sister cell and periclinal division of one of the daughter cells thus formed result in two jacket cells and a primary androgonial cell (Fig. 124*E–F*). Development of the gametophyte halts for a time at this 13-celled stage when it consists of one prothallial cell, four primary androgonial cells, and eight jacket cells. It is at this stage of development that the gametophyte is shed from the microsporangium of *S. Kraussiana*. Development is resumed after shedding of the microgametophyte, and each of the four primary androgonial cells may undergo six successive divisions. The 256 androcytes thus formed become metamorphosed into biflagellate antherozoids. There is a disintegration of the jacket layer and of the prothallial cell during the later stages in development of the androgonial tissue (Fig. 124*G*). Thus, a mature

[1] Duthie, 1923; Mitchell, 1910. [2] Lyon, 1901.

microgametophyte consists only of a mass of antherozoids swimming about within the old microspore wall (Fig. 124*H*). For some species it is definitely known that these later stages in development take place upon the soil.[1] For other species it is definitely known[2] that the dust-like, immature microgametophytes sift into the partially opened macrosporangia and there complete their development. The advantage of the incipient type of pollination found in these latter species is obvious.

The microgametophyte of *Selaginella* is so reduced in size and so compressed because of its development within the microspore wall that its homologies with gametophytes of homosporous pteridophytes are obscure. It is generally agreed that the prothallial cell is vegetative and homologous with the entire vegetative tissue of homosporous forms. There is considerable difference of opinion concerning the nature of the antheridial cell. Some[3] hold that it is the initial of a single antheridium. Others[4] think that the antheridial cell is one that divides to form, depending upon the species, two or four antheridial initials.

Macrogametophytes also begin to develop while the macrospore is still within the sporangium, but the stage of development at which the macrogametophyte is shed is extremely variable. The macrogametophyte may be ejected from the sporangium before any trace of cellular organization is evident;[1] it may be shed shortly after the first archegonia are formed;[5] or it may be retained within the sporangium until after fertilization and a considerable development of the embryo.[6]

The structure and development of the macrogametophyte vary from species to species. Development of that of *S. kraussiana*[7] begins with a conspicuous enlargement of the germinating macrospore and a secretion of a two-layered spore wall. Early in the enlargement there is a division of the macrospore nucleus, but this is not followed by cell division (Fig. 125*A*). Continued nuclear division results in a multinucleate protoplast with a conspicuous central vacuole and with the cytoplasm restricted to a thin layer next the spore wall (Fig. 125*C*). Enlargement of the multinucleate gametophyte slows down after a time, and the cytoplasmic layer becomes thicker and thicker, eventually obliterating the central vacuole. Long before this time, free cell formation at the pyramidal end of the macrogametophyte produces a cellular tissue two to three cells in thickness (Fig. 125*D–E*), which is separated from the remainder of the gametophyte by a fairly conspicuous diaphragm (Fig. 125*B*). The portion below the diaphragm, which is densely packed with starch, remains multinucleate until after the embryo has begun to develop, but it too eventually becomes multicellular. Shortly after the apical tissue

[1] Duthie, 1923. [2] Lyon, 1901. [3] Campbell, 1918; Slagg, 1932.
[4] Bruchmann, 1912. [5] Campbell, 1918. [6] Geiger, 1934; Lyon, 1901.
[7] Bruchmann, 1912; Campbell, 1902, 1918.

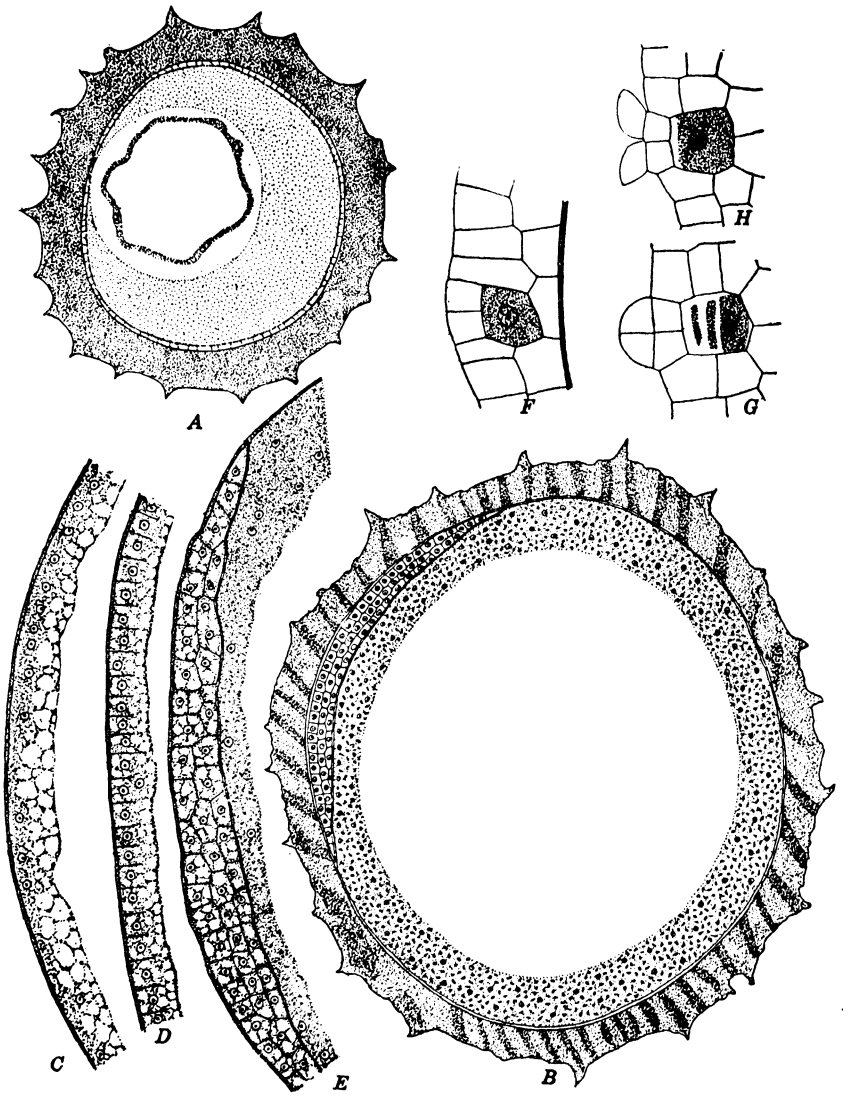

FIG. 125. *Selaginella kraussiana* A.Br. *A*, a very young macrogametophyte. *B* macrogametophyte just before the formation of archegonia. *C–E*, stages in development of cellular tissue of macrogametophyte. *F–H*, stages in development of archegonia. (*A–B*, × 160; *C–E*, × 325; *F–H*, × 485.)

is formed, it becomes exposed by a cracking of the portion of the spore wall external to it. This tissue may become green, and gametophytes that have fallen upon soil may even develop rhizoids.[1] However, this photosynthetic tissue is of minor importance as far as nutrition of gametophyte and developing embryo is concerned, since the reserve food derived from the parent sporophyte and stored in the lower portion of the gametophyte is of far greater importance in their nutrition.

Most of the superficial cells of the apical tissue are potential archegonial initials, and several of these generally develop into archegonia. An archegonial initial divides periclinally into a **primary cover cell** and a **central cell** (Fig. 125*F*). The central cell next divides periclinally into a **primary canal cell** and a **primary venter cell.** Periclinal division of the primary venter cell produces a **venter canal cell** and an **egg** (Fig. 125*G*). The primary canal cell does not divide but functions directly as the single **canal cell** of the mature archegonium. Meanwhile the primary cover cell, by two successive anticlinal divisions at right angles to each other, forms four **neck initials.** Transverse division of each of the neck initials results in a neck two cells in height, and one in which the outer tier of four cells projects above the level of the macrogametophyte (Fig. 125*G–H*). The spreading apart of the neck cells, after disintegration of neck canal cell and venter canal cell, leaves a free passageway for swimming of the antherozoid to the egg.

Fertilization may take place while the macrogametophyte is still within the sporangium[2] or after it has fallen to the ground. Several species are also known to form embryos apogamously. Apogamy may be due to a development of an archegonial initial into an embryo[3] or to a parthenogenetic development of eggs lying within unopened archegonia.[4] There are also several species that are presumptively apogamous since they produce macrospores only or viable macrospores and abortive microspores.[5]

The developing embryo of *Selaginella* always pushes deeply into the macrogametophyte by means of a **suspensor.** In some cases this is composed of a few cells;[1] in other cases it appears to be a one-celled structure.[6] The first division of the zygote is generally (if not always) transverse.

S. martensii Spring. is representative of those species in which all parts of the embryo but the suspensor come from the lower daughter cell formed by division of the zygote. The first division of this cell is vertical, and the two daughter cells thus formed also divide vertically (Fig. 126*B*). One of these four cells, by a diagonal vertical division, forms the apical

[1] Bruchmann, 1912. [2] Lyon, 1901. [3] Lyon, 1904.
[4] Bruchmann, 1912, 1919; Geiger, 1934. [5] Goebel, 1915.
[6] Bruchmann, 1913.

cell of the future stem (Fig. 126*C–D*). The remaining three cells, together with the sister cell of the apical cell, then divide transversely. All the cells, in both the upper and lower tier of four, then undergo repeated vertical and transverse division (Fig. 126*D–F*). Cell division is somewhat more active in one of the lower quadrants, and this eventually leads to a differentiation of the **foot** of the embryo. As is the case with embryos of other Pteridophyta, the foot is a haustorial organ absorbing food from the gametophyte. About the time the foot begins to be apparent, a superficial cell in each of two diagonally opposed quadrants in the upper tier begins to function as the apical cell of a **cotyledon.** The

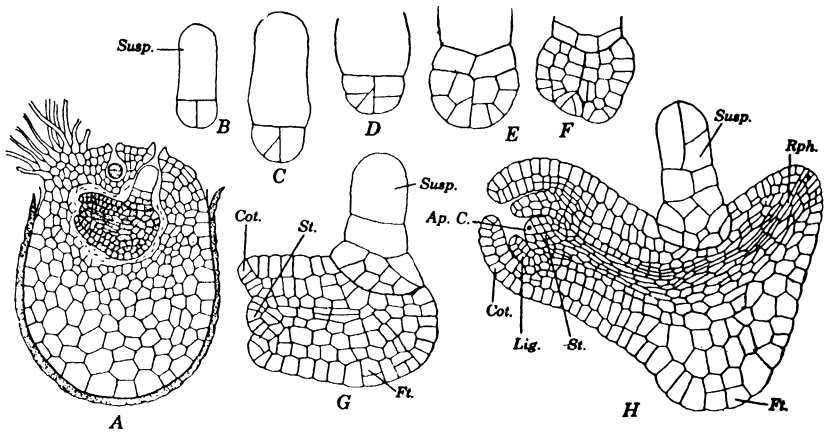

FIG. 126. *Selaginella martensii* Spring. *A*, macrogametophyte and embryo. *B–H*, stages in development of embryos. (*Ap. C.*, apical cell; *Cot.*, cotyledon; *Ft.*, foot; *Lig.*, ligule; *Rph.*, rhizophore; *St.*, stem; *Susp.*, suspensor.) (*After Bruchmann*, 1909.) (*A*, × 75; *B–G*, × 175; *H*, × 110.)

two cotyledons developing from these two apical cells are identical in appearance. They are similar to foliage leaves in having a ligule, but their internal structure is simpler. Cotyledonary development is accompanied by an active division of the apical cell of the stem. The portion of the embryo immediately posterior to the cotyledons develops into the hypocotyledonary portion of the stem. Soon after cotyledons and stem apex have begun to develop, there is a differentiation of an apical cell from a superficial cell on one flank of the foot. Segments cut off from this cell develop into a structure that is root-like in appearance but one that is considered[1] a rhizophore rather then a primary root.

A developing embryo eventually grows through the surrounding gametophytic tissue—the stem and its appendages growing upward and the rhizophore growing downward. This juvenile sporophyte is quite differ-

[1] Bruchmann, 1909, 1912.

ent from that of other pteridophytes in having the cotyledons borne directly on the stem and in having a conspicuous hypocotyledonary stem portion below the level of the cotyledons.

FAMILY 2. MIADESMIACEAE

Sporophytes of Miadesmiaceae had a vegetative structure typical of that for the order. The macrogametophytes were permanently retained within macrosporangia enveloped by an outgrowth from the sporophylls.

The single genus, *Miadesmia*, is known only from the Carboniferous. Its sporophytes resembled those of *Selaginella* in external appearance, and the leaves borne by it were ligulate. The internal organization of

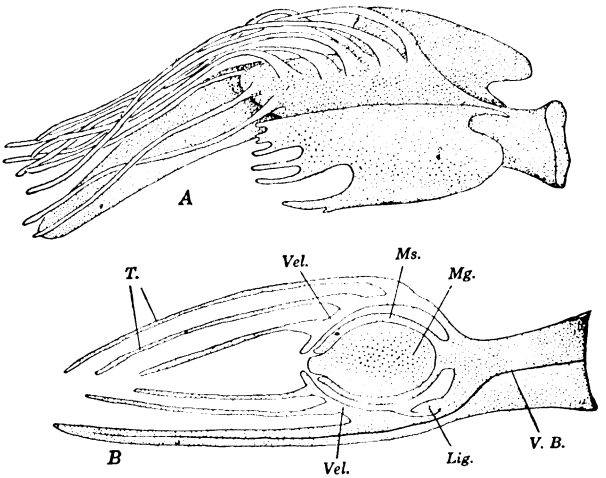

FIG. 127. *Miadesmia membranacea* Bern. *A*, reconstruction of a macrosporophyll. *B*, diagram of a vertical sagittal section of a macrosporophyll. (*Lig.*, ligule; *Mg.*, macrogametophyte; *Ms.*, macrosporangium; *T.*, tentacle; *V.B.*, vascular bundle; *Vel.*, velum.) (*A*, *after*, *and B*, *based upon Benson*, 1908.)

fossil remains of the stem also resembles *Selaginella*, especially in the trabeculae between stele and inner part of the cortex.[1]

The sporophylls were borne in lax strobili, but it is uncertain whether the microsporophylls and macrosporophylls were borne in the same strobilus. The difficulty in settling this question is due to the fact that both types of sporophyll were shed after they became mature. The macrosporangium (Fig. 127) was completely enveloped, except for a small micropyle-like opening, by an envelope growing up from the surface of the macrosporophyll and bearing on its surface numerous long outgrowths that have been called[2] "tentacles." The ensheathing structure surrounding a macrosporangium looks like an integument of a seed, but it is a structure of an entirely different nature and has been called[1] the **velum**

[1] Benson, 1908. [2] Scott, 1920.

because of homologies with the velum of *Isoetes* (see page 227). A macrosporangium contained a single macrogametophyte, which when mature protruded through the macrosporangial jacket but was not liberated from it. If, as has been suggested,[1] the mass of "tentacles" entrapped microspores or developing microgametophytes, there is good reason for thinking that fertilization was not siphonogamous but was by means of free-swimming antherozoids liberated from microgametophytes entrapped in the "tentacles."

The macrosporangium and envelope of Miadesmiaceae resemble seeds in having the macrogametophyte permanently retained within the macrosporangium. On the other hand, as just suggested, there is justification for thinking that they were not siphonogamous. It also seems probable that growth of the sporophyte was not interrupted at any stage between zygote and maturity. Because of the apparent lack of siphonogamy and any dormant period in the "seed," the Miadesmiaceae and the Lepidocarpaceae (see page 216) should be considered pseudospermatophytes rather than true spermatophytes.

ORDER 3. LEPIDODENDRALES

Sporophytes of Lepidodendrales were of tree-like proportions and had secondary tissues formed by means of a cambium. The leaves were microphyllous, ligulate, and deciduous. Roots were borne on rhizophores that were often of large diameter because of secondary thickening. Sporophylls were borne in strobili and all members of the order were heterosporous.

The known fossil record indicates that the Lepidodendrales appeared in the Upper Devonian, were an important element in the flora of Carboniferous coal swamps, and become extinct during the Permian. Leaf scars on fossil stems of them are so distinctive in shape and arrangement that members of the order can be identified from casts and impressions. Many species are also known as petrefactions.

In spite of their tree-like size and secondary thickening, stems of Lepidodendrales were of a primitive type as far as their exarch primary xylem is concerned. As is the case with other members of the division, there were no leaf gaps in portions of the vascular cylinder above the departure of leaf traces. Leaves of Lepidodendrales were relatively large, arranged spirally or in vertical rows, and each had a ligule at its base.

Subterranean portions of sporophytes are so much alike in genera referred to the order that it is impossible to distinguish between genera on this basis. Remains of subterranean portions of Lepidodendrales, which were first considered a separate genus (*Stigmaria*) are of widespread occurrence as casts but are also known as petrefactions. A stigmarian "root

[1] Scott, 1920.

system" consisted of four horizontal branches radiating from the base of the erect trunk of a sporophyte. These horizontal branches, which were often dichotomously branched, approximated in size the aerial portions of the plant. They increased in diameter by a secondary thickening of the vascular cylinder and through the formation of a periderm. The surface in older parts of each branch was rather closely beset with small circular scars, each marking the former position of a rootlet. Fossil remains of portions of branches near the ultimate dichotomies have been found with attached rootlets instead of scars. The rootlets, which were usually but a few millimeters in diameter and rarely more than 25 cm. in length, grew in all directions in the soil. Often they penetrated decaying vegetable matter lying on the ground, as is evidenced by the frequent occurrence of stigmarian rootlets within the softer tissues of contemporary vegetation. Fossil remains of stigmarian rootlets almost always have a space between the cortex and the excentrically located stele. This space is often interpreted as an artifact resulting from imperfect preservation of the inner cortical tissues. The occurrence of a similar space and a similar excentric location of the stele in roots of *Isoetes* (Fig. 138, page 227) seems to show that the space in stigmarian rootlets is not an artifact.

From the physiological standpoint the stigmarian portion of lepidodendrads is comparable to a root system. From the anatomical standpoint, the primary branches are stem-like since the primary vascular tissue is siphonostelic. However, the short lateral appendages borne by the dichotomously forking horizontal branches are more root-like than stem-like in structure. The most probable interpretation of the stigmarian "root system" is that it consisted of four rhizophores similar in nature to those of *Selaginella*.[1] Namely, it consisted of horizontally growing leafless branches which bore numerous true adventitious roots.

The Lepidodendrales are divided into four families.

FAMILY 1. LEPIDODENDRACEAE

The Lepidodendraceae include a number of arborescent genera in which the aerial portion was freely branched and with the strobili borne at the tips of branches. The trunk and its branches had spirally arranged leaf scars lying close to one another.

Over a hundred species have been described for *Lepidodendron*, the best-known member of the family. This genus appeared in the Upper Devonian, flourished abundantly throughout the Carboniferous, and disappeared during the Permian. Well-preserved remains have been found in various parts of the world. A majority of the species were tall trees, in some cases reaching an estimated height of 40 meters. The trunk was a straight shaft that did not branch until some distance above the ground;

[1] Scott, 1920; Wordsell, 1910.

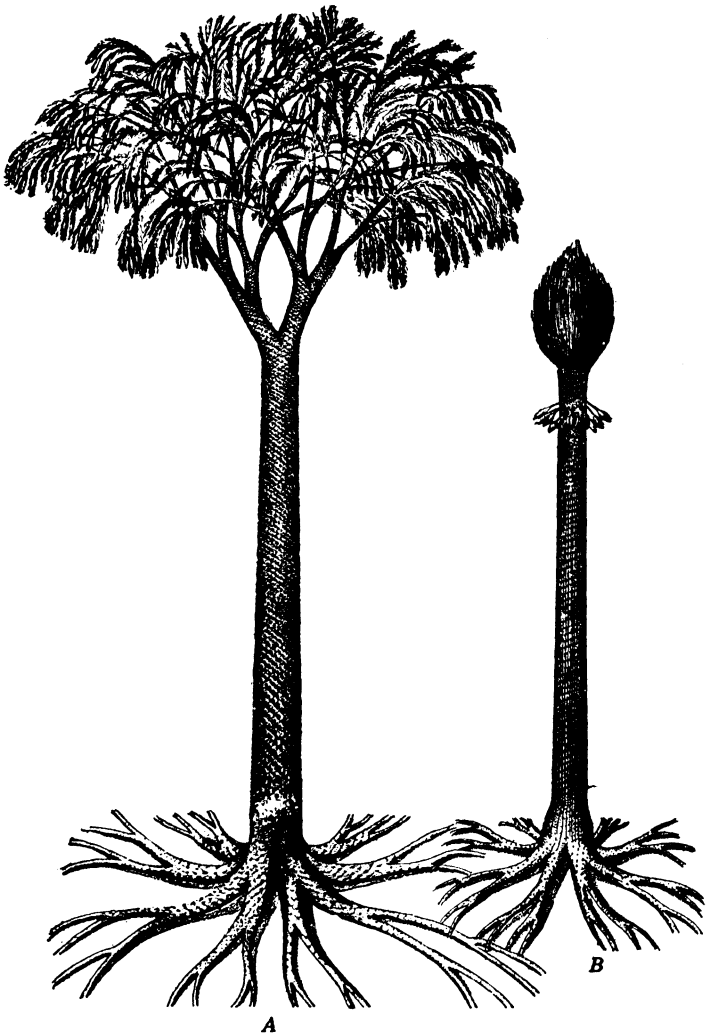

FIG. 128. *A*, reconstruction of *Lepidodendron obovatum* Sternb. *B*, reconstruction of a species of *Sigillaria*. (*After Hirmer*, 1927.)

above this was a dichotomously branched crown with the smaller branches clothed with spirally arranged leaves (Fig. 128*A*). The leaves, which were ultimately shed from the tree, were simple, acicular to linear, and up to 18 cm. in length. Certain species are known in which a typical trunk of *Lepidodendron* is attached to a typical stigmarian "root system."

Most species of the genus had a secondary thickening of the stem, but certain species seem to have lacked a cambium. The central cylin-

der of the stem was protostelic or siphonostelic, but in either case the protoxylem was exarch in position and polyarch (Fig. 129*A*). The steles were small in proportion to the size of the cortex, and the latter was frequently complicated in structure. In *L. vasculare* Binney (*L. selaginelloides* Sternb.) the cortex consisted of the following parts:[1] (1) a parenchymatous **inner cortex,** homogeneous except for the leaf traces; (2) a **secretory zone** composed of intermingled large and small cells, many of which were filled with a dark-colored substance; (3) a

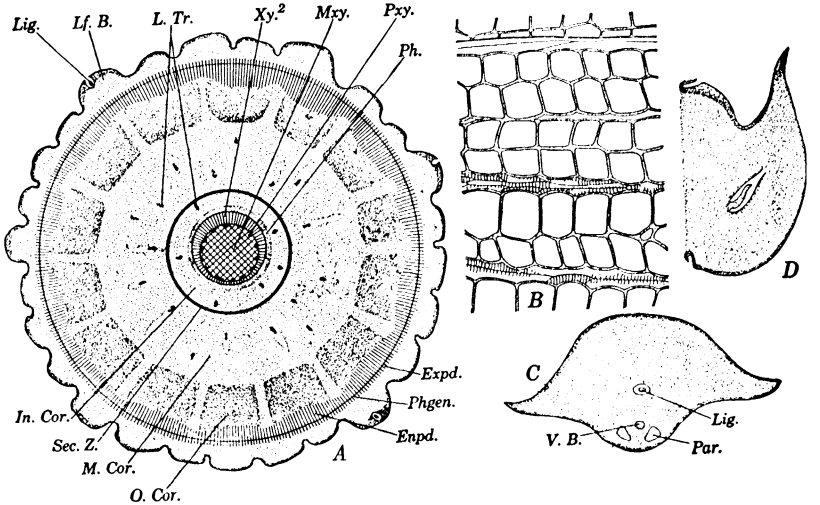

FIG. 129. *A–B, Lepidodendron vasculare* Binney. *A*, transverse section of a stem. *B*, transverse section of a portion of the secondary xylem. *C–D, Lepidodendron aculeatum* Sternb. Transverse and vertical sections of leaf base. (*Enpd.*, endophelloderm; *Expd.*, exophelloderm; *In. Cor.*, inner cortex; *L. Tr.*, leaf trace; *Lf. B.*, leaf base; *Lig.*, ligule; *M. Cor.*, middle cortex; *Mxy.*, metaxylem; *O. Cor.*, outer cortex; *Par.*, parichnos; *Phgen.*, phellogen; *Ph.*, phloem; *Pxy.*, protoxylem; *Sec. Z.*, secretory zone; *V. B.*, vascular bundle; Xy^2, secondary xylem.) (*B*, × 40; *C–D*, × 2.)

middle cortex, similar in appearance to the inner cortex; (4) an **outer cortex** consisting of alternate radial masses of thick- and thin-walled elements. Early in the ontogeny of this stem and even before secondary thickening of the vascular cylinder, there was the differentiation of a **periderm** in the outer cortex. This was formed by a **phellogen** that cut off many more **endophelloderm** elements toward its inner face than **exophelloderm** elements toward its outer face.

Secondary thickening of the stele of *L. vasculare* was due to a **cambium** that formed secondary xylem toward the interior and secondary phloem toward the exterior. The appearance of the secondary tissues in *Lepidodendron* differs from that of corresponding tissues in gymnosperms and

[1] Seward, 1910.

angiosperms in that the cells in the cambium do not exactly correspond with the radial elements in the secondary xylem. In many cases the cambial activity of *L. vasculare* was restricted to one side of the vascular cylinder; later it encircled the entire cylinder. Stems of these plants, therefore, had an excentric cylinder of secondary wood. The secondary xylem of *Lepidodendron* consisted of radial rows of tracheids in which groups of tracheids were laterally separated from one another by **wood rays** (Fig. 129*B*). Some rays were uniseriate and one to many cells in height; other rays were multiseriate. Cells in the xylem portion of the rays were radially elongate and had spirally thickened walls. Relatively little secondary phloem was formed external to the cambium. In the few cases where this has been found well preserved, it seems to be composed of elongate thin-walled elements.

The only portions of leaves in most petrifactions of *Lepidodendron* are the leaf bases which persist after the leaves have fallen away. When cut close to their attachment to the stem, the leaf bases are triangular in cross section; when cut farther out, they are rhomboidal (Fig. 129*C*). In the median vertical axis and close to the lower epidermis, the leaf base has a single small vascular bundle. This is flanked on either side by a **parichnos.** These are bundle-like strands of parenchymatous tissue that parallel the vascular bundle for some distance but eventually become indistinguishable from the mesophyll cells of the leaf. Because of its association with aerenchyma tissue in the leaf and because of its inward extension into the cortex, it is thought[1] that the parichnos had the function of taking in air through the leaf, or the leaf base, and conducting it inward to the stem and downward to the subterranean portion of the plant. Leaf bases of *Lepidodendron* usually have a small **ligule** on the upper surface. In many leaves, as in those of *L. aculeatum* Sternberg, the ligule was so deeply embedded in a flask-shaped cavity that it appears to be a central structure when the leaf base is seen in transverse section (Fig. 129*C*). The distal portions of the leaf were essentially like those of *Selaginella* or *Lycopodium.*[2]

Numerous fossil lepidodendraceous strobili are known. These are generally referred to the genus *Lepidostrobus,* but in certain cases the strobili have been found attached to a branch identical in structure with that of *Lepidodendron.* According to the species, the strobili were 2.5 to 30 cm. long and 1 to 7.5 cm. broad. They bore numerous densely crowded sporophylls (Fig. 130*A*). In most cases these were spirally arranged, but in a few instances they were verticillate. Each sporophyll bore a single sessile elongate sporangium on its adaxial face. Just beyond the sporangium the sporophyll had a small ligule. Sporangia of certain species have been shown to be incompletely septate in a manner

[1] Weiss, 1907. [2] Scott, 1920.

somewhat similar to those of *Isoetes*. It has been suggested[1] that these septa or trabeculae were concerned with the nutrition of the spore mass rather than with mechanical support of the sporangial jacket.

In spite of the fact that a few strobili of *Lepidostrobus* have been found only with small-sized spores, there is considerable evidence for presuming that all species were heterosporous.[2] In the cases where the

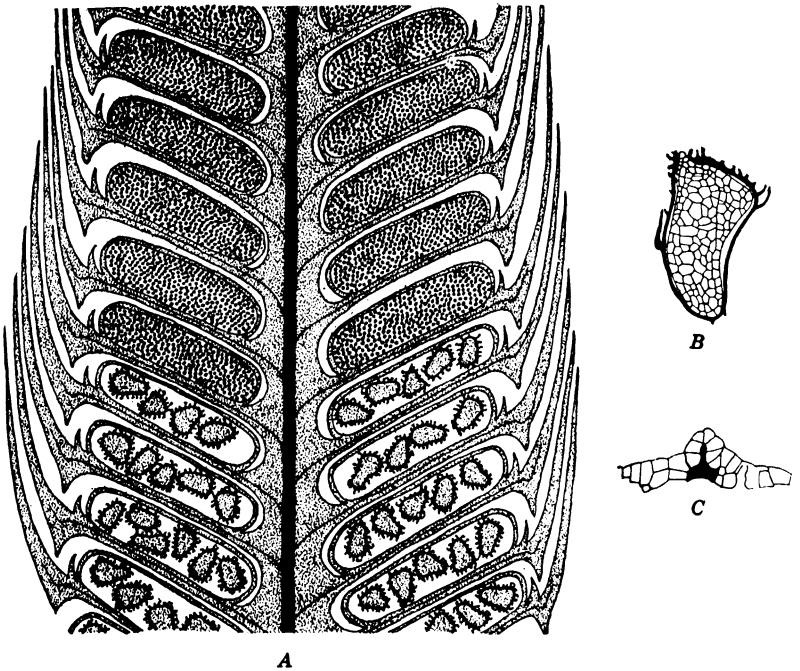

FIG. 130. *A*, diagram of a portion of a strobilus of *Lepidostrobus* in vertical section. *B–C*, macrogametophyte and archegonium of *Lepidostrobus veltheimianus* Sternb. (*B–C*, *after Scott*, 1920.) (*B*, × 25; *C*, × 135.)

cones are known to be heterosporous, the upper sporophylls bear microsporangia and the lower ones macrosporangia. The macrosporangia regularly contained more than four macrospores, but the number was small and probably never more than 16. The macrospores began to develop into macrogametophytes while still within the sporangium. The discovery of cellular macrogametophytes with archegonia[3] (Fig. 130*B–C*) shows that the macrogametophytes were quite like those of *Selaginella*.

[1] Bower, 1894. [2] Scott, 1920. [3] Gordon, 1910.

FAMILY 2. LEPIDOCARPACEAE

The Lepidocarpaceae differ from other families of the order in their permanent retention of macrogametophytes within the macrosporangia. The vegetative structure of sporophytes was as in Lepidodendraceae. Strobili were borne in the same manner, but a strobilus had only microsporophylls or only macrosporophylls, never both.

Two of the genera in the family are known only from their fructifications. A third genus, *Lepidocarpon*, is also based upon the fructification; but it has been suggested[1] that *Lepidophlois*, a genus separated from

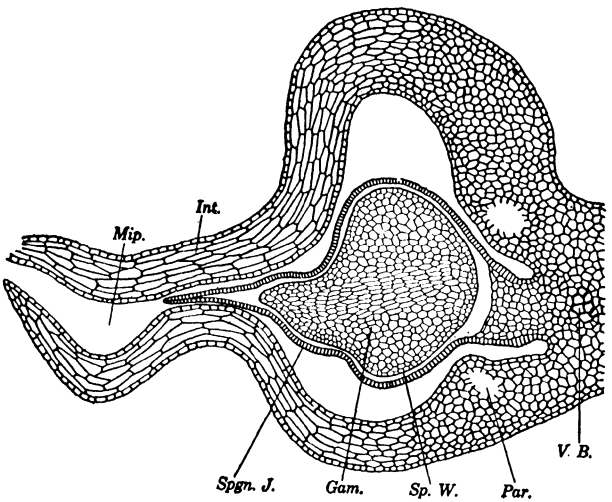

FIG. 131. *Lepidocarpon lomaxi* Scott. Diagrammatic longitudinal section of "seed." (*Gam.*, macrogametophyte; *Int.*, integument; *Mip.*, micropyle; *Par.*, parichnos; *Sp. W.*, wall of macrospore; *Spgn. J.*, jacket of macrosporangium; *V. B.*, vascular bundle.) (× 55.)

Lepidodendron on the basis of leaf scars, is the sporophyte of *Lepidocarpon*. *Lepidocarpon* has been found in England and in the Mississippi Valley of the United States.

Its strobili bore but one kind of sporophyll. Microsporophylls were much like those of *Lepidodendron*. Each macrosporophyll bore an elongate macrosporangium in which the upper side of the jacket layer was prolonged into a crest whose apex split open after the macrospores were formed. As seen when cut vertically, a macrosporangium is surrounded by an enveloping tissue that is often called the integument (Fig. 131). According to one interpretation[2] the "integument" is a special structure growing up from the surface of the macrosporophyll; according to another interpretation[3] the "integument" results from an upturning of

[1] Schopf, 1941. [2] Schopf, 1941; Scott, 1901.
[3] Arnold, 1947; Hoskins and Cross, 1941.

flattened portions of the macrosporophyll lateral to the macrosporangium. The latter interpretation seems the more probable. A macrosporangium contained four spores, only one of which developed into a mature macrogametophyte.[1] According to the species, a mature macrogametophyte completely or incompletely filled the macrosporangium. Fertile macrogametophytes have been found in one species.[2] They had several archegonia somewhat like those of *Lycopodium*. The macrosporangial cavity of this species with mature macrogametophytes also contained numerous spores; some identified as microspores of *Lepidocarpon*, others identified as spores of ferns. Certain species of *Selaginella* have partially developed microgametophytes sifting into open macrosporangia, and there maturing and producing antherozoids which fertilize eggs of macrogametophytes within the macrosporangium.[3] On this account, there is reason for believing that *Lepidocarpon* did the same but unlike *Selaginella* did not have an eventual liberation of macrogametophyte and embryo from the macrosporangium. Macrosporophylls of *Lepidocarpon* were eventually shed from a strobilus and it is very probable that development of an embryo into a sporophyte continued after a macrosporophyll had fallen to the ground.

Paleobotanists usually use the term seed for the structure borne by a macrosporophyll. It is comparable to the seeds of gymnosperms and angiosperms in having the macrogametophyte permanently retained within the macrosporangium. Its development differs from that of a true seed in the following respects: there is no formation of a pollen tube; the macrosporangium is not enclosed by an integument; and there is no formation of a seed coat. There is also a strong probability that growth of the sporophyte was continuous from zygote to maturity. Thus, as in the case of the Miadesmiaceae (see page 209), the Lepidocarpaceae are to be considered pseudospermatophytes rather than true spermatophytes.

FAMILY 3. BOTHRODENDRACEAE

The Bothrodendraceae differ from other families of the order in having strobili that were borne in two vertical rows on opposite sides of major branches. A strobilus had both micro- and macrosporophylls.

Bothrodendron, the type genus, occurred chiefly in the Lower Carboniferous and possibly in the Upper Devonian. Its sporophyte was a tree with much the same proportions as *Lepidodendron*. The lower part of this tree was massive and unbranched; the upper part was repeatedly branched into progressively smaller dichotomies (Fig. 132). The ligulate leaves, which were restricted to the finer branchlets, are comparable in

[1] Hoskins and Cross, 1941; Scott, 1901. [2] Andrews and Pannell, 1941.
[3] Geiger, 1934; Lyon, 1901.

size and arrangement to those of *Lycopodium*. The "root system" was of the stigmarian type typical of Lepidodendrales.

B. mundum (Will.) Lomax, which is here selected to show internal organization of the stem, had the smaller branches protostelic and the

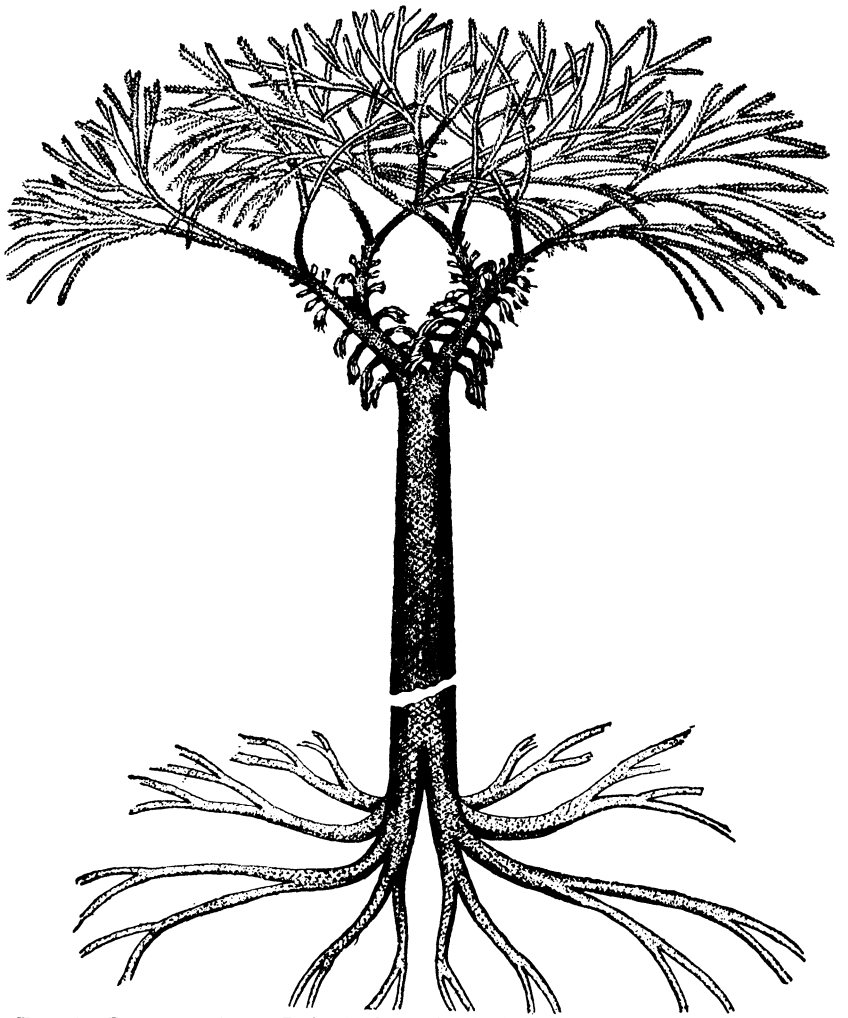

FIG. 132. Reconstruction of *Bothrodendron minutifolium* Boulay. (*After Hirmer*, 1927.)

larger ones siphonostelic (Fig. 133*A*). In either case the protoxylem was exarch. Most specimens of this species are without secondary thickening, but one stem with a conspicuous development of secondary xylem has been recorded.[1] The cortex of *B. mundum* was several times broader than

[1] Williamson, 1889.

the stele. The exterior portion of it, which contained numerous leaf traces, was composed of radially arranged thick-walled cells. The inner portion of the cortex, except for that immediately external to the stele, is always lacking in specimens. This shows that the inner cortex was a delicate thin-walled tissue.

The sporophylls were in strobili borne at the tips of special lateral branches lying in two vertical rows, one on either side of a major branch. *B. mundum* has been shown[1] to have been heterosporous, with both kinds of sporophyll in the same strobilus, and with microsporophylls borne above macrosporophylls (Fig. 133*B*).

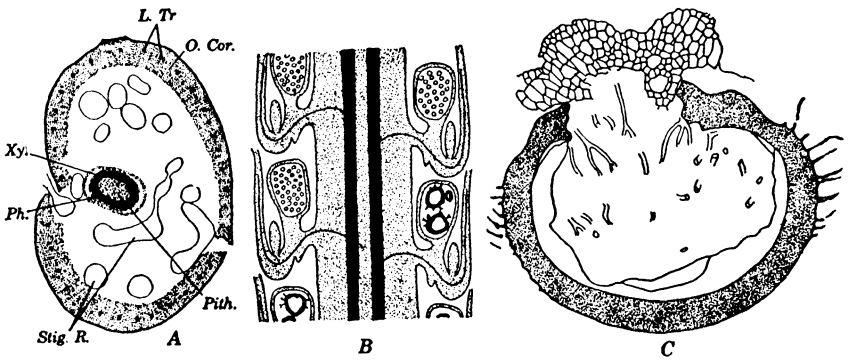

FIG. 133. *A–B, Bothrodendron mundum* (Will.) Lomax. *A*, transverse section of a stem. *B*, longitudinal section of a portion of a strobilus. *C*, gametophyte of *Bothrodendron* sp. (*L. Tr.*, leaf trace; *O. Cor.*, outer cortex; *Ph.*, phloem; *Stig. R.*, stigmarian rootlets; *Xy.*, xylem.) (*B*, *after Watson*, 1908; *C*, *after McLean*, 1912.) (*A*, × 2; *B*, × 6.)

A single fossil macrogametophyte, found external to a macrosporangium, has been referred[2] to *Bothrodendron*. This gametophyte has a pad of cellular tissue external to the apex of the old macrospore wall (Fig. 133*C*). Within the cellular portion of the macrogametophyte are several archegonia-like cavities. On the ventral side of the gametophytic tissue, and projecting into the cavity of the old macrospore, are several rhizoid-like outgrowths. It is thought that these were fungi rather than rhizoids.

FAMILY 4. SIGILLARIACEAE

The Sigillariaceae differ from other Lepidodendrales in having had a columnar, sparingly branched trunk in which the leaf scars were in vertical series and often lying between vertical ridges on the surface of the stem. Strobili were borne at the tips of short, pendant, fertile branches borne in a transverse series below vegetative branches. Both micro- and macrosporophylls were produced by a single strobilus.

[1] Watson, 1908. [2] McLean, 1912.

Sigillaria, with a hundred or more species, is widespread in Carboniferous deposits, but most of the species are known as casts or compressions. These are referred to the genus because of the distinctive leaf scars. The trunk of *Sigillaria*, which was unbranched or with a few major dichotomies at its apex, was a columnar shaft that tapered but slightly from base to apex (Fig. 128*B*). The discovery of trunks more than 2 meters in diameter and the discovery of trunks in which the known portions are more than 22 meters in length shows that the genus included some of the largest arborescent lycopods. The apex of a trunk terminated in a tuft of numerous grass-like leaves, and in certain species these were more than a meter in length.[1] Leaves of certain species had two parallel veins instead of a single vein. The basal portion of a sigillarian tree was a typical stigmarian system.

Petrified remains of *Sigillaria* are of much less frequent occurrence than are those of *Lepidodendron*, but enough material has accumulated

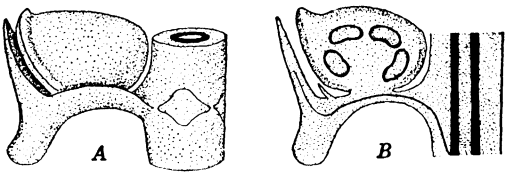

FIG. 134. *Mazocarpon oedipternum* Schopf. *A*, reconstruction of a sporophyll. *B*, diagram of a vertical section through a macrosporophyll and a macrosporangium. (*A*, *after*, *and B*, *based upon Schopf*, 1941.)

to give a general knowledge of the internal organization of the sporophyte. Practically all stems thus far found have a siphonostelic vascular cylinder. The protoxylem was exarch and polyarch. There was regularly a formation of secondary xylem. The structure of the cortex was quite like that of *Lepidodendron*.

Pendant branches, each terminating in a strobilus, were borne in transverse whorls below vegetative branches and were shed after spore production was completed. The genera *Sigillariostrobus* and *Mazocarpon* are to be considered fructifications of *Sigillaria*. *Sigillariostrobus* is known from impressions and compressions; *Mazocarpon* is known from petrified remains in coal balls. *Mazocarpon* was heterosporous and with microsporophylls borne above the macrosporophylls of a strobilus. Macro- and microsporophylls and the sporangia borne by them were quite similar in external appearance. Macrosporangia (Fig. 134) of some species contained more than four spores[2] and those of other species contained four macrospores.[3] The *Mazocarpon* type of macrosporangium differed from those of all other Lepidodendrales in having the macrospores embedded within a tissue instead of lying free from one another. Mature gameto-

[1] Scott, 1920. [2] Benson, 1918. [3] Schopf, 1941*A*.

phytes have been found[1] within macrosporangia. These macrogametophytes resemble those of *Selaginella* and *Isoetes* except that they have but one archegonium.

ORDER 4. ISOETALES

The Isoetales have herbaceous sporophytes with a massive rhizophore at the base of the stem. The leaves are microphyllous and ligulate. The sporophytes are heterosporous, and with or without the sporophylls grouped in definite strobili. Antherozoids, known only for the single living genus, are multiflagellate. Members of the order are known from the Triassic to the present.

Isoetes differs so markedly from other living pteridophytes that its systematic position was long a matter of dispute. During recent years a majority of botanists, with or without reservations, have adhered to the view that its affinities are with the lycopodiaceous pteridophytes. Features favoring this view include the lycopsidan vascular organization, the ligulate leaves, and the single sporangium on the adaxial face of a sporophyll. There are a number of additional features which, when taken collectively, seem to show that *Isoetes* has more in common with Lepidodendrales than with other lycopods. These include the presence of a stigmaria-like rhizophore; roots with the same distinctive structure as stigmarian rootlets; a vestigial parichnos in the leaves; a lepidodendroid trabeculation of sporangia; and a regular formation of more than four macrospores within a macrosporangium.

Many botanists include only *Isoetes* and its fossil relative *Isoetites* among the Isoetales. The phylogenetic connection between *Isoetes* and *Pleuromeia* has been admitted by many, but Seward[2] is one of the few who have formally assigned *Isoetes* and *Pleuromeia* to the same taxon. He places them in the same family (Isoetaceae) but the families that he recognizes among lycopods are the equivalent of orders in most other systems of classification. As will be shown on later pages, *Isoetes* and *Pleuromeia* have a similar stem structure. The two are also alike in their ligulate leaves, structure of their roots, and their trabeculate sporangia. On the other hand, except for its peculiar rhizophore, *Pleuromia* has much in common with Lepidodendrales. Thus, it is a connecting link between *Isoetes* and Lepidodendrales, but one whose affinities are more with the former than the latter. For this reason the Pleuromeiaceae (*Pleuromeia* and its relative *Nathorstiana*) seem in a more natural position when placed in the Isoetales than when placed in a separate order.

FAMILY 1. PLEUROMEIACEAE

Sporophytes of Pleuromeiaceae had an upright unbranched stem with foliage leaves in the upper portion and a single strobilus at the apex of

[1] Schopf, 1941*A*. [2] Seward, 1910.

the stem. At the base of the stem was a massive rhizophore with very short arms.

Pleuromeia, the most fully known member of the family, is a fossil with a chronological range limited to the Middle Triassic. The sporophyte attained a height of about 2 meters and consisted of an erect unbranched stem subtended by a massive rhizophore (Fig. 135). The upper part of the axis was densely clothed with spirally arranged, long, narrow leaves, each of which had a ligule at its base.[1] The lower part of an axis had numerous spirally arranged leaf scars.

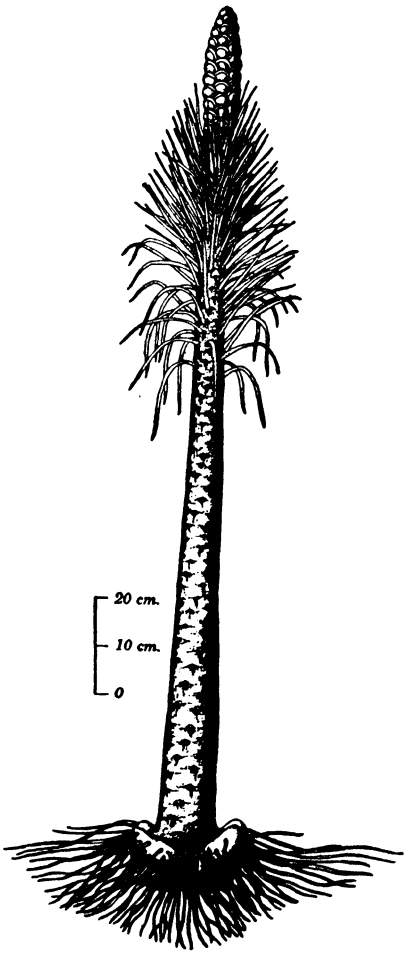

FIG. 135. Reconstruction of *Pleuromeia sternbergii* Corda. (*After Hirmer*, 1933.)

An axis terminated in a single strobilus with closely overlapping shield-shaped sporophylls. *Pleuromeia* was heterosporous, but with macro- and microsporophylls borne on separate sporophytes. Each sporophyll bore a single sporangium and these have been described as being borne on the underside of the sporophyll. This description of an atypical position of sporangia for a member of the Lepidophyta has been thought[2] to be due to a misinterpretation of an adaxially borne sporangium bulging toward the abaxial side of the sporophyll. The sporangia were relatively large and had the same internal trabeculation as in those of *Lepidostrobus* and *Isoetes*.

The stelar portion of an axis was actinostelic and with the protoxylem exarch. The only secondary thickening of an axis resulted from the activity of a phellogen arising toward the exterior of the cortex. This produced a thick periderm quite similar to that found in Lepidodendrales. The rhizophoric portion of the sporophyte differed from the stigmarian type of rhizophore in having each of the four rhizophores

[1] Hirmer, 1933; Mägdefrau, 1931. [2] Walton, 1940.

unbranched and growing but very little in length. However, each of the four massive rhizophores bore rootlets on the lower surface and these were identical in structure with stigmarian rootlets.

FAMILY 2. ISOETACEAE

Sporophytes of Isoetaceae have a corm-like stem that is not externally differentiated into axis and rhizophore. The sporophylls, which bear their sporangia on the adaxial face, are not arranged in definite strobili. The sporophytes are heterosporous and antherozoids produced by the male gametophytes are multiflagellate. This family contains two genera: *Isoetes*, a genus of living plants, and *Isoetites*, a fossil genus with a record extending back to the Lower Cretaceous.

Isoetes has about 65 species, 19 of which occur in the United States.[1] A large majority of the species are hydrophytes that grow immersed in water or that grow on swampy land. A few species, including certain ones found in southern California, grow in habitats that are completely dry for a portion of the year.

The plant body of *Isoetes* is 5 to 50 cm. tall. It consists of a very short, two- or three-lobed, corm-like "stock" which bears a densely crowded rosette of stiff awl-shaped leaves on its upper surface (Fig. 136). The lowest (outermost) leaves on the stock are sterile; successively within them are macrosporophylls, microsporophylls, and leaves with immature sporangia.[2] The lower surface of the stock bears many dichotomously branched roots. These appear to cover the entire lower surface; in reality, they are in two or three groups accordingly as the stock is two- or three-lobed.

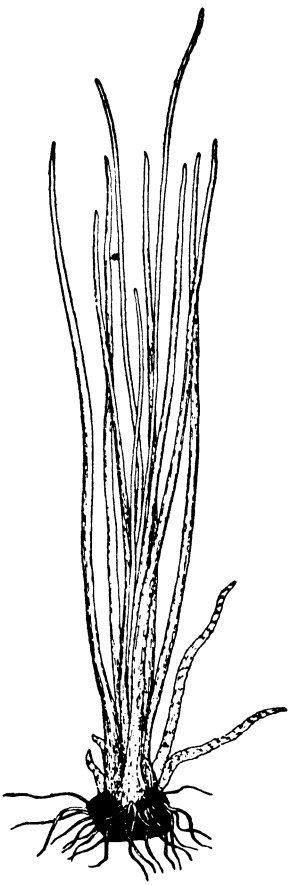

FIG. 136. *Isoetes bolanderi* Engelm. (*Natural size.*)

The term stock has been proposed[3] for the tuberous axis bearing the roots and leaves, since it has been interpreted both as a stem[4] and as a stem combined with a stigmarian type of rhizophore.[5] When stripped of its

[1] Pfeiffer, 1922. [2] Osborn, 1922; R. W. Smith, 1900. [3] Lang, 1915.
[4] Scott and Hill, 1900; Stokey, 1909. [5] Lang, 1915; West and Takeda, 1915.

leaves and roots, the stock has, according to the species, two or three deep vertical furrows that make it, respectively, deeply two- or three-lobed. Even in this denuded condition, the external form gives no indication of its true morphological nature. The answer to this question rests upon the analysis of the vascular system. Vertical sections of two-lobed stocks, cut both parallel to and at right angles to the furrows, taken in

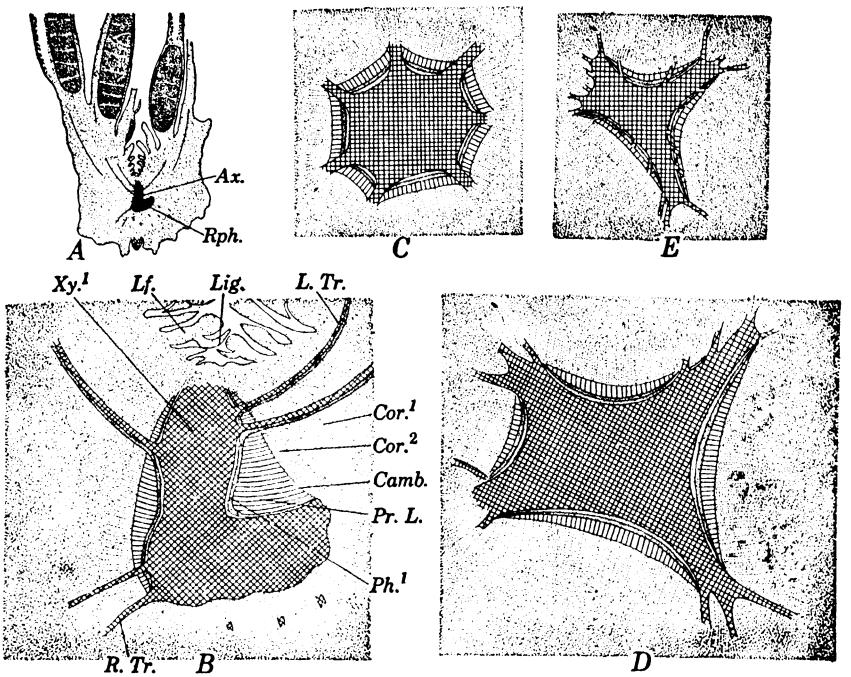

FIG. 137. *Isoetes nuttallii* A.Br. *A*, vertical section of "corm" and bases of leaves borne by it. *B*, diagram of vascular portion of Fig. *A*. *C*, diagram of transverse section through vascular portion of axis of Fig. *A*. *D–E*, diagrams of transverse sections through upper and lower portions of vascular tissue of rhizophore portion of Fig. *A*. (*Ax*, axis; *Camb.*, cambium; *Cor.*[1], primary cortex; *Cor.*[2], secondary cortex; *Lf.*, leaf; *Lig.*, ligule; *L. Tr.*, leaf trace; *Ph.*[1], primary phloem; *Pr. L.*, prismatic layer; *Rph.*, rhizophore; *R. Tr.*, root trace; *Xy.*[1], primary xylem. (*A*, × 5; *B–E*, × 60.)

conjunction with serial transverse sections, show that the portion of the vascular system connected with the leaf traces is a vertical cylinder (Fig. 137*A–C*). The lower portion of the vascular system, connected with steles of the roots, is a spade-shaped structure flattened in the plane of the surface furrows on the stock. Three-lobed stocks differ from the foregoing in that the lower part of the vascular system consists of four radiating arms. One pair of arms diverge widely from each other. The other pair are more or less fused with each other (Fig. 137*D–E*). Thus, the lower portion of the vascular system appears to be triradiate. When taken by it-

self, the vascular system of *Isoetes* shows a remarkable resemblance to the plant body of *Pleuromeia*. In *Pleuromeia* the plant body is externally differentiated into an unbranched erect axis subtended by a massive recurved rhizophore. In *Isoetes* the plant body is so telescoped and the cortex is so thick that differentiation into axis and rhizophore is not externally evident. However, the differentiation into axis and rhizophore does become apparent when the vascular system is taken by itself and viewed as a three-dimensional object.

The growing point of the axis lies in a shallow depression at the distal end of the stock. Growth seems to be initiated by a group of meristematic cells rather than by a single apical cell. Vertical elongation of the stock is very slight, and the mature tissues lie a very short distance back from the embryonic region. The stelar portion of the mature region differs sharply from the cortical region, but the two are not delimited by an endodermis. The vascular cylinder of the axis is protostelic in organization. In very young portions of the stem, it consists of a central core of xylem ensheathed by a layer of phloem. The xylem consists of parenchyma intermingled with very short spiral and reticulate tracheids. Numerous leaf traces depart from the stele, and, as in other Lycopodinae, these are without gaps.

Maturation of the primary tissues already described is followed by the differentiation of a cambium just external to the phloem. There is great diversity of opinion as to functioning of this cambium and as to the nature of the tissues formed by it. It has been held[1] that the cambium forms derivatives toward its inner face only, but there is a good evidence to show that it cuts off a secondary cortex externally and a secondary tissue internally. The secondary tissue cut off internally has been interpreted as secondary xylem,[2] as secondary phloem,[3] and as a secondary tissue containing both tracheids and sieve tubes.[4] Probably the best solution of the difficulty is to follow the practice of the older anatomists and to refer to this tissue as the **prismatic layer.** The first few derivatives cut off inward from a cambial cell may mature into reticulate tracheids (secondary tracheids), but all the later-formed derivatives mature into sieve tubes or into parenchymatous cells. The sieve tubes are of the same size as the parenchymatous cells but may be distinguished from the latter by the sieve plates on their walls and by the lack of starch within their protoplasts.

Except for the leaf traces, the primary cortex in the stem portion of the stock consists of a homogeneous, starch-filled, parenchymatous tissue with conspicuous intercellular spaces. The radial diameter of the mature cortex is several times that of the vascular cylinder (Fig. 137*A*). This,

[1] Lang, 1915*A*. [2] Stokey, 1909. [3] West and Takeda, 1915.
[4] Scott and Hill, 1900.

in conjunction with the lack of vertical elongation, frequently results in a stock broader than it is tall. The stem portion of the stock produces a new set of leaves each year. As the new leaves develop, the old leaves are sloughed off by the formation of an abscission layer in the outer portion of the cortex. In certain cases the abscission layer is a layer of mucilage-filled cells. The cortex in older portions of the stem is externally bounded by a scar tissue formed by this abscission of the outer portion of the cortex, and the outermost cells of the scar tissue may be sclerified.

There is also a cortical region external to the rhizophore portion of the stock. Development of cortical tissue is greater on the lateral than on the lower face of the rhizophore. The production of a smaller amount of cortical tissue external to the lower face of the rhizophore is the reason for the vertical grooves evident on the surface of the stock. The growing apex of the rhizophore portion of the stock also produces a new set of roots every year, and they lie in a row on either side of the median axis of each lobe. Accordingly as the stock is two or three lobed, there is a formation of either two or three double rows of roots each year. Roots formed in previous growing seasons come to lie farther and farther back from the growing apices of the rhizophore as new sets of roots are formed each year. These old roots may persist for more than one year, or they may function for one year only and then be sloughed off by the formation of an abscission layer at the surface of the cortex of the rhizophore.[1]

The embryonic apex of an *Isoetes* root has an apical meristem instead of a single apical cell. Now and then the apical meristem becomes divided into two portions which grow at equal rates and so produce the characteristic dichotomy of the roots. Posterior to the apical meristem the root becomes differentiated into stele and cortex (Fig. 138). The vascular cylinder matures into a monarch protostele. The xylem and phloem of this stele are collateral and so oriented that the xylem is on the side of the root next to, and the phloem on the side away from, the rhizophore. At the periphery of the stele is an endodermal layer, readily recognizable because of the Casparian strips in the radial walls. Portions of the roots extending outward from the stock contain a large C-shaped intercellular space in their cortices. This space results from a breaking down of cortical cells external to the phloem side of the stele. The occurrence of a similar cavity in stigmarian "rootlets" furnishes another reason for linking *Isoetes* with the Lepidodendrales.

The leaves, both fertile and sterile, taper abruptly from a broad base to an elongate acicular portion. Each leaf bears a single ligule on the adaxial surface and at the juncture of the acicular and basal portions. The ligule is similar in structure to that of *Selaginella*. Within the leaf

[1] Osborn, 1922.

is a single vascular bundle, continuous with a leaf trace departing from the central cylinder. The bundle is collateral throughout its entire length, but sometimes it tends to become concentric toward the tip of the leaf. Sporophylls of certain species have the lower portion of the bundle flanked on either side by a mucilage canal. These canals are thought to be homologous with the parichnos strands found in leaves of Lepidodendrales.[1] The awl-shaped portion of the leaf is traversed longitudinally by four cylindrical air chambers that may be transversely septate.

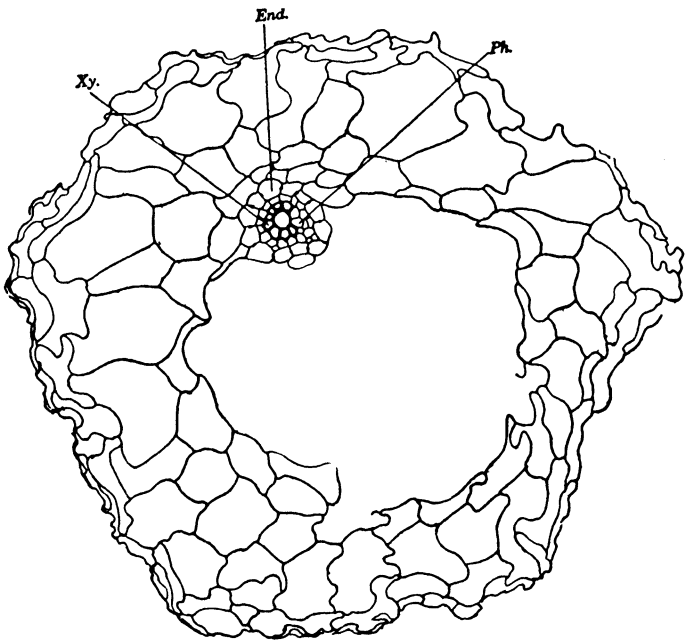

FIG. 138. *Isoetes nuttallii* A.Br. Transverse section of root. (*End.* endodermis; *ph.*, phloem; *Xy.*, xylem.) (× 215.)

The mesophyll lateral to the air chambers may be wholly parenchymatous, or it may contain four longitudinal strands of sclerenchyma, so located that they alternate with the air chambers. The superficial layer of a leaf is a well-defined epidermis in which there are stomata if the plant does not grow submerged in water.

Each sporophyll bears a single flattened sporangium between the ligule and leaf base, and on the adaxial face. The sporangium lies within a depression in the leaf base which is completely or incompletely roofed over by a membranous outgrowth (the **velum**) arising just below the ligule (Fig. 139*A*).

[1] T. G. Hill, 1906.

Early stages in the ontogeny of macro- and microsporangia are alike. The first evidence of sporangial development[1] is the periclinal division of a group of embryonic epidermal cells somewhat below the ligule. Cells in the outer layer formed by this division are jacket initials; those of the inner layer are archesporial cells (Fig. 139*C*). The velum is developed from epidermal cells between the sporangial initials and the ligule. Development of the velum proceeds rapidly, and it is a clearly evident structure before the sporangial initials divide periclinally (Fig. 139*B*).

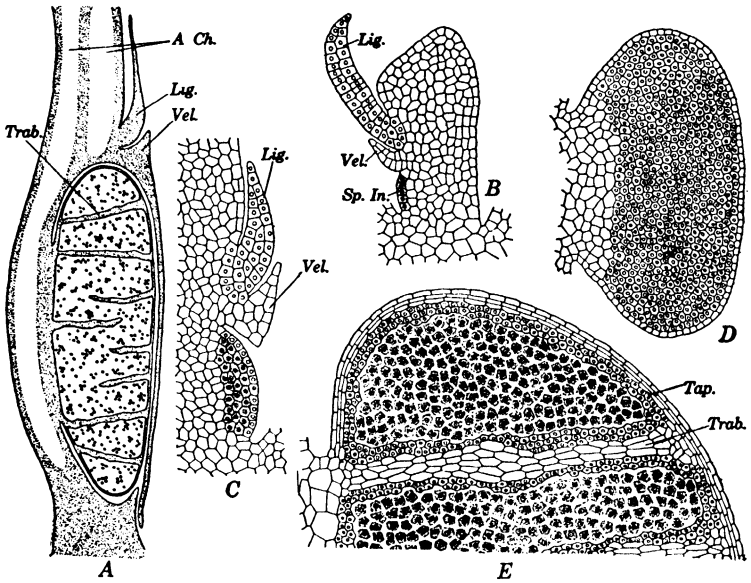

FIG. 139. *Isoetes nuttallii* A.Br. *A*, vertical section of base of a microsporophyll bearing a mature microsporangium. *B*, a young microsporophyll with the primordium of a microsporangium. *C–E*, stages in development of microsporangia. (*A. Ch.*, air chambers; *Lig.*, ligule; *Sp. In.*, sporangial initials; *Tap.*, tapetum; *Trab.*, trabecula; *Vel.*, velum.) (*A*, × 14; *B–E*, × 140.)

The margin of the velum toward the sporangium develops much more extensively than does the margin toward the ligule. Downward development of the velum margin may continue until the sporangium is completely overarched, or it may cease before overarching is completed. The archesporial cells divide and redivide to form a massive sporogenous tissue (Fig. 139*D*). Late in development of the sporogenous tissue, it becomes differentiated into blocks of fertile cells laterally separated from one another by plates and columns of sterile cells. The sterile cells eventually mature into the **trabeculae** that incompletely divide the cavity within the mature sporangium. The sporogenous cells adjacent to the

[1] Bower, 1894.

trabeculae, as well as those adjacent to the sides of the sporangium, become a tapetum that is generally two cells in thickness (Fig. 139*E*). The remaining sporogenous cells are all potential sporocytes. The jacket layer of the sporangium remains one cell in thickness for a considerable time, but, as tapetal differentiation takes place, it may become a layer three or four cells in thickness.

All fertile cells in microsporangia are potential sporocytes, and most of them form tetrads in the usual manner. Only a limited number of fertile cells of macrosporangia are potential macrospore mother cells. These cells begin to enlarge early in development of the sporogenous tissue[1] and become densely filled with cytoplasm. Eventually 40 to 80 of the enlarged sporogenous cells divide to form four macrospores each. The remaining fertile cells of the macrosporangium, both large and small, disintegrate while the reduction divisions are taking place.

Sporangia of most species of *Isoetes* remain indehiscent after they are fully mature, and the spores are liberated by a death and decay of the sporophylls. The spores thus freed usually remain close to the plant that produced them, but they may be scattered by the wind or through the agency of worms.[2] In at least one species there is a dehiscence of the sporangia after abscission of the sporophylls from the stock.

Development of microspores into microgametophytes begins immediately after they are liberated from the sporangium and is completed within a few days. Germination begins with a migration of the nucleus to one end of the microspore.[3] After this, the microspore divides asymmetrically into a small cell (the prothallial cell), which does not divide again, and a large cell (the antheridial initial) which undergoes several divisions (Fig. 140*B*). The first division of the antheridial initial is transversely diagonal to the long axis of the old microspore (Fig. 140*C*). The daughter cell nearest the prothallial cell is the first cell of the jacket layer of the antheridium. This cell does not divide, but its sister cell divides in a plane perpendicular to the previous plane of division (Fig. 140*D*). Of the two daughter cells thus formed, the one farthest from the prothallial cell becomes the second cell of the jacket layer. Its sister cell divides in a plane approximately parallel to the preceding plane of division. One daughter cell thus formed becomes the third cell of the jacket layer; the other divides periclinally into the fourth jacket cell and the primary androgonial cell (Fig. 140*E*). The primary androgonial cell, by two successive divisions, forms four androcytes, each of which becomes metamorphosed into an antherozoid bearing a tuft of some 15 flagella near one pole (Fig. 140*F–G*). Metamorphosis of androcytes into antherozoids is accompanied by a disintegration of the prothallial cell

[1] R. W. Smith, 1900. [2] Duthie, 1929.
[3] Belajeff, 1885; Campbell, 1918; Liebig, 1931.

and the four jacket cells. Shortly after this, the antherozoids are liberated by a dehiscence of the old microspore wall along its straight face.

The nucleus of a germinating macrospore may lie in the apical or in the basal portion of the spore.[1] In either case, germination begins with a series of nuclear divisions. Multinucleate macrogametophytes of *Isoetes* differ from those of *Selaginella* in that their protoplasts never have a conspicuous central vacuole at any stage of development. During the later multinucleate stages the nuclei become more numerous in the apical portion of the gametophyte. It is here that the first cells are formed as a result of free cell formation[2] by means of cell plates produced between the

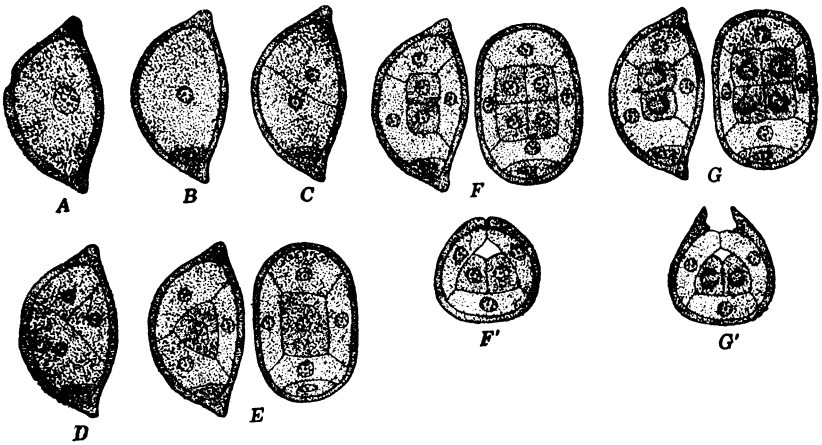

FIG. 140. Diagrams showing the development of microgametophyte of *Isoetes*. *A–D*, in vertical section perpendicular to flat surface of spore wall. *E–G*, in vertical section perpendicular to and parallel to flat surface of spore wall. *F*[1]–*G*[1], in transverse section. (*Diagrams based upon Liebig*, 1931.)

nuclei (Fig. 141*A*). The lower portion of the gametophyte eventually becomes cellular, but this may be delayed until the embryo is fairly well advanced (Fig. 142*E*). The first-formed prothallial tissue, which becomes exposed by a cracking of the old spore wall,[3] lacks chlorophyll but it may develop numerous rhizoids.[4]

Two or three of the superficial cells in the prothallial tissue generally function as archegonial initials. If fertilization does not take place within archegonia developed from these initials, other superficial cells function as archegonial initials. Formation of additional archegonia continues until fertilization does take place or until the reserve food supply of the gametophyte is exhausted. The first division of an initial is periclinal and into a primary cover cell and a central cell (Fig. 141*C*). Two succes-

[1] Campbell, 1891; La Motte, 1933. [2] Campbell, 1891.
[3] Campbell, 1891; Liebig, 1931. [4] La Motte, 1933.

sive divisions of the primary cover cell form four neck initials and from these is developed a neck three or four cells in height (Fig. 141*D*). Meanwhile, the central cell divides into a primary canal cell and a primary venter cell. The primary canal cell may become binucleate, but this is rarely followed by a division to form two canal cells. The primary venter cell divides transversely into a venter canal cell and an egg. The last steps in archegonial development consist of a disintegration of the venter and canal cells and a spreading apart of the neck cells (Fig. 141*E*).

Embryos of *Isoetes* (Fig. 142) differ from those of other lycopods in their lack of a suspensor and in their precocious differentiation of initials of the four parts of the embryo at the four-celled stage of development. Division of the zygote is diagonally vertical and at an angle of about

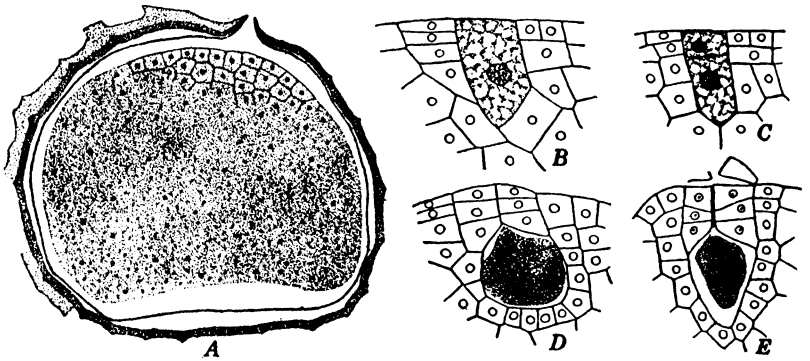

FIG. 141. *Isoetes braunii* Dur. *A*, vertical section of a young macrogametophyte. *B–E*, stages in development of archegonia. (*A*, × 110; *B–E*, × 215.)

20 degrees to the vertical axis of the archegonium.[1] Both daughter cells divide transversely. In the four-celled embryo thus formed, one of the two cells in the **epibasal half,** the half nearest the neck of archegonium, is the initial cell of the **primary root** and the other is the initial cell of the **stem.** In the **hypobasal half** of the four-celled embryo, the half farthest from the archegonial neck, one of the two cells is the initial cell of the **foot** and the other is the initial cell of the **cotyledon.** Certain families of ferns also have the cotyledon, stem, foot, and primary root each developing from a cell of the four-celled embryo, but in them (Fig. 234, page 356) the epibasal half of the four-celled embryo gives rise to cotyledon and primary root instead of stem and primary root.

Cell division in the stem quadrant of a young embryo is at a slower rate than in other quadrants. Within a very short time the embryo becomes longitudinally differentiated, with the cotyledon at one pole and the primary root at the other.[1] At first the embryo lies so that longitu-

[1] La Motte, 1937.

dinal axes of cotyledon and primary root lie diagonal to the vertical axis of the archegonium, but later on they come to lie at right angles to it. Development of an embryo is at a rapid rate. About a week after fertilization the cotyledon has developed to a stage where it begins to grow through the surrounding gametophytic tissue (**calyptra**) and in a few more days the primary root does the same.[1] At this time the only evidence of development in the stem quadrant is the formation of a ligule-like structure, the "cotyledonary sheath" (Fig. 142*E*). A developing sporophyte begins to become self-sustaining after the primary root has grown

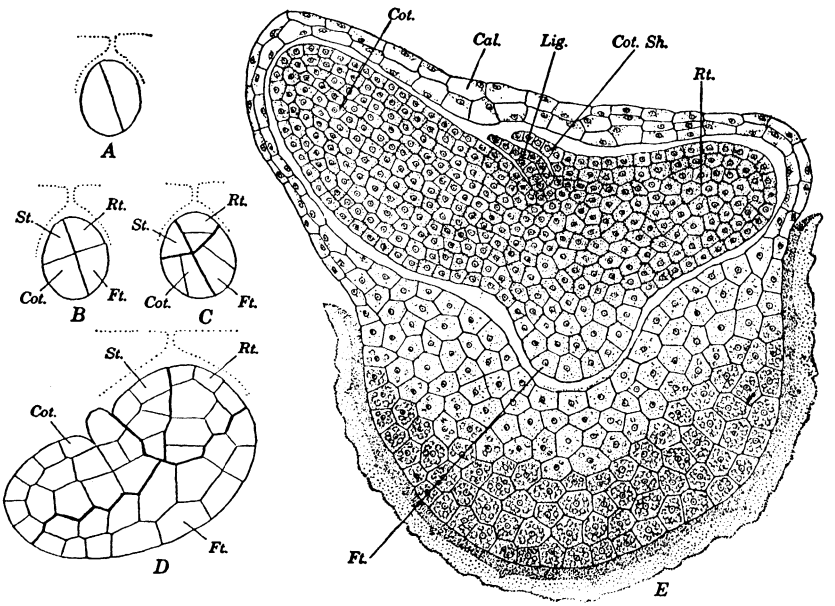

FIG. 142. *A–D*, *Isoetes lithophila* Pfeiffer. Early stages in development of embryo, and with portions derived from each of the four initials outlined with a heavy line. *E*, *Isoetes braunii* Dur. Diagrammatic vertical section through macrogametophyte and embryo. (*Cal.*, calyptra; *Cot.*, cotyledon; *Cot. Sh.*, cotyledonary sheath; *Ft.*, foot; *Lig.*, ligule; *Rt.*, primary root; *St.*, stem.) (*A–D*, *after La Motte*, 1937.)

down into the soil and the cotyledon has grown up into the air. Following this, the very immature stem quadrant begins to grow and to form the various parts of the mature sporophyte.

Gravity has no effect on the parts into which the four initials of the four-celled embryo grow. This was demonstrated[1] by placing macrogametophytes with zygotes so that the vertical axis of the archegonium was at various angles to the direction of gravity, and by rotating macrogametophytes on a clinostat. Although gravity has no effect on relation of the four initials one to another, it does influence the direction of growth of

[1] La Motte, 1937.

cotyledon and primary root at the stage when they are beginning to emerge from the macrogametophyte. Macrogametophytes maintained at right angles to the force of gravity from the zygote stage onward always had the cotyledon growing directly upward and the primary root growing directly downward (Fig. 143*A*). When such gametophytes were inverted at the two-celled embryo stage (about 24 hours after fertilization), or at any later stage in early embryonal development, the cotyledon grew downward for a considerable time and the primary root grew upward. Then, as they were emerging from the macrogametophyte, the tip of the cotyledon began to grow upward and the tip of the primary root began to grow downward (Fig. 143*B*). Macrogametophytes were also placed so that the archegonial axis was parallel to the force of gravity

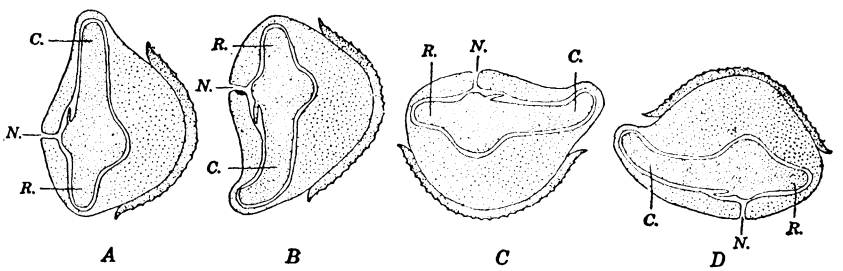

FIG. 143. *Isoetes lithophila* Pfeiffer. Diagrams of embryos showing direction of growth when macrogametophyte is kept in a fixed position. *A*, longitudinal axis of archegonium horizontal. *B*, the same, but macrogametophyte turned 180 degrees after 24 hours. *C–D*, longitudinal axis of archegonium vertical. (*C.*, cotyledon; *N.*, neck of archegonium; *R.*, primary root.) (*Based upon La Motte*, 1937.)

from the zygote stage onward. Irrespective of whether archegonia faced toward or away from the center of the earth, cotyledon and primary root grew at right angles to the force of gravity until they were beginning to emerge from the macrogametophyte. Then the growing tip of the cotyledon began to grow upward and the tip of the primary root began to grow downward (Fig. 143*C–D*).

Bibliography

Andrews, H. N., and Eloise Pannell. **1941.** *Ann. Missouri Bot. Gard.* **29**: 19–29. 4 pl. 2 figs. [Gametophyte, *Lepidocarpon.*]

Arnold, C. A. **1939.** *Contr. Mus. Paleont. Univ. Michigan* **5**: 271–314. 10 pl. 1 fig. [*Protolepidodendron.*]

1947. An introduction to paleobotany. New York. 433 pp. 187 figs.

Barclay, B. D. **1931.** *Bot. Gaz.* **91**: 452–461. 19 figs. [Anatomy, *Selaginella.*]

Belajeff, W. **1885.** *Bot. Zeitg.* **43**: 793–802, 808–819. 1 pl. [Microgametophyte, *Isoetes.*]

Benson, Margaret. **1908.** *Phil. Trans. Roy. Soc. London B* **199**: 409–425. 5 pl. [*Miadesmia.*]

1918. *Ann. Bot.* **32**: 569–589. 2 pl. 4 figs. [Strobili, Sigillariaceae.]

Bower, F. O. **1894.** *Phil. Trans. Roy. Soc. London B* **185**: 473–572. 11 pl. [Sporangia, Lycopodinae.]

1903. *Ann. Bot.* **17**: 278–280. 1 fig. [Sporophylls, *Lycopodium.*]
1908. The origin of a land flora. London. 727 pp. 359 figs.
1935. Primitive land plants. London. 658 pp. 449 figs.
Bruchmann, H. **1898.** Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien. Gotha. 111 pp. 7 pl.
1905. *Flora* **95**: 150–166. 2 pl. [Rhizophore, *Selaginella.*]
1909. *Ibid.* **99**: 12–51. 44 figs. [Macrogametophyte, *Selaginella.*]
1910. *Ibid.* **101**: 220–267. 35 figs. [Gametophyte, *Lycopodium.*]
1912. *Ibid.* **104**: 180–224. 67 figs. [Gametophytes, *Selaginella.*]
1913. *Ibid.* **105**: 337–346. 16 figs. [Suspensor, *Selaginella.*]
1919. *Ibid.* **113**: 168–177. 10 figs. [Apogamy, *Selaginella.*]
Campbell, D. H. **1891.** *Ann. Bot.* **5**: 231–256. 3 pl. [Gametophytes, *Isoetes.*]
1902. *Ibid.* **16**: 419–428. 1 pl. [Gametophytes, *Selaginella.*]
1918. The structure and development of mosses and ferns. 3d ed. New York. 708 pp. 322 figs.
Chamberlain, C. J. **1917.** *Bot. Gaz.* **63**: 51–65. 2 pl. [Gametophyte, *Lycopodium.*]
Chang, C. Y. **1927.** *Ibid.* **83**: 288–306. 18 figs. [Rhizome, *Pteridium.*]
Copeland, E. B. **1902.** *Ann. Bot.* **16**: 327–364. 1 pl. [Stomata, *Lycopodium.*]
Darrah, W. C. **1938.** *Bot. Mus. Leaflets Harvard Univ.* **6**: 118–136. 4 pl. [*Selaginellites.*]
Duerden, H. **1929.** *Ann. Bot.* **43**: 451–457. 4 figs. [Macrosporangia, *Selaginella.*]
Dupler, A. W. **1922.** *Bot. Gaz.* **74**: 331–332. 1 fig. [Sporophyll, *Lycopodium.*]
Duthie, A. V. **1923.** *Trans. Roy. Soc. S. Africa* **11**: 131–144. 20 figs. [Strobili, gametophytes, *Selaginella.*]
1924. *Ibid.* **11**: 275–295. 26 figs. [Strobili, *Selaginella.*]
1929. *Ann. Bot.* **43**: 411–412. [Spore dispersal, *Isoetes.*]
Eames, A. J. **1936.** Morphology of vascular plants. Lower groups. New York. 433 pp. 215 figs.
Farmer, J. B. **1890.** *Ann. Bot.* **5**: 37–62. 2 pl. 1 fig. [Anatomy, *Isoetes.*]
Geiger, H. **1934.** *Flora* **129**: 140–157. 10 figs. [Macrogametophyte, *Selaginella.*]
Goebel, K. **1905.** Organography of plants. Part II. English ed. Translated by I. B. Balfour. Oxford. 707 pp. 417 figs.
1915. *Flora* **108**: 324–326. [Apogamy, *Selaginella.*]
Gordon, W. T. **1910.** *Ann. Bot.* **24**: 821–822. 2 figs. [Macrogametophyte, *Lepidodendron.*]
Haberlandt, G. **1918.** *Beitr. Allgem. Bot.* **1**: 293–300. 1 pl. [Gametophyte, *Lycopodium.*]
Halle, T. G. **1908.** *Ark. Bot.* **7**, No. 6: 1–17. 3 pl. [*Selaginellites.*]
Härtel, K. **1938.** *Beitr. Biol. Pflanzen* **25**: 125–168. 44 figs. [Apical meristem, *Lycopodium.*]
Harvey-Gibson, R. J. **1894.** *Ann. Bot.* **8**: 133–206. 4 pl. [Anatomy, *Selaginella.*]
1896. *Ibid.* **10**: 77–88. 1 pl. [Ligule, *Selaginella.*]
1897. *Ibid.* **11**: 123–155. 1 pl. [Leaf, *Selaginella.*]
1902. *Ibid.* **16**: 449–466. 2 pl. [Root, *Selaginella.*]
Hieronymus, G. **1900.** Selaginellaceae. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. Teil 1. Abt. 4. Pp. 621–715. 21 figs.
Hill, J. B. **1914.** *Bot. Gaz.* **58**: 61–85. 28 figs. [Anatomy, *Lycopodium.*]
1919. *Ibid.* **68**: 226–231. 5 figs. [Anatomy, *Lycopodium.*]
Hill, T. G. **1906.** *Ann. Bot.* **20**: 267–273. 2 pl. [Parichnos, *Isoetes.*]
Hirmer, M. **1927.** Handbuch der Paläobotanik. Bd. 1. Berlin. 708 pp. 817 figs.
1933. *Palaeontographica* **78**, Abt. B: 47–56. 15 figs. [*Pleuromia.*]
1938. Geographie und zeitliche Verbreitung der fossilen Pteridophyten. In F. Verdoorn, Manual of pteridology. The Hague. Pp. 474–495.
Holloway, J. E. **1910.** *Trans. New Zealand Inst.* **42**: 356–370. 4 pl. 8 figs. [Anatomy, *Lycopodium.*]

1916. *Ibid.* **48**: 253–303. 2 pl. 102 figs. [Vegetative multiplication, *Lycopodium.*]
1917. *Ibid.* **49**: 80–93. 2 pl. 24 figs. [Vegetative multiplication, *Lycopodium.*]
1920. *Ibid.* **52**: 193–239. 5 pl. 75 figs. [Gametophyte, *Lycopodium.*]
Hoskins, J. H., and A. T. Cross. **1941.** *Amer. Midland Nat.* **25**: 523–547. 16 figs. [*Lepidocarpon.*]
Jeffrey, E. C. **1902.** *Phil. Trans. Roy. Soc. London B* **195**: 119–146. 6 pl. [Anatomy, pteridophytes.]
1917. The anatomy of woody plants. Chicago. 478 pp. 306 figs.
Jones, C. E. **1905.** *Trans. Linn. Soc. Bot. London* 2 ser. **7**: 15–35. 3 pl. [Anatomy, *Lycopodium.*]
Kidston, R. **1897.** *Trans. Roy. Soc. Edinburgh* **39**: 33–62. 3 pl. 2 figs. [Strobili, Sigillariaceae.]
Kräusel, R., and H. Weyland. **1929.** *Abhandl. Senckenbergischen Naturf. Ges. Frankfurt a/M.* **41**: 317–359. 15 pl. 34 figs. [*Protolepidodendron.*]
1932. *Senckenbergiana* **14**: 391–403. 18 figs. [*Protolepidodendron.*]
La Motte, C. **1933.** *Amer. Jour. Bot.* **20**: 217–233. 17 figs. [Macrogametophyte, *Isoetes.*]
1937. *Ann. Bot.* N.S. **1**: 695–716. 1 pl. 20 figs. [Embryo, *Isoetes.*]
Lang, W. H., **1899.** *Ann. Bot.* **13**: 279–317. 2 pl. [Gametophyte, *Lycopodium.*]
1915. *Mem. and Proc. Manchester Lit. Phil. Soc.* **59**: No. 3: 1–28, 6 figs. [Anatomy, *Isoetes.*]
1915A. *Ibid.* **59,** No. 8: 29–59. 4 pl. 1 fig. [Anatomy, *Lycopodium.*]
Lang, W. H. and Isabel C. Cookson. **1935.** *Phil. Trans. Roy. Soc. London B* **224**: 421–449. 4 pl. [Silurian pteridophytes.]
Liebig, Johanna. **1931.** *Flora* **125**: 321–358. 3 pl. 18 figs. [Microgametophyte, *Isoetes.*]
Lindsey, Marjorie. **1915.** *Ann. Bot.* **29**: 223–230. 1 pl. 3 figs. [*Bothrodendron.*]
Lyon, Florence M. **1901.** *Bot. Gaz.* **32**: 124–141, 170–194. 5 pl. [Gametophytes, *Selaginella.*]
1904. *Ibid.* **37**: 280–293. 16 figs. [Sex organs, pteridophytes.]
Ma, Roberta M. **1931.** *Bull. Torrey Bot. Club* **57**: 277–284. 1 pl. [Chloroplasts, *Selaginella.*]
McLean, R. C. **1912.** *New Phytol.* **11**: 305–318. 2 pl. 2 figs. [Macrogametophyte, *Bothrodendron.*]
Mägdefrau, K. **1931.** *Beih. Bot. Centralbl.* **48**: 119–140. 5 pl. 9 figs. [*Pleuromia.*]
Mitchell, Gertrude. **1910.** *Ann. Bot.* **24**: 19–33. 2 pl. [Strobilus, *Selaginella.*]
Osborn, T. G. B. **1922.** *Ibid.* **36**: 41–54. 15 figs. [Root, *Isoetes.*]
Pfeiffer, Norma E. **1922.** *Ann. Missouri Bot. Gard.* **9**: 79–232. 8 pl. [Isoetaceae.]
Pritzel, E. **1900.** Lycopodiales. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. Teil 1. Abt. 4. Pp 563–606. 27 figs.
Saxelby, E. Mary. **1908.** *Ann. Bot.* **22**: 21–33. 1 pl. [Root, *Lycopodium.*]
Schopf, J. M. **1941.** *Amer. Midland Nat.* **25**: 548–563. [Lepidocarpaceae.]
1941A. *Illinois Geol. Surv., Rept. of Investigations* **75**: 1–40. 6 pl. 5 figs. [*Mazocarpon.*]
Scott, D. H. **1901.** *Phil. Trans. Roy. Soc. London B* **194**: 291–333. 6 pl. [*Lepidocarpon.*]
1920. Studies in fossil botany. 3d ed. Vol. 1. London. 434 pp. 190 figs.
Scott, D. H., and T. G. Hill. **1900.** *Ann. Bot.* **14**: 413–454. 2 pl. 2 figs. [Anatomy, *Isoetes.*]
Seward, A. C. **1910.** Fossil plants. Vol. 2. Cambridge. 624 pp. 265 figs.
1913. *New Phytol.* **12**: 85–89. 1 pl. [*Selaginellites.*]
Slagg, R. A. **1932.** *Amer. Jour. Bot.* **19**: 106–127. 4 pl. 15 figs. [Microgametophyte, *Selaginella.*]
Smith, G. M. Cryptogamic botany. Vol. 2. New York. 380 pp. 224 figs.
Smith, R. W. **1900.** *Bot. Gaz.* **29**: 225–258, 323–346. 8 pl. [Sporangia, *Isoetes.*]

1920. *Ibid.* **69:** 426–437. 21 figs. [Bulbils, *Lycopodium.*]
Spessard, E. A. **1922.** *Ibid.* **74:** 392–413. 3 pl. [Gametophyte, *Lycopodium.*]
1928. *Ibid.* **85:** 323–333. 2 pl. 9 figs. [Young sporophyte, *Lycopodium.*]
Steel, Jessie K. **1923.** *Proc. Linn. Soc. New South Wales* **48:** 287–300. 19 figs. [Anatomy, *Selaginella.*]
Stokey, Alma G. **1907.** *Bot. Gaz.* **44:** 57–63. 2 pl. 1 fig. [Root, *Lycopodium.*]
1909. *Ibid.* **47:** 311–335. 3 pl. [Anatomy, *Isoetes.*]
Sykes, M. G. **1908.** *New Phytol.* **7:** 41–60. 2 pl. 8 figs. [Sporangia, *Lycopodium.*]
Sykes, M. G., and W. Stiles. **1910.** *Ann. Bot.* **24:** 523–536. 1 pl. [Strobilus, *Selaginella.*]
Treub, M. **1888.** *Ann. Jard. Bot. Buitenzorg.* **7:** 141–150. 4 pl. [Gametophyte, *Lycopodium.*]
1890. *Ibid.* **8:** 1–37. 12 pl. [Embryo, *Lycopodium.*]
Turner, J. J. **1924.** *Bot. Gaz.* **78:** 215–225. 7 figs. [Anatomy, *Lycopodium.*]
Uphof, J. C. T. **1920.** *Ann. Bot.* **34:** 493–517. 13 figs. [Rhizophore, *Selaginella.*]
Walton, J. **1940.** Introduction to the study of fossil plants. London. 188 pp. 139 figs.
Wardlaw, C. W. **1924.** *Trans. Roy. Soc. Edinburgh* **53:** 503–532. 18 figs. [Size and internal morphology.]
1925. *Ibid.* **54:** 281–308. 17 figs. [Anatomy, *Selaginella.*]
Watson, D. M. S. **1908.** *Mem. and Proc. Manchester Lit. Phil. Soc.* **52,** No. 3: 5–16. 1 pl. 2 figs. [Strobilus, *Bothrodendron.*]
Weiss, F. E. **1907.** *Ibid.* **51,** No. 8: 1–22. 1 pl. 8 figs. [Parichnos.]
West, C., and H. Takeda. **1915.** *Trans. Linn. Soc. Bot. London.* 2 ser. **8:** 333–376. 8 pl. 20 figs. [Anatomy, *Isoetes.*]
Wettstein, R. von. **1935.** Handbuch der systematischen Botanik. 4th ed. 1152 pp. 709 figs.
Wigglesworth, Grace. **1907.** *Ann. Bot.* **21:** 211–234. 1 pl. 4 figs. [Young sporophyte, *Lycopodium.*]
Williamson, W. C. **1889.** *Phil. Trans. Roy. Soc. London B* **180:** 195–214. 4 pl. [Lepidodendrales.]
Wordsell, W. C. **1910.** *New Phytol.* **9:** 242–253. 2 figs. [Rhizophore, *Selaginella.*]
Zimmermann, W. **1930.** Die Phylogenie der Pflanzen. Jena. 452 pp. 250 figs.

CHAPTER 9

CALAMOPHYTA

Members of the division Calamophyta, which include the horsetails and allied forms, have a sporophyte differentiated into stem, leaves, and roots. Foliage leaves are generally borne in transverse whorls upon stems or branches with a protostelic or siphonostelic vascular cylinder. The sporangia are borne upon a distinctive appendage, the sporangiophore, borne in numbers at the terminus of the stem.

The Calamophyta differ from other pteridophytes in a number of respects. Irrespective of whether the leaves are scale-like or expanded, they are never arranged alternately. Usually there is a whorl of leaves at each node. Correlated with this is a longitudinal ribbing of the stem surface and one in which there are parallel ribs extending the length of each internode. In most cases the ribs of an internode alternate with those of abutting internodes. Ribbing of the stem surface is so characteristic a feature that one is justified in assigning to the Calamophyta fossil plants known only from casts or impressions of their stems.

The arrangement of appendages borne by the stem is also distinctive. In the filicinean and lycopodian series, branches always arise axillary to leaves; in the Calamophyta, leaves and branches alternate with each other at the nodes.

The fertile portion of the sporophyte also differs from that of other Pteridophytes. The appendages bearing sporangia are usually called **sporangiophores,** and this term is especially suitable since there is considerable evidence showing that these structures are not sporophylls. The sporangiophores are always borne on the terminal portion of certain branches. This portion of a branch is usually called a **strobilus.** but the application of this term to fertile portions of sporophytes is inappropriate if sporangiophores are something other than sporophylls. There are several types of sporangiophore among the Calamophyta. In the primitive forms referred to the Hyeniales the sporangiophore is cylindrical, once or twice dichotomously forked, and with the ultimate dichotomies recurved and each terminating in a single sporangium (Fig. 146*C*). Such a structure is, perhaps, but little different from a sporophyll. Among the Sphenophyl-

lales the sporangium-bearing appendages consist of two portions, a branched fertile portion resembling the sporangiophore of Hyeniales, and a simple or forked leaf-like sterile portion. The fertile portion always lies on the adaxial face of the sterile portion and is more or less united with it (Fig. 150). For this reason the whole appendage might be considered a sporophyll with adaxial sporangia. However, the vascular supply to the fertile portion is more or less distinct from that to the sterile portion. On this account the fertile portion is usually referred to as the sporangiophore and the sterile portion as the bract. Among the Equisetales the sporangiophores are generally associated with bracts. In some cases, as *Palaeostachys* (Fig. 153*A*), the sporangiophores seem to be axillary to bracts, but the vascular supplies to bract and sporangiophore are independent of each other. More frequently bracts and sporangiophores are in separate whorls. The whorls of sporangiophores and bracts may alternate with each other, as in *Calamostachys* (Fig. 153*B*); or there may be two or more whorls of sporangiophores between two successive whorls of bracts. Some genera have many whorls of sporangiophores before there is a whorl of bracts. *Equisetum*, with a single whorl of rudimentary bracts (the annulus) below the sporangiophores, is an extreme example of this type.

There are two types of foliage leaf among the Calamophyta. The Sphenophyllales have flattened, entire or incised, wedge-shaped leaves with a dichotomously branched venation (Fig. 147*B–D*). There is good ground for interpreting these leaves as macrophyllous and as having arisen by lateral fusion of members of a psilophyte branch system. The Equisetales have microphyllous leaves if a microphyllous leaf is defined as one with a single unbranched axial vein. The leaf of Equisetales may have been evolved in the same way that the microphyllous leaf of lycopods is thought to have arisen (see page 137). On the other hand, it is equally possible that they originated in an entirely different manner and by reduction from a macrophyllous type.

The primary vascular tissue of a stem may be protostelic, but more frequently it is siphonostelic. Siphonic steles of Calamophyta have the internodal portions of the vascular cylinder dissected by parallel perforations extending vertically through the entire internode. Dissection of the vascular cylinder in lycopodian siphonosteles is due to branch gaps only. It has been held[1] that perforations of equisetaceous siphonosteles are of a similar nature. The correctness of the interpretation of equisetaceous perforations as appendicular gaps is open to question. Typical appendicular gaps, whether a branch gap or a leaf gap, always abut directly on the trace which underlies them (Fig. 91*A*, page 145). In Calamophyta there is always nodal wood intervening between the departing trace

[1] Jeffrey, 1899.

(either leaf or branch) and the lacuna above. Thus, perforations in vascular cylinders of Calamophyta are not strictly comparable to the perforations in cylinders of other pteridophytes. Furthermore, branch traces of Calamophyta do not have a constant orientation with respect to the perforations above them. In some cases, as *Equisetum* (Fig. 144*A*), the perforations in the internode above lie directly above the traces. In other cases, as *Archaeocalamites* (Fig. 144*B*), the perforations in the internode above lie between the traces. In view of the foregoing, it is better to consider the perforations of the vascular cylinder of Calamophyta as something other than branch gaps.

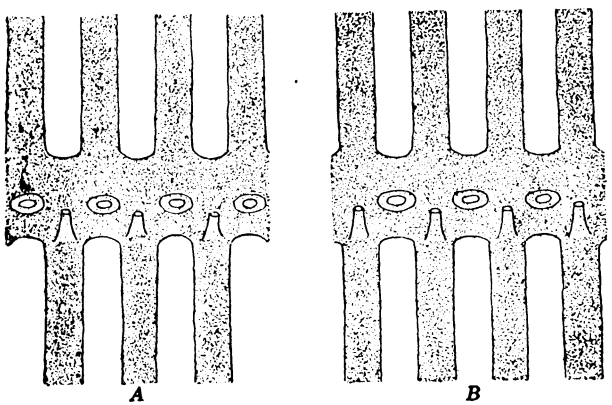

FIG. 144. Diagrams of vascular anatomy of nodes of Calamophyta. *A*, *Equisetum*. *B*, *Archaeocalamites*. (*Diagrams based upon Jeffrey*, 1917.)

Genera definitely ascribable to the Calamophyta are known from as far back as the Lower Devonian (Fig. 145). Evolution within the division was quite rapid, and in the Carboniferous there was a variety of species, including some that were arborescent and grew to a height of 25 meters. At this time the horsetails were a conspicuous element in the vegetation of the earth. The equisetaceous flora that was so abundant during the Carboniferous became almost extinct during the unfavorable climate of the Permian. The only family known from as far back as the Carboniferous that did not become extinct is the Equisetaceae. This family attained its maximum diversity in the Lower Mesozoic and one genus (*Equisteum*) is found in the flora of today.

There is a widespread belief that the Calamophyta were evolved from the Psilophytales, but no attempts have been made to visualize the manner in which psilophytes evolved the whorled arrangement of appendages characteristic of Calamophyta. In the Hyeniales, the oldest known and most primitive order of the Calamophyta, the whorled arrangement of appendages is not so pronounced as in more advanced orders of the divi-

sion. The manner in which a fertile branched portion of a psilophyte gave rise to the type of sporangiophore found in Hyeniales has been suggested on page 139. Evolution from the primitive type found in Hyeniales was in two directions. The Sphenophyllales, typified by *Sphenophyllum*, constitute one line. In this evolutionary line the stem was protostelic, with macrophyllous leaves and with a dichotomous venation. The

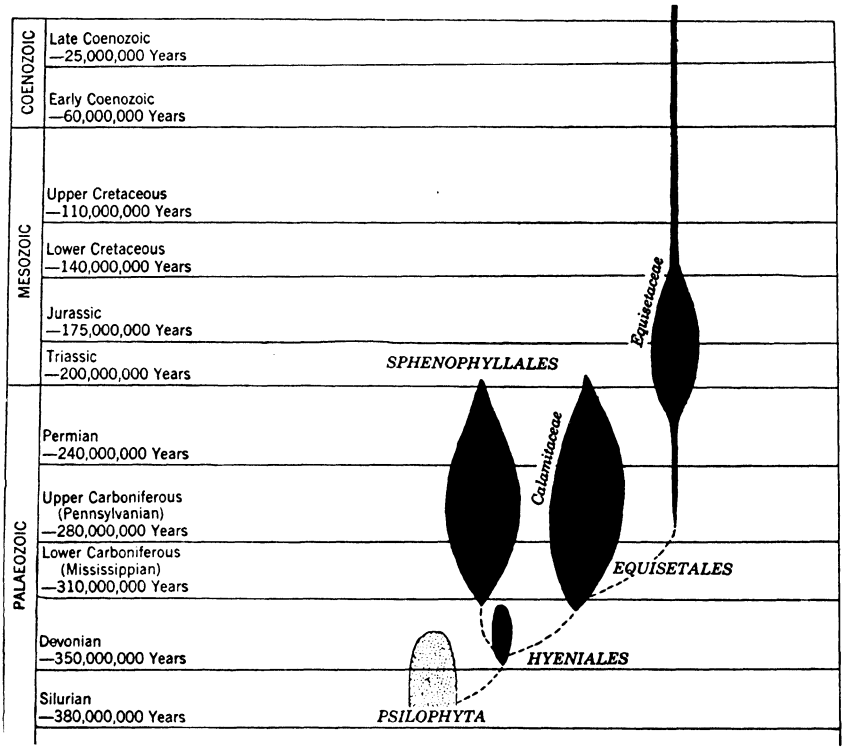

FIG. 145. Diagram showing the geological range and suggested interrelationships among the Calamophyta.

Equisetales, the other evolutionary line, have siphonostelic stems and have leaves with a single unbranched vein.

There is but one class, the Equisetinae. The members of this class are divided into three orders on pages to follow. Some botanists[1] think that the Equisetaceae and Calamitaceae differ sufficiently from each other to be placed in separate orders. It has also been held[2] that *Pseudobornia* differs so markedly from other Equisetinae that it should be placed in a separate order.

[1] Arnold, 1947. [2] Arnold, 1947; Hirmer, 1927.

ORDER 1. HYENIALES

Sporophytes of the Hyeniales had a jointed stem, but one in which the whorled arrangement of leaves was not conspicuous. The leaves were elongate, narrow, and once or twice forked at the apex. The sporangiophores were cylindrical, were once or twice dichotomously branched, and had the apex of each branch recurved and terminating in a single sporangium. The sporangiophores were borne in lax strobili without sterile appendages. Hyeniales are known only in the fossil condition and from the Devonian.

The Hyeniales include two genera, *Hyenia* and *Calamophyton*, both known only from the Middle Devonian. These two genera are of particular interest in that they have certain features more like those of Psilophyta than those of Equisetinae.

The known fossil remains of these plants are chiefly aerial shoots, but one species of *Hyenia* has been found with a stout rhizome.[1] The height which aerial shoots of *Calamophyton* attained is unknown, but branch systems 20 cm. long have been found. The branching of *Calamophyton* is atypical for Equisetinae in that it is dichotomous (Fig. 146*A*). Small branches of this genus have the articulation characteristic of Equisetinae; large branches have a somewhat obscure articulation. Specimens of *Calamophyton* are sufficiently well preserved to show that the stem was siphonostelic and had a triangular mass of primary xylem surrounding a triangular pith. The xylem consisted largely of scalariform tracheids. It is thought that there was secondary thickening in older parts of the stem, but this is not definitely established.

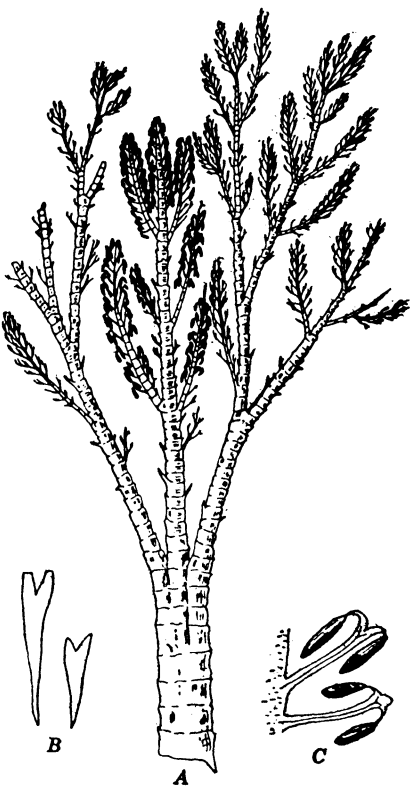

FIG. 146. *Calamophyton primaevum* Kräusel and Weyland. *A*, reconstruction of aerial shoot. *B*, foliage leaves. *C*, sporangiophores. (*After Kräusel and Weyland*, 1926.)

[1] Kräusel and Weyland, 1932.

The leaves of *Calamophyton* were restricted to the branchlets and were borne in whorls as is typical of Equisetinae. The leaves were 8 to 10 mm. long, narrowly cuneate, and once- or twice-forked at the expanded distal end (Fig. 146*B*). Lower down on the shoot the leaves were replaced by spiny outgrowths which are interpreted as persistent leaf bases.

Fertile branches of *Calamophyton* were about the same length as those bearing leaves but were much stouter. Fertile branches were lax strobili which bore sporangiophores only, never sterile appendages of a bract-like nature. As is the case with the leaves, the sporangiophores were borne in whorls. Each sporangiophore was about 10 mm. long and consisted of a cylindrical stipe that was bifurcate at the distal end.[1] The bifurcations were reflexed and each terminated in a narrowly ovoid sporangium some 2 to 3 mm. long (Fig. 146*C*).

ORDER 2. SPHENOPHYLLALES

Sporophytes of the Sphenophyllales had stems with longitudinally ridged internodes and whorls of leaves at the nodes. The leaves were sessile, wedge-shaped, entire or dichotomously divided, and with a dichotomously branched venation. The primary vascular cylinder of a stem was an actinostele and the primary xylem was triarch or hexarch. There was a formation of secondary vascular tissues. The fertile portion of a sporophyte was a strobilus with densely crowded whorls of appendages, each differentiated into a sporangiophoric and a bract-like portion. Sporophytes were homosporous or primitively heterosporous. Members of the order are known only in a fossil condition and from the Upper Devonian to the Triassic.

Sphenophyllum is the only member of the order in which there is adequate knowledge of both the vegetative and fertile portions of the sporophyte. This genus appeared in the Upper Devonian, flourished throughout the Carboniferous, and became extinct in the Triassic. The aerial shoots had a slender, irregularly branched, central axis less than 1 cm. in diameter. The small diameter in proportion to the great length indicates that the plants were partially supported by adjoining plants, if not actually vine-like in habit. The stem had the longitudinally ribbed internodes typical of Calamophyta; but, unlike most of the Equisetales, ribs of successive internodes did not alternate with one another. The number of leaves at each node was some multiple of three. The number was most frequently 6 but it was sometimes as high as 18. Leaves at one node were directly above and not alternate with those of adjoining nodes. Leaves of certain species were entire; those of other species were dichotomously divided into several lobes (Fig. 147*B–D*). Some species had both types of leaf on the same shoot. Certain of these heterophyllous species had en-

[1] Kräusel and Weyland, 1926.

tire leaves in the upper part of the shoot and dissected leaves in the lower part. At one time this was thought to be similar to the heterophylly in certain aquatic species of *Ranunculus*, and the inference was drawn that *Sphenophyllum* was an aquatic plant in which only the lower part of the shoot was submerged. The finding of shoots with dissected leaves above entire leaves (Fig. 147*A*) shows the incorrectness of this inference. Taken as a whole, the leaf surface was greater than the stem surface. This indicates that the leaves were the chief photosynthetic organs of the plant.

The internal organization of the shoot was unique, and students seeing a cross section of a stem for the first time often think that it is a cross

FIG. 147. *A*, reconstruction of shoot of *Sphenophyllum cuneifolium* Sternb. *B–D*, leaves of *Sphenophyllum*. *B*, *S. emarginatum* Bgt. *C*, *S. majus* Bronn. *D*, *S. cuneifolium* Sternb. (*B–D*, *after Zeiller in Arnold.* 1947.)

section of a root. At the center of the stem was a triangular mass of primary xylem (Fig. 148). This was an actinostele and had the exarch protoxylem restricted to the angles of the actinostele. Most species had but one protoxylem mass at each angle, but some had two protoxylem masses. Stems of the latter type were hexarch even though the actinostele was triangular in outline. Little is known concerning the organization of the primary phloem. The cortex external to the stele was relatively narrow and consisted of thick-walled elements at the exterior and thin-walled elements toward the interior.[1]

Stems of all species of *Sphenophyllum* were thickened secondarily by means of a cambium. The cambium arose just outside the primary xylem and completely encircled it. The secondary xylem was dimorphic in the sense that elements radial to the protoxylem were smaller in diameter

[1] Williamson and Scott, 1894.

than those radial to the metaxylem. There were two elements in the secondary wood; pitted tracheids and parenchyma. The tracheids were laid down in radial rows and had their pits largely restricted to the radial walls. The xylem parenchyma was composed of elongate cells whose long axes were parallel to the long axes of the tracheids. The parenchyma is usually evident only in the angles between the tracheids. The parenchymatous portion of the secondary xylem is interpreted as a series of wood rays[1] and not as a wood parenchyma. The cambium also formed

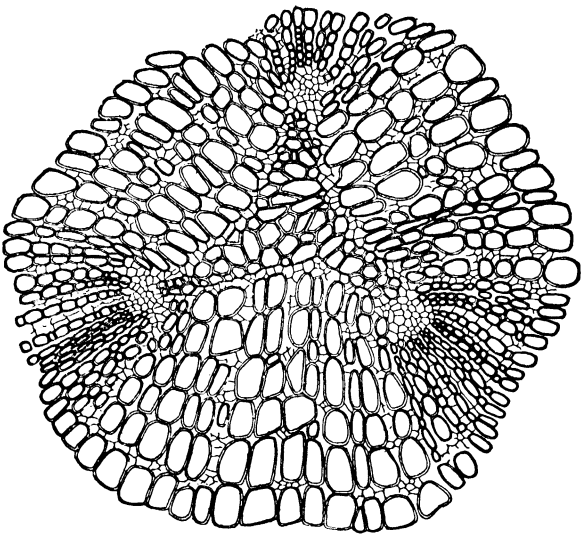

FIG. 148. *Sphenophyllum plurifoliatum* Williamson. Transverse section of xylem cylinder of stem. (× 40.)

secondary phloem at its outer face. This was composed of radially arranged, thin-walled elements. Sooner or later after cambial activity began, there was a development of a periderm in the inner portion of the cortex. The regular radial arrangement of cells in the periderm suggests that it was formed by a cambial layer similar to the cork cambium of seed plants. Ultimately there was a sloughing off of all cortical tissues external to the periderm. As is the case with many seed plants, the cork cambium became inactive after a time, and a new cork cambium was developed from tissues internal to the original cork cambium. Because of this the bark at the outside of a stem sometimes consisted of two or more concentric layers of periderm.

Roots were adventitious and borne along the internodes. They increased in diameter by cambial activity. The primary xylem was usually

[1] Jeffrey, 1917.

diarch, but sometimes it was triarch (Fig. 149). Unlike the stem, secondary elements radial to the protoxylem were not smaller than the others. The root also had a well-developed periderm formed by a cork cambium which seems to have arisen in the pericycle. The root was unusual in that the relatively narrow cortex persisted after the periderm was well developed.

There is considerable diversity in structure of strobili associated with plant bodies of the *Sphenophyllum* type. In the case of *S. dawsoni* Williamson the strobilus was over 1 cm. in diameter and several centimeters in length. Its central axis was 2 to 3 mm. in diameter and bore

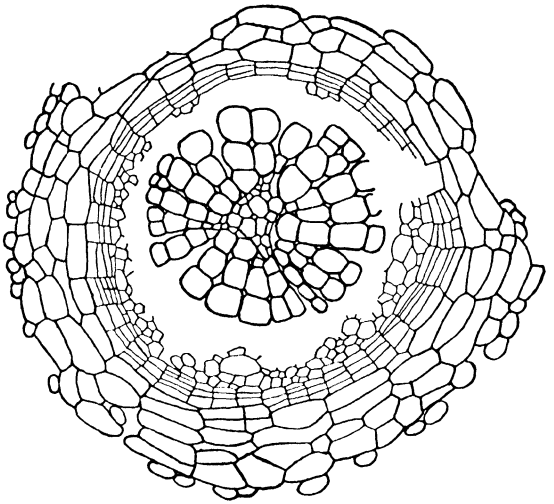

FIG. 149. *Sphenophyllum* sp. Transverse section of root.

numerous whorls of bracts at equidistant intervals. The 14 to 20 bracts of each whorl were free from one another at their apices and laterally united at their bases (Fig. 150). These cup-like whorls of bracts were so nested one above the other that the apical portion of one whorl ensheathed the basal portions of the next two or three whorls above (Fig. 150*A*). Although not definitely known, it is thought that bracts of successive whorls were superimposed, not alternate. Axillary to each bract was a single three-pronged sporangiophore that was partially united with the bract. The sporangiophores were of two sorts, those with two long distal prongs and one short median one, and those with one long distal prong and two short median ones (Fig. 150*B*). These alternated with one another in each whorl. Each prong of a sporangiophore, whether long or short, was reflexed and terminated in a single sporangium. The general

appearance of prong and sporangium is similar to that of an anatropous ovule. *Sphenophyllum* was usually homosporous, but strobili have been found[1] in which there is a 20 per cent difference in size of spores in adjacent sporangia. This is considered an incipient type of heterospory.

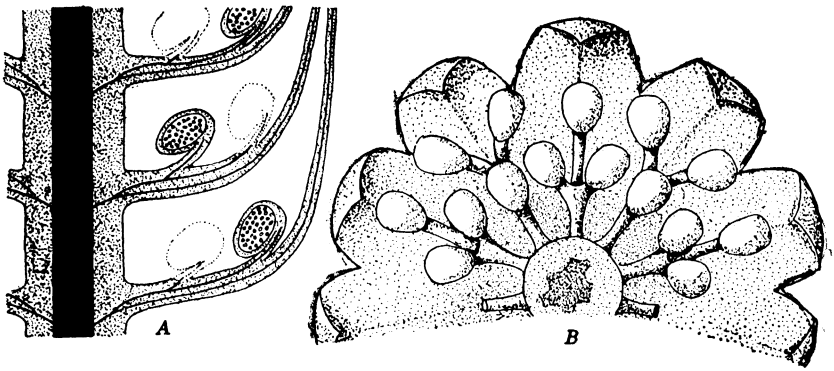

FIG. 150. *Sphenophyllum dawsoni* Williamson. Diagrams of strobilus in vertical and transverse section. (*Based upon Hirmer*, 1927.)

ORDER 3. EQUISETALES

Sporophytes of Equisetales have a branched stem in which the branches are generally borne in transverse whorls. Internodes of stem and branches are longitudinally ribbed and generally with ribs of successive internodes alternating with one another. Each node of stem and branches bears a whorl of leaves that are usually small and scale-like. The vascular cylinder is an endarch siphonostele, entire at the nodes and longitudinally perforate through the internodes. Some genera have a secondary thickening of the vascular cylinder; other genera lack it. Fertile portions of a sporophyte are strobili with transverse whorls of sporangiophores that are usually shield-shaped at the distal end. Strobili of some genera have whorls of bracts distinct for the sporangiophores. Sporophytes may be homosporous or heterosporous.

The Equisetales appeared in the Upper Devonian and reached their greatest diversity in the Upper Carboniferous. Most of them disappeared during the Permian but one genus, *Equisetum*, has persisted until today. There are three families, the two most important of which are discussed on pages to follow.

FAMILY 1. CALAMITACEAE

The Calamitaceae had a tree-like sporophyte in which there was considerable secondary thickening of stem and branches. The strobili had alternate whorls of sporangiophores and sterile bracts.

[1] Scott, 1920.

The Calamitaceae appeared in the Upper Devonian, were most abundant during the Carboniferous, and became extinct early in the Triassic. These giant horsetails, together with the giant lycopods, were the dominant element in the flora of the Carboniferous and remains of them are almost always present in deposits containing Carboniferous plants. As is the case with other groups of fossil plants, certain species are known only from their stems, others only from their twigs, and still others only from their roots, rhizomes, or strobili. In a few cases all parts of a single species are known. Thus, the leafy twigs known as *Annularia radiata* Brongniart and the fructification known as *Calamostachys ramosa* Weiss have been shown[1] to belong to the stem known as *Calamites ramosus* Artis.

Casts of the central cavity of the trunk of Calamitaceae have been found which are 3 to 8 meters in length and up to 30 cm. in breadth. From this it has been estimated that the plant was a tree 20 to 30 meters tall. *Calamites* (Fig. 151) is one of the members of the family which was arborescent. In spite of its tree-like proportions, it had a horizontal underground rhizome with aerial branches, just as does the present-day *Equisetum*. Fossil specimens of rhizomes are differentiated into nodes and internodes, and have a whorl of adventitious roots at

[1] Scott, 1920.

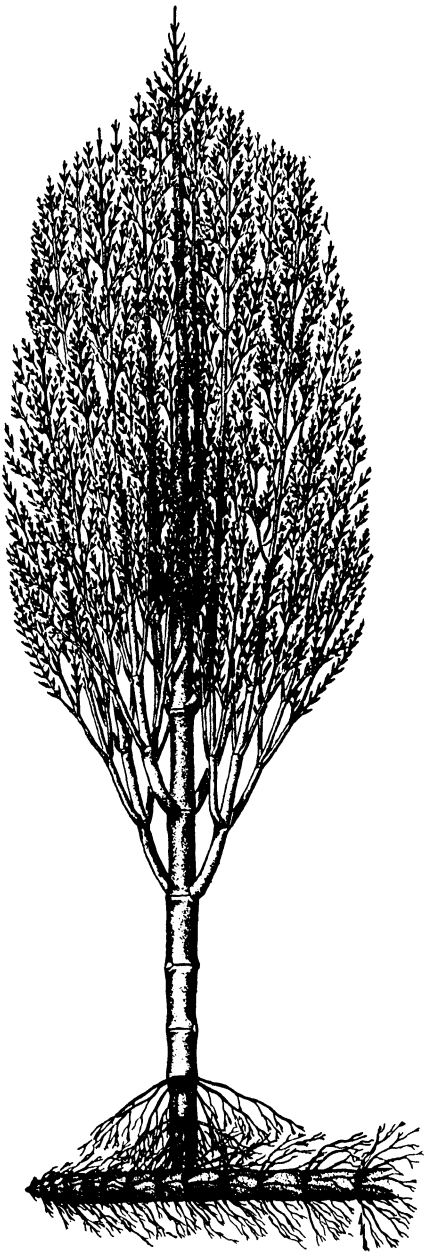

FIG. 151. Reconstruction of *Calamites* sp. (*After Hirmer*, 1927.)

each node. Their considerable size shows that they formed secondary wood. Specimens have been found with erect branches arising from the upper side of the rhizome. The fact that several of the lowermost nodes in the erect branches have whorls of adventitious roots shows that the rhizome grew at some distance below the surface of the soil. Erect branches were generally constricted where they adjoined the rhizome, a condition probably due to lessened cambial activity in this region. The arborescent aboveground portion of the erect shoots has a conspicuous central axis bearing whorls of lateral branches. In some species the lateral branches persisted for a long time and became nearly as thick as the central axis. Such plants looked like an *Equisetum* of tree-like proportions. Other species shed their lateral branches after a time. Such plants, which had a naked central axis bearing a tuft of branches at the apex, looked somewhat like palms. The surface of a *Calamites* stem had the same longitudinally ribbed internodes as that of the present-day *Equisetum*, but the ribs of successive internodes were sometimes above, instead of alternate with, one another.

The stem of *Calamites* was internally differentiated into epidermis, cortex, and stele. The structure of the cortex is seen to best advantage in the fossil forms of young twigs. Here it has been shown that fossil twigs have a cortex with an inner region of thin-walled parenchyma and an outer region of thick-walled cells. Sometimes the latter are in longitudinal strands as in *Equisetum*.[1] The cortex differs from that of *Equisetum* in that there are no vertical cavities (vallecular canals) in the internodes.

The stele of *Calamites* was siphonostelic. The pith internal to the vascular cylinder was solid at the nodes and hollow at the internodes. Young twigs had parallel strands of vascular tissue extending the whole length of the internodes. The protoxylem was toward the inner face of the bundle, and it matured in centrifugal succession. The metaxylem external to the protoxylem was composed of scalariform tracheids. The protoxylem elements (both annular and spiral tracheids) disintegrated immediately after they matured, leaving, precisely as in *Equisetum*, a vertical cavity (**carinal canal**) at the inner face of each metaxylem mass. The stelar organization thus far described is almost identical with that of *Equisetum*. Fossil stems of *Calamites* differ markedly from those of *Equisetum* in that they have a cambium. Secondary xylem formed toward the inner face of the cambium was composed of radial rows of tracheids (Fig. 152*A*). The first-formed secondary tracheids were scalariform; later-formed ones were generally pitted and had the pits restricted to the radial walls. The cylinder of secondary wood attained a thickness of 6 cm. or more, but did not have a differentiation of annual rings. This shows that the plant retained its foliage throughout the year and that climatic conditions were

[1] Scott, 1920

approximately uniform throughout the year. Secondary thickening was accompanied by the formation of a periderm in the outer portion of the cortex. The periderm often became a bark several centimeters in thickness.

The roots of *Calamites*, to which the generic name *Astromeylon* was originally applied, differed in structure according to their size. Small rootlets had di-, tri-, or tetrarch actinosteles[1] with the protoxylem exarch and with the typical alternation of masses of phloem with the protoxylem points. Such roots had a cambium, but it formed only a limited amount of secondary xylem. As in *Equisetum*, the endodermis seems to have been a double layer. External to the endodermis was a thin-walled paren-

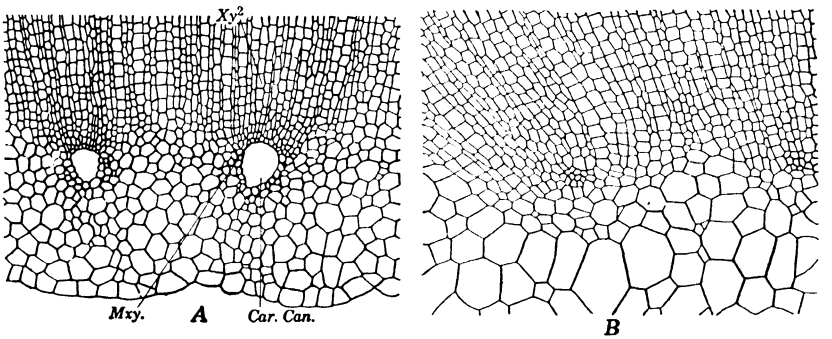

FIG. 152. *Calamites* sp. *A*, transverse section of a portion of a stem. *B*, transverse section of a portion of a root. (*Car. Can*, carinal canal; *Mxy.*, metaxylem; $Xy.^2$, secondary xylem.) (*A*, × 10; *B*, × 30.)

chyma with conspicuous intercellular spaces, and at the outside of the cortex was a zone of thick-walled cells similar in appearance to the exodermis in roots of many angiosperms. Larger roots had a polyarch actinostele, in which the center was either solidly filled with parenchyma or was hollow. The primary xylem superficially resembled that of a stem but differed in that it was exarch and did not have a disintegration of the protoxylem to form carinal canals. Roots of this type produced a considerable amount of radially arranged secondary xylem (Fig. 152*B*). Polyarch roots had a periderm, and the cork cambium producing it probably arose in the outer portion of the cortex.

Each node of a *Calamites* stem had a single whorl of leaves. In some species the leaves of a whorl were free from one another; in other species the leaves were laterally united along their lower margins. Although the leaves were generally of small size, their structure shows that they were photosynthetic organs. In one type of fossil leaf found in association with a *Calamites*-like stem, the internal structure resembles that of a pine

[1] Williamson and Scott, 1894.

leaf. This leaf has a single axial vascular bundle surrounded by a sheath. External to this is a radiate palisade tissue with conspicuous intercellular spaces. The palisade layer is surrounded by an epidermis, one cell in thickness, in which there are numerous stomata.

Several types of strobili have been found on the fossil calamitean type of plant body. Although decidedly different in organization, they are all alike in having had transverse whorls of sporangiophores and transverse

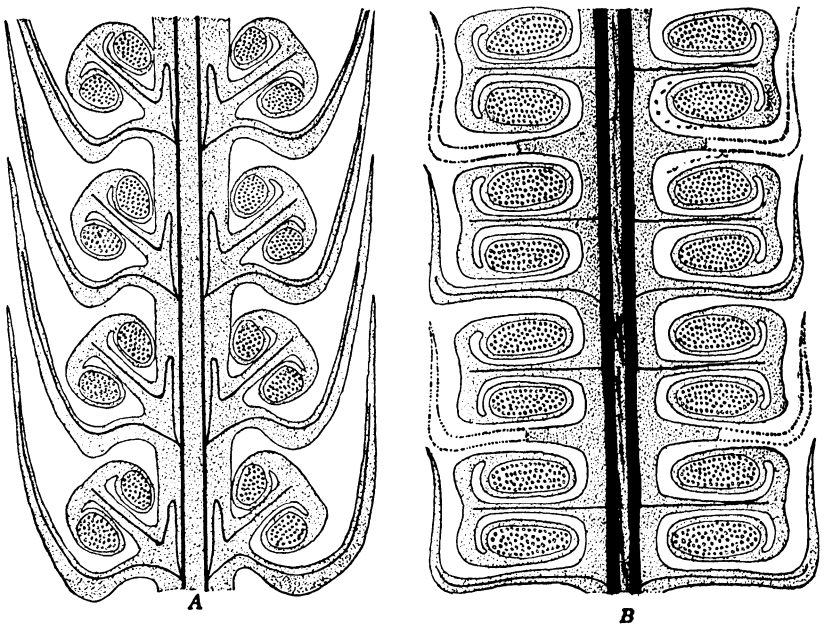

FIG. 153. Diagrams of vertical sections of strobili of Calamitaceae. *A*, *Palaeostachys*. *B*, *Calamostachys*. (*Based upon Scott*, 1920.)

whorls of bracts. In the case of the fructification genus known as *Calamostachys* the sporangiophores had cruciately branched apices with the tip of each branch recurved toward the sporangiophore base and each bearing a single sporangium.[1] The whorls of bracts and sporangiophores were alternate with and equidistant from one another on the central axis (Fig. 153*B*). Other types of strobili had several equidistant whorls of sporangiophores between two successive whorls of bracts. In still other cases, as *Palaeostachys* (Fig. 153*A*), the sporangiophores were axillary to the bracts. However, the sporangiophores were not true appendages of the bracts because the two had entirely independent vascular supplies.

[1] Lacey, 1943.

Some fossil calamitean fructifications are homosporous; others are heterosporous and have macrospores triple the diameter of microspores.[1] Generic distinctions are not based solely on this character and in certain cases, as in *Calamostachys*, the same genus may have both homosporous and heterosporous species. There is also variation in the manner in which the two types of sporangia were borne. In some fossil sporangia, as *Calamostachys binneyana* Carruthers, three sporangia of a sporangiophore are macrosporangia and one a microsporangium. In other cases, as *C. casheana* Williamson, all sporangiophores in a whorl bear macrosporangia, all bear microsporangia, or both kinds may be present in the same whorl. Macro- and microsporangia of *Calamostachys* were identical in size. The smaller number of spores in macrosporangia resulted from abortion of certain of the young spores shortly after or during the tetrad stage in spore development.[1]

FAMILY 2. EQUISETACEAE

The Equisetaceae differ from the Calamitaceae in the absence of secondary tissues in the stem, and in the lack of distinct whorls of bracts in the strobili.

Equisetites, the oldest known member of the family, has been found as far back as early in the Upper Carboniferous. It was herbaceous and quite like the *Equisetum* of today. The Equisetaceae are thought to have evolved by reduction from a calamitean type, but there is the possibility that they originated in the ancestral stock leading to the Calamitaceae. The Equisetaceae reached their greatest diversity in the Triassic. By the time of the Lower Cretaceous, *Equisetites* was the only persisting genus and derivatives from it are found in the present-day *Equisetum*.

Equisetum, with about 25 species, is world-wide in distribution, except for Australia, and the various species grow in a variety of habitats. Certain species grow in ponds and marshes; others grow in damp shaded places; and still others grow in exposed, relatively dry habitats. Most of the species have sporophytes that are less than a meter in height, but the aerial branches of *E. giganteum* L. of tropical South America may grow to a height of 12 meters. However, this species is vine-like in habit, and its stem, which is but 0.5 to 2.0 cm. in diameter, clambers over adjacent trees.

The sporophyte of *Equisetum* has a horizontal, much branched, perennial, subterranean rhizome which often penetrates to more than a meter below the surface of the soil. The rhizome is conspicuously differentiated into nodes and internodes. At each node is a whorl of small, slender, scale-like leaves, more or less laterally united with one another to form a brown sheath around the node. Alternating with each leaf at a

[1] Williamson and Scott, 1894.

node is a branch primordium. Branch primordia of the rhizome may immediately develop into branches, either aerial or subterranean, or they may remain dormant for an indefinite period. Sometimes the primordia develop into short rounded branches one internode long. These tubers are capable of developing into new plants when separated from the parent rhizome and thus afford a means of propagating the sporophyte generation vegetatively. Nodes of the rhizome also bear whorls of slender much-branched adventitious roots. These usually function for one growing season only.

Aerial branches from rhizomes of most species are of two sorts, sterile and fertile (Fig. 154*A*). Sterile branches are green and have a whorl of lateral branches at each node. Frequently the lateral branches bear whorls of similar, but smaller, branches. Fertile branches of most species are colorless, are unbranched, and have a single strobilus at the branch apex. Fertile branches of this type usually appear above ground, attain their full development, and shed their spores before the vegetative branches appear. Other species, as *E. palustre* L. (Fig. 154*B*), have green, branched, fertile shoots with a strobilus at the apex of each lateral branch. Fertile shoots of this type persist after the spores are shed and function as vegetative organs.

The general organization of the stem is the same in aerial and in subterranean portions but is best exemplified by aerial branches. Each internode of an aerial branch is longitudinally ribbed and has the ribs alternate with the leaves of the subtending node. Since the leaves of successive internodes are alternate, ribs of successive internodes are alternate.

Internodes of *Equisetum* have definitely arranged vertical cavities extending the length of the internode. Primary branches of aerial shoots have a conspicuous space (the **central canal**) occupying most of the pith. Internodes of small branches and of the rhizome lack a central canal. At the inner face of each internodal vascular bundle is another space, the **carinal canal.** The carinal canals lie in a ring and each one is internally radial to a rib of the stem surface. External to the carinal canals and alternate with them is a ring of larger intercellular spaces (**vallecular canals**) that lie in the cortex. These various intercellular spaces are not alike in function: the central and carinal canals are usually water-filled; the vallecular canals always contain air.

The stem of *Equisetum* is organized into epidermis, cortex, and stele. The limits between cortex and stele are clearly marked in certain species, as *E. arvense* L., because of the endodermis surrounding the entire stele. The demarcation between the two is not clearly evident in other species, as *E. giganteum* L., where each vascular bundle is encircled by an endodermal layer.

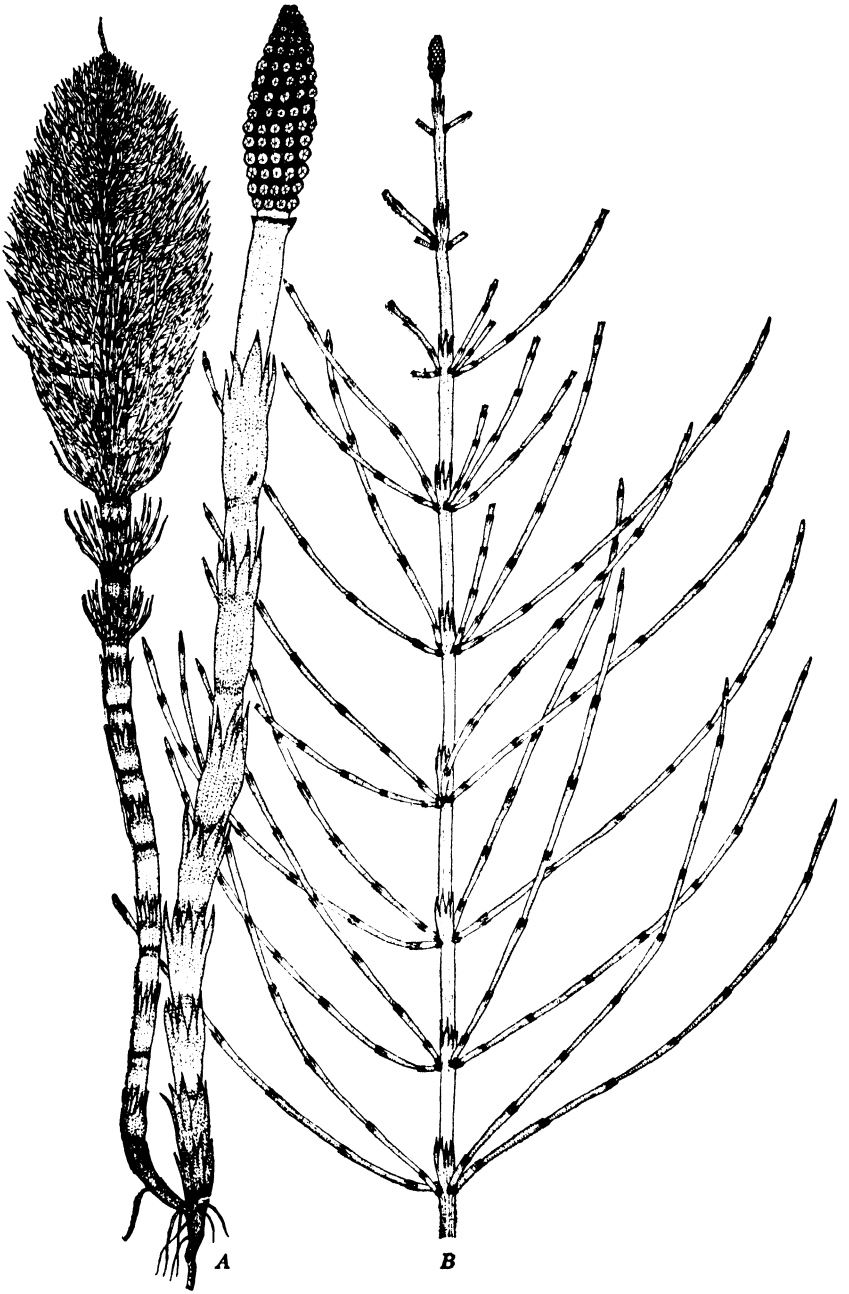

FIG. 154. *A*, *Equisetum telmateia* Ehrh. *B*, *Equisetum palustre* L. (× ½.)

The epidermal layer of *Equisetum* has highly silicified cell walls in which the silica may be uniformly deposited or may be deposited in granules. Stomata are largely restricted to aerial branches and to portions of the epidermis between longitudinal ridges of the internodes. The development of a stoma is unusual in that there are two successive longitudinal divisions of the initial, the two innermost cells maturing into a pair of guard cells and the two outermost into a pair of accessory cells. Silica deposited in walls of guard cells is in transverse bands radial to the stoma.

The cortex of an aerial branch is highly differentiated. Beneath each of the externally evident ribs of the internode is a vertical rod-like mass of sclerenchyma. The sclerenchyma may be restricted to the peripheral portion of the cortex or, as in *E. giganteum*, may extend inward to the central cylinder. In addition there are frequently smaller vertical masses of sclerenchyma in the periphery of the cortex and at the bases of the grooves between the ribs. The columns of sclerenchyma, especially those internal to the ridges, are the chief mechanical elements of a branch. The peripheral portion of the cortex lateral to the sclerenchyma is a chlorenchyma with intercellular spaces that are especially conspicuous just beneath the stomata. Since the leaves are small and have but few chloroplasts, the chlorenchyma of the cortex is of major importance in the photosynthetic work of the aerial branch.

Cross sections of internodes show a well-defined ring of vascular strands toward the periphery of the stele. In very young bundles the protoxylem, consisting of a few annular and spiral tracheids, lies toward the inner face of the bundle. The maturation of the protoxylem is in centrifugal succession,[1] but this is exceedingly difficult to determine in older stems because the protoxylem elements separate from one another as growth continues, and they are in a more or less disorganized condition within the carinal canals thus formed. External to the carinal canal is a phloem mass composed of phloem parenchyma and of sieve tubes with sieve plates in the diagonal walls. On both lateral flanks of the phloem is a small metaxylem mass consisting of scalariform tracheids. The vascular strands of the internode are laterally separated from one another by parenchymatous cells similar in size and appearance to those of the pith. The peripheral portion of the stele, the pericycle, is one cell in thickness (Fig. 155*A–B*).

The vascular skeleton of the *Equisetum* stem is siphonostelic. Nodal portions of this hollow cylinder (the **nodal wood**) are uninterrupted; internodal portions are longitudinally perforate and have each perforation running the length of an internode. As already noted (page 239) these perforations do not seem to be branch gaps, as some maintain,[2] but are structures different in nature from true gaps. The internodal strands of

[1] Eames, 1909. [2] Jeffrey, 1917.

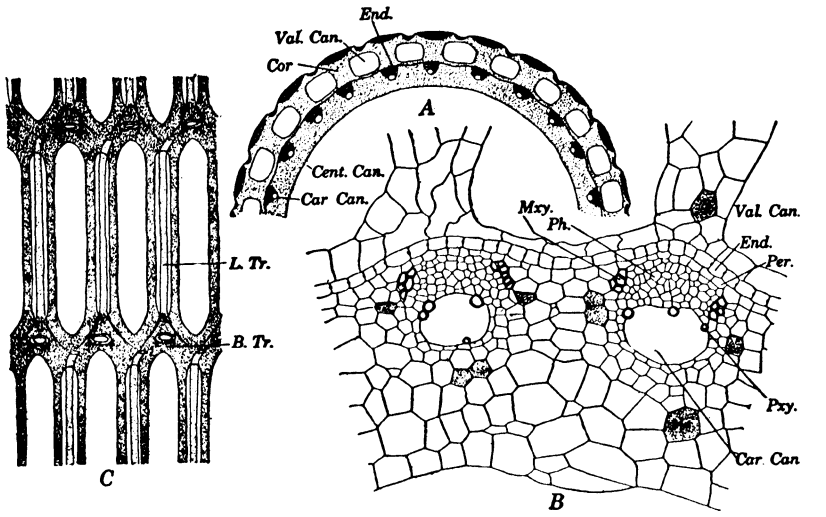

FIG. 155. *A–B*, *Equisetum telmateia* Ehrh. Transverse sections through internode of shoot. *C*, diagram of vascular skeleton of *Equisetum*. (*B. Tr.*, branch trace; *Car. Can.*, carinal canal; *Cent. Can.*, central canal; *Cor.*, cortex; *End.*, endodermis; *L. Tr.*, leaf trace; *Mxy.*, metaxylem; *Per.*, pericycle; *Ph.*, phloem; *Pxy.*, protoxylem; *Val. Can.*, vallecular canal.) (*A*, × 7; *B*, × 110.)

vascular tissue (the so-called vascular bundles) between the perforations contain both metaxylem and protoxylem. The vascular supply to a leaf trace consists wholly of protoxylem. This arises at a node, extends vertically through the node above, and departs at the succeeding node[1] (Fig. 155*C*). The metaxylem of the internode joins directly with the nodal wood above and below. Branch traces, which lie alternate with the leaf traces, join immediately with the nodal metaxylem beneath them.

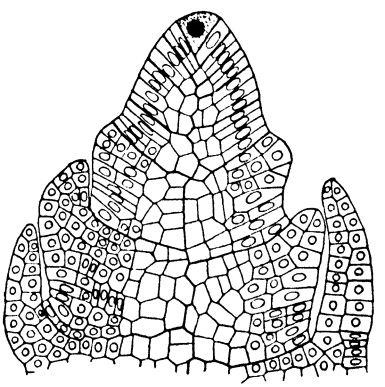

FIG. 156. *Equisetum telmateia* Ehrh. Vertical section of apex of a shoot. Portions derived from successive segments from the apical cell are outlined with a heavy line. (× 110.)

Terminal growth of rhizome and branches is initiated by a pyramidal apical cell with three cutting faces (Fig. 156). Each segment cut off by the apical cell ultimately develops into a sector of the stem. The first division of the segment is anticlinal, the upper and lower cells thus formed developing, respectively, into a nodal and an internodal sector of the stem. Each of the two cells then

[1] Browne, 1922.

divides periclinally. The small inner cell thus formed contributes to the pith; the elongate outer cell contributes to all other parts of the sector. Lateral branch initials arise several nodes back from the apical cell. When the stem is seen in longitudinal section, they appear to be axillary in origin, but this is not actually the case because the superficial stem cell functioning as the branch initial lies midway between two adjoining leaves.

All the roots borne at nodes of the rhizome and aerial branches are adventitious in origin. Primordia of adventitious roots arise from the

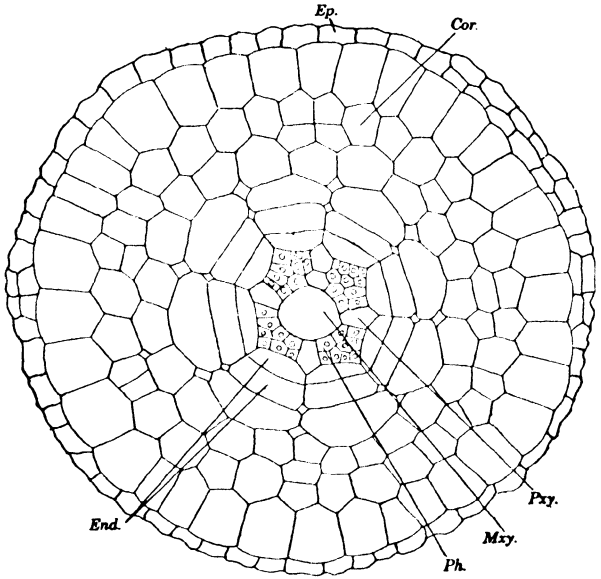

FIG. 157. *Equisetum telmateia* Ehrh. Transverse section near growing apex of a root. (*Cor.*, cortex; *End.*, endodermis; *Ep.*, epidermis; *Mxy.*, metaxylem; *Ph.*, phloem; *Pxy.*, protoxylem.) (× 215.)

lower side of branch primordia at the node, not directly from the node itself. In the case of rhizomes the branch primordia usually remain dormant, and the root primordia develop vigorously. In aerial branches the opposite condition obtains, the branch primordia developing vigorously and the root primordia remaining dormant.

A young root primordium differentiates a group of initials, which form the root cap, and a pyramidal apical cell, which forms the root proper. The stele of a root is tri- to hexarch, and with three to six protoxylem points surrounding a single axial metaxylem element (Fig. 157). The angles between the protoxylem are completely filled with phloem. *Equisetum* is unusual in that it lacks a pericycle. Instead, there is an endodermal layer two cells in thickness, and one in which the inner layer

functions as a pericycle if there is a production of secondary branches. The cortical tissue external to the endodermis is three or four cells in thickness. A short distance posterior to the root cap, its cell walls are of uniform thickness; farther back from this, the outer portion of the cortex is thick-walled and constitutes an exodermis.

Strobili of *Equisetum* have several whorls of densely crowded peltate appendages which bear the sporangia (Fig. 158*A*). In spite of the fact that occasional tetratological appendages are leaf-like, it is better, for reasons already given (page 139), to call the appendages sporangiophores, not sporophylls. Immediately below the sporangiophores, the central axis bears a small ring-like outgrowth, the **annulus**. This structure is often interpreted as a vestigial remainder of the bracts characteristic of strobili of Calamitaceae. However, the fact that annuli of certain species regularly bear small sporangia shows that the annulus may be sporangiophoric in nature.

Each sporangiophore has a slender stalk. The free end is expanded into a flattened disk which lies at right angles to the stalk. The disk is generally hexagonal in outline because of crowding by disks of adjoining sporangiophores. The sporangia, of which there are 5 to 10, are borne in a ring and on the side of the disk facing the central axis of the strobilus (Fig. 158*B–C*). Each sporangium is an elongate cylinder with a rounded apex. When fully mature, the sporangia open along a single longitudinal line of dehiscence.

The sporangia of *Equisetum* are of the eusporangiate type (page 269) in the sense that they are not entirely derived from a single initial cell. However, all the sporogenous tissue in a sporangium can be traced back to a single superficial cell of the young sporangiophore.[1] The first division of this initial is periclinal. The inner daughter cell contributes only to the sporogenous tissue; the outer daughter cell contributes both to the sporogenous tissue and to the portion of the sporangial jacket radial to the sporogenous tissue (Fig. 158*F*). The remainder of the jacket layer is derived from cells lateral to the original initial. The jacket ultimately becomes a tissue several cells in thickness, in which the innermost cell layer functions as a tapetum (Fig. 158*G–H*). During the course of spore development, there is a disintegration of the tapetal layer and of all but the two outermost layers of jacket cells. Thus, when fully mature, the sporangium has a jacket two cells in thickness, in which cells of the outermost layer have spirally thickened walls (Fig. 158*I*).

There is a disintegration of about a third of the spore mother cells shortly before the reduction divisions begin. The remaining spore mother cells separate from one another, assume a spherical shape, and float about in the plasmodial liquid resulting from disintegration of tapetum and

[1] Bower, 1894.

spore mother cells. This liquid persists until the spores are well along toward maturity. The spore secretes a wall composed of four concentric layers.[1] The outermost layer (**exosporium**) is laid down in four spiral strips. Later the four strips split away from the remainder of the wall except for one common point of attachment. These strips remain tightly coiled about the spore until the sporangium dehisces. The strips are hygroscopic, coiling and uncoiling accordingly as the air is moist or dry (Fig. 158*D–E*). The strips are called **elaters,** but it should be noted

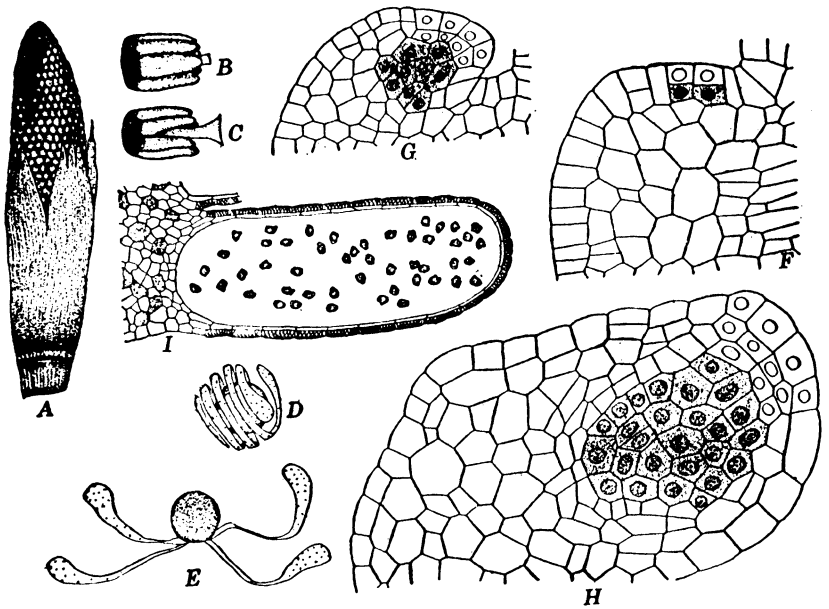

FIG. 158. *Equisetum telmateia* Ehrh. *A*, strobilus. *B–C*, sporangiophores. *D–E*, spores with coiled and uncoiled elaters; *F–I*, stages in development of sporangia. (*A*, × ⅔; *B–C*, × 5; *D–H*, × 210; *I*, × 40.)

that they are different in nature from the elaters of Bryophyta. The function of the elaters is uncertain. Possibly their expansion may assist in dehiscence of the sporangium; possibly their expansion and contraction may assist in spore dispersal. Mature spores are relatively large and contain numerous chloroplasts. Similar to other pteridophytes whose spores contain chloroplasts, they remain viable for only a few days after they are shed.

When developing under natural conditions, the gametophytes of *Equisetum* are generally found growing upon clayey soil and in the mud belt along the banks of streams. The first cell division in the develop-

[1] Beer, 1909.

ment of a gametophyte takes place 10 to 12 hours after the spore is sown. One of the two daughter cells is small and develops into the first rhizoid, the other is large and develops into the remainder of the thallus.[1] Division and redivision of the larger cell are in irregular sequence and produce a small cushion-like tissue, several cells in thickness, which bears numerous rhizoids on its lower surface. Cells in the upper portion of the cushion contain chloroplasts, those in the lower portion are colorless. The entire margin of the cushion is meristematic in nature. If growth is uniform throughout the meristematic region, the result is a circular gametophyte, if growth is more active at one side the result is a gametophyte of irregular shape. Rather early in development of the gametophyte the upper surface sends forth irregularly shaped upright plates (Figs. 159*A*, 161*A*). These densely crowded green lobes completely cover the disk below. Gametophytes of *Equisetum* are long-lived and certain of them grown in culture have persisted for more than two years.[2] Those of most species rarely become a centimeter in diameter, but in *E. debile* Roxb. they may become 3 cm. in diameter.[3]

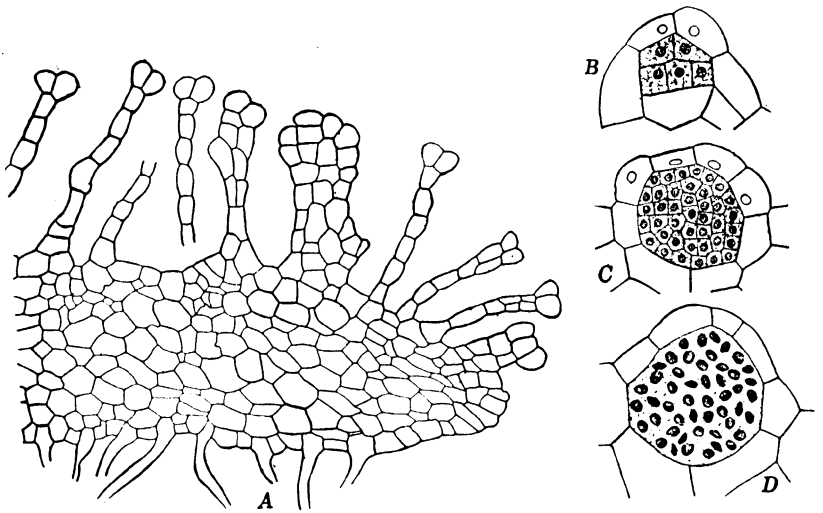

FIG. 159. *A*, *Equisetum debile* Roxb. Vertical section of a portion of a gametophyte. *B–D*, *Equisetum telmateia* Ehrh. Stages in development of antheridia. (*A*, × 55; *B–D*, × 210.)

If conditions of growth are favorable, the first sex organs are formed when the gametophytes are 30 to 40 days old. The initials developing into sex organs are in the meristematic region of the cushion. The mature sex organs lie between plates somewhat in from the margin of a thallus, because the marginal meristem continues marginal growth and

[1] Campbell, 1918; Kashyap, 1914; Walker, 1931.
[2] Walker, 1931. [3] Kashyap, 1914.

a formation of vertical plates. There has been considerable debate as to whether *Equisetum* is homothallic or heterothallic. In the case of *E. arvense* L. it has been shown[1] that about half of the spores develop into gametophytes which produce only antheridia no matter how the cultural conditions are changed. The remaining half of the spores develop into gametophytes which produce archegonia when cultural conditions are favorable. If fertilization does not take place, the prothallia with archegonia may then develop antheridia.

An initial developing into an antheridium is a superficial cell of the meristematic region. This initial divides periclinally into an outer cell (the jacket initial) and an inner cell (the primary androgonial cell). Subsequent development[2] is identical with that of eusporangiate ferns. The jacket initial develops into a jacket layer one cell in thickness, and one with a triangular opercular cell as in the Eusporangiatae. Division and redivision of the primary androgonial cell result in a considerable number of androgonial cells (Fig. 159*B*-*C*). Two blepharoplasts become evident at the androcyte mother cell stage of development,[3] and one goes to each of the two androcytes formed by a mother cell. The androcytes are metamorphosed into spirally coiled antherozoids with numerous flagella (Fig. 159*D*).

Archegonial initials are also superficial cells of the marginal meristem. The first division of the initial is periclinal (Fig. 160*A*). The outer daughter cell is the primary cover cell. The inner daughter cell is the mother cell of the central cell. The primary cover cell divides quadrately to form four primary neck cells. Transverse division of these cells results in an archegonial neck three or four cells in height and one that projects vertically above the thallus (Fig. 160*C*-*D*). The central cell divides transversely into a primary canal cell and a primary venter cell (Fig. 160*B*). Some species rarely have a division of the primary canal cell; other species regularly have it dividing vertically into two boot-shaped neck canal cells. In all cases there is an asymmetrical transverse division of the venter cell to form a venter canal cell and an egg (Fig. 160*C*). The last step in archegonial development is the usual disintegration of all axial cells but the egg.[4]

Fertilization is effected by the antherozoid swimming down the canal of the archegonium. Frequently many antherozoids enter the venter, but only one of them penetrates the egg.[5] Unlike most other pteridophytes, several sporophytes may develop on the same prothallus (Fig. 161*A*). In *E. debile* it is not unusual to find 8 to 10 young sporophytes on a single gametophyte and as many as 15 have been observed.[6]

[1] Schratz, 1928. [2] Campbell, 1918. [3] Sharp, 1912.
[4] Campbell, 1918; Jeffrey, 1899; Kashyap, 1914; Sethi, 1928; Walker, 1921.
[5] Sethi, 1928. [6] Kashyap, 1914.

The first division of the zygote is usually transverse.[1] The cell walls of the next division are usually at right angles to the first (Fig. 160*E*). Although the embryo thus has the early differentiation into quadrants typical of leptosporangiate ferns, the four quadrants do not give rise, respectively, to stem, root, cotyledon, and foot. In some cases, as *E. debile*,[2] the whole of the lower (hypobasal) half of the embryo develops into a foot (Fig. 160*F*); in other cases, as *E. arvense*,[3] both foot and root come from the hypobasal half. Rather early in the development of the

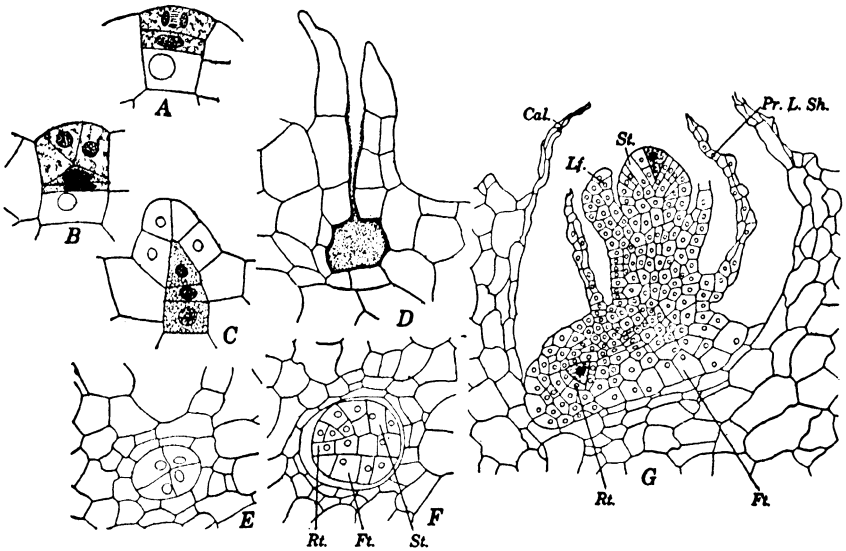

FIG. 160. *A–C, Equisetum telmateia* Ehrh. Stages in development of archegonia. *D–G, Equisetum debile* Roxb. *D*, an old archegonium. *E–F*, young embryos. *G*, embryo at an advanced stage of development. (*Cal.*, calyptra; *Ft.*, foot; *Lf.*, Leaf; *Pr. L. Sh.*, primary leaf sheath; *Rt.*, root; *St.*, stem.) (*A–B*, × 325; *C–D*, × 210; *E–G*, × 110.)

upper (epibasal) half of the embryo, there is a differentiation of the apical cell of the stem. The cells lateral to this develop into the first leaf sheath of the young stem. Typically there are three leaves in this first sheath, but there may be two or four leaves. These leaves, unlike the first leaves developed by embryos of other pteridophytes, are small, scale-like, and of little importance as photosynthetic organs when the sporophyte begins to manufacture its own food. If the entire hypobasal half of the embryo has developed into a foot, the apical cell of the root is differentiated from a superficial cell of the epibasal half that lies near the hypobasal half. Growth and elongation of the stem and root portions of the embryo are

[1] Campbell, 1918, 1928; Jeffrey, 1899; Walker, 1921.
[2] Campbell, 1928. [3] Sadebeck, 1878.

rapid. The root grows directly downward through the underlying gametophytic tissues and into the soil. The stem portion of the embryo bursts through the neck of the archegonium (the calyptra) and grows upright. The stem is differentiated into nodes and internodes and has a whorl of leaves (generally three) at each node. Apical development of this branch

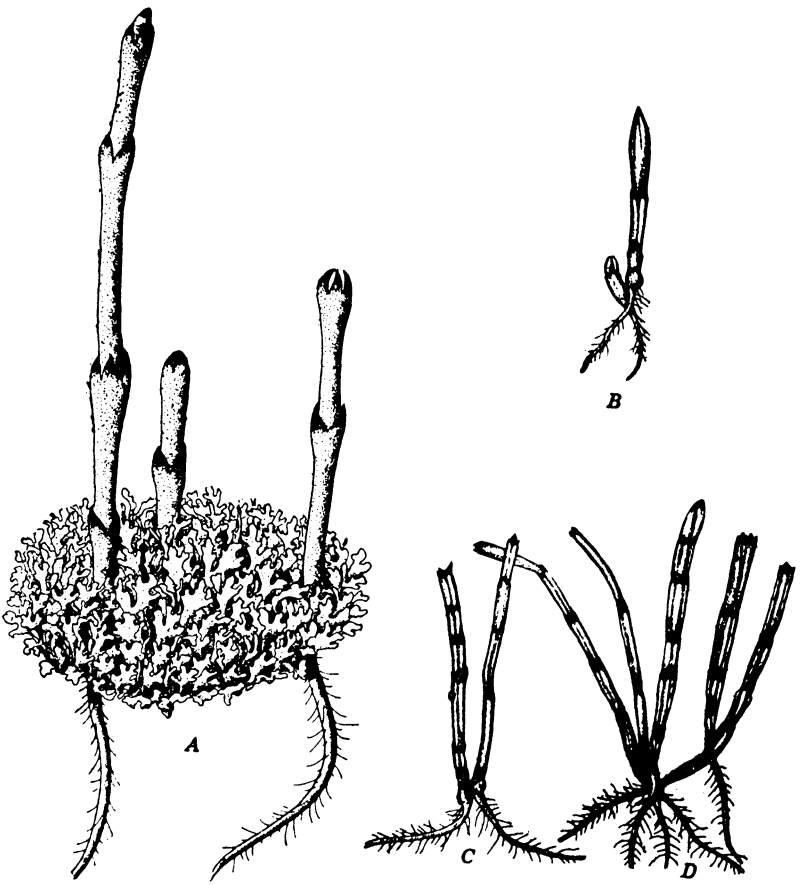

FIG. 161. *A*, *Equisetum* sp. Gametophyte with young sporophytes. *B–D*, *Equisetum hiemale* L. Young sporophytes. (*B–D*, *after Jeffrey*, 1899.)

is limited, and all growth ceases after it has become 10 to 15 internodes long. A secondary branch then grows out from the base of the primary branch (Fig. 161*B*). This branch differs in generally having four to five leaves at the nodes. Growth of this branch, like that of the first, is limited (Fig. 161*C*). It has been shown for *E. debile*,[1] and the same is probably

[1] Campbell, 1928.

true of other species, that the secondary branch is endogenous in origin and arises from tissues of the primary root. The second branch has a root of its own and one which is developed adventitiously near its base. The young sporophyte successively produces several additional erect secondary branches of limited growth (Fig. 161*D*). Presumably these branches also arise endogenously. Eventually there is a formation of a secondary branch that does not grow erect but bends downward, grows into the soil, and develops into a rhizome capable of unlimited growth.

Bibliography

Arnold, C. A. **1947.** An introduction to paleobotany. New York. 433 pp. 187 figs.

Beer, R. **1909.** *New Phytol.* **8**: 261–266. [Spores, *Equisetum.*]

Bower, F. O. **1894.** *Phil. Trans. Roy. Soc. London B* **185**: 473–572. 11 pl. [Sporangia, *Equisetum.*]

Browne, Isabel M. P. **1922.** *Bot. Gaz.* **73**: 447–468. 7 figs. [Anatomy, *Equisetum.*]

Campbell, D. H. **1918.** The structure and development of mosses and ferns. 3d ed. New York. 708 pp. 322 figs.

1928. *Ann. Bot.* **42**: 717–728. 1 pl. 10 figs. [Embryo, *Equisetum.*]

Eames, A. J. **1909.** *Ibid.* **23**: 587–601. 1 pl. [Anatomy, *Equisetum.*]

Hirmer, M. **1927.** Handbuch der Paläobotanik. Bd. 1. Munich. 708 pp. 817 figs.

Jeffrey, E. C. **1899.** *Mem. Boston Soc. Nat. Hist.* **5**: 155–190. 5 pl. [*Equisetum.*]

1917. The anatomy of woody plants. Chicago. 478 pp. 306 figs.

Kashyap, S. R. **1914.** *Ann. Bot.* **28**: 163–181. 45 figs. [Gametophyte, *Equisetum.*]

Kräusel, R., and H. Weyland. **1926.** *Abhandl. Senckenbergischen Naturf. Ges. Frankfurt a/M.* **40**: 115–155. 15 pl. 46 figs. [*Calamophyton.*]

1932. *Senckenbergiana* **14**: 274–280. 7 figs. [*Hyenia.*]

Lacey, W. S. **1943.** *New Phytol.* **42**: 98–102. 3 figs. [*Calamostachys.*]

Sadebeck, R. **1878.** *Jahrb. Wiss. Bot.* **11**: 575–602. 3 pl. [Embryo, *Equisetum.*]

Schratz, E. **1928.** *Biol. Zentralbl.* **48**: 617–639. [Gametophytes, *Equisetum.*]

Scott, D. H. **1920.** Studies in fossil botany. 3d ed. Vol. 1. London. 434 pp. 190 figs.

Sethi, M. L. **1928.** *Ann. Bot.* **42**: 729–738. 1 pl. 1 fig. [Gametophyte, *Equisetum.*]

Sharp, L. W. **1912.** *Bot. Gaz.* **54**: 89–119. 2 pl. [Antherozoids, *Equisetum.*]

Walker, Elda R. **1921.** *Ibid.* **71**: 378–391. 2 pl. 3 figs. [Gametophyte, *Equisetum.*]

1931. *Ibid.* **92**: 1–22. 54 figs. [Gametophyte, *Equisetum.*]

Williamson, W. C., and D. H. Scott. **1894.** *Phil. Trans. Roy. Soc. London B* **185**: 863–959. 15 pl. [*Calamites, Calamostachys, Sphenosphyllum.*]

CHAPTER 10

PTEROPHYTA

The Pterophyta have a sporophyte differentiated into stem, leaves, and roots. The vascular cylinder of stems, when siphonostelic, differs from that of other pteridophytes in having leaf gaps. The leaves are macrophyllous and usually differentiated into a petiole and a dissected blade with a central axis (**rachis**). Unlike other pteridophytes the leaf bears many sporangia on either the margin or the abaxial face of the leaf blade. Practically all members of the division are homosporous and among living members have the spores developing into small, green, free-living gametophytes that are frequently heart-shaped and with sex organs restricted to the ventral side.

From the standpoint of geographical distribution in the flora of today, about 10 per cent of the genera of ferns are either cosmopolitan or pantropical, and the rest are endemic to restricted or rather broad geographical areas.* There are no strictly endemic genera in Europe and only one in the portion of North America north of Mexico. Less than 1 per cent of the known genera are endemic to Africa; 39 per cent of the known genera are endemic to Central and South America or to the Caribbean. The richest of all areas is the Indo-Malayan–South Pacific area, to which fully 50 per cent of all known genera are endemic.

The restriction of a given species to a definite area depends upon a number of factors. One factor limiting the ability of a fern to spread to new territory is not the ability of its spores to travel long distances by air or other agencies, but their ability to survive during transport. One would not expect to find *Hymenophyllum javanicum* Spr. or *Dipteris conjugata* (Kaulf.) Reinw. jumping over long stretches of unfavorable territory because their spores have been shown[1] to remain viable for only about a week. Another factor in extension of range of ferns is lodgment of spores in a place suitable for their germination and development into a gametophyte, because conditions favorable for growth of gametophyte

* These data are based upon the genera recognized by Copeland (1947) and the geographical distribution he gives for them.

[1] Stokey, 1940, 1945.

and young sporophyte are even more rigorously limited than are those required by the adult sporophyte.[1]

Temperature, water relations, the amount of illumination, and the nature of the substratum jointly determine whether or not a particular species will grow in a given area or habitat. Temperature restricts the vast majority of genera of ferns to portions of the earth with a tropical or subtropical climate because they are unable to endure the more rigorous climates of other parts of the earth. In past geological periods when the earth's climate was much more equable than that of today, certain families now found only in the tropics and subtropics were much more widely distributed (see pages 325 and 328).

The intensity of illumination is an important factor in restricting ferns to particular habits. Relatively few ferns are "sun ferns" capable of growing where they are exposed to full sunlight. *Pteridium aquilinum* (L.) Kuhn of temperate regions and the various *Gleichenia* species of tropical and subtropical regions are examples of sun ferns that thrive in open spaces and disappear when too densely shaded by other vegetation invading the area. The light relations of ferns growing in more or less shaded habitats is seen to best advantage in tropical rain forests. Here there is a vertical zonation of species from those growing on the ground to the various epiphytic ones ranging from those restricted to the bases of tree trunks to those restricted to the crowns of trees. In these forests the gradient in light intensity ranges from approximately 1 per cent at the ground level to 100 per cent at the treetops.[1]

Water relations are equally important in causing the vertical zonation of ferns in tropical rain forests. At the ground level the relative humidity may be 100 per cent. Thus, ferns growing on the ground and on the base of tree trunks are essentially hydrophytes. Epiphytic ferns in the crown of trees are facultative xerophytes since the substratum on which they are growing loses much water during the day and there may be successive days when the substratum is not wetted. A majority of ferns of temperate climates grow in habitats where the substratum never becomes dry. These include the mesophytic ferns of woodlands and ravines and the hydrophytic ferns of marsh and swamp as well as those, such as *Azolla*, that grow floating in water. Very few ferns are true xerophytes, but a number of them are facultative ones and are able to withstand drought for a considerable time. Examples of them are the ferns growing in areas with a long dry season, as the Pacific Coast of the United States, and the ferns growing on exposed cliffs that become dry between successive rains.

When conditions of temperature, light, and moisture are favorable the presence of a particular fern in a given locality is dependent upon a suitable substratum. The pH reaction of substrata upon which a particular

[1] Holttum, 1938.

species grows may be toward the acid side, toward the basic side, or ranging from acid to basic. This is especially the case with rock ferns. For example, the pH found[1] for the substratum of *Asplenium pinnatifidum* Nutt. is 4.5 to 5.5, that for *Pellea glabella* Nutt. is 6.5 to 8, and that for *Polypodium vulgare* L. is 5.0 to 8.5. Ferns of woods and swamps[2] are

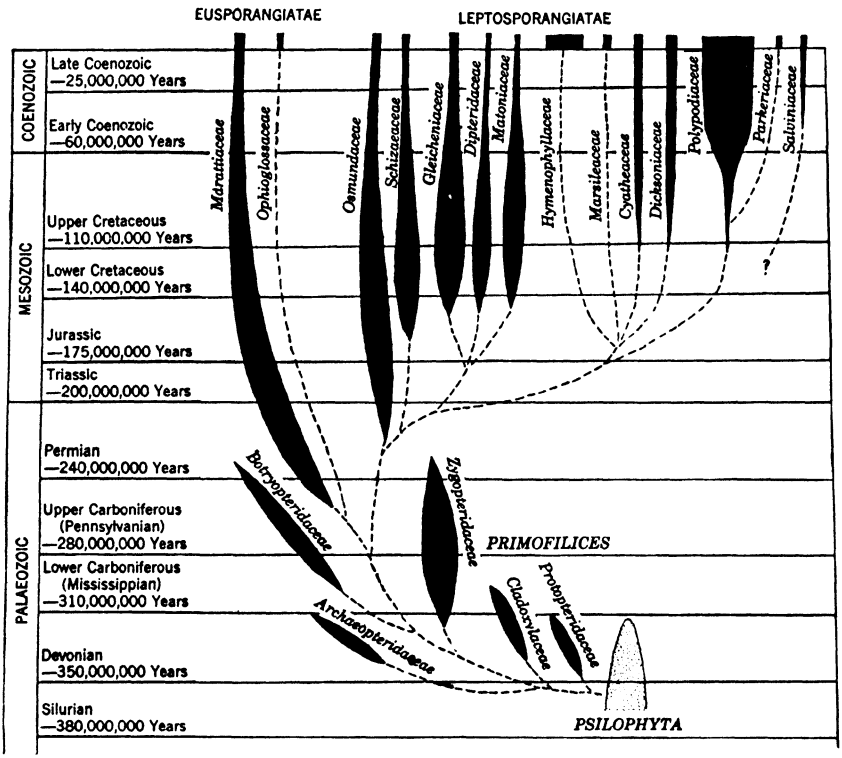

FIG. 162. Diagram showing the geological range and the suggested interrelationships among the Pterophyta.

rarely found where the pH of the substratum is over 7.5, a feature correlated with the fact that most of them grow in a substratum rich in humus.

From the standpoint of distribution in time, the Pterophyta are known from as far back as the Devonian (Fig. 162). However, members of the Pterophyta were a less conspicuous element in the flora of the next two periods, the Lower and Upper Carboniferous, than were the Lepidophyta and Calamophyta. This does not mean that evolution of the filicinean series was at a slower rate. The reverse was the case, and, at least by the Lower Carboniferous, evolution in the filicinean series had progressed be-

[1] Wherry, 1920, 1922. [2] Wherry, 1921.

yond the pteridophytic level. Although the filicinean series gave rise to seed plants at an early date, evolution continued at the pteridophytic level. Most of the Pterophyta evolved during the Carboniferous periods become extinct during the Permian, but in the succeeding Triassic and Jurassic there was an evolution of several new series (families) most of which have survived until today (Fig. 162).

Evolution of the characteristic filicinean stem and leaf appears to have come about through metamorphosis of the erect portion of a psilophyte. The manner in which a branch of a psilophyte evolved into the megaphyllous leaf has been discussed on page 136. Certain of the oldest ferns, as *Cladoxylon* (Fig. 166). had leaves closely resembling the hypothetical modified branch of a psilophytan sporophyte. Sporangia of ancient ferns afford additional evidence that the filicinean leaf is a modified psilophytan branch. Thus, sporangia of these ferns were vertically elongate, had a jacket layer more than one cell in thickness, and opened vertically by a longitudinal splitting of the jacket. They were borne singly and terminally on appendages resembling foreshortened branches of Psilophytales. Evolution of the filicinean shoot involved but little change in the majority of Primofilices and the stem had the same protostelic organization as in shoots of Psilophyta. Sporophytes of Pterophyta have an organ, the root, that was not present in the Psilophytales. The origin of this organ is obscure. It may have appeared *de novo*, or it may have arisen by a modification of prostrate branches of the psilophytan sporophyte.

Evolution from the primitive type of filicinean sporophyte involved changes in external form, changes in internal structure, and changes in its sporangial characters. Undoubtedly, also, there were changes in the gametophytic generation but these can only be inferred since gametophytes of fossil Pterophyta are unknown. A comparison of admittedly advanced and primitive characters affords a means of determining the general evolutionary tendencies within the division. In using these various characters in establishing phylogenetic relationships between present-day ferns it must be borne in mind that some of the admittedly primitive features, such as venation of the blade, may have arisen by reduction from a more advanced type instead of persisting from a primitive ancestral type. When taken as a whole, the following are among the general evolutionary tendencies among ferns.[1]

Habit and External Morphology. Ferns with an upright radially symmetrical sporophyte are more primitive than those with a prostrate dorsiventrally symmetrical one.

Stele of Stem. A protostelic vascular cylinder is more primitive than a solenostelic or dictyostelic one, and exarch protoxylem is more primitive than mesarch or endarch protoxylem.

[1] Bower, 1923; Holttum, 1949; Wagner, 1953.

Leaf Trace. A single trace departing to a leaf is a more primitive condition than is a dissection of the trace into several meristeles.

Leaf Blade. Evolution of leaf blades involved an advance from dichotomous to monopodial and pinnate branching. An open venation where the forked veins have free ends is more primitive than a closed venation where the veins form a reticulum.

First-formed Leaves. The first few leaves formed by a young sporophyte may be different from those formed later, and those of two ferns may differ markedly even when later-formed leaves of the two seem much alike.

Sporangial Structure and Dehiscence. A jacket layer more than one cell in thickness is more primitive than a jacket layer one cell in thickness. An **annulus** (the mechanism causing dehiscence) at one side of a sporangium and causing vertical dehiscence is more primitive than a vertical annulus causing a transverse dehiscence of a sporangium.

Spore Output. Sporangia producing a large and indefinite number of spores are more primitive than those with a definite number that is some multiple of two; and a large definite number is more primitive than a small definite number.

Differentiation of Spores. The heterospory found in a few genera is a more advanced character than is the homospory characteristic of most genera.

Position and Protection of Sporangia. A production of sporangia at the margin of a blade is a more primitive condition than a production of them on the abaxial face. Abaxial sporangia scattered over the blade are more primitive than those produced in groups (**sori**), and naked sori are more primitive than those protected by a covering (**indusium**).

Sequence of Sporangial Development. A simultaneous development of all sporangia on a blade is more primitive than a development of them in succession; and a sorus developing them in basipetalous succession is more primitive than one in which sporangia of various ages are intermingled.

Vegetative Structure of Gametophyte. Spore germination into a plate-like germling is considered more primitive than germination into a filamentous germling,[1] and a wedge-shaped or ribbon-like mature gametophyte with a longitudinally thickened axis is more primitive than a heart-shaped gametophyte with a thickened cushion posterior to the apical notch.

Sex Organs. An antheridium embedded in the gametophyte is more primitive than an emergent one; and emergent antheridia with a small number of jacket cells and antherozoids are more advanced than those with a larger number.

[1] Stokey, 1951.

Embryology. A late differentiation of an embryo into cotyledon, stem, root, and foot is more primitive than a differentiation into initials of these parts at the four- or eight-celled stage.

All the foregoing primitive or advanced features are not characteristic of any particular genus or family of living ferns. A fern or group of ferns may be advanced in certain respects and less advanced in others. For example, the highly advanced heterospory of *Marsilea* is associated with relatively primitive vegetative and sporangial characters of the sporophyte. On the other hand, the Marattiales have an advanced vegetative organization of the sporophyte and primitive features in sporangia and gametophyte. Thus in evaluating the evolutionary level attained by any genus or family the critical characters must be balanced one against the other.

All the Pterophyta are generally placed in a single class, the *Filicinae.* Filicinae of the Palaeozoic differ so markedly from other ferns that they are placed in a separate subclass called[1] the *Primofilices.* Living ferns and those evolved later than the Permian fall into two distinct series: those whose sporangia develop in a **eusporangiate** manner (from more than one initial cell) and those that develop in a **leptosporangiate** manner (from a single initial cell). When first recognized,[2] this distinction was made the basis for separating all pteridophytes into two primary series, the *Eusporangiatae* and the *Leptosporangiatae,* but within a fairly short time the term became restricted to the Filicinae and used as a basis for distinguishing two subclasses. Subclasses based upon mode of initiation of sporangial development are not so trivial as they appear because they are correlated with marked differences in structure of mature sporangia, and distinctive antheridial and embryonal characters. Furthermore, it is not necessary to know the early ontogeny of the sporangia of a particular fern because its mature structure shows whether it should be placed in the Eusporangiatae or Leptosporangiatae.

SUBCLASS 1. PRIMOFILICES

The Primofilices differ from other subclasses of the Filicinae in having sporangia that were borne on pedicels with a vascular bundle. The sporangia were elongate, had a jacket layer more than one cell in thickness, and opened by a longitudinal slit or a terminal pore. The vascular bundle of rachis and petiole of many genera was quite different from that of other ferns.

The Primofilices[1] (also known as the Inversicatenales,[3] the Coenopterideae,[4] or the Palaeopteridales)[5] are an extinct group of pteridophytes that practically all paleobotanists place in the filicinean series. Their geo-

[1] Arber, 1906. [2] Goebel, 1880–1881. [3] Bertrand and Cornaille, 1904.
[4] Seward, 1910. [5] Bertrand, 1933.

logical range is from the Middle Devonian to the Permian. The reproductive portions of Primofilices show a much greater resemblance to fertile portions of Psilophytales than do those of "modern" ferns known from the Triassic onward. Sporangia of Primofilices were borne singly or in clusters and terminally on branch-like pedicels with a central vascular strand.

Many of the Primofilices are of the type known as coenopterid ferns. The most conspicuous of the vegetative differences between coenopterid and "modern" ferns are in the leaf-like appendages borne by the stem. These were branched and at times with the primary axis intermediate in nature between a rachis and a true branch of the stem. The primary axis has a vascular bundle that was more or less H-shaped, E-shaped, or C-shaped as seen in cross section.

There are also certain Devonian pteridophytes that merit consideration as members of the Primofilices. The Devonian pteridophytes called[1] the *Protopteridales* have been variously considered members of the Psilophyta,[2] members of the Pterophyta,[3] and a group intermediate between Psilophyta and Pterophyta.[4] There is some justification for each of these views, but the vegetative organization seems to warrant holding that they have progressed sufficiently from the psilophytic type to be included among the Filicinae. If they do belong here they should be placed among the Primofilices.

Another problematical group is the one called[1] the *Archaeopteridales*. For a long time these were thought to be pteridosperms but their sporangia show[5] that they were heterosporous ferns. In spite of being heterosporous, the structure of their sporangia was of such a primitive type that the Archaeopteridales should be placed among the Primofilices.

Still another problem of classification is that of the affinities of the cladoxyloids. Some[2] place them among the Psilophytales; others place them among the Primofilices and either as a separate order[6] or as a family of the Coenopteridales.[7] Although standing considerably apart from other members of the Protopteridales they seem to be sufficiently related to them to be put in that order.

ORDER 1. PROTOPTERIDALES

Sporophytes of Protopteridales had an erect axis bearing appendages of a leaf-like nature that were more or less divided and with the segments flattened. Fertile appendages were branched and with each ultimate branchlet terminating in a single sporangium.

[1] Zimmermann, 1930. [2] Kräusel, 1938. [3] Arnold, 1947; Zimmermann, 1938.
[4] Hirmer, 1938. [5] Arnold, 1939.
[6] Hirmer, 1927; Zimmermann, 1930. [7] Arnold, 1947.

FAMILY 1. PROTOPTERIDACEAE

The Protopteridaceae had a monopodially or radially branched axis whose branched appendages were divided into flattened segments. Fer-

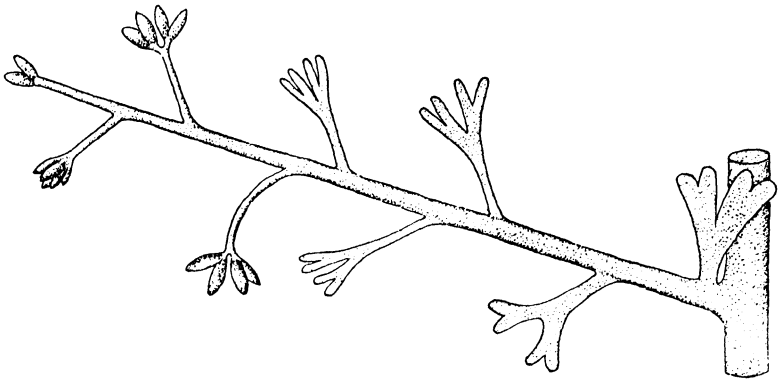

FIG. 163. Reconstruction of a branch of *Protopteridium minutum* Halle. (*After Halle*, 1936.)

tile appendages were dichotomously branched and with a single sporangium at the tip of each ultimate dichotomy.

The two genera found to be most widely distributed are *Protopteridium* and *Aneurophyton*, both known only as carbonized compressions whose internal structure is unknown. *Protopteridium*, as represented by *P. minutum* Halle (Fig. 163), had a sympodially branched axis bearing appendages of a leaf-like nature. The sterile appendages were borne in the lower part of a branch, were dichotomously divided, and with the flattened segments lacking evident veins.[1] The fertile appendages were borne toward the distal end of branches of the axis. They were dichotomously branched into four to six prongs and each terminated in a single sporangium. A sporangium was ovoid to spindle-shaped, sometimes almost cylindrical, and with an acute apex. At one side of the jacket was a vertical band of cells, presumably an annulus that caused a longitudinal dehiscence of the sporangium. A sporangium contained numerous spores.[1]

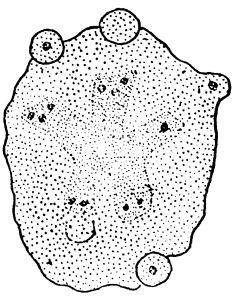

FIG. 164. *Iridopteris eriensis* Arnold. Diagram of a transverse section of a stem. (*Based upon Arnold*, 1940.)

Certain genera known only from their stems might also be placed in the Protopteridaceae pending discovery of other portions of their sporophytes. They have been placed[2] in two families distinct from the Proto-

[1] Halle, 1936. [2] Arnold, 1940.

pteridaceae. The stems of these plants were actinostelic and with mesarch protoxylem. The most advanced of these genera is *Iridopteris* (Fig. 164). It had an actinostele with five arms and traces departing from the tip of each arm. The traces connected with the bases of appendages that are

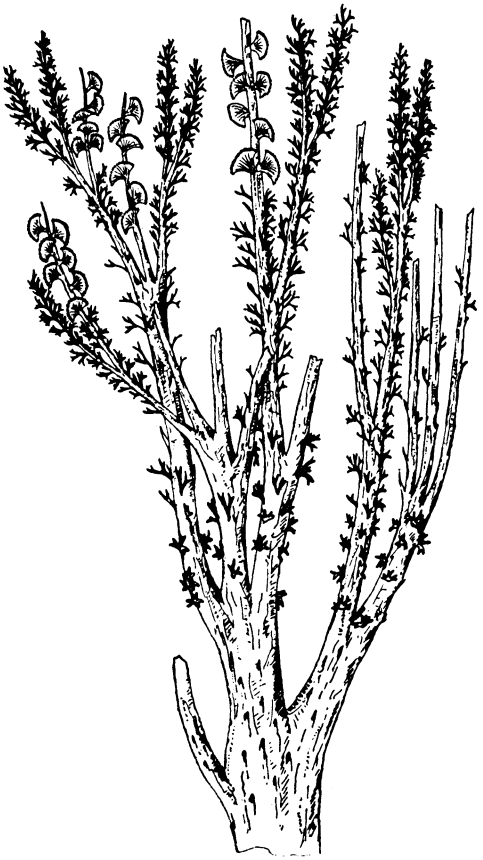

FIG. 165. Reconstruction of shoot of *Cladoxylon scoparium* Kräusel and Weyland. (*After Kräusel and Weyland*, 1926.)

thought to be leaf-like in nature,[1] and the evidence indicates that these were borne in a spiral succession.

FAMILY 2. CLADOXYLACEAE

The Cladoxylaceae had dichotomously branched stems that were polystelic and with each stele actinostelic and with secondary thickening. The stem bore numerous small leaves that were dichotomously branched

[1] Arnold, 1940, 1947.

in one plane. Certain of the leaves were sterile; others were fertile and with each ultimate dichotomy terminating in a single sporangium.

There are about half a dozen species of *Cladoxylon*, a genus known only from the Middle Devonian to the Lower Carboniferous. *C. scoparium* Kräusel and Weyland, a species of the Middle Devonian, is the only one in which leaves are known.[1] This species is based on a single specimen about 22 cm. long and so embedded in rock that there is an upwardly diverging series of branches. The largest branches are about 1.5 cm. in diameter and their divergence suggests that they were borne on a common axis. The branches are dichotomously forked and leaf-bearing (Fig.

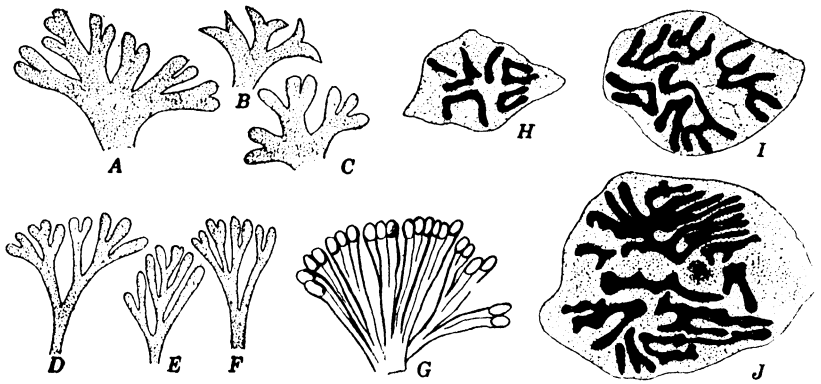

FIG. 166. *Cladoxylon scoparium* Kräusel and Weyland. *A–C*, sterile leaves from lower branches. *D–F*, sterile leaves from upper twigs. *G*, fertile leaf. *H–J*, transverse sections of the same stem at different levels. (*After Kräusel and Weyland*, 1926.) (*A–G*, × 2½; *H–J*, × 8.)

165). The smaller upper branches bore numerous spirally arranged leaves and the lower branches bore a few scattered leaves.

Branches of *C. scoparium* had a homogeneous cortical region surrounding a number of radially elongate, flattened steles. Serial sections cut at 5-mm. intervals on the same branch show a downwardly progressive increase both in number of steles and in complexity of their outline (Fig. 166*H–J*), but the method by which the number of steles was increased as a branch became older is unknown. Possibly, as in certain present-day palms, maturation of certain of the vascular strands was long delayed. The xylem of a stele contained both scalariform and pitted elements. Steles of certain species have the primary xylem completely or incompletely encircled by secondary xylem.

The leaves of *C. scoparium* were relatively small and rarely over 2 cm. long. Sterile leaves on lower portions of the shoot were broadly wedge-shaped, dichotomously incised, and with a broad to narrow base (Fig.

[1] Kräusel and Weyland, 1926.

166*A–C*). Those on upper branches had narrower dichotomies and a narrow petiole-like base (Fig. 166*D–F*). The fertile leaves (Fig. 166*G*) were broadly fan-shaped, dichotomously forked, and with each ultimate dichotomy terminating in a single sporangium that contained many spores. The structure of the sporangial jacket is unknown.

ORDER 2. COENOPTERIDALES

The Coenopteridales had erect stems that were monostelic and usually protostelic. The leaves were borne spirally, were of relatively large size,

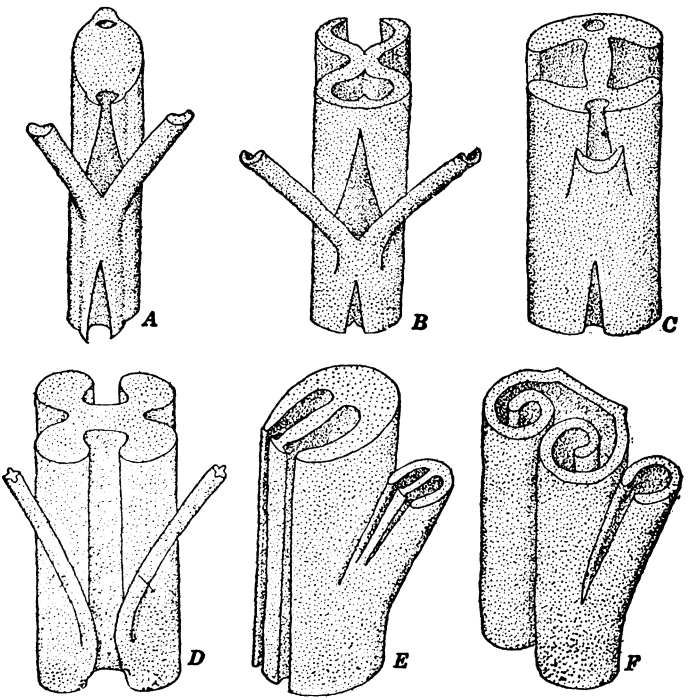

FIG. 167. Stereodiagrams of xylem of rachis of Coenopteridales. *A*, *Dineuron pteroides* Bertr. *B*, *Diplolabis roemeri* (Solms) Bertr. *C*, *Etapteris bertrandi* Scott. *D*, *Stauropteris* sp. *E*, *Botryopteris americana* Graham. *F*, *Anachoropteris involuta* Hoskins. (*A–C*, *after Posthumus*, 1925; *D*, *after Zimmermann*, 1930; *E–F*, *after Darrah*, 1941.)

and were with or without all parts lying in one plane. Sporangia were generally pedicellate and borne terminally on the ultimate divisions of a leaf.

Some paleobotanists[1] think that the sporophytes of certain genera attained a size comparable to that of the tree ferns of today. Leaves of coenopterid ferns were of two distinct types. One type of leaf, the **phyllophore,**[2] had a primary axis intermediate between a stem and a typical

[1] Darrah, 1941; Sahni, 1933. [2] Bertrand, 1933.

rachis. The primary feature of a phyllophore is the bilateral symmetry in two planes of the bundle of the rachis (Fig. 167*A–D*). This is correlated with the fact that all secondary segments of the phyllophore were not borne in the same plane (Fig. 169). The vascular bundle of petiole and rachis of the other type of coenopterid fern was bilaterally symmetrical in one plane only (Fig. 167*E–F*). This is correlated with the fact that all secondary segments of the leaf were borne in one plane as in "modern" ferns.

Similar to certain present-day ferns the stems and petioles of some coenopterid ferns bore the small blade-like outgrowths called **aphlebiae.** All aphlebiae of vascular plants are not homologous structures and the problem of their nature[1] is an unsettled one.

Genera with phyllophores have been placed[2] in a suborder with three families; and the other genera in a second suborder, also with three families. Genera with phyllophores seem sufficiently related to one another to be placed in a single family. When sporangia of the remaining genera are taken into consideration they differ enough to be placed in two families.

FAMILY 1. ZYGOPTERIDACEAE

The Zygopteridaceae include all genera in which the leaf was a phyllophore. The stems were erect or clambering and had a more or less complicated actinostelic central cylinder. The sporangia were borne in pedicellate clusters on the ultimate segments of a leaf. The jacket layer of a sporangium was more than one cell in thickness and had a definite or indefinite annulus. Members of this family have been found from the Middle Devonian to the Permian.

The type genus, *Zygopteris,* was originally based upon a discovery of petioles with a distinctive type of H-shaped vascular bundle. The type species of the genus, *Z. primaria* (Cotta) Corda, has been shown[3] to have had a stem referable to the stem genus *Botrychioxylon* and a leaf referable to the leaf genus *Etapteris.* This does not mean that all the various species recognized in *Etapteris* were borne on a *Botrychioxylon* type of stem, or that all *Botrychioxylon* stems had an *Etapteris* type of leaf. The sporophyte of *Z. primaria* grew erect and it is thought[3] to have been a tree fern. The stem (Fig. 168) was relatively slender and partially held erect by a surrounding sheath of intermingled leaf bases and adventitious roots. The stem is quite unusual for ferns in having had the stellate primary xylem encircled by radially arranged secondary wood elements. Leaf traces connecting leaf base and stele of the stem were more or less cylindrical and with secondary wood. Adventitious roots arose directly from the stem and sometimes from the leaf base. They were usually

[1] Browne, 1935; Darrah, 1941; Hirmer, 1927.
[2] Bertrand, 1933. [3] Sahni, 1933.

diarch, though sometimes triarch, and with a considerable amount of secondary xylem lateral to the metaxylem of the primary xylem.

The vascular bundle in the rachis was H-shaped and without secondary wood (Fig. 167*C*). The general structure of the leaf (phyllophore) is better known for species referable to *Etapteris* than it is for the *Etapteris* type of leaf borne by *Zygopteris*. Leaves of *Etapteris* were large and one species, *E. diupsilon* (Will.), had a rachis up to 2 cm. in diameter. The leaves were pinnately divided and had the pinnae borne alternately on the rachis. Each of the primary pinnae immediately forked into two pinnules lying at an angle to the plane in which the pinnae were borne (Fig. 169). There were generally pinnules of a secondary order and these were also at an angle to the pinnules on which they were borne. Certain of the pinnules of a leaf were fertile; others were sterile.

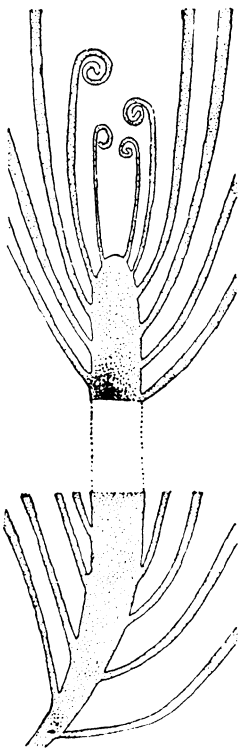

FIG. 168. Reconstruction of vertical sections through upper and lower portion of *Zygopteris primaria* (Cotta) Corda. (*Based upon Sahni*, 1933.)

E. lacattei Renault has been found in a fertile condition.[1] Its sporangia were borne terminally on di- or trichotomously branched pedicels that were without flattened appendages. Typical H-shaped vascular bundles have been noted within certain portions of the pedicels. The jacket of a sporangium seems to have been more than one cell in thickness and with a disintegration of all but the outermost cell layer when mature. On opposite sides of the sporangial jacket, and extending from base to apex, was an annulus several cells in breadth (Fig. 170). The sporangia contained a large number of small spores and there is some indication that the young spores were surrounded by a tapetum.

FAMILY 2. BOTRYOPTERIDACEAE

The Botryopteridaceae had leaves in which the vascular bundle was bilaterally symmetrical in one plane only. The sporangia were borne in pedicellate tufts on primary divisions of a leaf. Members of this family are known from the Lower Carboniferous to the Permian.

Botryopteris, the type genus, is of frequent occurrence in coal balls found in Europe and in the United States. Very few compressions show-

[1] Renault, 1876.

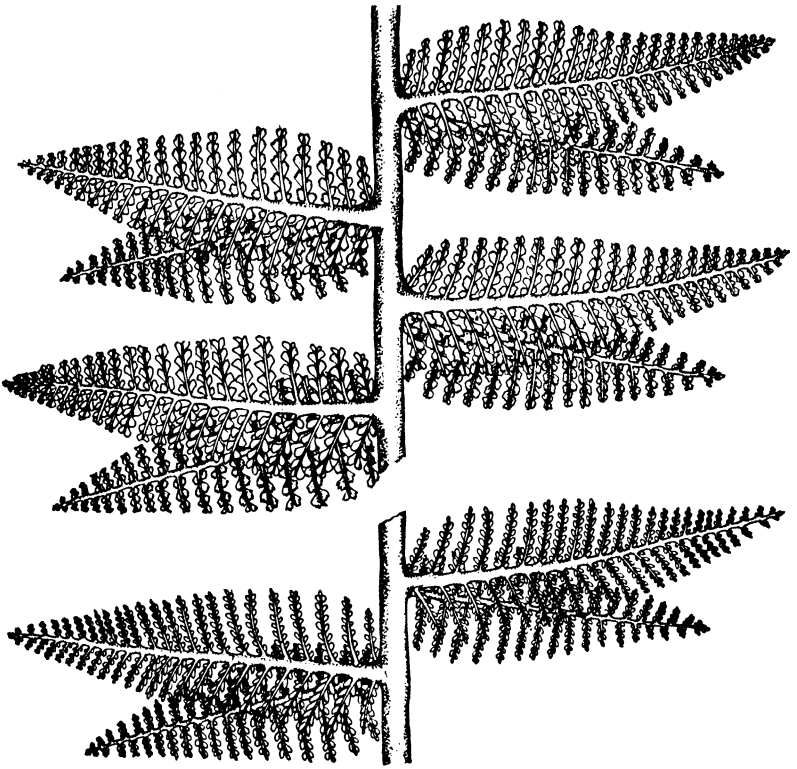

FIG. 169. Reconstruction of leaf of *Etapteris lacattei* Renault. (*After Hirmer in Wettstein*, 1933.)

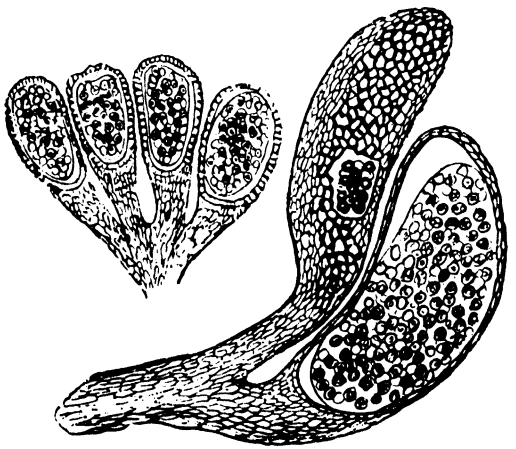

FIG. 170. Sporangia of *Etapteris*. (*From Renault*, 1876.)

ing the general habit of the sporophyte have been found. However, so many sections of various parts of the sporophyte are known that it is possible to visualize its general appearance. It had an upright, more or less branched stem that was 1 to 15 mm. in diameter. The leaves were borne spirally along a stem and sometimes with a definite $\frac{2}{5}$ phyllotaxy. The lower part of a stem had numerous adventitious roots, and several of them were borne in the vicinity of each node.

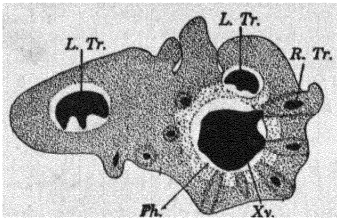

FIG. 171. *Botryopteris ramosa* Williamson. Diagram of a transverse section of a stem. (*L. Tr.*, leaf trace; *Ph.*, phloem; *R. Tr.*, root trace; *Xy.* xylem.) (*Based upon Scott*, 1920.) (× 4.)

The stele of a stem (Fig. 171) was surrounded by a broad homogeneous cortex with a well-defined endodermis.[1] The stele was protostelic and with a layer of phloem surrounding a cylindrical mass of xylem. Roots were diarch and with a general structure much like that of roots of many present-day ferns.

The rachis of a leaf had a more or less **E**-shaped vascular bundle (Fig. 167*E*), with the three prongs of the **E** abaxial and each tipped with a small mass of protoxylem. The rachis bore alternately arranged pinnae with **E**-shaped bundles, and there is questionable evidence that the pinnae bore flattened pinnules with a dichotomously branched venation.[2]

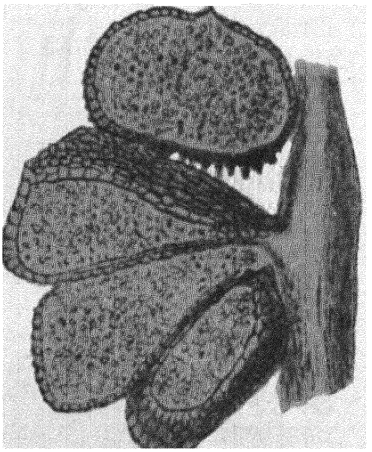

FIG. 172. Sporangia of *Botryopteris*. (*From Renault*, 1875.)

Pinnae of *Botryopteris* have been found bearing sparingly branched[3] or much-branched[4] appendages with vascular strands. Each ultimate branch of an appendage terminated in a single sporangium (Fig. 172). A sporangium had a jacket layer two cells in thickness[3] and with superficial cells on one side differentiated into an annulus. All spores within sporangia were of the same size.

FAMILY 3. ANACHOROPTERIDACEAE

The Anachoropteridaceae had a rachis with a **C**-shaped vascular bundle that was bilaterally symmetrical in but one plane. The sporangia were

[1] Benson, 1911; Scott, 1920. [2] Darrah, 1941.
[3] Renault, 1875. [4] Darrah, 1939.

borne in sori on the margins of flattened pinnules. Members of this family have been found in the Lower and Upper Carboniferous. The family consists of a fairly well known genus (*Anachoropteris*) and another one (*Gyropteris*) known only from fragments of the leaf base.

The vascular bundle of petiole and rachis of *Anachoropteris* was C-shaped and with revolute free margins (Fig. 167*F*). The outline of the petiole shows that the convex face of the bundle was toward the stem; not away from it as in "modern" ferns with C-shaped bundles. The major portion of the xylem of a bundle consisted of metaxylem and on its convex face were four small groups of protoxylem.[1] Nonvascular portions of petiole and rachis had a subepidermal zone of sclerenchyma and had parenchyma inward from it.

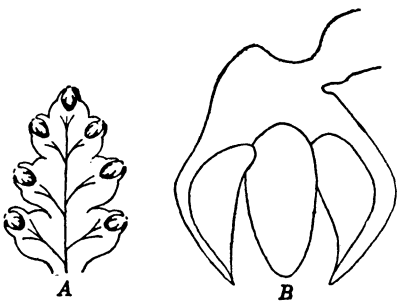

FIG. 173. *Anachoropteris pulchra* Corda. *A*, fertile pinnule. *B*, sporangia. (*A*, *after Hirmer*, 1927; *B*, *after Kubärt*, 1917.)

The sori were synangial in nature (see page 298) and each contained four sporangia.[2] One synangium was borne at the apex and others along the lateral margins of a flattened pinnule (Fig. 173). Each synangium was surrounded by a cup-like sheath of leaf tissue, several cells in thickness, and there is some indication that the sporangia were laterally separated from one another by thin-walled parenchyma. The jacket of a sporangium seems to have been one cell in thickness and without an annulus. The sporangia were large and with an estimated spore output of over 5,000 spores.[2] It is thought that sporangia opened apically and that they spread apart from one another when they opened.

The manner in which sporangia are borne by leaves of *Anachoropteris* shows a close approach to that in the Marattales. Thus, of all the Primofilices, the Anachoropteridaceae may be the most nearly related to "modern" ferns.

ORDER 3. ARCHAEOPTERIDALES

The Archaeopteridales had pinnately divided leaves with all pinnae and pinnules in the same plane. A pinna bore sterile pinnules only, fertile pinnules only, or both. Fertile pinnules had their sporangia restricted to the adaxial side and borne on simple or branched pedicels. At least certain members of the order were heterosporous.

There is but one family, the Archaeopteridaceae, known only from the Devonian. Several species have been described for *Archaeopteris*, a genus of scarce occurrence in Middle Devonian and abundant in Upper Devo-

[1] Bertrand, 1913; Scott, 1920. [2] Kubärt, 1917.

nian deposits. *Svalbardia*, a Devonian genus thought[1] to be related to *Archaeopteris*, probably should be placed in the family.

Archaeopteris is known only from carbonized compressions of leaves. Although unknown, the stem is thought[2] to have been erect and short, rather than prostrate and elongate. The leaves were large and those of *A. hibernica* (Forbes) Dawson are known[3] to have attained a length of

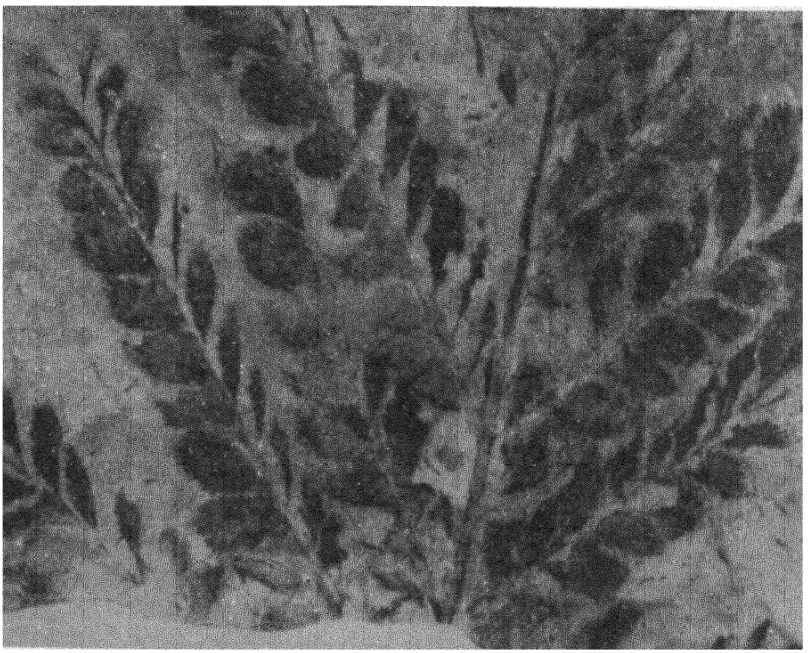

FIG. 174. *Archaeopteris latifolia* Arnold. Portion [illegible] **Arnold, 1947.)**

nearly 2 meters. A leaf had a rachis that bore subopposite pairs of pinnae. In addition, a rachis bore a pair of stipules at its base and at irregular intervals bore small flattened appendages more or less similar to aphlebiae. A pinna bore alternately arranged pinnules. Some pinnae had sterile pinnules only (Fig. 174); others had fertile pinnules only; and still others had both sterile and fertile pinnules (Fig. 175*A*). The sterile pinnules were flattened, oval to wedge-shaped, and with entire or incised apices. The vein of sterile pinnules was repeatedly dichotomous and extended to the apex of a pinnule.

At one time paleobotanists thought that *Archaeopteris* was a pteridosperm and that fertile portions found upon leaves were male fructifications. Today it is almost universally agreed that *Archaeopteris* is a fern

[1] Høeg, 1942. [2] Arnold, 1939. [3] T. Johnson, 1911.

whose sporangia were borne in a psilophyte-like manner comparable to that of other Primofilices. The sporangia terminated branched or unbranched pedicels borne adaxially on a pinnule. The one species whose spores are known[1] was heterosporous and with micro- and macrosporangia intermingled with one another on the same pinnule. Both kinds of sporangia were approximately the same length, but the breadth of macrosporangia was about double that of microsporangia (Fig. 175*B*). Macrosporangia contained either 8 or 16 macrospores, and microsporangia contained more than a hundred microspores. The heterospory was pronounced, the macrospores having a diameter about ten times that of microspores (Fig. 175*C–D*).

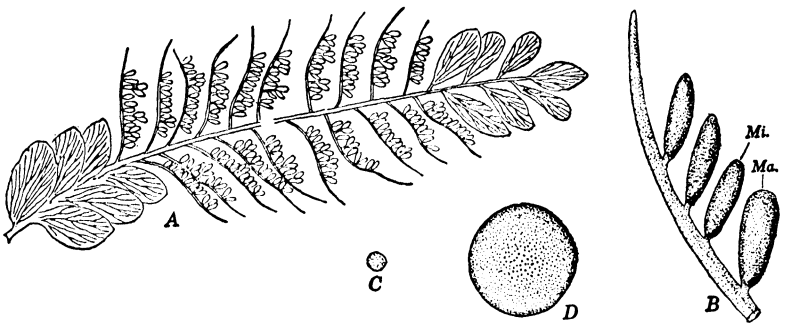

FIG. 175. *A*, *Archaeopteris hibernica* (Forbes) Dawson. Pinna with sterile and fertile pinnules. *B–D*, *Archaeopteris latifolia* Arnold. *B*, reconstruction of a portion of a fertile pinnule with microsporangia (*Mi.*) and a macrosporangium (*Ma.*). *C*, microspore. *D*, macrospore. (*A*, *after Schimper*, 1869; *B–D*, *based upon Arnold*, 1939.) (*C–D*, × 500.)

Although among the most ancient of known ferns, *Archaeopteris* has certain features more advanced than other ferns of the Devonian and Carboniferous. From the vegetative standpoint its leaves resemble those of "modern" ferns more than they do those of ancient ferns. From the reproductive standpoint it is more advanced than other Palaeozoic ferns in being heterosporous.

SUBCLASS 2. EUSPORANGIATAE

The Eusporangiatae produce their sporangia either upon a specialized portion (the **fertile spike**) of a leaf blade, or produce them in sori borne on the abaxial face of a leaf blade. Sporangia contain an indefinite large number of spores and have a jacket layer more than one cell in thickness. Each sporangium develops from a group of initial cells. Antheridia of living species are embedded in the gametophyte and contain many antherozoids. The subclass is known from the Carboniferous to the present day.

[1] Arnold, 1939.

Sporangia of Eusporangiatae resemble those of Primofilices in having a jacket layer more than one cell in thickness, but differ in not being like those of psilophytes. Sporangia are immediately distinguished from those of Leptosporangiatae by their development from more than one initial cell, their jacket more than one cell in thickness, and the large and indefinite number of cells within them.

The Eusporangiatae are of two general types, one known only in the living condition, the other with living representatives and a fossil record extending back to the Carboniferous (Fig. 162). The differences between the two are so great that they are placed in separate orders.

ORDER 1. OPHIOGLOSSALES

The Ophioglossales differ from all other Filicinae in having the sporangia borne on an outgrowth, the **fertile spike,** projecting adaxially from a leaf and near the juncture of blade and petiole.

No fossil members of the order are known. According to the most recent monograph[1] there are three genera. Two of these, *Ophioglossum* (with 28 species) and *Botrychium* (with 23 species), are world-wide in distribution; the third (*Helminthostachys*) is monotypic and found only in the Indo-Malayan region. These three genera are placed in a single family, the Ophioglossaceae.

Despite the lack of a fossil record to show their antiquity, there is a general agreement that the Ophioglossales are a primitive stock. It has been held[2] that they are "an imperfectly modernized relic of the Palaeozoic flora" and a relic that represents a blind evolutionary series from the Primofilices of the Carboniferous. They are a group in which, according to the criteria listed on page 267, there has been considerable progress in evolution of vegetative parts of the sporophytes as against a retention of primitive characters in parts concerned with reproduction in both sporophyte and gametophyte.

Ophioglossum, the genus discussed on succeeding pages, is a somewhat specialized member of the order and somewhat more advanced than the other two genera. Its fertile spike (Fig. 176*A–B*) seems to represent a condensation from the branched condition found in the more primitive *Botrychium* (Fig. 176*C*). Other reasons for considering *Ophioglossum* more advanced than *Botrychium* are the closed venation of leaves of all species, and the division of the leaf traces into several strands in certain species.[2] It is a more favorable genus for study of vegetative structure of the sporophyte since there is no obvious secondary thickening as in *Botrychium.*

The sporophyte of most species of *Ophioglossum* has a short, upright, subterranean stem. A few species (including *O. pendulum* L.) have a

[1] Clausen, 1938. [2] Bower, 1926.

markedly dorsiventral stem. Branching of the sporophyte is generally due to a formation of buds in the axils of leaves. Occasionally, however, it is due to a dichotomy of the stem apex.[1] The stem bears numerous adventitious roots (Fig. 176*A*). As a rule these are borne singly below the leaf scars of previous seasons and the leaf, or leaves, of the current season. A majority of the species produce but one leaf each year. Some species, especially those growing in the tropics, may produce four or five leaves in a single season. The leaves are borne in an irregular

FIG. 176. *A–B*, *Ophioglossum moluccanum* Schlecht. *A*, sporophyte. *B*, fertile spike. *C*, leaf of *Botrychium silaifolium* Presl. (*A*, × ⅔; *B*, × 2½; *C*, × ⅓.)

spiral on the stem. Sometimes they appear to be in a two-ranked arrangement, but there is no true dorsiventrality in the insertion of these leaves.[2] The embryonic leaf at a stem apex of species producing but one leaf a year develops slowly for three years and then grows above ground and unfolds the fourth year. Unfolding leaves of *Ophioglossum* do not have the spiral uncoiling (circinate vernation) so characteristic of Filicinae. A fully expanded leaf is sharply differentiated into blade and petiole. In all but one species there is a single fertile spike at the juncture of blade and petiole. This is usually unbranched, but it may have one or two irregular branchings. *O. palmatum* L. is exceptional in

[1] Petry, 1915. [2] Petry, 1914.

that it has several small fertile spikes in the region where blade and petiole adjoin. The blades of all species but *O. palmatum* are entire and narrowly linear to broadly ovate in outline. In *O. palmatum* the blade is palmately incised into a number of narrow segments. The venation of the blade is always reticulate and, according to the species, is with or without small veinlets ending blindly within the larger meshes (Fig. 179*A*). There is no midrib, but the veins near the central axis of the blade may be more conspicuous than others.

There is a single inconspicuous pyramidal apical cell with three cutting faces[1] at the apex of a stem. Derivatives cut off from the apical cell divide and redivide to form an embryonic tissue that becomes differentiated into stele, cortex, and epidermis when it matures. The first-matured (lowermost) portion of a stem may have an endodermis delimiting stele and cortex;[2] higher up there is no endodermis. Here the innermost cortical cells and the outermost stelar cells are so similar in appearance that it is impossible to tell where one region leaves off and the other begins. Cases have been found[2] where the basal portion of the stem is protostelic and the upper portion siphonostelic. Generally, however, the stem is siphonostelic throughout its entire length. The siphonostele may be solenostelic and may have but one leaf gap when cut at any particular level, but more often there is an overlapping of gaps and a dictyostelic condition (Fig. 177*A–B*). A large majority of the species have a single leaf trace departing at each gap and transversing the cortex without branching. A few species, including *O. palmatum* L.[3] and *O. pendulum* L.,[4] have two traces departing at each gap and a division of each trace into several strands before it runs into the leaf base.

The xylem portion of a meristele is endarch in arrangement and has the protoxylem lining the entire inner face of the xylem mass (Fig. 177*C*). The metaxylem is composed of irregularly shaped reticulate tracheids whose length is rarely more than six times the breadth. A small amount of secondary thickening has been observed in the stem of *O. vulgatum* L.[5] All the phloem lies external to the xylem. Generally it is a layer four or five cells in thickness, but that of *O. pendulum*[4] is uniformly a single layer of cells separated from the xylem by a layer of parenchyma three to five cells in thickness. The pith internal to the xylem is usually a homogeneous thin-walled parenchyma of relatively large cells, but sometimes, as in *O. pendulum*, there may be small strands of xylem within the pith.[4] The cortical portion of the stem is also generally a uniform thin-walled parenchyma. In some cases[6] a periderm is differentiated in the superficial portion of the cortex, but this never has a functional phellogen.

[1] Campbell, 1918. [2] Bower, 1911*A*. [3] Bower, 1911*B*. [4] Petry, 1914.
[5] Boodle, 1899. [6] Campbell, 1911; Maheshwari and Singh, 1934.

The roots of *Ophioglossum* are without root hairs and have the free faces of the epidermal cells thickened and suberized (Fig. 178). The cortex is massive and has the innermost cell layer differentiated into an endodermis with well-defined Casparian strips. The remainder of the cortex consists of two concentric regions of approximately equal

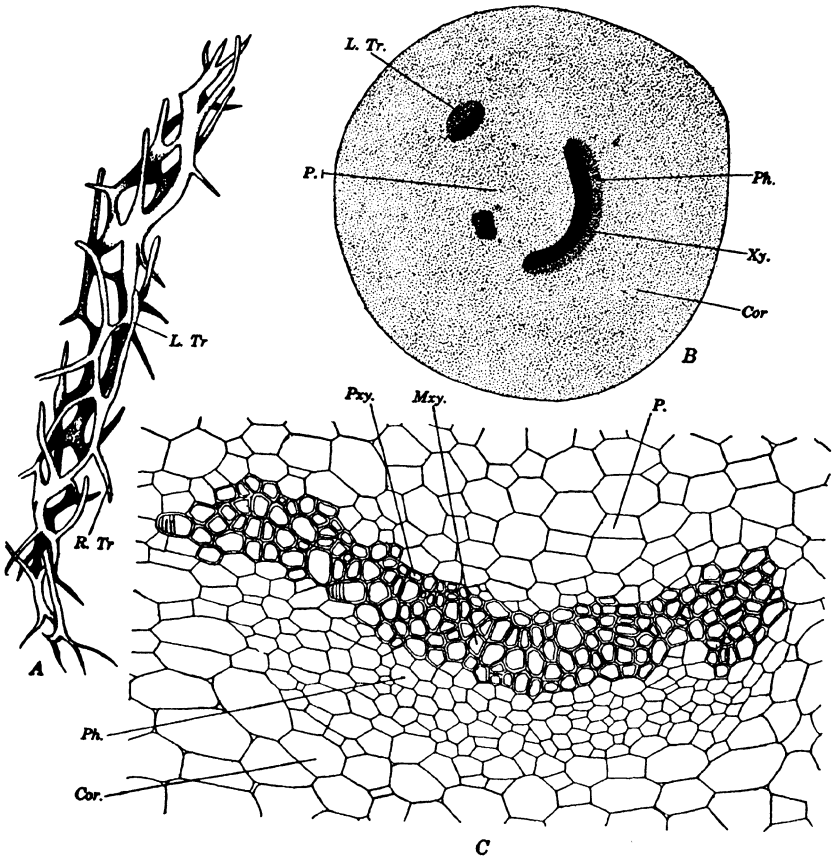

FIG. 177. *Ophioglossum vulgatum* L. *A*, vascular skeleton of the stem. *B*, transverse section of the stem. *C*, transverse section of a meristele. (*Cor.*, cortex; *L. Tr.*, leaf trace; *Mxy.*, metaxylem; *P*, pith; *Ph.*, phloem; *Pxy.*, protoxylem; *R. Tr.*, root trace; *Xy.*, xylem.) (*A*, *after Rostowzew*, 1891). (*B*, × 21; *C*, × 160.)

thickness. The outer region is composed of angular cells without intercellular spaces, and a mycorhizal fungus is generally present in this portion of the cortex. This fungus is obviously a phycomycete, but, owing to the lack of fruiting bodies, it is impossible to determine whether or not it is identical with the oömycete (*Stigeosporium marattiacearum* West) found in roots of Marattiales. The inner region of the cortex has

rounded cells with intercellular spaces. Cells in this region frequently contain starch grains. The stele of a root is generally monarch or diarch. Tri- and tetrach steles have been observed in a few species. Diarch steles have the usual plate of xylem with a protoxylem mass at each pole. There is a mass of phloem on either side of the xylem. Each of the phloem masses is separated from the xylem by a parenchymatous tissue

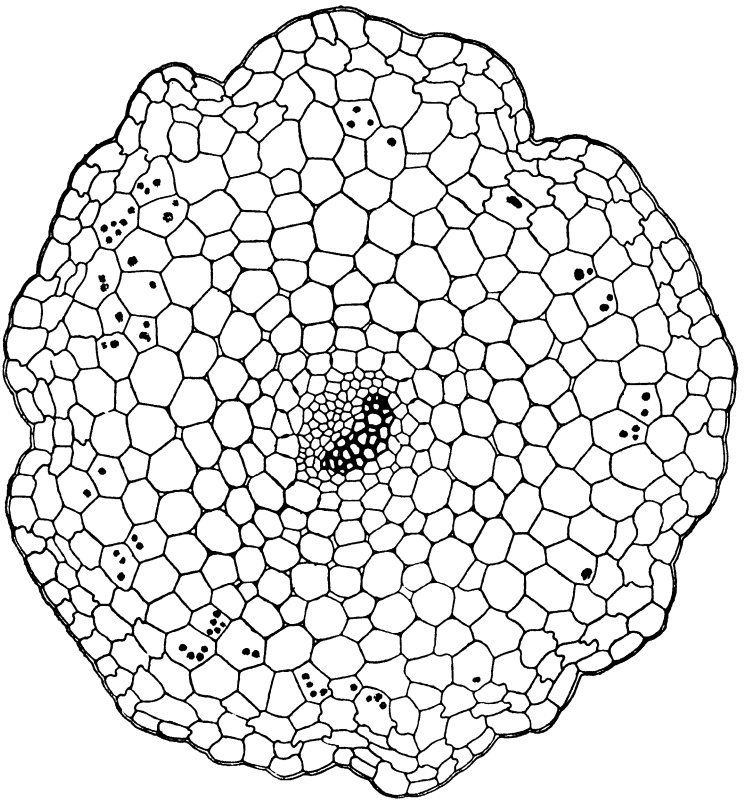

FIG. 178. *Ophioglossum vulgatum* L. Transverse section of a root. (× 120.)

two to three cells in thickness. Some monarch roots have the xylem and phloem radial to each other. Others have the xylem and phloem masses with their broader sides facing each other (Fig. 178). It is very probable that monarch steles of the latter type have been derived from diarch steles by a suppression of one of the phloem masses. Evidence supporting this assumption is the occasional incomplete suppression of the second phloem mass[1] and the occurrence of two protoxylem points on the xylem mass.

[1] Boodle, 1899.

The trace, or pair of traces, departing to a leaf always become divided into strands that lie parallel to one another throughout the length of the petiole. Certain of these strands in a petiole run to the fertile spike; others run to the sterile blade. Exclusive of the vascular strands, the interior of a petiole is composed of a spongy parenchyma that may or may not have conspicuous cavities in the central region. Parenchyma cells just beneath the epidermis frequently contain numerous chloroplasts. The epidermal layer of a petiole is not heavily cutinized. The sterile blade has a structure resembling that of a petiole. If the species is one with erect leaves, stomata are present in equal numbers on both faces of the blade; if, as in *O. reticulatum* L., the leaf lies more or less horizontally, there are more stomata in the upper epidermis.[1] The mesophyll

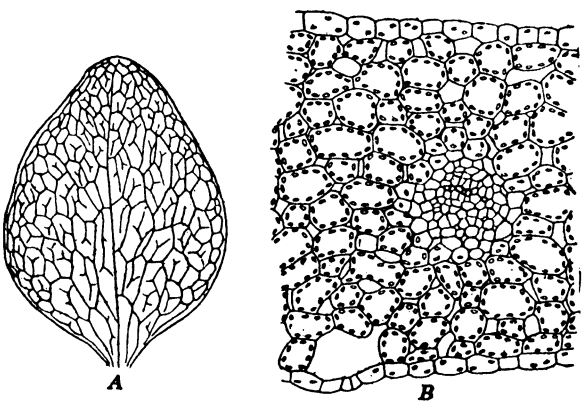

FIG. 179. *A*, *Ophioglossum moluccanum* Schlecht. Surface view of a leaf blade. *B*, *Ophioglossum pendulum* L. Transverse section of a leaf blade. (*A*, × ¾; *B*, × 80.)

of a blade is composed of vascular tissue and a spongy parenchyma in which all the cells contain chloroplasts (Fig. 179*B*).

A very young fertile spike is a conical hump of meristematic tissue which grows by means of a pyramidal apical cell with four cutting faces. The four quadrants recognizable in transverse sections cut just back of the apex of the spike correspond to the four cutting faces of the apical cell.[2] They are so oriented that two lie in a plane perpendicular to the sterile blade, and two in a plane parallel to it. As development continues, there is the differentiation of a vertical strip of cells in the epidermal layer of the two quadrants in the plane parallel to the leaf blade. Each strip, which is two to three cells broad and several cells tall, is a **sporangiogenic band.**[2] The two bands become three or four cells in thickness soon after they are recognizable (Fig. 180*A*). At this time there is a differentiation of the hypodermal region of the band into alternate

[1] Campbell, 1911. [2] Bower, 1896.

superimposed blocks of archesporial cells and sterile cells (Fig. 180*B*). Each group of archesporial cells divides and redivides to form a large number of sporogenous cells. The portion of the band external to each archesporium divides periclinally to form a jacket layer that is several cells in thickness when the sporangium is mature (Fig. 180*C*). There are also a division and redivision of the sterile cells vertically separating the sporangia one from another and the ultimate maturation of an irregularly branched vascular strand within each sterile mass. As the sporogenous tissue continues development, it becomes surrounded by a poorly

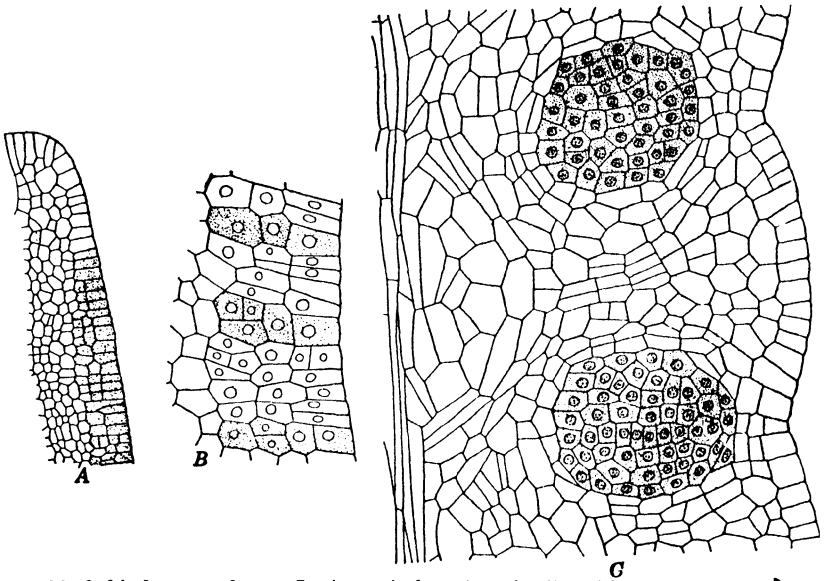

FIG. 180. *Ophioglossum vulgatum* L. *A*, vertical section of spike with sporangiogenic band. *B–C*, very early and somewhat later stages in development of sporangia. (*A–B*, *after Bower*, 1896.) (*A*, × 75; *C*, × 160.)

defined tapetum (Fig. 181). This has been described as arising from the outermost sporogenous cells,[1] but it seems more probable that it comes from cells immediately external to the sporogenous mass. The tapetum ultimately breaks down into a plasmodial mass, with persistent nuclei, that invades the space between the isolated spore mother cells.[2] Each sporangium of the spike opens by a transverse cleft after the spores are mature (Fig. 176*B*), but there is no special mechanism (annulus) causing an opening of the sporangial jacket. Dehiscence seems to result from a drying out and shrinking of the sterile tissues within the spike.

The morphological nature of the fertile spike has been argued at length. There is no need of discussing whether or not it is a single sep-

[1] Bower, 1908. [2] Bower, 1896; Burlingame, 1907.

tate sporangium,[1] since this hypothesis has been rejected by its proponent.[2] During recent years practically all those considering the question are in agreement that it is pinna-like in nature. The pinna-like nature is more evident in *Botrychium*, where the sterile blade is pinnately divided, than it is in *Ophioglossum*, where the blade is entire. It has been held[3] that the spike represents a single pinna, but it is more probable that it represents the fusion of the two basal pinnae of a leaf.[4] One of the reasons for the latter interpretation is that the fertile spike has the same vascular supply as would go to a pair of pinnae. If the plant is abnormal

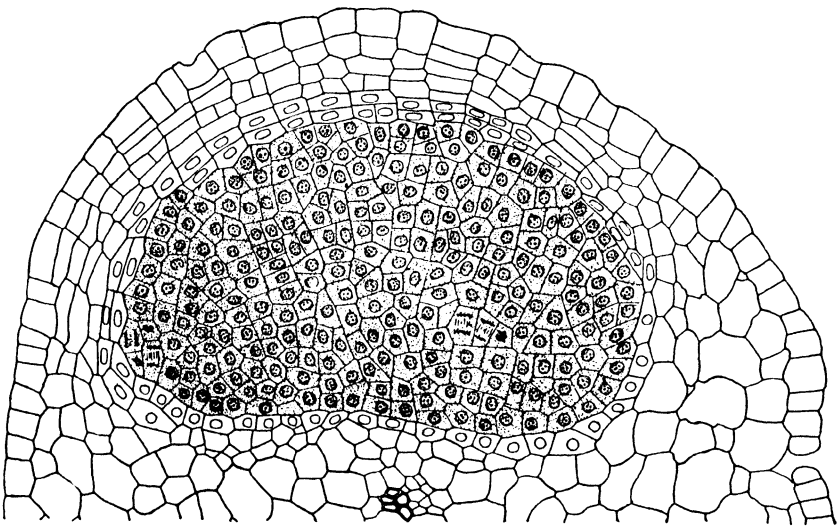

FIG. 181. *Ophioglossum vulgatum* L. Transverse section through a portion of a fertile spike. (× 160.)

and has a pair of fertile spikes instead of one, each spike has the vascular supply that would ordinarily go to a single pinna. The pinna nature of the spike is shown most strikingly by *Botrychium lanuginosum* Wall., a species found in southeastern Asia. Here[5] the spike is inserted in the middle of the blade and in the position of the third to the sixth leaflet from the base.

The gametophyte of *Ophioglossum* may be wholly subterranean in habit and obtain all its food through the agency of a mycorhizal fungus, or it may have small green lobes above ground. Germination of spores to form gametophytes may take place after shedding or may be greatly delayed.[6] In either case, the young gametophyte does not develop beyond the three- or four-celled stage unless it becomes infected with the my-

[1] Bower, 1896, 1908. [2] Bower, 1911*A*, 1926. [3] Goebel, 1915.
[4] Chrysler, 1910. [5] Chrysler, 1925. [6] Campbell, 1911.

corhizal fungus. The spore divides transversely into a lower and an upper cell. Subsequent development is chiefly by division and redivision of the lower cell, but there is a certain amount of division in the upper cell. The fungus which becomes the mycorhizal endophyte always enters through the lower cell (Fig. 182*A*). The largest gametophytes that have been grown from spores consisted of but 13 cells.[1] They were globose and without rhizoids. Possibly there was an apical cell at this stage, but this could not be determined with certainty. Mature gametophytes[2] are irregularly cylindrical to conical and, according to the species, unbranched (Fig. 182*B*) or profusely branched. In most species the gametophyte is perennial, but in *O. moluccanum* Schlecht. it seems to be an annual.[1] The growing apex of a prothallus has a single apical cell with three or four cutting faces. The region immediately posterior to the apical cell is colorless; the remainder of the prothallus is brownish. According to the species, the gametophyte has numerous rhizoids in the older portion[1] or lacks them.[3] There is little differentiation of tissue within a gametophyte, except that cells toward the interior may be somewhat elongate. The apical portion of the thallus and the outer cells in older portions are free from fungi. Interior cells in older parts of a gametophyte are sparingly or abundantly infected with a mycorhizal fungus. These interior cells may also contain numerous starch grains.

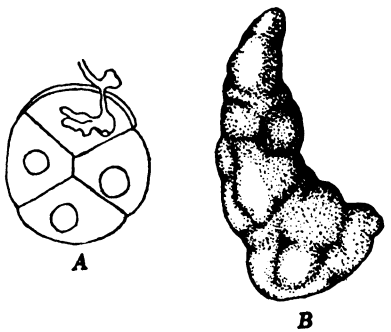

FIG. 182. *Ophioglossum pendulum* L. *A*, four-celled gametophyte. *B*, mature gametophyte. (*A*, *after Campbell*, 1907.) (*A*, × 265; *B*, × 5.)

Sex organs generally begin to develop near the growing tip, sometimes even in a segment but once removed from the apical cell. In *O. pendulum* L. most of them arise in acropetalous succession. Antheridia and archegonia are formed in irregular sequence, and the two are generally indiscriminately intermingled on the lobes of a thallus. The ratio between the two is quite variable, and it is not uncommon to find either antheridia or archegonia markedly predominating on a particular gametophyte.

The antheridium arises from a superficial cell of the gametophyte.[2] This initial divides periclinally into an outer cell (the jacket initial) and an inner cell (the primary androgonial cell). The jacket initial always divides anticlinally and generally into two daughter cells of equal

[1] Campbell, 1907. [2] Bruchmann, 1904; Campbell, 1907; Lang, 1902.
[3] Bruchmann, 1904.

size (Fig. 183*A*). One of these daughter cells, by anticlinal division in a plane diagonal to the first wall, forms two daughter cells—one approximately triangular, the other approximately rectangular. The triangular cell functions in the same manner as an apical cell and successively cuts off a series of cells from each of its three sides. After it has stopped cutting off segments it is known as the **opercular cell** (Fig. 183*E*). As the antheridium approaches maturity the opercular cell becomes brownish and ultimately disintegrates. Eventually there is an escape of the antherozoids through this triangular pore. Division of the primary androgonial cell to form two androgonial cells may be anticlinal or periclinal. In either case the next division is in the opposite plane so that the four androgonial cells lie in two tiers (Fig. 183*A*). Division and redivision is

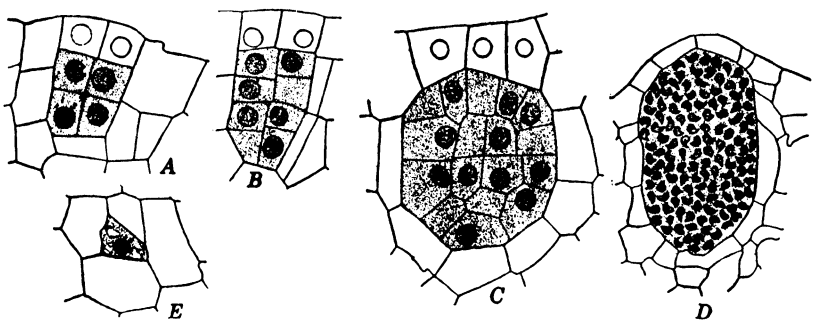

FIG. 183. *Ophioglossum pendulum* L. *A–D*, vertical sections through antheridia at various stages of development. *E*, transverse section through the jacket of an antheridium showing the opercular cell. (*A–C*, *E*, × 215; *D*, × 140.)

long continued in the androgonial tissue (Fig. 183*B–D*), and it has been estimated[1] that an antheridium contains several thousand androgonial cells. Members of the last cell generation of androgonial cells, the androcyte mother cells, have two blepharoplasts at one side of the nucleus.[1] When an androcyte mother cell divides to form two androcytes, each receives one of the blepharoplasts. The first noticeable change in the metamorphosis of an androcyte into an antherozoid is an elongation of the blepharoplast. As metamorphosis continues the blepharoplast becomes coiled into two or more turns and the nucleus also becomes coiled. Shortly after this there is a development of several flagella at the anterior portion of the blepharoplast. The end result is the coiled multiflagellate antherozoid characteristic of all Filicinae. The narrowly coiled anterior portion of the antherozoid consists mainly of blepharoplast and cytoplasm; the broad, loosely coiled posterior portion is mainly nucleus.

Archegonia also arise from a single superficial cell of the prothallus. Division of an archegonial initial is periclinal and into a primary cover

[1] Campbell, 1907.

cell and an inner cell (Fig. 184*A*). This is followed[1] by a periclinal division of the inner cell into a central cell, which lies next the primary cover cell, and a basal cell (Fig. 184*B*). Next to follow is an anticlinal division of the primary cover cell, after which the two daughter cells divide anticlinally to form the four quadrately arranged neck initials (Fig. 184*C*). Diagonally transverse division of each of the neck initials results in a neck composed of two tiers of four cells each (Fig. 184*D*). Accordingly as the cells in one or both tiers divide transversely, the mature neck is three or four cells in height (Fig. 184*E–G*). In either case it is a structure that projects but slightly above the surface of the gametophyte. As the neck is developing there is a periclinal division of the central cell into a

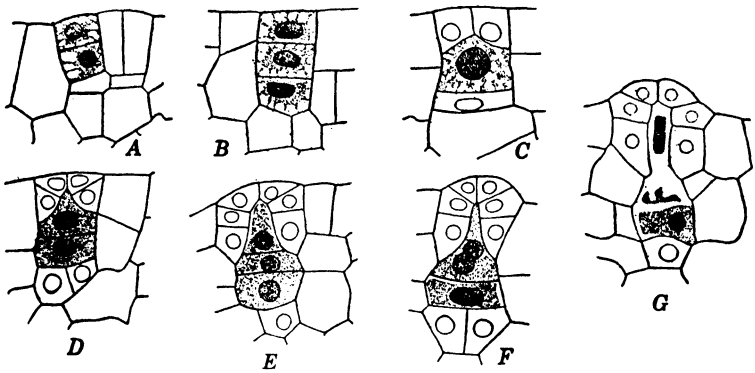

FIG. 184. *Ophioglossum pendulum* L. Vertical sections through archegonia at various stages of development. (× 215.)

primary canal cell and a primary venter cell (Fig. 184*D*). The primary canal cell elongates vertically and pushes out into the neck. Its nucleus generally divides, but this is rarely followed by a division into two canal cells. Shortly before the archegonium is mature there is a division of the primary venter cell into a venter canal cell (which immediately disintegrates) and an egg (Fig. 184*E*). The venter canal cell is such a transitory structure in the ontogeny of an archegonium that it is rarely demonstrable.[2] The last step in archegonial development is a disintegration of the canal cell (or cells) and an opening of the archegonial neck (Fig. 184*G*).

Development of an embryo into a self-sustaining sporophyte with cotyledon and primary root may take a single year (*O. moluccanum* Schlecht.),[2] or it may require several years (*O. vulgatum* L.).[3] Early stages in embryonal development are best known in *O. pendulum* L.,[2] but even here there are many gaps in the developmental history. All species investigated have an approximately transverse division of the zygote

[1] Bruchmann, 1904; Campbell, 1907; Lang, 1902.
[2] Campbell, 1907. [3] Bruchmann, 1904.

(Fig. 185*A*). The meager evidence at hand makes it uncertain whether the hypobasal cell (that farthest from the archegonial neck) develops only into the foot[1] or into the foot and primary root.[2] Irrespective of its precise point of origin, there is an early differentiation of an apical cell in the root portion of an embryo (Fig. 185*B–D*). In some species, including *O. vulgatum*,[2] development of root and foot so overshadows that

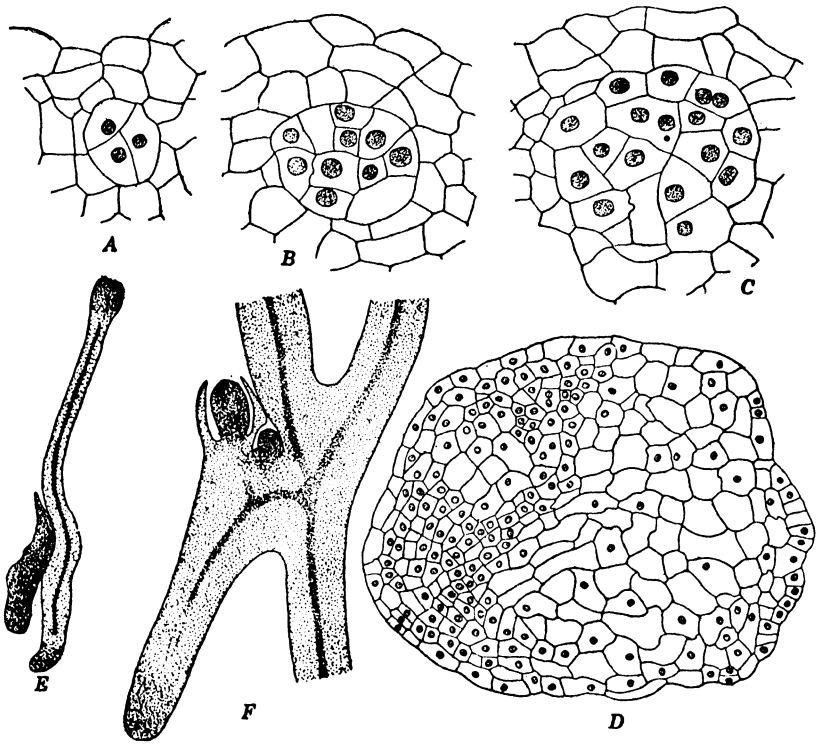

FIG. 185. *A–D, Ophioglossum pendulum* L. Vertical sections through young embryos at various stages of development. *E–F, Ophioglossum moluccanum* Schlecht. *E*, vertical section through a gametophyte and a young sporophyte. *F*, vertical section through a somewhat older sporophyte. (*A–C*, × 160; *D*, × 80; *E*, × 10; *F*, × 20.)

of cotyledon and stem that the young sporophyte appears to be all root for a considerable time after it protudes from the gametophyte. In other species, including *O. moluccanum*,[1] the cotyledon and root grow at an equal rate (Fig. 185*E*). The method of formation of the cotyledon from the epibasal (upper) half of an embryo is unknown. Cotyledonary growth is due to an apical cell, but it is uncertain whether this is differentiated early or late in ontogeny of the epibasal half. After primary root and cotyledon are well along in their development, there is an appearance of

[1] Campbell, 1907. [2] Bruchmann, 1904.

the apical cell of the stem. This appears in the region where cotyledon and root adjoin, and seems to be a superficial cell of the embryonic sporophyte. Development of the stem by means of this apical cell takes place very slowly. The first, second, third, and successively formed leaves on a stem appear to arise in the same manner as do those of other ferns, namely, as meristematic outgrowths slightly posterior to the stem's apical cell.* However, the growth and maturation of leaf tissues greatly overshadow those of stem tissues. Thus the young stem is composed mainly of leaf bases and tissues of adventitious roots formed in association with these leaves (Fig. 185*F*). Later on, when the sporophyte has formed several leaves, there may be a less marked predominance of leaf portions over the stem portion of the plant.

ORDER 2. MARATTIALES

The Marattiales include all the Eusporangiatae in which sporangia are borne on the abaxial face of leaf blades. The sporangia are grouped in sori; and in most genera those of a sorus are laterally adherent to form a **synangium,** but this character is not universal throughout the order. Leaves of Marattiales differ from those of other living ferns in having a pair of stipules at the base of the petiole. Marattiales also differ from other living ferns, except the Ophioglossales, in the eusporangiate development of a sporangium from a group of initial cells, and in structure of the antheridia.

The living species are placed in six genera;[1] some genera with numerous species, others with but one or two species. In addition to the living representatives there are a number of fossil genera that have been referred to the order, either because of the synangial nature of their sori, or because of stem structure. While the systematic position of certain of these genera may be dubious, that of others seems to be sufficiently well established to warrant the statement that members of the order are found as far back as the Middle Carboniferous.[2]

The Marattiales have a number of features in common with the Ophioglossales. These include the eusporangiate formation of sporangia, similarities in ontogeny and structure of sex organs, and late differentiation of cotyledon, root, and stem in the embryo. The presence of so many common features indicates that the two have a mutual ancestry. On the other hand, the marked differences in structure of the mature sporophyte and in the method in which the sporangia are borne seem to indicate that they diverged from each other long ago. The six liv-

* Campbell (1911) holds that all parts of the sporophyte but the cotyledon and primary root are formed from an adventitious bud that arises in the primary root.

[1] Christensen, 1938; Copeland, 1947.

[2] Arnold, 1947; Hirmer, 1927; Scott, 1920; Seward, 1910.

ing genera of Marattiales are so alike that they are generally placed in a single family, the Marattiaceae.

Marattia, the type genus of the family and order, ranges widely throughout tropical regions of both hemispheres. There are some 26 species. Although none of these occurs in the United States, six species are known from Mexico, Central America, and the West Indies.[1]

FIG. 186. *Marattia alata* Smith. Young sporophyte from which all but one of the leaves have been removed. (× ⅓.)

The adult sporophyte of *Marattia* possesses an upright, tuberous, conical, fleshy stem which bears a crown of pinnately divided leaves at its apex (Fig. 186). Each leaf has a pair of stipules at its base and the stem surface below the leaves is covered with leaf scars, each with two persistent stipules. The stem has numerous long adventitious roots, each inserted below a leaf or a leaf scar. In the largest species of *Marattia* the

[1] Underwood and Benedict, 1909.

stem may be half a meter or more in diameter and the leaves 3 or 4 meters in length.

The growing apex of a young stem has a single apical cell. Later on this is replaced by a group of meristematic initials.[1] Young stems and the first-matured portions of old stems generally have an endodermal layer at the inner face of the cortex; later-matured parts of a stem rarely contain an endodermis.[1] The cortex in both old and young stems is wholly parenchymatous. The cortex of *Marattia*, similar to that in all other members of the family, contains numerous mucilage canals and tannin-filled cells.[2]

The vascular cylinder in the first-formed portion of a stem is protostelic. At the level of the third or the fourth leaf, there is an abrupt transition to a siphonostelic organization.[3] The protostelic and lowermost siphonostelic portions of the vascular cylinder have a single trace departing to each leaf. In the later-formed portions of the siphonostele there are two traces to each leaf. Shortly above the level where the stem has become siphonostelic, there is a strand of vascular tissue (the **commissural strand**) that runs diagonally across the pith at each node. The relationship of this strand to the vascular skeleton appears to better advantage in *Danaea* (Fig. 187*C*), a member of the family that has longer internodes than does *Marattia*. Stems of older plants of *Marattia* have the commissural strand broken up into strands that lie in a ring internal to the vascular cylinder. It is the presence of this ring of strands, as well as the numerous leaf traces and root traces, that makes transverse sections of old stems so difficult of interpretation (Fig. 187*B*). It is not improbable that very old stems may have the vascular tissues in three or more concentric rings.[4]

The root system of *Marattia* is composed of a number of adventitious roots, one of which is generally formed below each leaf. The vascular tissue of a root may connect with the vascular cylinder of the stem just below departure of a leaf trace, or it may connect with the system of commissural strands internal to the main vascular cylinder.[4] Each of the roots may bear several irregularly distributed lateral roots. The chief difference between the internal organization of older roots in Marattiales, of which *Marattia* (Fig. 188) is quite typical, and that of roots in other Filicinae is the polyarch actinostelic organization of the vascular cylinder. In *Marattia* the number of protoxylem points may be as high as twelve.[5] The cortex is a uniform parenchyma with numerous mucilage canals. The first-formed roots generally contain a mycorhizal oömycete (*Stigeosporium marattiacearum* West) within their cortices. Later-formed roots generally lack the endophyte.[6]

[1] Charles, 1911. [2] West, 1915. [3] Brebner, 1902; Charles, 1911; West, 1917*A*.
[4] West, 1917*A*. [5] Campbell, 1911. [6] West, 1917.

Very young leaves have a precocious growth of their stipules to form a protective sheath around the young blade and petiole; later on there is an elongation of the leaf tip beyond the stipulary sheath. This elongation is by the spiral uncoiling (circinate vernation) characteristic of most Filicinae. Well-developed leaves of *M. alata* Smith may be 2 to 3 meters in length and have a petiole 5 to 6 cm. in diameter. The blade of *M. alata* is three to five times pinnately compound and has the ultimate

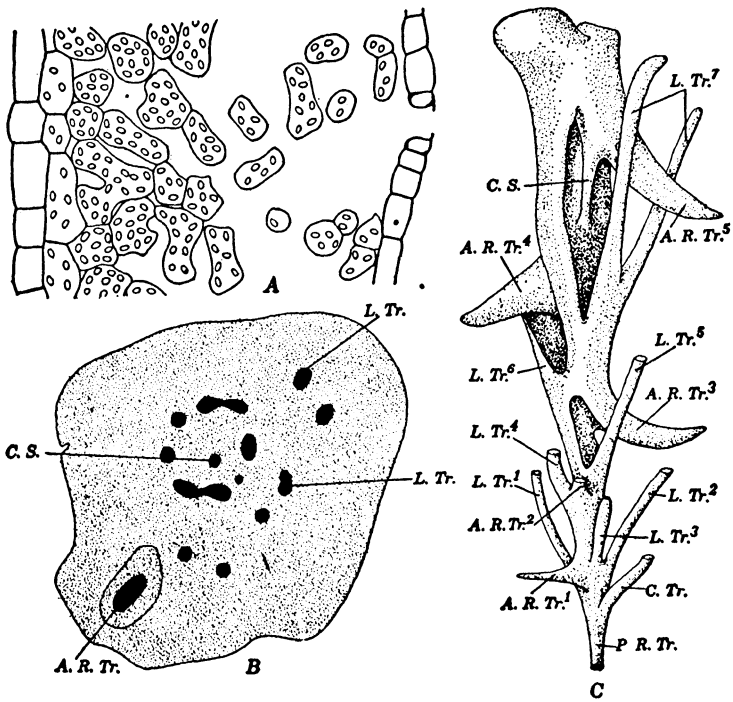

FIG. 187. *A*, *Marattia fraxina* Smith. Transverse section of a leaf. *B*, *Marattia alata* Smith. Transverse section of stem. *C*, *Danaea alata* Smith. Stereodiagram of vascular system of stem. (*A.R.Tr.*, adventitious root traces; *C.S.*, commissural strand; *C.Tr.*, cotyledonary trace; *L.Tr.*, leaf trace; *P.R.Tr.*, primary root trace.) (*C*, *after West;* 1917*A*.) (*A*, × 215 *B*, × 3.)

pinnules about 2 cm. long. A pinnule has a conspicuous main vein (midrib) and alternately disposed lateral veins. Certain of the lateral veins are simple; others are dichotomously forked. In either case their apices end blindly near the margin of the pinnule. The internal organization of a blade resembles that of an angiosperm in that there is a compact palisade-like tissue beneath the upper epidermis and a loose spongy tissue next the lower epidermis (Fig. 187*A*). Stomata are restricted to the lower epidermis. Sooner or later there is the formation of an abscis-

sion layer at the base of the petiole. When the leaf falls away, it leaves a clean-cut leaf scar, flanked on either side by a persistent stipule.

The sporangia of *Marattia* are borne in more or less linear sori. These lie below the lateral veins, on the lower side of a pinnule, and some distance in from the margin of the pinnule (Fig. 189*A*). The sporangia in each sorus are in two rows and laterally fused with one another to form a **synangium** (Fig. 189*F–H*). The number of sporangia in a synangium ranges from 12 to 36.

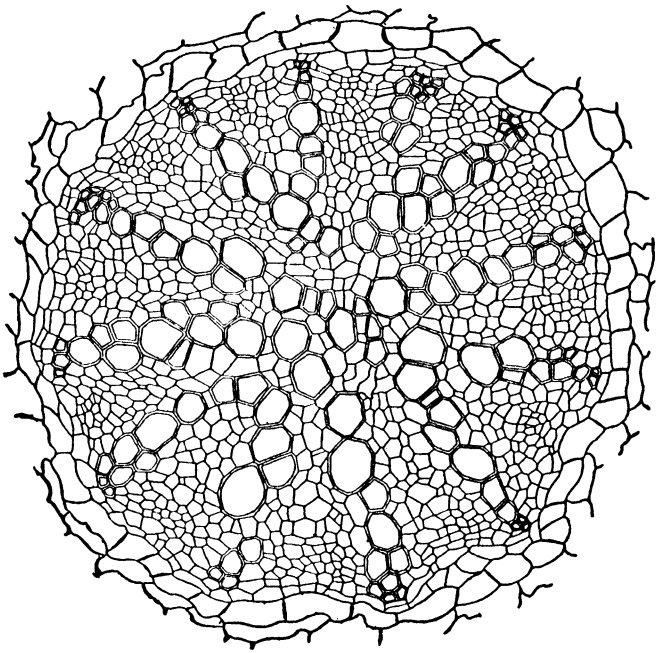

FIG. 188. *Marattia alata* Smith. Transverse section of stele of root. (× 160.)

The first evidence of sporangial development is a greater accumulation of cytoplasm in certain epidermal cells lying in localized areas on the underside of a pinnule.[1] At first each area, the receptacle of a sorus, is flush with the leaf surface; soon the sides of the receptacle, but not the axial portion, become somewhat elevated (Fig. 189*B–C*). Elevation of the receptacle above the leaf surface is accompanied by a development of unbranched multicellular hairs from immediately adjoining epidermal cells. Development of the individual sporangia generally begins with a periclinal division of a single cell in the receptacle, the sporangial initial (Fig. 189*C*). Occasionally a sporangium has more than one initial cell.

[1] Bower, 1897.

The outer daughter cell formed by periclinal division of an initial cell is the jacket initial; the inner cell is the archesporial cell. Division and redivision of the archesporial cell eventually result in a sporogenous tissue of some 500 spore mother cells (theoretically 512).[1] Since all spore mother cells are functional, there is a potential output of 2,048 spores in a sporangium. Formation of the sporogenous tissue is accompanied by periclinal and anticlinal division of the jacket initial to form the apical portion of the jacket layer (Fig. 189*D–E*). The remainder of the jacket layer is derived from cells lateral to the sporangial initial. Sporangial development in *Marattia*, as in all other Marattiales, is, therefore, of the

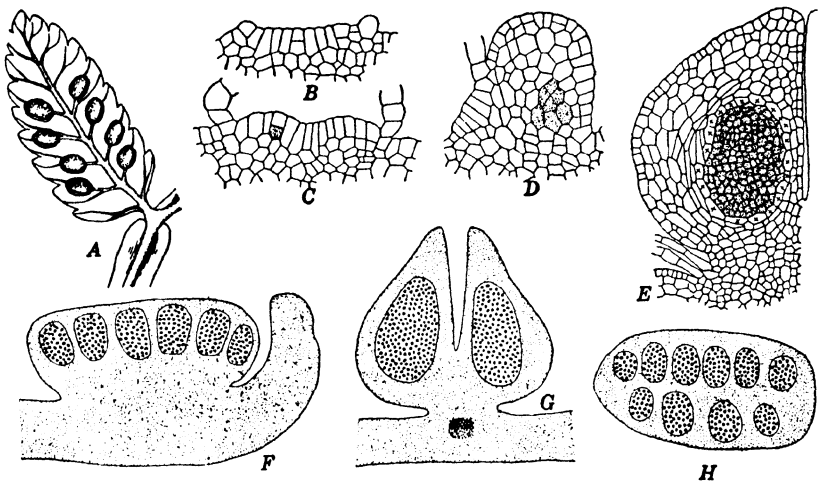

FIG. 189. *A*, *Marattia alata* Smith. Fertile pinnule. *B–H*, *Marattia fraxina* Smith. *B–E*, stages in development of a synangium. *F–G*, longitudinal vertical and transverse sections of a mature synangium. *H*, horizontal section of a mature synangium. (*B–E*, *after Bower*, 1897.) (*A*, × 1½; *B–D*, × 150; *E*, × 75; *F–H*, × 21.)

eusporangiate type. The jacket eventually becomes a tissue several cells in thickness and one in which the jacket cells immediately next the sporogenous mass function as a tapetum. The outer cells on the free face of a jacket become thick-walled. Drying out of these cells causes the two halves of a synangium to spread apart in a manner very much like the opening of a book. Spreading apart of a synangium is followed by a vertical dehiscence of each of the exposed sporangia.

Gametophytes of Marattiales (Fig. 190*A–C*) are dark green in color, are fleshy in texture, and have an external appearance resembling that of certain anacrogynous liverworts, including *Riccardia* (page 63). They are among the largest of gametophytes of pteridophytes and may attain a length of 2.5 to 3.5 cm.[2] Germination of a spore of *Marattia* begins with

[1] Bower, 1897. [2] Campbell, 1908; Stokey, 1942.

a rupture of the outer layer of the spore wall and a protrusion of a primary cell that enlarges to several times the original spore diameter before it divides. The first division of a primary cell usually cuts off a rhizoid-bearing cell, although there may be a formation of four or five cells before an appearance of the first rhizoid.[1] An apical cell may be differentiated as early as the four-celled stage but in most cases it is differentiated at a somewhat later stage. As growth continues the gametophyte becomes a small circular plate more than one cell in thickness (Fig. 190*D–E*). Further growth is at the distal end and the gametophyte

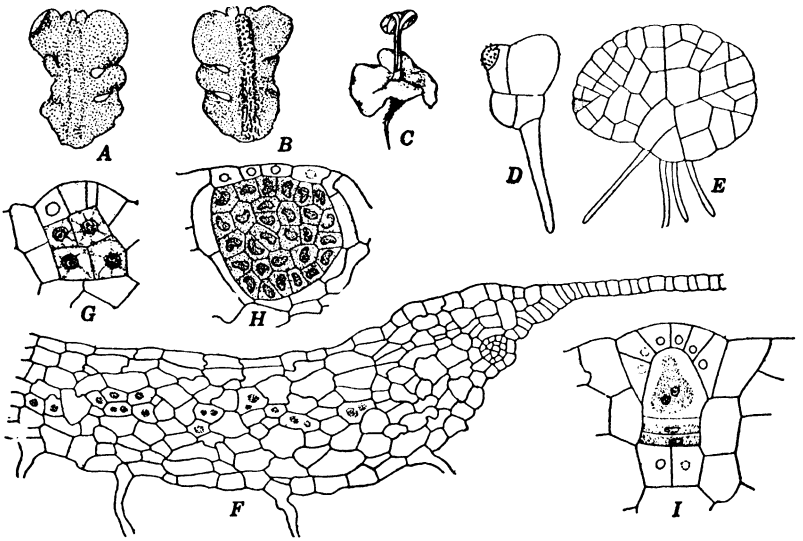

FIG. 190. *A–B, Marattia douglasii* Baker. Dorsal and ventral views of a gametophyte. *C, Danaea elliptica* Smith. Gametophyte and young sporophyte. *D–E, Marattia fraxina* Smith. Early stages in development of gametophyte. *F–I, Marattia douglasii. F*, transverse section of a portion of a mature gametophyte. *G–H*, stages in development of antheridia. *I*, a nearly mature archegonium. (*D–E, after Jonkman*, 1880.) (*A–C*, × 1½; *F*, × 80; *G–I*, × 325.)

gradually becomes elongate. It has a midrib several cells in thickness, and one flanked on either side by a thin wing one cell in thickness for some distance inward from the free margin. When grown in culture for several years a gametophyte may become branched at the distal end.[2] Gametophytes of Marattiales growing under natural conditions regularly contain an endophytic fungus (Fig. 190*F*) which is thought[3] to be more of a parasite than a mycorhizal symbiont. That the presence of this fungus is not essential for growth of gametophytes of Marattiales is shown by the development of spores sown on a sterile substratum into mature gametophytes free from fungi.[2]

[1] Jonkman, 1880; Stokey, 1942. [2] Stokey, 1942. [3] West, 1917.

When grown in cultures started from spores, gametophytes of *Marattia* do not form antheridia until they are about eight months old and do not form archegonia until they are about a year old.[1] Antheridia are first formed on the ventral side of the midrib; but after formation of archegonia has commenced, antheridia may also be formed on the dorsal side. Formation of archegonia is restricted to the ventral side of the midrib. Development of antheridia in *Marattia* (Fig. 190*G–H*) and in other Marattiales[2] is similar to that in *Ophioglossum*. A mature antheridium lies deeply embedded in a gametophyte, contains many antherozoids, and

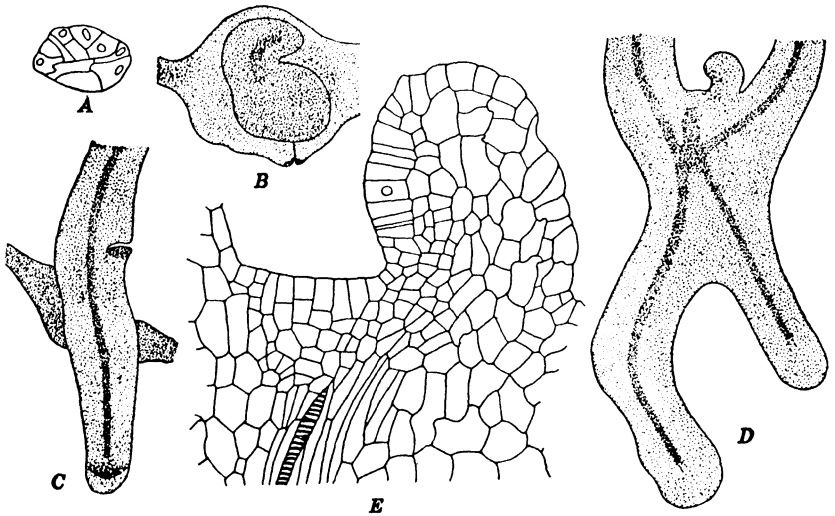

FIG. 191. *Marattia douglasii* Baker. *A–B*, young embryos. *C–D*, young sporophytes. *E*, stem apex of sporophyte in Fig. *D*. (*A*, *after Campbell*, 1911; *B*, *after Campbell*, 1894.) (*A*, × 100; *B*, × 45; *C–D*, × 21; *E*, × 160.)

opens by means of an opercular cell. Archegonial development[2] and structure of the mature archegonium (Fig. 190*I*) are also similar to those in *Ophioglossum*.

Our knowledge of embryonal development in all Marattiales is imperfect because[3] "a very large number of prothallia must be examined before a small series of embryos can be secured." Division of the zygote of Marattiales is transverse instead of vertical as in other Leptosporangiatae. Such early stages of embryonal development as are known for *Marattia* show[3] that the epibasal daughter cell of the zygote (that nearest the archegonial neck) gives rise to the foot of the embryo and the other (hypobasal) daughter cell gives rise to the primary root, cotyledon, and stem. The first two or three divisions are in fairly regular sequence but

[1] Stokey, 1942. [2] Campbell, 1894, 1911; Haupt, 1940; Stokey, 1942.
[3] Campbell, 1911.

there is soon a disappearance of any regularity of division (Fig. 191*A*). Differentiation of root, cotyledon, and stem is not apparent until the embryo has become a massive many-celled structure. The cotyledon arises in the portion of the embryo farthest from the neck of the archegonium and near the free face of the hypobasal half of the embryo. Early stages in cotyledonary development may possibly have an apical cell, but this cell is not definitely recognizable until the cotyledon has attained a considerable size. Unlike the cotyledon of Leptosporangiatae (which curves around the growing point of the gametophyte), the cotyledon of *Marattia* grows upward through the middle of the gametophyte (Fig. 191*B*). The two sides of a cotyledon growing through the gametophyte elongate at unequal rates and thus, similar to young foliage leaves, it has a curved apex. Development of the primary root is due to an apical cell differentiated endogenously along the plane where epibasal and hypobasal halves of the embryo adjoin.[1] The primary root developed from this apical cell grows directly downward into the soil. The cotyledon and primary root are well-matured structures, with a single continuous vascular strand, before there is any production of stem tissues. This is formed by means of an apical cell differentiated in the epidermis and at the juncture of cotyledon and primary root. Development of the young stem is overshadowed by that of leaves produced by it, but by the time the second or third leaf has matured there is an evident protostelic stele within the stem (Fig. 191*C–E*).

SUBCLASS 3. LEPTOSPORANGIATAE

The Leptosporangiatae differ from other ferns in having a sporangium with a jacket layer one cell in thickness, a definite number of spores within a sporangium, a development of a sporangium from a single initial cell (a leptosporangiate mode of development), and a differentiation of the tapetum from a single internal cell of a developing sporangium. Sporangia are borne marginally or abaxially, and when grouped in sori are not laterally united to form a synangium. Antheridia differ from those of other ferns in being small, more or less emergent, and containing a relatively small number of antherozoids. Many members of the subclass have a distinctive type of embryonal development in which the foot, primary root, cotyledon, and stem of a young sporophyte are each referable to a single cell of the four-celled embryo. There are no characteristic vegetative features distinguishing sporophytes of Leptosporangiatae from those of other Pterophyta.

Pterologists are not in accord concerning the number of species and genera among living Leptosporangiatae. Of the two most recent sur-

[1] Campbell, 1894.

veys, one[1] recognizes approximately 6,400 species and 235 genera, and the other[2] recognizes approximately 9,000 species and 300 genera.

The geological record (Figs. 95, 162) shows that the Leptosporangiatae are a less ancient group than other ferns or other pteridophytes, and that only one family is known from as far back as the Permian. Certain families found in the flora of today (including the Osmundaceae, Schizaeaceae, Gleicheniaceae, and Matoniaceae) reached their climax during the Lower Cretaceous. Other families of the present-day flora appear to be more numerous today than at any time in the past.

The homosporous Leptosporangiatae are universally placed in a single order, the *Filicales*. The two heterosporous families (Marsiliaceae and Salviniaceae) have individual sori or groups of sori enclosed by a many-celled envelope superficially resembling a seed coat, the whole constituting what is called a **sporocarp.** Because of their heterospory, their formation of a sporocarp, and their aquatic habit, the two families are often placed in a separate taxon variously called the Salviniales, the Hydropteridae, and the Rhizocarpae, the last of these three names being based upon the erroneous idea that the sporocarps are borne directly on the roots. There has long been a realization[3] that the two families are not closely related to each other and that the unique features common to the two (heterospory and formation of a sporocarp) are due to parallel evolution instead of a common origin. There is justification for thinking that the heterosporous Leptosporangiatae differ so markedly from the homosporous ones that they should not be put in the Filicales. On the other hand, the phylogenetic relationship between the Marsiliaceae and Salviniaceae is so remote that they should be placed in separate orders, the *Marsiliales* and the *Salviniales.*

ORDER 1. FILICALES

The Filicales are to be distinguished from other orders of the Leptosporangiatae by their homospory.

When segregated on the basis of structure and development of fertile portions of leaves the homosporous genera fall into three groups.[4] The most primitive genera belong to the Simplices characterized by **simple sori** in which all sporangia develop simultaneously. The Gradatae are a more advanced group with a **gradate sorus** characterized by development of sporangia in a basipetalous succession. The most advanced group is the Mixtae with a **mixed sorus** in which the sporangia develop in an irregular sequence. In addition to the type of sorus many other characters are taken into consideration in grouping the homosporous genera in families. During the past quarter century four quite different groupings

[1] Christensen, 1938. [2] Copeland, 1947. [3] Campbell, 1895. [4] Bower, 1899.

into families have been proposed[1] by botanists familiar with a wide variety of ferns. All four systems are in agreement in grouping the primitive genera with simple sori into four families (Osmundaceae, Schizaeaceae, Gleicheniaceae, Matoniaceae). Among the families with a gradate sorus the only ones recognized in all four systems are the Hymenophyllaceae and the Cyatheaceae. There are two radically different treatments of genera with a mixed sorus. One[2] is to divide them into many families; the other[3] is to place them in a single family—the Polypodiaceae. Opinion concerning the number and composition of families to be recognized among genera with mixed sori is so divided[4] that for the present it seems better to follow the grouping of all into the Polypodiaceae, but with full realization that this is an artificial family when defined in this manner.

FAMILY 1. OSMUNDACEAE

The Osmundaceae have all sporangia on a leaf developing simultaneously, and have the sporangia borne abaxially and either in distinct or indistinct sori that are without indusial protection. The sporangia are massive, contain a large number of spores, and dehisce longitudinally by means of a shield-shaped annulus at one side of the sporangial jacket. Leaf traces and the vascular bundle of a rachis are C-shaped.

There are several reasons for regarding the Osmundaceae as the most primitive of Leptosporangiatae with a simultaneous development of sporangia. Among these reasons are the pseudoeusporangiate nature of the sporangium, the shield-shaped annulus of a sporangium, the cordate type of gametophyte, the relatively large number of antherozoids in an antheridium and their escape through an opercular cell, and the relatively late differentiation of parts of an embryo.

There are three living genera of Osmundaceae, *Osmunda*, a cosmopolitan genus with 12 to 14 species; *Leptopteris*, a South Pacific genus with 6 species; and *Todea*, a monotypic genus found in South Africa, Australia, and New Zealand. There are also a number of fossil genera in which the distinctive anatomy of the stem shows that they should be referred to the Osmundaceae. Among them are the oldest of the Leptosporangiatae, since they are known with certainty from as far back as the Upper Permian.[5]

The sporophyte of *Osmunda* has a short, upright or creeping stem that is invested with persistent remains of old sclerenchymatous leaf bases. The stem has numerous adventitious roots, two of which arise at each leaf base. Stems usually bifurcate into two branches of equal size; and

[1] Bower, 1926, 1928; Christensen, 1938; Copeland, 1947; Holttum, 1949.
[2] Copeland, 1947; Holttum, 1949. [3] Bower, 1928; Christensen, 1938.
[4] Ching, 1940; Copeland, 1947; Holttum, 1949. [5] Arnold, 1952.

occasionally one of the branches bifurcates again.[1] The apex of each branch bears a crown of pinnate or bipinnate leaves. Some species have two kinds of leaves, fertile and sterile. If the leaves are dimorphic, the fertile ones appear before the sterile ones when a new set of leaves is unfolded. Other species have all leaves fertile and the production of sporangia restricted to pinnae at the middle (Fig. 192) or at the apex of a blade.

The first-developed portion of a stem may have a central cylinder with a protostelic organization;[2] later-developed portions of the central

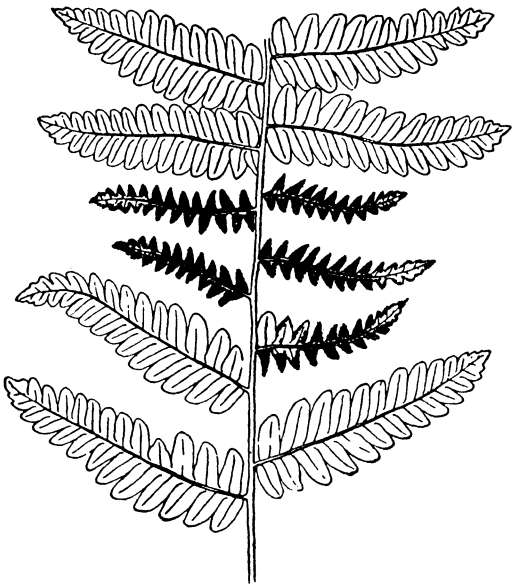

FIG. 192. *Osmunda claytoniana* L. Portion of a leaf with fertile pinnules. (× ½.)

cylinder are always dictyostelic and have numerous overlapping narrow leaf gaps (Fig. 193*C*). Cortex and stele are delimited from each other by a well-defined endodermis. This is unusual because it is not interrupted at the leaf gaps. The outer portion of the cortex is dark brown in color and has highly sclerified cells; the inner portion is colorless and parenchymatous. Both portions of the cortex contain numerous spirally arranged, C-shaped leaf traces, each surrounded by an endodermal layer (Fig. 193*A*). The outermost region in the dictyostelic portion of stele is a pericycle that is two to four cells in thickness (Fig. 193*B*). Internal to the pericycle is a continuous sheath of phloem that is thicker in portions external to the leaf gaps. The inner portion of the phloem differs from

[1] Faull, 1901. [2] Gwynne-Vaughan, 1911.

that in most ferns in having its cells with their long axes diagonal or tangential to the long axis of the stele.[1] Between phloem and xylem is the so-called xylem sheath, a layer four to six cells in thickness. The meristeles of the xylem ring are oval to U-shaped in outline, and each generally has a small protoxylem mass that is mesarch in position. The metaxylem is composed of large scalariform tracheids. Some species

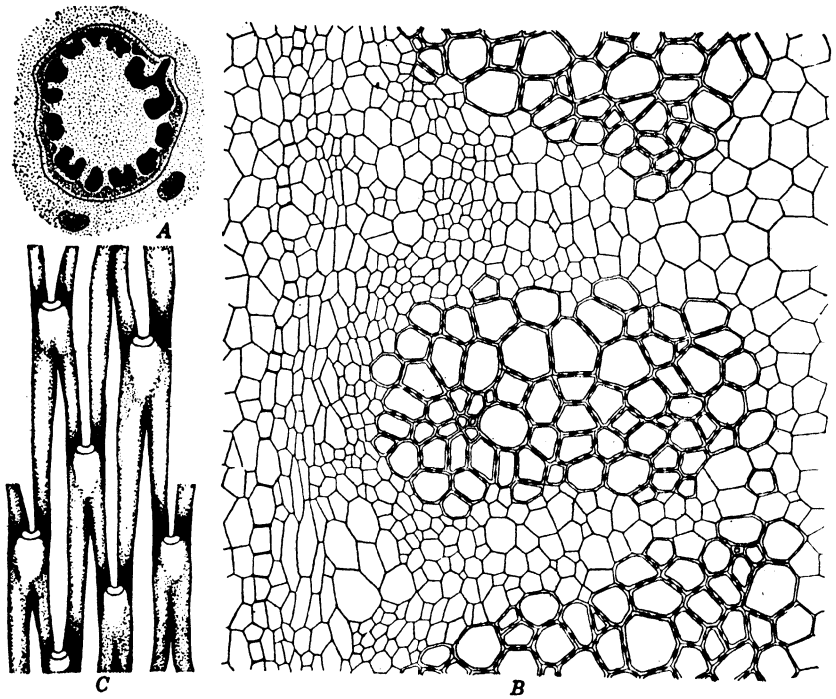

FIG. 193. *A–B, Osmunda claytoniana* L. *A*, transverse section of stele and inner portion of cortex. *B*, enlarged portion of stele in Fig. *A*. *C, Osmunda regalis* L. Stereodiagram of a portion of the stele. (*C, after Lachmann in Kidston and Gwynne-Vaughan*, 1907.) (*A*, × 5; *B*, × 120.)

have a homogeneous pith internal to the xylem; others, including *O. cinnamomea* L., have one or more strands of sclerenchyma in the pith. *O. cinnamomea* may also have an endodermal layer internal to the xylem,[1] but this is not always clearly distinguishable.

The two adventitious roots formed below each leaf arise endogenously and at the base of the leaf trace or immediately below it. A root has a broad cortex with small thick-walled cells at the exterior and progressively larger and thinner-walled cells inward to the endodermis. In most cases the vascular cylinder is diarch but occasionally it is triarch.[1]

[1] Faull, 1901.

The single trace departing to a leaf runs diagonally upward through the cortex without branching and without a disappearance of the ensheathing endodermal layer. The xylem of a leaf trace is C-shaped in cross section and has a small protoxylem mass in the concave side toward the stele. It is surrounded on all sides by a layer of phloem. The petiole of an *Osmunda* leaf differs from those of most other Leptosporangiatae in the stipule-like expansions at its base. The single bundle running the length of a petiole is similar in shape to a leaf trace but is without a conspicuous endodermal layer. The blade of the leaf may be pinnately or bipinnately divided. Pinnae have the open venation typical of primitive ferns. The internal structure of a pinna is much like that in other Leptosporangiatae.

Sporangia of *Osmunda* are first recognizable as small convex protuberances on the pinnae or pinnules.[1] There is one conspicuous cell (the sporangial initial) in each protuberance. *Osmunda* differs from typical Leptosporangiatae in that the whole sporangium is not referable to this initial. Instead, the massive stalk is formed in whole or in part from cells adjoining the initial. The sporangial initial divides periclinally into an outer cell (the jacket initial) and an inner cell (the archesporial cell). The shape of the archesporial cell is variable; most frequently it is a truncate pyramid (Fig. 194*A*). Division of the jacket initial and its daughter cells is always anticlinal. Thus the tissue derived from it is a layer one cell in thickness. The archesporial cell functions as an internal apical cell and cuts off a flat cell from each of its faces, including that next to the jacket initial (Fig. 194*B–C*). After cutting off these flat cells, the archesporial cell functions as the primary sporogenous cell. The flat cells cut off by the archesporial cell have been called tapetal cells[2] because they have been thought to be similar to the tapetal initials of typical leptosporangiatae. In the case of *O. claytoniana* L. the layer of flattened cells internal to the jacket layer never develop the dense protoplasts typical of tapetal cells (Fig. 194*E–F*). Instead, they have more watery protoplasts from early spore mother cell stages onward. Furthermore, they do not disintegrate even after the spores have well-developed walls. On this account these cells are to be interpreted as a thin-walled layer of the jacket, but a layer that is of no importance in spore protection or sporangial dehiscence. The primary sporogenous cell undergoes a series of divisions to form a large number of sporogenous cells, theoretically 64 or 128. In *O. claytoniana* L. the outer layer of sporogenous cells functions as a tapetum after the cessation of division, and the remaining sporogenous cells function as spore mother cells (Fig. 194*F*). During meiosis the tapetal cells elongate greatly and their walls disappear. Eventually the elongating tapetal cells push between the dividing spore mother cells

[1] Bower, 1889. [2] Bower, 1889, 1899.

and fuse with one another to form a plasmodial reticulum that eventually disappears during the course of spore-wall formation. Late in sporangial development there is a thickening of the walls in a group of jacket cells at one side of the sporangium. This annulus may be a plate, or it may be a transverse band (several cells broad and two to three cells tall) that extends a considerable distance around the circumference of the sporangium.[1] Perpendicular to the annulus, and extending over the sporangial

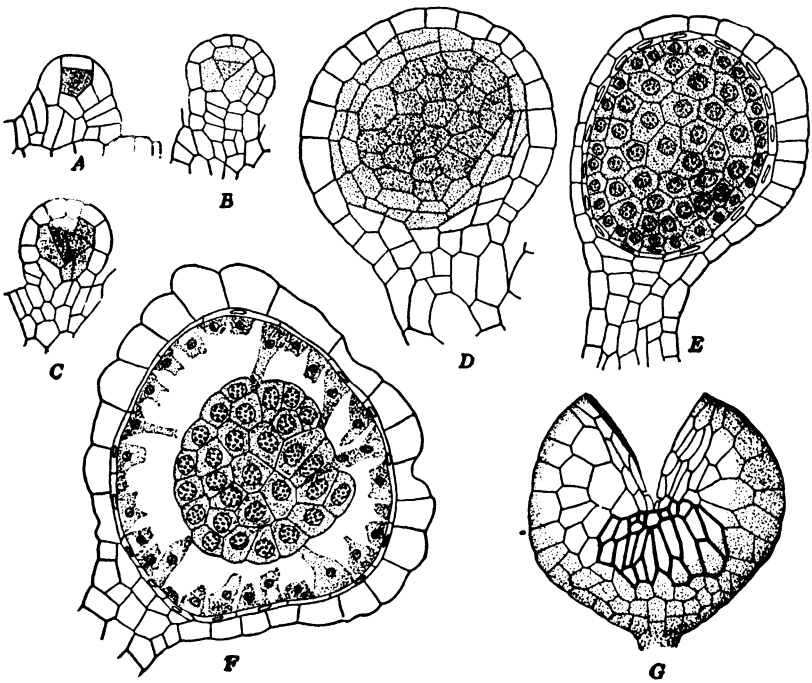

FIG. 194. *A–D, Osmunda regalis* L. Early stages in development of sporangia. *E–G, Osmunda claytoniana* L. *E–F*, late stages in development of sporangia. *G*, surface view of a sporangium after dehiscence. (*A–D, after Bower*, 1889.) (*A–D*, × 160; *E–G*, × 215.)

apex and nearly down to the stalk, is a band of elongate thin-walled cells—the future zone of vertical dehiscence of the sporangium (Fig. 194*G*).

Spores of *Osmunda* contain chloroplasts when they are ripe. This accounts for their rapid germination when sown, and may possibly account for the short time they remain viable when stored. When germination takes place there is a bursting of the outer spore-wall layer (the exospore) along the three ridges of the spore wall and a protrusion of the spore contents, still enclosed by the two inner spore-wall layers. The first division, generally at right angles to the long axis, forms two daugh-

[1] Williams, 1928.

ter cells of unequal size. The larger cell develops into the gametophyte; the smaller elongates and becomes the first rhizoid.[1] This rhizoid, unlike rhizoids of most other ferns, contains chloroplasts. The larger cell divides transversely to form a file of three or four cells whose terminal cell, by two successive diagonal divisions, then differentiates an apical cell that alternately cuts off derivatives right and left for some time. The apical cell projects ahead of the rest of the thallus during early stages of

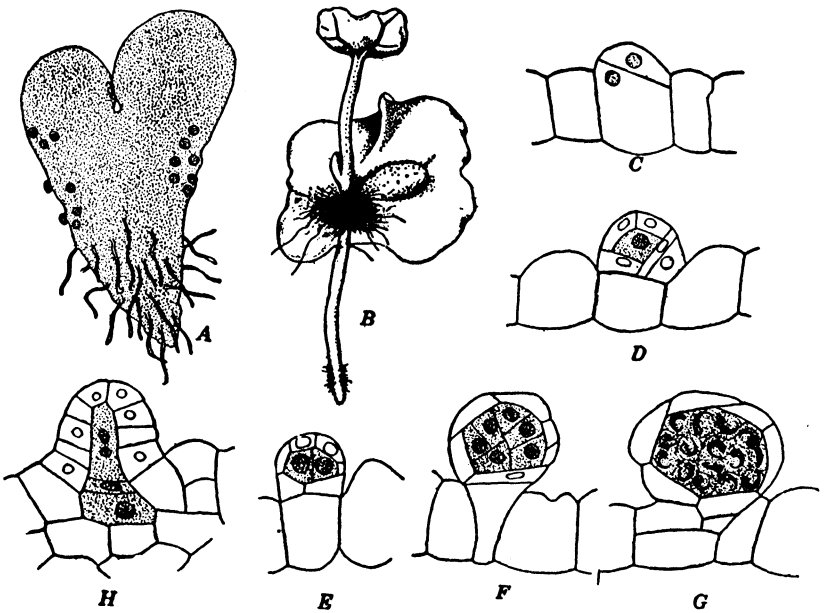

FIG. 195. *A*, *Osmunda cinnamoema* L. ventral view of gametophyte. *B*, *Osmunda claytoniana* L. Gametophyte and young sporophyte. *C–H*, *Osmunda cinnamoema* L. *C–G*, stages in development of antheridia. *H*, archegonium. (*B*, *after Campbell*, 1892.) (*A*, × 21; *B*, × 6; *C–H*, × 325.)

prothallial growth. Later on, because of rapid cell division in its derivatives, the apical cell comes to lie in a depression at the anterior end of the gametophyte (Fig. 195*A*). The two-sided apical cell is eventually replaced by one with four cutting faces or is replaced by a group of two or three initials that cut off daughter cells dorsally and ventrally as well as laterally. This results in a wedge-shaped gametophyte with a longitudinal midrib and one similar in appearance to those of Marattiales.

Young gametophytes have antheridia only and produce them either marginally or terminally. Antheridia are also formed on mature gametophytes with archegonia. Here they are formed on the ventral side of the lateral wings. Antheridial development[1] begins with a protrusion of a

[1] Campbell, 1892.

cell above its neighbors and the cutting off of a small cell, the antheridial initial, by a diagonal wall (Fig. 195*C*). By two successive diagonal divisions, the initial forms a pyramidal cell and two flattened cells. The pyramidal cell functions in the manner of an apical cell with three cutting faces and cuts off tabular cells on the side toward the gametophyte. The cells thus cut off constitute the basal part of the antheridium. If several tabular cells are cut off, a pedicel is formed, and the mature antheridium stands considerably above the surface of the gametophyte. After cutting off one or more segments from each basal face, the pyramidal cell divides periclinally into a jacket initial and a primary androgonial cell that are separated from each other by a curved wall. The jacket initial divides anticlinally (Fig. 195*D*). Its daughter cells also divide anticlinally and by oblique walls. The last-formed jacket cells meet to enclose a triangular cell that lies either at the top or at the side of the antheridium. This cell is thrown off when the antheridium is mature and is very suggestive of the opercular cell in Eusporangiatae. Coincident with the first division of the jacket initial, there is a vertical division of the primary androgonial cell (Fig. 195*E*). The two androgonial cells thus formed divide, and their daughter cells redivide to form a hundred or more androcytes (Fig. 195*F–G*). This number is very high for a leptosporangiate fern. Metamorphosis of the androcytes into antherozoids is essentially as in *Ophioglossum*.

Archegonia are formed on the ventral side of old gametophytes and over the entire midrib (*O. claytoniana* L.) or only along its edges (*O. cinnamoema* L.)[1] The general sequence of archegonial development is quite similar to that in *Ophioglossum*. In fact, there are but minor differences between archegonial development in Eusporangiatae and in Leptosporangiatae. The chief differences in the two are in the length of the neck and the amount of its curvature. *Osmunda* has an archegonial neck eight cells in height, which stands erect to the prothallus (Fig. 195*H*).

Division of the zygote is vertical and in a plane parallel to the neck of the archegonium.[2] The two daughter cells also divide vertically, but in a plane at right angles to the first plane of division. Transverse division of each cell results in an eight-celled embryo with the cells in two tiers of four (Fig. 196*B*). *Osmunda* differs from most other Leptosporangiatae in that the cotyledon, stem, primary root, and foot are not each referable to a specific cell of the four-celled embryo.[3] Instead, cotyledon, stem, and primary root of *Osmunda* are derived from one half of the eight-celled embryo, and the foot from the other half. In *O. cinnamoema* L. the half of the eight-celled embryo next the archegonial neck develops into cotyledon, stem, and primary root, and the other half develops into the foot.[3] *O. claytoniana* L. may have cotyledon, stem, and root derived from one

[1] Campbell, 1892*A*. [2] Campbell, 1892; Cross, 1931. [3] Cross, 1931.

daughter cell of the zygote and the foot derived from the other daughter cell. In either case the embryo is far advanced beyond the octant stage before its various parts are clearly recognizable (Fig. 196*C–D*). The cotyledon and stem are each due to the activity of a special apical cell. These cells are superficial (epidermal) and lie close to each other. The root initial arises in the same half of the embryo, but endogenously and near the foot.[1] Up to this time enlargement of the embryo has been accompanied by an enlargement of the archegonium and adjoining gametophytic tissue into an enclosing sheath, the calyptra. Shortly after this

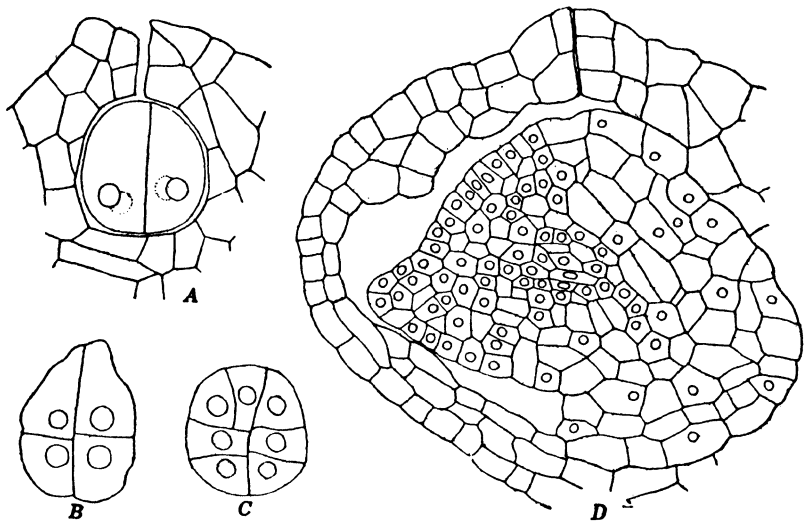

FIG. 196. *Osmunda claytoniana* L. Stages in development of embryo. (*A–C*, × 325; *D*, × 215.)

the root and cotyledon burst through the calyptra, the cotyledon growing laterally to the side of the gametophyte and then growing upward.[2] This growth of the cotyledon along the underside of the gametophyte, instead of an upward growth through it, is a feature distinguishing Leptosporangiatae from Eusporangiatae with thallose gametophytes. However, *Osmunda* differs from other Leptosporangiatae in having the cotyledon curve around the side of the gametophyte instead of around the apical end (Fig. 195*B*).

Gametophytes grown from spores may form sporophytes apogamously instead of by a union of gametes.[3] Apospory has been noted both under natural conditions and when young sporophytes are wounded.[4] In both cases the aposporously produced gametophytes are apogamous.

[1] Cross, 1931. [2] Campbell, 1892. [3] Brown, 1920.
[4] Manton, 1932; Sarbadhikari, 1939.

FAMILY 2. SCHIZAEACEAE

The Schizaeaceae have their sporangia borne singly along a leaf margin and have all sporangia developing simultaneously. A sporangium dehisces longitudinally by means of a transverse ring-shaped annulus at the distal end.

There are several reasons for placing the family at a low phylogenetic level among leptosporangiate ferns. These include the simple leaf trace, the open venation of leaf blades, the simultaneous development of sporangia, the terminal annulus, the relatively large spore output, the cordate gametophytes of most genera, and the structure of antheridia.

The family has four living genera, *Schizaea*, with 30 species; *Lygodium*, with 40 species; *Anemia*, with 90 species; and *Mohria*, with 1 to 3 species. Species of the first three genera are usually found only in the tropics; *Mohria* is South African. There are also several fossil genera with the same unique type of sporangium that is found only in living genera referred to the family. *Seftenbergia*, a genus of the Upper Carboniferous, has been placed with[1] or without[2] reservations in the Schizaeaceae. Thus the family has a claim to being the oldest known one of the Leptosporangiatae. In any case, the family is known with certainty from as far back as the Jurassic.

One species of the type genus (*Schizaea*) occurs in the United States. This species, *S. pusilla* Pursh (Fig. 196*A*), is found only in *Sphagnum* swamps in the Pine Barrens of New Jersey. It is considered[3] a stranded relic from preglacial ages when tropical plants grew far to the north.

Most species of *Schizaea* have a short upright rhizome but a few of them have a horizontal one. Occasional individuals of various species have one or two dichotomous branchings of the rhizome.[4] Leaves and adventitious roots are borne spirally on the stem. Very young leaves may be in a 1:3 spiral arrangement, corresponding to the three cutting faces of the apical cell, but there is soon an obliteration of any definite phyllotaxy. Some species, including *S. pusilla* Pursh[5] and *S. rupestris* R. Br.,[6] have two sorts of leaves, sterile and fertile. Sterile leaves of these species have a few crowded pinnae at their apices, the two rows of pinnae lying parallel to each other and approximately perpendicular to the axis of the leaf (Figs. 197*A*, 200*A*). The pinnate portion of a fertile leaf looks much like a double comb. Other species have all leaves fertile. Leaves of these species may be like the fertile leaves of dimorphic species, or they may have one or more dichotomous branchings and a

[1] Bower, 1926. [2] Arnold, 1947; Hirmer, 1938. [3] Maxon, 1925.
[4] Bartoo, 1930; Boodle, 1903; Tansley and Chick, 1903.
[5] Bartoo, 1930. [6] Bartoo, 1929*A*.

comb-like double row of pinnae at the tips of the ultimate dichotomies (Fig. 197*B*).

The vascular organization of the stem in the Schizaeaceae ranges from a simple protostele (*Lygodium*) to a dictyostele (*Mohria*). The first formed portion of vascular cylinder of *Schizaea* may be protostelic;[1] later-formed portions are always siphonostelic and ectophloic. The pith internal to the ring of xylem may be homogeneous or heterogeneous. In the latter case[2] it contains small spindle-shaped masses of tracheids with or without a surrounding endodermal layer (Fig. 198). The cortex is

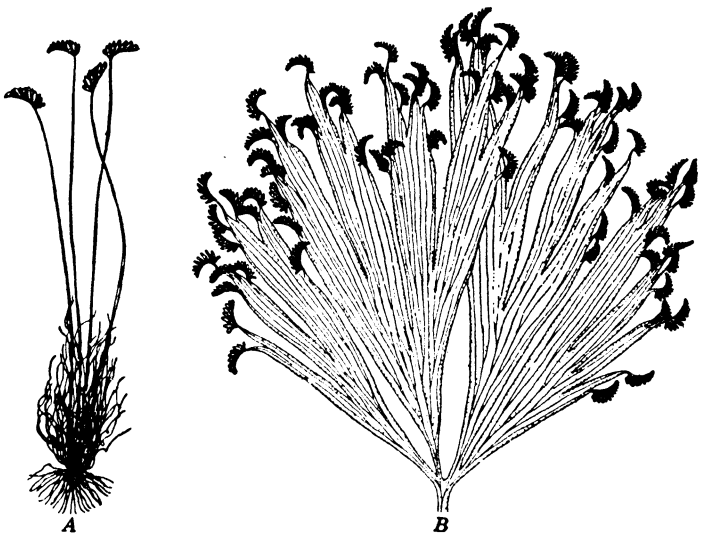

FIG. 197. *A*, *Schizaea pusilla* Pursh. *B*, leaf of *Schizaea elegans* (Vahl.) Sw. (× ½.)

generally but a few cells in diameter.[3] Cortical cells are usually sclerified and they may contain considerable starch. There is a well-defined endodermal layer toward the inner face of the cortex. A study[4] of the histogenesis of this layer in *S. pusilla* Pursh shows that it and the pericyclic layer internal to it are derived from the innermost layer of the cortex. Thus, in this species both endodermis and pericycle are cortical in nature. Among species where the pericycle is more than one cell in thickness, as *S. dichotoma* J. Sm.,[5] the endodermis seems to be the innermost cortical layer. Whatever its nature, the endodermis is similar to that of *Osmunda* in that it is not interrupted when a leaf trace departs from the stele.

[1] Bartoo, 1930; Boodle, 1903; Thompson, 1920.
[2] Boodle, 1903; Thompson, 1920. [3] Boodle, 1901; Tansley and Chick, 1903.
[4] Bartoo, 1930. [5] Thompson, 1920.

Adventitious roots of *Schizaea* arise endogenously. In *S. pusilla* Pursh they originate from a single cell of the innermost layer of the cortex.[1] This cell soon gives rise to an apical cell with three lateral cutting faces. The formation of cortical and stelar tissues from segments cut off by the apical cell is in diagrammatic sequence.[2] The stele of a root is

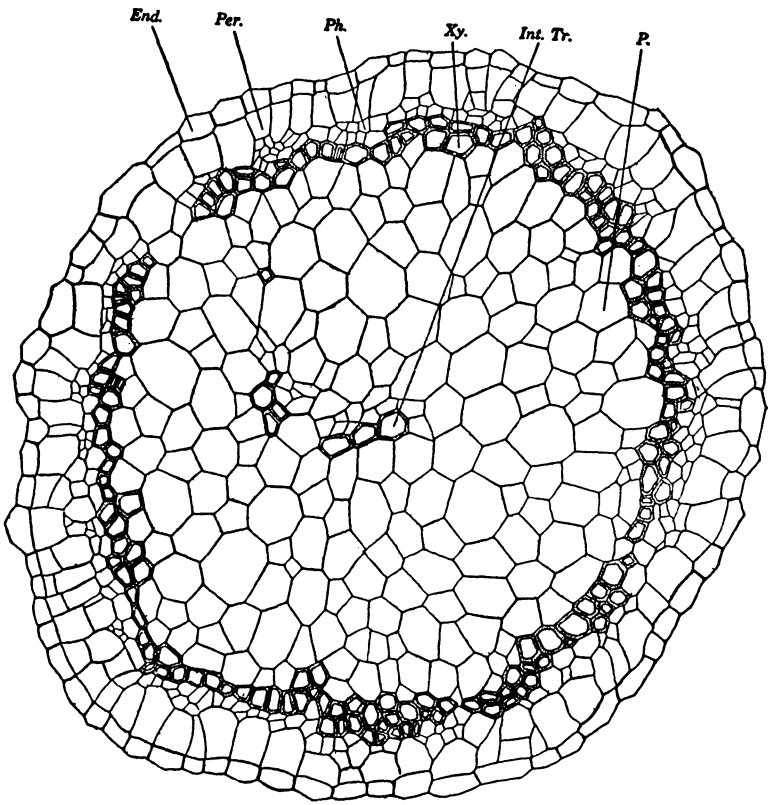

FIG. 198. *Schizaea molacceana* Br. Transverse section of stele and endodermis of stem. (*End.*, endodermis; *Int. Tr.*, internal tracheids; *P.*, pith; *Per.*, pericycle; *Ph.*, phloem; *Xy.*, xylem.) (× 160.)

very small and diarch, phloem and xylem each containing only four to six elements when seen in cross section (Fig. 199). Phloem and xylem are surrounded by a ring of six pericyclic cells. This is successively enclosed by a ring of six endodermal cells and a ring of six cortical cells. The radial arrangement of cells in the pericyclic, endodermal, and innermost cortical layers shows that they have been derived from a common mother-cell layer. The cortex, including the endodermis, is generally three cells

[1] Bartoo, 1930. [2] Bartoo, 1929*A*, 1930.

in thickness. One peculiar feature of the root is the conspicuous thickening of radial and inner tangential walls in the cell layer immediately external to the endodermis. The epidermal layer in young parts of a root has root hairs. Some species have a persistence of the epidermis and its hairs;[1] others have an eventual sloughing off of the epidermis.[2]

Leaves are formed from a single superficial cell three or four removed from the apical cell of the rhizome. This cell gives rise to a leaf initial with two cutting faces. Developing leaves have the spiral uncoiling (circinate vernation) typical of most ferns. The petiole of an unfolding

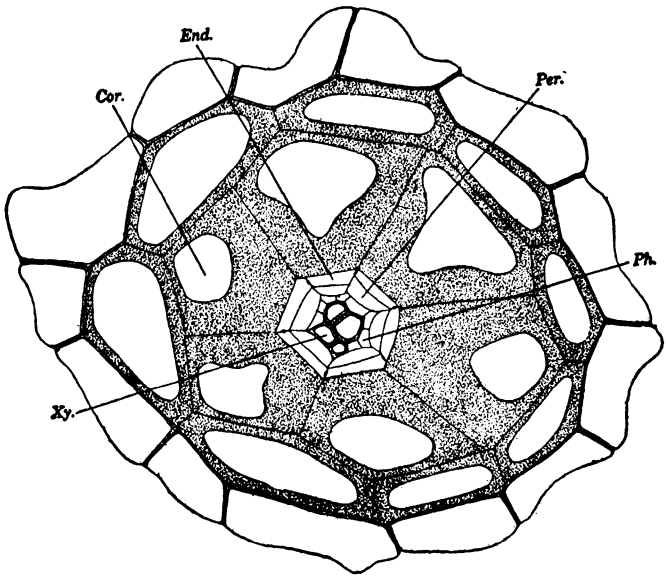

FIG. 199. *Schizaea molacceana* Bk. Transverse section of root. (*Cor.*, cortex; *End.*, endodermis; *Per.*, pericycle; *Ph.*, phloem; *Xy.*, xylem.) (× 215.)

leaf has a single vascular bundle, continuous with a single trace running through the cortex to the stele. Both the trace and the petiolar bundle are surrounded by a pericycle and an endodermis derived from a common cell layer.[3] Sterile leaves of some dimorphic species have no expansion of the distal portion into a blade (*S. pusilla* Pursh); those of other species have an expanded blade with an open venation (*S. rupestris* R. Br.). Species in which all leaves are fertile have a similar expansion or lack of expansion in the sterile portion beneath the fertile pinnules.

Fertile leaves of *Schizaea* (Fig. 200*A*) look as if the sporangia were borne on the upper (adaxial) sides of pinnules that face one another, but the relative position of xylem and phloem in the pinnules (Fig. 200*F*)

[1] Bartoo. 1929*A*, 1930. [2] Boodle, 1901. [3] Bartoo, 1930.

shows that in reality the pinnules are apposed back to back and that the sporangia are borne on the lower (abaxial) face. Sporangial development in *Schizaea* is strictly leptosporangiate, and each sporangium and its stalk is referable to a single initial cell. These initials lie in two rows, one along either margin of a pinnule. The sporangia matured from a file of marginal initials generally lie in a single row, but in some species they are alternately pressed right and left to form a double row.[1] Sporangial

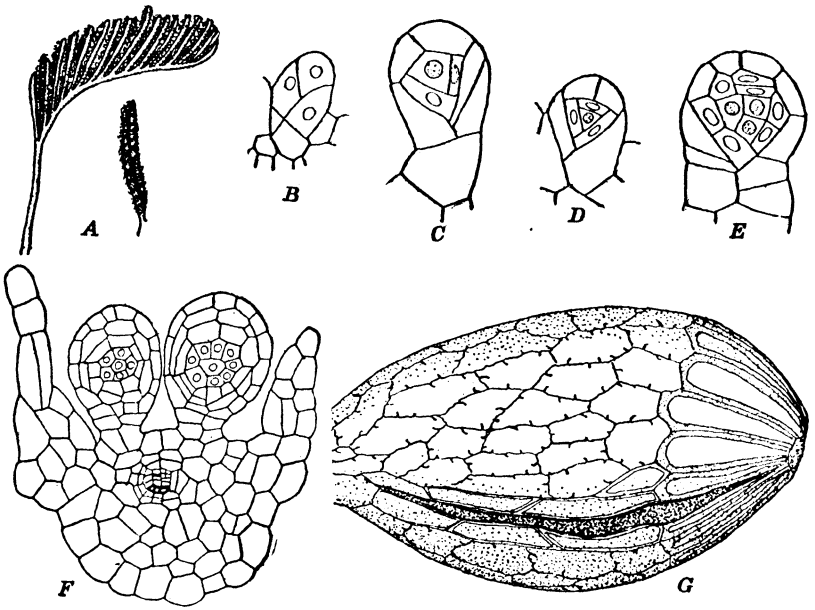

FIG. 200. *A*, *Schizaea pusilla* Pursh. Leaf and pinna. *B–F*, *Schizaea rupestris* R.Br. *B–E*, stages in development of sporangia. *F*, transverse section of a young fertile leaf. *G*, *Schizaea bifida* Sw. Surface view of a sporangium after dehiscence. (*B–E*, *after Bartoo*, 1929*A*; *F*, *after Bower*, 1918.) (*A*, × 1½; *F*, × 60; *G*, × 180.)

development[2] begins with a protrusion of an initial and its transverse division into an inner and an outer cell. The inner cell, which contributes to the base of the stalk, may divide once or twice. The outer cell, by three successive diagonal divisions, gives rise to a pyramidal apical cell that cuts off a variable number of segments from each of its three lateral cutting faces (Fig. 200*B*). The last three segments cut off contribute to the sporangial jacket; those cut off previously go to form the stalk. Apical growth terminates with a periclinal division that forms a flat outer cell (a jacket initial) and an inner pyramidal cell (the archesporial cell). The archesporial cell functions as an internal apical cell and successively cuts off a tabular tapetal initial from each of its four

[1] Bower, 1918. [2] Bartoo, 1929*A*; Bower, 1918.

cutting faces (Fig. 200*C–D*). Division of the tapetal initials is both periclinal and anticlinal, and produces a tapetal layer two cells in thickness. The cell remaining after cutting off of the tapetal initials is the primary sporogenous cell. Cell divisions in development of the sporogenous tissue from the primary sporogenous cell are always simultaneous, and, accordingly as there are four or five successive divisions, there are 16 or 32 spore mother cells. During the meioses to form the 64 or 128 spores, there is a disintegration of the tapetum into a plasmodial mass that gradually disappears as the spores ripen. Similar to other Leptosporangiatae, the jacket initials develop into a jacket layer one cell in thickness. The cells

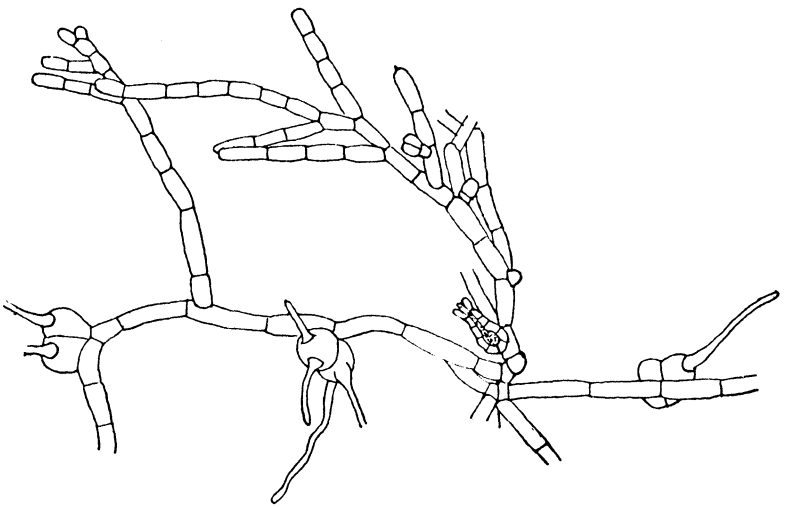

FIG. 201. *Schizaea pusilla* Pursh. Gametophyte. (*After Britton and Taylor*, 1901.) (× 30.)

at the distal end of the jacket are so oriented that their long axes are radial to a single central cell. There are about 15 of these cells, and the thickening of their walls results in the distal annulus that causes a longitudinal dehiscence of a sporangium (Fig. 200*G*). Although the sporangia are strictly marginal in origin, they appear to lie some distance in from the margin when mature. This apparently nonmarginal position results from the proliferation of a protective flap (indusium) as the sporangia are developing (Fig. 200*F*).

Gametophytes of *Schizaea* are atypical in that they are protonema-like branched filaments.[1] Gametophytes of many ferns show a filamentous tendency when growing in moist habitats and under faint illumination, but environmental conditions do not account for the filamentous gametophyte of *Schizaea*.[2] The filamentous prothallus of *Schizaea* might

[1] Britton and Taylor, 1901; Thomas, 1902. [2] Thomas, 1902.

be interpreted as a primitive type in which there has been a persistence of the filamentous body of the ancestral algae. The fact that other members of the family, *Anemia*[1] and *Lygodium*,[2] have a cordate gametophyte with a longitudinal midrib shows that this is not the case. A more attractive interpretation of the filamentous gametophyte of *Schizaea* is the hypothesis[3] that it represents a permanent retention of a juvenile stage that is of but short duration in most ferns.

The filamentous gametophytes of *S. pusilla* Pursh[4] have unicellular colorless rhizoids that arise from short branches with swollen cells containing an endophytic fungus (Fig. 201). The pale color of chloroplasts in the remainder of the plant suggests that the fungus is mycorhizal in nature. Antheridia and archegonia, both of which develop on the same gametophyte, are formed on one-celled lateral branches. Mature antheridia have a one-celled pedicel; archegonia may be sessile or may have a basal cushion of a few cells. The details of development of sex organs have been worked out more thoroughly in *Lygodium* than they have in *Schizaea*. Antheridia of *Lygodium*[1] are emergent and generally contain 128 antherozoids. This is a large number for a leptosporangiate fern and is to be considered a primitive character. Archegonia of *Lygodium*[5] have necks four to five cells in height that curve away from the apical notch of a prothallus. One primitive feature in an archegonium is the rather frequent occurrence of four nuclei within the neck canal cell.

The only studies on the early embryogeny of Schizaeaceae have been on *Lygodium*.[5] Here the first two divisions of a zygote are vertical. As in many other leptosporangiate ferns, the foot, primary root, cotyledon, and stem are each formed from one quadrant of the four-celled embryo.

FAMILY 3. GLEICHENIACEAE

The Gleicheniaceae have all sporangia on a leaf developing simultaneously and have them produced in small sori without indusial protection. The sporangia are subsessile and dehisce longitudinally by a transversely oblique annulus.

There are numerous features indicating that the family stands at a low evolutionary level among the Leptosporangiatae. Among these are the vascular organization, the simple leaf traces, the open venation of pinnules, the simultaneous development of all sporangia on a pinnule, the unprotected sori, the vertical dehiscence of sporangia, the relatively large spore output per sporangium, the cordate gametophytes with a midrib, the large number of antherozoids in an antheridium, and the triangular opercular cell of the antheridial jacket.

[1] Twiss, 1910. [2] Rogers, 1923; Twiss, 1910. [3] Goebel, 1930.
[4] Britton and Taylor, 1901. [5] Rogers, 1927.

There are 120 to 130 species in the family and all but one or two are frequently referred to *Gleichenia*. The present-day practice[1] is to segregate the species into half a dozen genera. *Gleichenia*, in the broad interpretation of the genus, is widely distributed throughout tropical and subtropical regions. Fossils from the Carboniferous have been assigned to the family, but with strong reservations. The Gleicheniaceae were conspicuous in the flora of the Upper Mesozoic and appear to have reached their greatest geographical distribution during the Cretaceous. At this time they ranged as far north as the western coast of Greenland. Changes

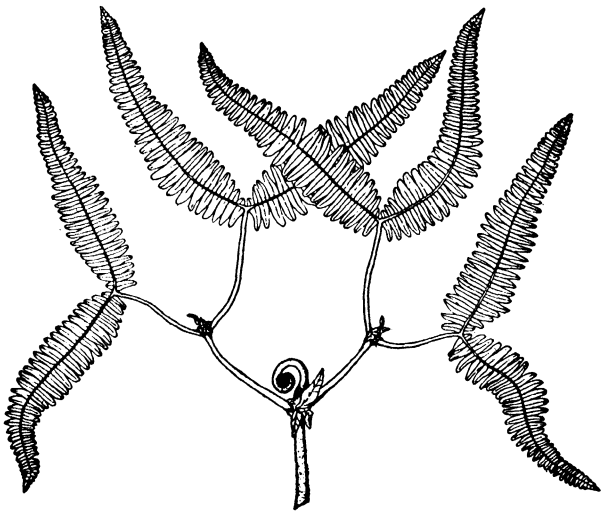

FIG. 202. Leaf of *Gleichenia pectinata* Presl. (× ⅛.)

in climatic conditions toward the close of the Cretaceous drove them toward the equator where the environment more nearly coincided with conditions that had ceased to exist in the higher latitudes.

Sporophytes of *Gleichenia* generally have creeping, dichotomously branched rhizomes with long internodes. Leaves are restricted to the upper side of a rhizome and appear to be borne in a single row even when the arrangement is three-ranked. The leaves of certain species are repeatedly forked and capable of attaining a length of 50 meters or more. Growth of these clambering vine-like leaves over the other vegetation results in an impenetrable thicket. *Gleichenia* is often a serious menace to agriculture in the tropics because of its encroachment upon cultivated fields. The forking of a leaf appears to be a dichotomous branching. Actually, there is an arrestation of terminal development of a leaf and a continued growth of the two lowermost pinnae (Fig. 202). The pinnae

[1] Christensen, 1938; Copeland, 1947; Holttum, 1949.

are bipinnate and the pinnules borne by them have an open venation (Fig. 204*A*).

Stems of almost all species have protostelic vascular cylinders that may be incipient actinosteles (Fig. 203*A*). Two species are known to be siphonostelic.[1] Protostelic stems[2] have a massive central core of xylem which is composed of tracheids intermingled with thin-walled parenchyma (Fig. 203*B*). A short distance inward from the periphery of the xylem, and

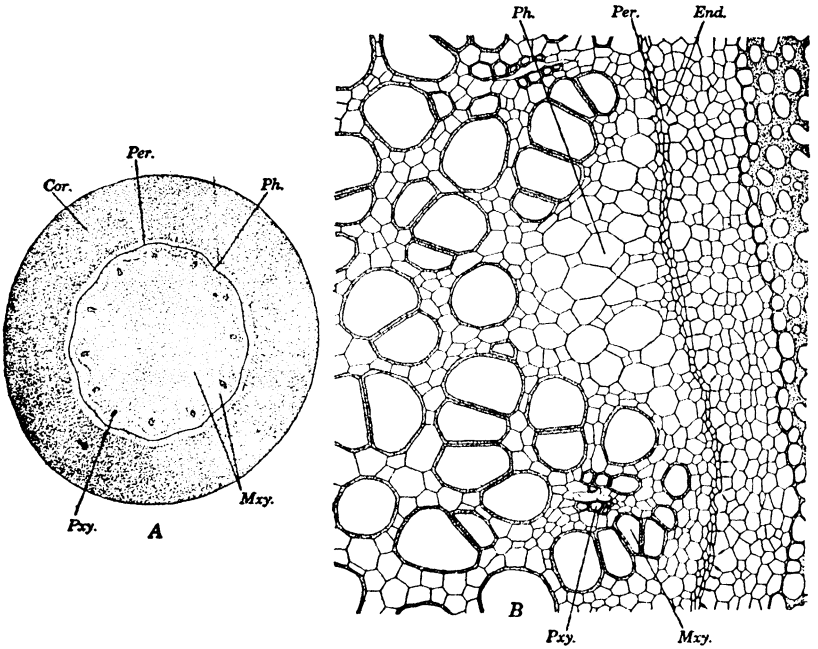

FIG. 203. *Gleichenia dichotoma* (Willd.) Hook. *A*, transverse section of rhizome. *B*, enlarged portion of stele and inner cortex of Fig. *A*. (*Cor.*, cortex; *End.*, endodermis; *Mxy.*, metaxylem; *Per.*, pericycle; *Ph.*, phloem; *Pxy.*, protoxylem.) (*A*, × 11; *B*, × 120.)

hence in a mesarch position, are a variable number of protoxylem elements. There is frequently a pulling apart of parenchymatous cells adjacent to the protoxylem to form small cavities similar in nature to the carinal canals in *Equisetum* (see page 254). The primary xylem is completely encircled by a layer of phloem, and it, in turn, is encircled by a narrow zone of pericyclic cells. An endodermis with typical Casparian strips surrounds the pericycle. The cortex of a rhizome may be wholly sclerenchymatous, or it may have a narrow layer of thin-walled parenchyma just outside the endodermis. Leaf traces departing from the stele are C-shaped and undivided until after they enter a petiole. Traces of

[1] Boodle, 1901*A*; Boodle and Hiley, 1909. [2] Boodle, 1901*A*.

most species have three protoxylem masses on the concave side facing the stele, but some species have more protoxylem masses.

Adventitious roots are borne on the underside of a rhizome and either in three rows or irregularly distributed along the rhizome. They are freely branched and with di- to tetrarch steles.[1]

Sporangia are borne in naked sori that generally lie in two rows, one on either side of and a short distance out from the midrib of a pinnule (Fig. 204*A*). The margin of a sorus bears a ring of four to seven or eight sporangia, and according to the species the center of the sorus is without

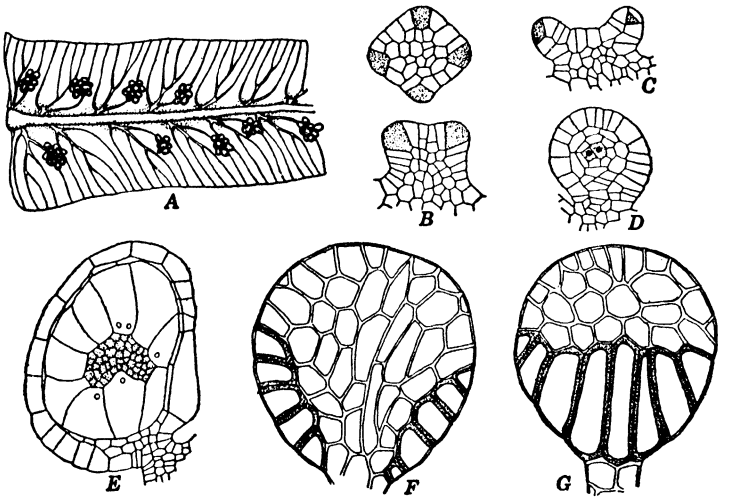

FIG. 204. *A*, *Gleichenia pectinata* Presl. Ventral view of a fertile pinnule. *B–E*, *Gleichenio flagellata* R.Br. *B*, young receptacle with sporangial initials. *C–E*, stages in development of sporangia. *F–G*, *Gleichenia pectinata* Presl. Ventral and dorsal views of a mature sporangium. (*B–E*, *after Bower*, 1899.) (*A*, × 4; *B–D*, × 150; *E*, × 75; *F–G*, × 120.)

sporangia or has one to six of them. When examined superficially, a sorus looks like a synangium, but this is not the case because the individual sporangia are not fused with one another.

The receptacular portion of a sorus becomes elevated above the surface of the pinnule before development of sporangia commences.[2] Sporangial initials may be differentiated over the entire top of a receptacle or only along the margin of the top (Fig. 204*B*). Development of a sporangium is strictly leptosporangiate (Fig. 204*C–E*). The tapetal initials develop into a tapetum two cells in thickness, but one in which only the inner cell layer contributes to the nutrition of developing spores. The outer tapetal layer develops into a tissue that seems to be a portion of the sporangial jacket. Accordingly as there are five, six, seven, or eight

[1] Boodle, 1901*A*. [2] Bower, 1899.

cell generations from archesporial cell to sporocytes there are 128, 256, 512, or 1,024 spores within a sporangium. During maturation of the jacket layer there is a differentiation of a linear obliquely transverse annulus (Fig. 204*F–G*) that causes a vertical dehiscence of the sporangium. Species with sporangia restricted to the margin of the receptacle have the sporangia dehiscing toward the center of the receptacle, but this is not always the case where there are also sporangia on the central portion of the receptacle.

Germination of spores is relatively slow and the spore wall does not crack open until two or three weeks after spores are sown on a suitable substratum.[1] According to the species the germling developing from a spore is a filamentous, plate-like, or massive structure. The mature gametophyte is cordate, with a thick midrib and with thin lateral wings that are frequently much ruffled. The first antheridia are formed when a

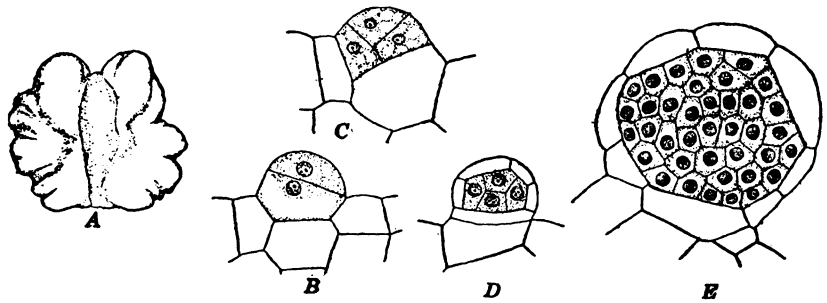

FIG. 205. *A. Gleichenia dichotoma* (Willd.) Hook. Dorsal view of a gametophyte. *B–E*, *Gleichenia pectinata* Presl. Stages in development of antheridia. (*A*, × 3; *B–E*, × 325.)

gametophyte is two to three months old; the first archegonia are formed about a month later.[1]

Antheridia are produced in abundance on the ventral side of both midrib and wings. Occasionally they are also produced on the dorsal side of a gametophyte. Early stages of antheridial development (Fig. 205*B–D*) are quite similar to those of *Osmunda*.[2] Development of the antheridial jacket layer is also similar, and there is a formation of a small triangular opercular cell at the apex of the jacket. The number of androgonial cells formed by the primary androgonial cell may be even larger than in *Osmunda* and there may be as many as 500 androcytes (Fig. 205*E*).

Archegonia are formed only on the ventral side of the midrib and in acropetalous succession. The initial cell of an archegonium is differentiated just a few cells back from the apical initials of a gametophyte. Development of an archegonium from an archegonial initial is quite similar to that in other ferns (Fig. 206*A–C*). The primary canal cell is usually binucleate and at times it divides into two canal cells.[2] Mature arche-

[1] Stokey, 1950. [2] Campbell, 1908; Stokey, 1950.

gonia (Fig. 206*D*) have long necks that are 7 to 14 cells in height and are directed toward the gametophyte's growing apex, and are either straight or curved.

Stages in embryonal development are exceedingly rare despite the fact that most gametophyte produce archegonia in abundance. The few early stages that have been observed[1] seem to show that, as in many other leptosporangiate ferns, differentiation of an embryo into foot, primary root, cotyledon, and stem occurs early and possibly at the eight-celled stage. The half of an embryo nearest the gametophyte's apex gives rise

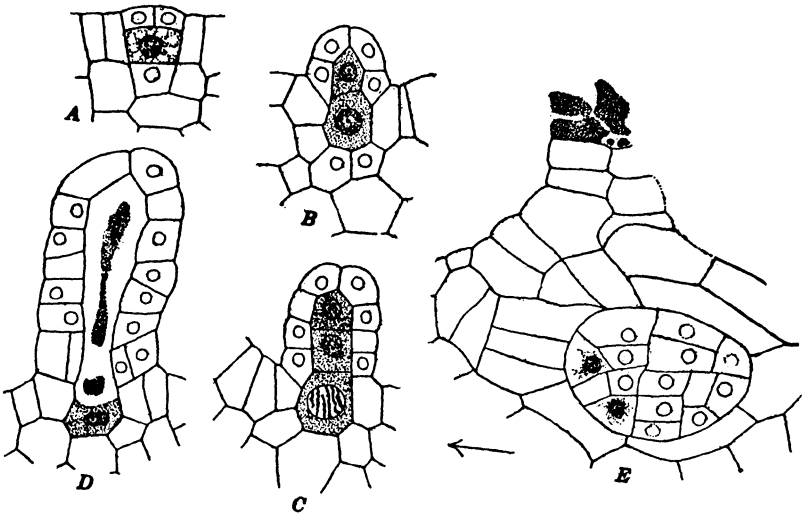

FIG. 206. *Gleichenia pectinata* Presl. *A–D*, stages in development of archegonia. *E*, embryo—the arrow points to the apex of the gametophyte. (× 325.)

to the cotyledon and stem, and the other half gives rise to the primary root and the foot (Fig. 206*E*). These four parts of an embryo also have a definite orientation with respect to one another, the cotyledon and primary root always lying next to each other and on the side of the embryo facing the archegonial neck. Cotyledon, stem, and primary root each develop from an apical cell, and it is also very probable that these apical cells are differentiated at the eight-celled stage of embryonal development.

FAMILY 4. MATONIACEAE

The Matoniaceae differ from other primitive Leptosporangiatae with a simultaneous development of sporangia in having the sporangia dehisce transversely and in having the sori protected by an umbrella-shaped indusium.

[1] Campbell, 1908.

The leaf architecture and certain sporangial features are similar to those in Gleicheniaceae. The Matoniaceae show considerable evolutionary progress over the Gleicheniaceae in their more elaborate vascular organization, their indusial protection of sori, and their transverse dehiscence of sporangia by means of a vertical annulus.

The Matoniaceae appeared later in the Triassic, presumably as an offshoot from the Gleicheniaceae. During the Jurassic and Lower Cretaceous

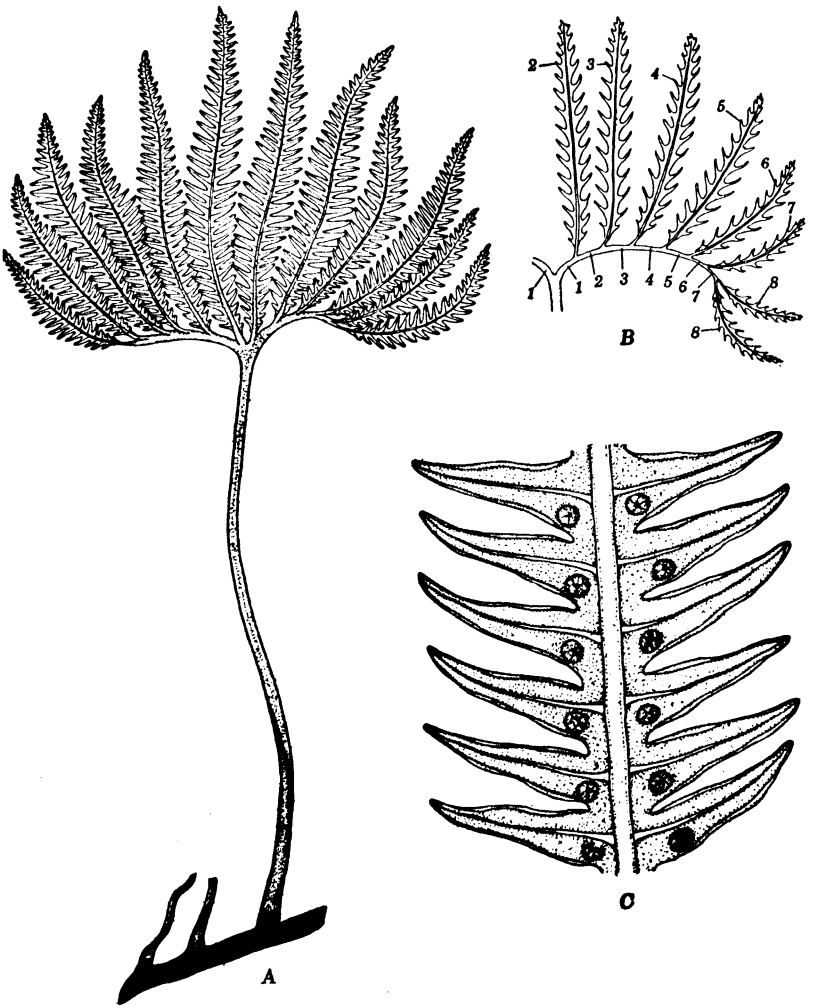

FIG. 207. *Matonia pectinata* R.Br. *A*, sporophyte. *B*, diagram of a leaf blade showing relationship of successive dichotomies; 1–1, 2–2, 3–3, etc. *C*, portion of a fertile pinna. (*A*, × ½; *C*, × 2.)

the family become widespread and with a distribution comparable to that of the cosmopolitan bracken fern in the flora of today.[1] The Matoniaceae, similar to the Gleicheniaceae, were driven toward the tropics by climatic changes toward the close of the Cretaceous. But in contrast with the widespread tropical persistence of present-day Gleicheniaceae, the Matoniaceae have disappeared from the tropical flora of today except in the Malayan region. Here there are two genera (*Matonia* and *Phanerosorus*), each with two species.

Matonia has a creeping, dichotomously branched rhizome. In *M. pectinata* R. Br. this is about 7 mm. in diameter and of indefinite length. A rhizome bears leaves at intervals along the upper side (Fig. 207*A*), but one striking peculiarity of *M. pectinata* is the intermingling of young and

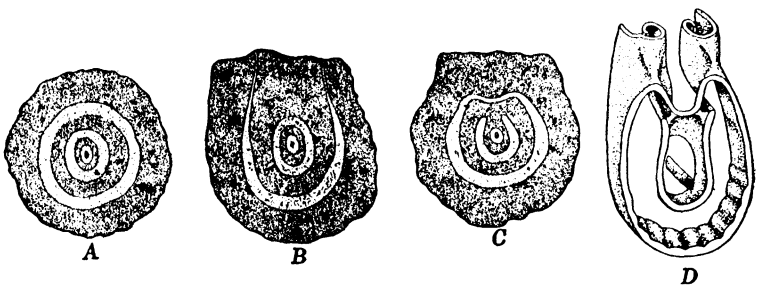

FIG. 208. *Matonia pectinata* R.Br. *A–C*, transverse sections below, through, and above a node of a rhizome. *D*, stereodiagram of the vascular tissues of a node. (*D*, *after Tansley and Lulham*, 1904.) (× 3⅓.)

old leaves along a rhizome. Leaves, which may attain a height of more than 2 meters, seem to have palmately divided leaves. Actually, there is a repeated dichotomous branching (up to 20 or more times) of the blade and one in which successive forkings are always restricted to the dichotomy facing the leaf base (Fig. 207*B*). Lateral veins of the pinnules have one or more bifurcations. Anastomoses between branches of the lateral veins result in a more or less reticulate venation.

Stems of very young sporophytes have a protostelic vascular cylinder.[2] The protostele is replaced by an amphiphloic siphonostele after a stem has produced two to four leaves. With further development there is a change into a polycyclic condition. Early-formed polycyclic regions of a stem have a siphonostele surrounding a protostele; later-formed regions have the inner vascular cylinder siphonostelic. Steles at the apex of an old stem are tricyclic and with the innermost cycle protostelic or siphonostelic (Fig. 208).

The outer and middle siphonosteles of a tricyclic stele are connected with each other only at the nodes.[2] Connection is established by a

[1] Seward, 1899. [2] Tansley and Lulham, 1904.

downwardly projecting "compensating tongue" from the two edges of each leaf trace (Fig. 208*D*). Both the outer and the middle siphonosteles have a gap at each node, but that of the middle stele lies considerably anterior to that of the outer stele. Hence successive sections through a node show no gap in the middle stele until after a closure of the gap in the outer stele (Fig. 208*C*). Anterior to the gap of the middle stele and arising from the inner face is a simple vascular bridge that connects it with the innermost stele.

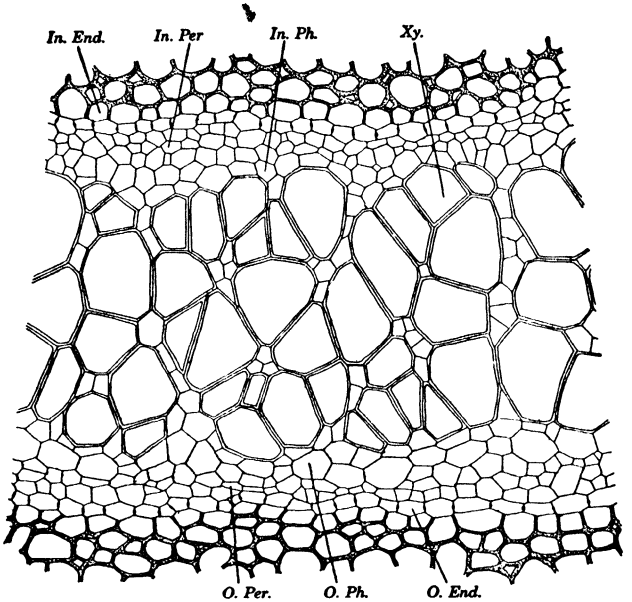

FIG. 209. *Matonia pectinata* R.Br. Transverse section through a portion of the middle siphonostele of a tricyclic rhizome. (*In. End.*, inner endodermis; *In. Per.*, inner pericycle; *In. Ph.*, inner phloem; *O. End.*, outer endodermis; *O. Per.*, outer pericycle; *O. Ph.*, outer phloem; *Xy.*, xylem.) (× 160.)

The xylem in all three siphonosteles consists of large tracheids intermingled with small, thin-walled, parenchymatous cells (Fig. 209). The outer siphonostele contains a variable number of small, mesarch, protoxylem masses that tend to lie toward the inner face of the xylem. There are also masses of protoxylem in the middle siphonostele. All three steles are amphiphloic, with the phloem on either side of the xylem but two or three cells in thickness. External to both the inner and outer phloem is a narrow belt of pericyclic tissue. There is a typical endodermal layer immediately external to and immediately internal to both the outer and the middle steles. The innermost siphonostele generally has an endodermal layer only at its outer face. At each node there is a single leaf trace departing from the outer siphonostele. The trace is C-shaped, un-

divided, and similar in appearance to the single bundle running the length of the petiole.

The sori generally lie in two rows on a pinna, one on either side of, and a short distance from, the midrib (Fig. 207*C*). Large leaves with deeply incised pinnae may have more numerous and irregularly distributed sori. All sporangia on a leaf develop simultaneously. As in *Gleichenia*, sporangial development is preceded by an elevation of the receptacle above the surface of a pinna.[1] There is soon an overarching of the receptacular apex to form an umbrella-shaped indusium with a massive stalk (Fig. 210*A*). Differentiation of the six to nine sporangial initials does not take place until the indusium is well along in its development. The initials are differentiated from superficial cells of the indusial stalk, and their development into sporangia is in typical leptosporangiate sequence, with

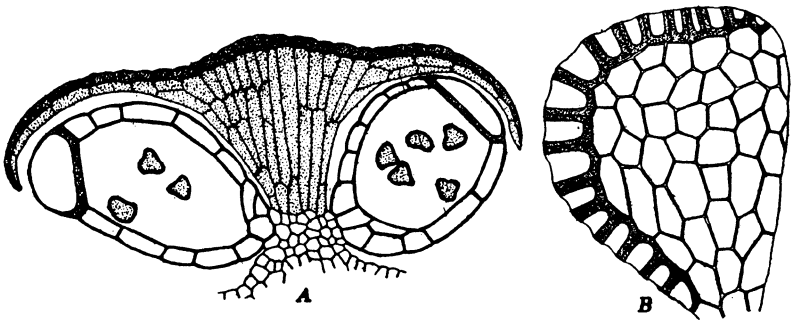

FIG. 210. *Matonia pectinata* R.Br. *A*, vertical section through a receptacle and indusium. *B*, surface view of a mature sporangium. (*A*, × 80; *B*, × 120.)

a potential formation of 64 spores.[1] Shortly after the sporangia are ripe there is a shedding of the indusium and a free exposure of the ring of sporangia surrounding the stump of the receptacle. Mature sporangia of *M. pectinata* (Fig. 210*B*) have a linear, obliquely vertical annulus that causes a transverse dehiscence of the sporangial jacket.

The structure of the gametophyte of *Matonia* is much the same as in *Gleichenia* and *Dipteris*.[2] So, also, are the development and structure of the sex organs. Division of the zygote is vertical. Relatively few stages in early development beyond the two-celled stage have been found,[2] but these indicate that there is an early differentiation into cotyledon, root, stem, and foot quadrants, and presumably at the eight-celled stage.

FAMILY 5. DIPTERIDACEAE

The Dipteridaceae have sori in which sporangial development is essentially simultaneous. The sori are without indusial protection but have numerous capitate hairs intermingled with the sporangia. Dehiscence of

[1] Bower, 1899. [2] Stokey and Atkinson, 1952.

sporangia is more or less transverse and by means of an obliquely vertical annulus.

There is but one genus with living species. This genus, *Dipteris*, is found only in the Malayan region and has eight species. *Dipteris* is usually placed among the polypodiaceous ferns[1] but there is good reason for following those[2] who place it in a separate family (Dipteridaceae) which also includes certain fossil genera of the Triassic and Jurassic. Three of the fossil genera assigned to the Dipteridaceae had lyre-shaped leaves; a fourth genus, of later origin, had leaves more like *Dipteris*. Except that the Dipteridaceae appeared somewhat earlier in the Triassic, the history of the family shows a remarkable parallelism to that of the Matoniaceae. Similar to the Matoniaceae they became widespread over Europe and North America during the Jurassic and disappeared from these continents during the Cretaceous. Similarly, also, present-day representatives are found only in the Malayan region.

Dipteris, the sole surviving genus, shows a curious intermingling of primitive and advanced characters. On the primitive side there is the relatively simple vascular structure, the major venation of blades, the nearly simultaneous development of sporangia, the cordate gametophytes with a midrib, occasional formation of sex organs on the dorsal side of a gametophyte, and the large number of antherozoids per antheridium. Advanced features include the double leaf trace, the reticulation of minor veins of a leaf blade, the small spore output per sporangium, and the nearly vertical annulus of a sporangium.

Sporophytes of *Dipteris* have creeping, dichotomously branched rhizomes that are covered with stiff brown scales. Leaves are borne on the upper side of a rhizome, and roots are irregularly distributed over its lower surface. The rhizome shows the same intermingling of old and young leaves as is found in *Matonia* (Fig. 211*A*). The blade of a leaf may have a repeated dichotomous branching into equal dichotomies (Fig. 211*B*) or it may have but one dichotomy and a repeated dichotomous branching of the main veins (Fig. 211*A*). Although both kinds of leaf have a primitive type of primary venation, the veinlets are of an advanced type in that they form a reticulum in which many of the ultimate veinlets end blindly.

Young sporophytes have rhizomes with a protostelic vascular cylinder but this soon gives way to a siphonostelic condition.[3] The siphonostele is amphiphloic and has an external and an internal endodermal layer. *D. conjugata* (Kaulf.) Reinw. has a single trace departing to the leaf at each node[4] (Fig. 212*A–B*). The first-formed portion of the siphonostele of

[1] Christensen, 1938; Copeland, 1947; Holttum, 1949.
[2] Bower, 1926; Seward and Dale, 1901. [3] de Bruyn, 1911.
[4] de Bruyn, 1911; Seward and Dale, 1901.

D. lobbiana (Hook.) Moore may also have but one trace to a leaf, but later-formed portions always have two traces.[1]

The sori may lie in two rows, one on either side of the midrib (Fig. 212*C*): or, as in *D. conjugata*, they may be irregularly distributed over the entire abaxial face of the blade. Two species have been shown[2] to have a simultaneous development of the sporangia on a leaf blade. Young sori of *D. conjugata* may produce sporangia in an irregular sequence.[2] However, the sorus of this species is only an incipient mixed sorus, since

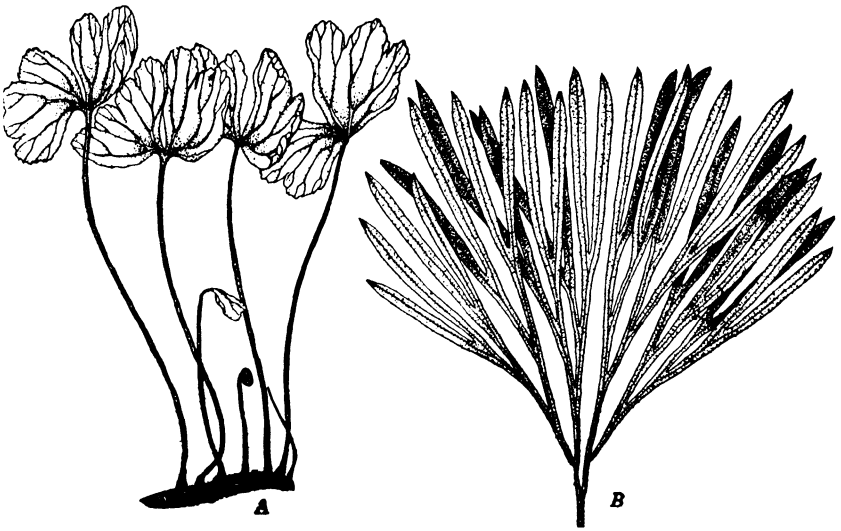

FIG. 211. *A*, sporophyte of *Dipteris conjugata* (Kaulf.) Reinw. *B*, leaf of *Dipteris lobbiana* (Hook.) Moore. (*A*, × ½; *B*, × ⅜.)

older sori do not have the intermingling of mature and developing sporangia typical for mixed sori. Sporangial development is strictly leptosporangiate, and sporangia have a relatively small (64) output of spores. The stalk of a sporangium consists of four vertical rows of cells, two of which are visible when a stalk is seen from the side. Mature sporangia have a vertically oblique annulus that almost completely encircles the sporangium (Fig. 212*D*). Dehiscence of a sporangium is approximately transverse but there is not a definite stomium in the region where the sporangial jacket ruptures.

Practically all knowledge about the gametophyte is from those of *D. conjugata* grown from spores in the laboratory.[3] A germinating spore usually gives rise to a small plate of cells and this eventually develops into a cordate gametophyte with a thick midrib and thin, ruffled, lateral wings (Fig. 213*A*). Sex organs are regularly formed on the ventral side,

[1] de Bruyn, 1911: Bower, 1915. [2] Armour, 1907. [3] Stokey, 1945.

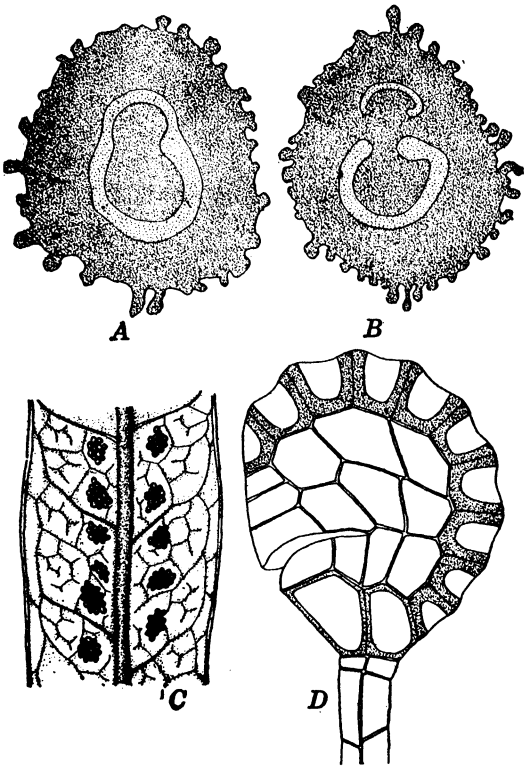

FIG. 212. *A–B*, *Dipteris conjugata* (Kaulf.) Reinw. Transverse sections just below (*A*) and through (*B*) a node of a rhizome. *C*, *Dipteris lobbiana* (Hook.) Moore. Portion of a fertile pinnule. *D*, *Dipteris conjugata*. Surface view of a mature sporangium. (*A–B*, × 8; *C*, × 3; *D*, × 190.)

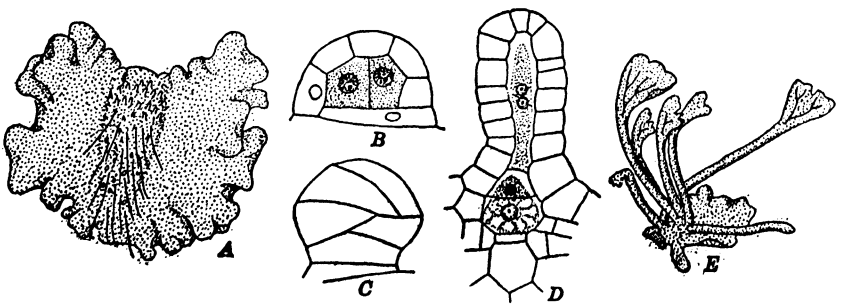

FIG. 213. *Dipteris conjugata* (Kaulf.) Reinw. *A*, ventral view of a mature gametophyte. *B–C*, vertical section and side view of an antheridium. *D*, archegonium. *E*, gametophyte with young leaves of an apogamous sporophyte. (*After Stokey*, 1945.)

but both antheridia and archegonia may be formed on the dorsal side. An antheridium (Fig. 213*B–C*), similar to that of Osmundaceae and Gleicheniaceae, has such primitive features as a jacket layer composed of several cells, a triangular opercular cell at the apex of the jacket, and a relatively large complement of antherozoids. The ontogeny of an archegonium is as in other leptosporangiates and when mature it has a long straight neck seven to nine cells in height and has a binucleate primary canal cell within the neck (Fig. 213*D*).

Although producing apparently normal archegonia in abundance and liberating antherozoids in abundance, no embryos were found when gametophytes were killed and cut in serial section.[1] On the other hand, there was regularly an apogamous production of young sporophytes (Fig. 213*E*).

FAMILY 6. HYMENOPHYLLACEAE

The Hymenophyllaceae differ from other homosporous Leptosporangiatae with a gradate sorus in having the sori borne marginally on leaves and in having each sorus surrounded by a cup-like or a two-lipped involucre (indusium). Practically all members of the family are "filmy ferns" in which the sporophyte has semitransparent leaves one cell in thickness. This feature cannot be considered a unique family character since *Leptopteris* (one of the Osmundaceae) is also a filmy fern.

Some 450 to 600 species are recognized in the family. These are usually segregated into two to four genera, but they have also been segregated[2] into 34 genera. If divided into three genera, the species with the sorus surrounded by a two-lipped involucre are placed in *Hymenophyllum*, and those with a cup-like involucre are placed in *Trichomanes* and in the monotypic *Cardiomanes*. The geological record of the family is uncertain, but one fossil genus (*Hymenophyllites*) known from as far back as the Upper Carboniferous seems to have much in common with present-day Hymenophyllaceae.

Hymenophyllaceae are found in greatest abundance and greatest variety in tropical rain forests. Here, most of the species are epiphytes, but a few of them are terrestrial in habit. In spite of their filmy leaves the sporophytes of many species are able to withstand desiccation and to recover after a considerable degree of drying and shriveling.[3] In this respect they resemble many liverworts and mosses, although their capacity to withstand desiccation is more limited.

The sporophyte shows several primitive features. Among these are the protostelic vascular cylinder, the dichotomous venation of leaves, and the marginal receptacles. These features point to a relationship with the lower Leptosporangiatae and tend to show that the Hymenophyllaceae

[1] Stokey, 1945. [2] Copeland, 1947. [3] Holloway, 1923; Shreve, 1911.

are a stock of relatively ancient origin. On the other hand, the gradate sorus and the nearly vertical annuli of sporangia show that there has been a considerable advance over primitive ferns as far as organization of the reproductive organs is concerned. Advance in structure of the fructification does not appear to have led to a higher type of fern because the plant body is ecologically restricted to a humid, feebly illuminated habitat. Thus, the Hymenophyllaceae may be looked upon as an evolutionary series ancient in origin and ending blindly because of ecological specialization.

Except for the indusia and receptacles there are no constant differences between *Hymenophyllum* and *Trichomanes*. With a very few exceptions, as *H. pulcherrimum* Col., the sporophyte of *Hymenophyllum* has a prostrate, creeping rhizome. This is sparingly branched because only occasionally is there a development of the axillary branch primordium formed at each node. Leaf primordia are formed in acropetalous succession and in a double row on the upper side of a rhizome. In many species, as in *H. australe* Willd., only one out of a half dozen successively formed primordia develops into a mature leaf. The others remain dormant, or they abort. Thus, there is a fairly long interval between successive mature leaves on a rhizome (Fig. 214). Since a dormant primordium may develop at any time into a leaf, it is not uncommon to find a spirally uncoiling young leaf between two fully mature ones. Irrespective of whether a leaf primordium continues development or not, a pair of adventitious roots is formed on the underside of a rhizome at each node. This accounts for the occurrence of several pairs of roots between two successive mature leaves. Intake of water through the roots is supplemented by absorption of water vapor condensing on the leaves. However, most species of *Hymenophyllum* seem to take in sufficient water through their roots to meet all needs of the plant.[1] A few species, as *H. cruentum* Cav., have an entire blade, but most of them have the blade divided into a succession of unequal dichotomies. Blades of the latter type always have a single vein in each shank of a dichotomy (Fig. 216*A*). Species with entire blades have a series of sori along the lateral margins, one at the terminus of each vein. Species with divided blades have a single sorus at the apex of each ultimate dichotomy. In both cases the receptacle is elevated but in neither does it project beyond the subtending indusium as in *Trichomanes*.

Stems of *Hymenophyllum*[2] have a relatively narrow cortex in comparison with those of most other ferns. All cells of the cortex may be thick-walled, or there may be thin-walled cells in the external portion and thick-walled ones in the internal portion. The vascular cylinder is protostelic. As is the case with most other ferns, the stele is externally

[1] Shreve, 1911. [2] Boodle, 1900.

delimited by an endodermal layer. The pericyclic layer internal to the endodermis may be one to several cells in thickness. It is always composed of thin-walled cells. Just within the pericycle is a layer of phloem, generally more than one cell in thickness. The phloem is separated from the xylem core by a band of conjunctive parenchyma one or more cells in thickness. There is considerable variation in structure of the xylem.

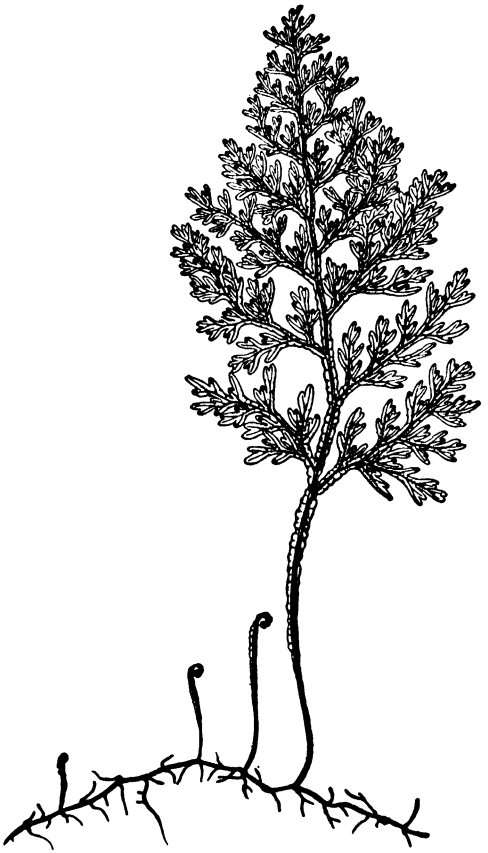

FIG. 214. *Hymenophyllum australe* Willd. Portion of a sporophyte. (× ½.)

Certain species with relatively large rhizomes, as *H. demissum* Swartz, have a continuous ring of metaxylem surrounding a central parenchymatous area in which the protoxylem is embedded. Other species with large rhizomes, as *H. scabrum* A. Rich., have the metaxylem ring transversely interrupted on either flank. Metaxylem elements in the ventral arc of an interrupted ring are of smaller diameter than those in the dorsal arc (Fig. 215*A*). Some species with small rhizomes have an obliteration of the

ventral arc of metaxylem. In such cases the protoxylem may be separated from the persistent dorsal arc by parenchyma (*H. cruentum* Cav.), or it may lie immediately next the lower face of the metaxylem (*H. fucoides* Swartz).

Leaf traces are similar in structure to the steles from which they depart, and there is no interruption of the vascular cylinder when a trace is given off. As noted, above, there is a rudimentary or vestigial branch

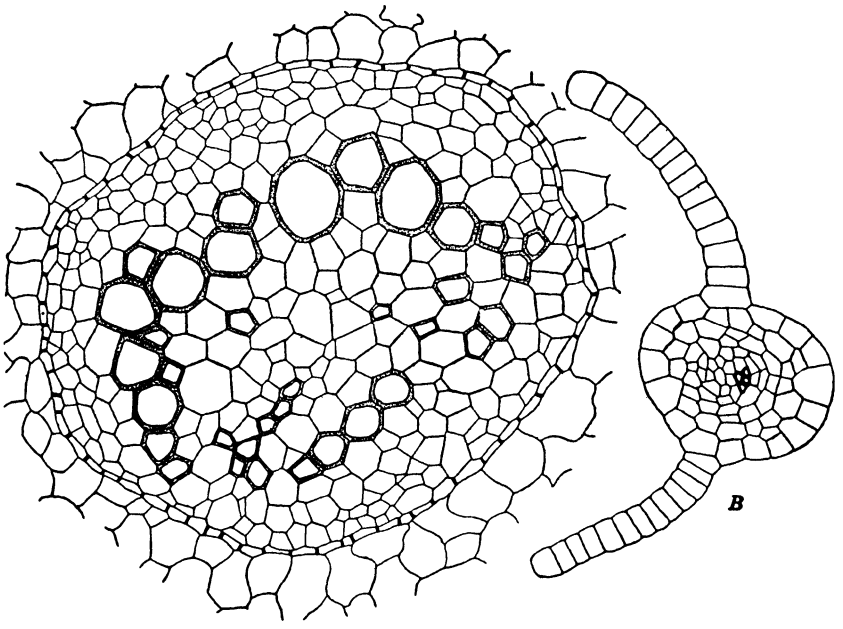

FIG. 215. *Hymenophyllum australe* Willd. *A*, Transverse section of stele and inner portion of cortex, of a rhizome. *B*, transverse section of a leaf. (*A*, × 325; *B*, × 140.)

primordium in the axil of each leaf. The vascular supply within a primordium does not connect directly with the central cylinder. Instead, it is joined with, or departs from, the leaf trace some distance above the region where the latter is united with the stele.[1]

The most conspicuous difference between roots of *Hymenophyllum* and those of other ferns is the lack of a root cap.[2] The structure of a root proper resembles that of other Leptosporangiatae. In most species the stele is diarch, but it may be monarch if the root is of small diameter.[1]

A majority of the species are true filmy ferns and, except for the veins, have leaves one cell in thickness (Fig. 215*B*). Veins of leaves with a blade one cell in thickness may contain xylem and phloem, or they may be

[1] Boodle, 1900. [2] Sadebeck, 1898.

pseudoveins in which there is no true vascular tissue. A few species, including *H. dilatatum* Swartz, have leaf blades several cells in thickness in which the cells are organized into a solid tissue without intercellular spaces. The thin filmy leaf typical of most species is thought[1] to be a secondarily developed type resulting from adaptation to a hydrophytic environment. The thicker-leaved species, as *H. dilatatum*, have been regarded as being nearer the ancestral type than are those species with filmy leaves.[2] However, the fact that the first-formed leaves of thick-leaved species are one cell in thickness[3] indicates that species with the thick-leaved type are derived from, instead of more primitive than, those with a filmy type of leaf blade.

The sori are developed singly and at the distal end of a vein. They are terminal in position if the blade is divided, and lateral if it is undivided. Receptacular development in *Hymenophyllum* is accompanied by the development of a subtending flap-like outgrowth, one cell in thickness, from both the adaxial and abaxial faces of the blade. The two-lipped indusium thus formed soon overarches the apex of a receptacle[4] and continues to ensheath the latter until the spores are shed (Fig. 216*A–B*). The first sporangial initials are differentiated at the apex of the receptacle and at a time when its basal portion is still meristematic. Succeeding sporangial initials appear in basipetalous succession, and sporangia at the receptacular apex may be at the spore-mother-cell stage before the lowermost initials are differentiated. Notwithstanding the gradate nature of the receptacle, the early stages in sporangial development resemble those of such primitive leptosporangiates as the Osmundaceae and the Gleicheniaceae. A sporangial initial is deeply embedded in the receptacle, and it produces only one or two stalk cells at each cutting face before dividing periclinally into jacket initial and primary archesporial cell (Fig. 216*B*). Succeeding stages of development are like those in typical leptosporangiates. The theoretical spore output[4] is generally 128 or 256, but it may be 512. A mature sporangium dehisces transversely by means of an obliquely vertical annulus (Fig. 216*C*).

There are two different kinds of gametophyte in the Hymenophyllaceae.[5] In *Hymenophyllum* and *Cardiomones* the gametophyte is an irregularly branched ribbon (Fig. 217*D*); in *Trichomanes* it is a profusely and irregularly branched uniseriate filament of cells (217*G*). These gametophytes are vegetatively simpler than gametophytes of most other Leptosporangiatae but the simplicity is generally considered a derived condition, not a primitive one.

Spores of *Hymenophyllum* germinate by dividing into three radiately arranged cells while still within the sporangium. *Trichomanes* may or may

[1] Bower, 1908, 1923. [2] Bower, 1908, 1926. [3] Holloway, 1923.
[4] Bower, 1899. [5] Holloway, 1944; Stokey, 1940.

not have a similar germination of spores within a sporangium.[1] In *Hymenophyllum* each of the three cells divides transversely after the spores are shed and in the resultant six-celled germling growth is independent in the three arms (Fig. 217*A–C*). Growth in two of the arms is soon checked by a development of the terminal cell into a rhizoid; growth of the third arm continues indefinitely, and it soon differentiates an apical

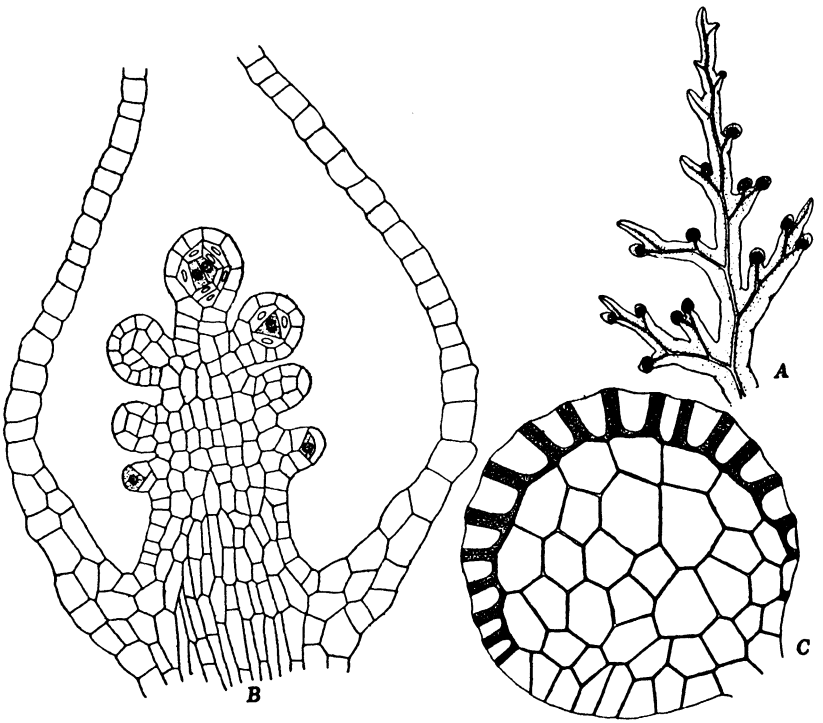

FIG. 216. *Hymenophyllum australe* Willd. *A*, tip of a fertile leaf. *B*, vertical section through a receptacle. *C*, surface view of a mature sporangium. (*A*, × 2; *B–C*, × 140.)

cell with two cutting faces. Later in development of the gametophyte the apical cell is replaced by a transverse row of initial cells in which cessation of division of those at the center of the row results in an apical branching of the gametophyte. Branches of the gametophyte, some of which grow upward from the substratum, are usually one cell in thickness and with rhizoids restricted to the marginal cells.

Sex organs of *Hymenophyllum* (Fig. 217*E–F*) are regularly formed on the ventral side and occasionally on the dorsal side. Antheridia are borne

[1] Stokey, 1940.

remote from one another and on or near the margins of branches.[1] Mature antheridia have a jacket layer composed of several cells and with a triangular opercular cell at the jacket's apex. Antheridia may contain over a hundred antherozoids. Archegonia of *Hymenophyllum* are restricted to localized areas, two cells in thickness, borne along the margins of branches. Development of an archegonium is in the manner characteristic of Leptosporangiatae and when mature it has a straight neck

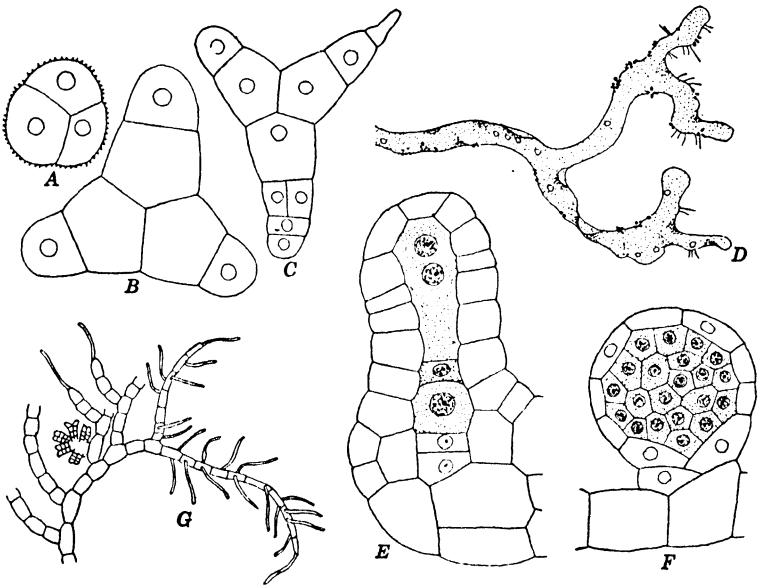

FIG. 217. *A–C, Hymenophyllum acanthoides* Ros. Early stages in development of gametophyte. *D-F, Hymenophyllum kurzii* Prantl. *D*, portion of a mature gametophyte with antheridia and archegonia, *E*, archegonium. *F*, antheridium. *G, Trichomanes bilabiatum* Nees. Portion of a mature gametophyte bearing an archegoniophore. (*A–C, after Stokey*, 1940; *D-G, after Stokey*, 1948.)

six to nine cells in height and has a binucleate primary canal cell within the neck. In the filamentous gametophyte of *Trichomanes*, antheridia may be produced directly on any filamentous branch, but all archegonia are formed on special globular or irregularly shaped multicellular structures (**archegoniophores**) borne here and there along the filamentous branches[1] (Fig. 217*G*).

The only member of the family where development of the embryo has been studied[2] is *Cardiomanes reniforme* (Forst.) Presl (*Trichomanes reniforme* Forst.). Division of its zygote is at right angles to the long axis of the archegonium, instead of parallel to the long axis as in most other Leptosporangiatae. Differentiation of the embryo into cotyledon, pri-

[1] Stokey, 1948. [2] Holloway, 1944.

mary root, stem, and foot does not occur until after the embryo has become a globular mass of many cells. When these organs are differentiated they are oriented with respect to one another in the manner characteristic of leptosporangiate ferns.

Three species of *Trichomanes* have been shown to be apogamous and two of these species have also been found to be aposporous.[1]

FAMILY 7. CYATHEACEAE

The Cyatheaceae have a gradate sorus bearing sporangia that dehisce transversely by means of an obliquely vertical annulus. The sori are borne abaxially on veins of pinnately compound leaves and usually have an involucrous indusium that covers the sorus when young, but an indusium may be lacking. Most members of the family are arborescent and with a crown of leaves at the stem apex.

The family is pantropical and southern in distribution, and containing five genera[2] if the Protocyatheaceae[3] are included in the family. Two of the genera are monotypic; the other three each have 100 to 300 species. Fossil cyatheaceous ferns, known either from their trunks or from their leaves, have been found as far back as the Jurassic.[4]

Cyathea, the type genus, has about 300 species, all of which are tree ferns. At one extreme are the species with a maximum height of approximately 20 meters; at the other are those with a maximum height of about 1 meter. Most species have unbranched stems terminating in a crown of bi- to quadripinnate leaves.

C. medullaris Sw. (Fig. 218), native to Australia and several islands of the South Pacific, is one of the hardier species that may be grown out of doors in this country in regions where the temperature does not fall more than a couple of degrees below the freezing point. It is also one of the species frequently grown in greenhouses. Mature plants growing under natural conditions in New Zealand attain a height of 6 to 15 meters.[5] In most cases the stem of *C. medullaris* is unbranched but it may have a single dichotomy. At the base of a stem and extending upward for a meter or more is a conical mass of adventitious roots. Above this for some distance upward the stem is smooth except for hexagonal leaf scars. Still higher up, the stem surface is clothed with a shaggy felt consisting of the half-decayed remains of old leaf bases and the adventitious roots borne by them. The stem terminates in a crown of 20 to 30 leaves with pinnately divided blades 1.5 to 4 meters long and a petiole whose length equals that of the blade. New leaves are produced throughout the growing season and have the same spiral uncoiling (circinate vernation) as do leaves of most other leptosporangiate ferns.

[1] Bower, 1883; Georgevitch, 1910; Stokey, 1948. [2] Christensen, 1938.
[3] Bower, 1926. [4] Arnold, 1947; Hirmer, 1938; Seward, 1910. [5] Cheeseman, 1925.

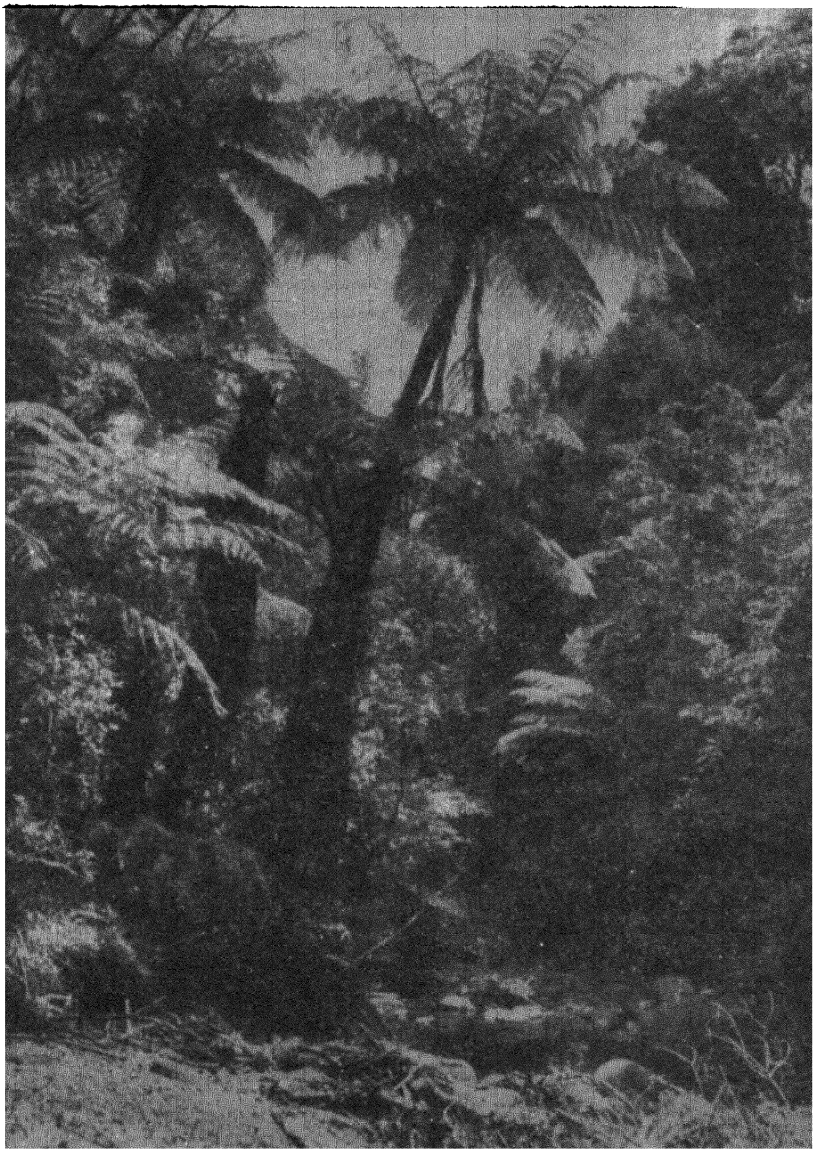

FIG. 218. Stand of *Cyathea medullaris* Sw. in a forest in New Zealand. (*Photograph by T. L. Lancaster. From Smith et al.*, 1942.)

Basal support and anchorage of a stem of *Cyathea* are due in large part to the conical, buttress-like, densely interwoven mass of adventitious roots at the base of a stem. The lowermost portion of a stem, exclusive of the root buttress, is an inverted cone that gradually broadens upward for some distance (Fig. 219). Above this the stem's diameter is constant up to the crown of leaves. There is no secondary thickening in stems of *Cyathea* or in those of other Cyatheaceae.

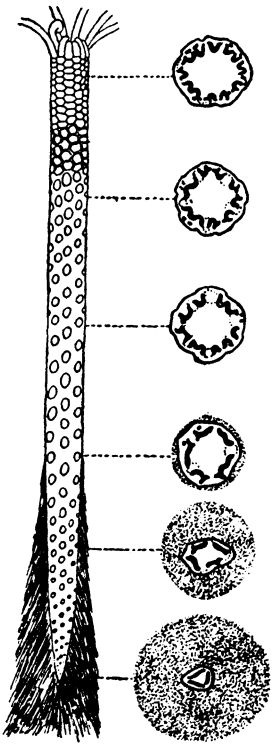

FIG. 219. *Cyathea* sp. Diagram of a stem showing the vascular organization at successive levels. (*After Ogura*, 1927.)

A stem has a narrow cortex and a broad central cylinder. The central cylinder shows an ontogenetic recapitulation of the stelar theory in being protostelic for the first one or two nodes, siphonostelic for the next few nodes, and a polycyclic dictyostele above this.[1] The outer portion of the polycyclic portion is a tubular dictyostele. Accordingly as it is cut at a low or a high level, there are[2] two or three to many overlapping leaf gaps (Fig. 219). The strands (meristeles) into which a leaf trace is divided are convexly arched and have their poles turned outward next to the leaf gaps. Internal and external to each meristele, and apparently a portion of it, is an arc of sclerenchyma. Each meristele is amphiphloic, completely encircled by an endodermal layer, and with a pericycle a few cells in thickness between endodermis and phloem.[2] The xylem of a meristele is composed of tracheids intermingled with parenchymatous cells. Internal to the outer ring of vascular tissue, and embedded in parenchyma, are rings and arcs of numerous (50 to 150) small vascular strands. These rings and arcs are much-dissected internal vascular cylinders[3] and comparable to much dissected internal cylinders of *Matonia*. The supply of traces to each leaf is extremely complex and is further complicated by the dissection of traces into meristeles. Some of the traces depart from the outer dictyostele and some depart from the internal dictyosteles. The relatively narrow cortex is differentiated into an outer sclerenchymatous region and an inner parenchymatous region containing numerous mucilage sacs.

[1] Ogura, 1927; Stephenson, 1907. [2] Ogura, 1927. [3] Godwin, 1932.

There are several adventitious roots at the base of each petiole. Some of the roots at a leaf base connect with the lower side of the leaf gap; others connect with the leaf traces. Although roots are formed in association with each leaf, those formed in association with leaves more than a meter above the ground remain short and never penetrate the soil. There are no unusual features in the structure of a root.[1]

Sori are developed as a leaf uncoils. Each pinnule bears two rows of sori, one on either side of the midrib (Fig. 220). Sori are first apparent as small swellings that soon become conical in shape.[2] Sometimes, as in *C. dealbata* Sw.,[2] the indusium formed at the base of a sorus grows more rapidly than the receptacle and soon becomes a cup-like sheath

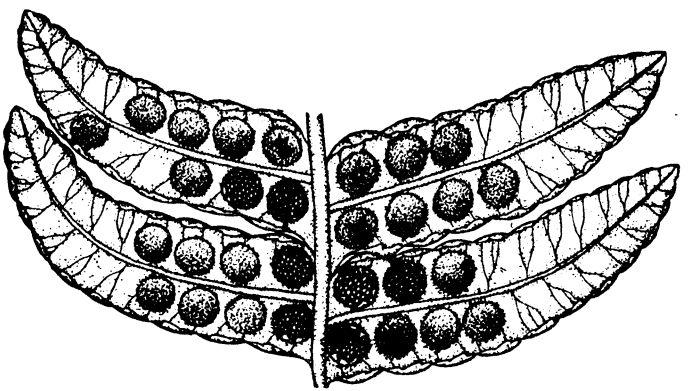

FIG. 220. *Cyathea medullaris* Sw. Fertile pinnules. (× 4.)

overarching it. In other cases, as in *C. medullaris* Sw., development of the indusium is relatively slow, and the only protection of young sporangia is that afforded by the precociously developing multicellular hairs from the receptacular surface (Fig. 221*A*). Some species have a somewhat larger cell at the apex of a young receptacle, but there is no evidence indicating that it is an apical cell.[2] Sporangial initials appear in basipetalous succession on a receptacle. Development of an initial into a sporangium is in the usual leptosporangiate manner, with the formation of a tapetum two cells in thickness (Fig. 221*A*). The archesporial cell of *C. dealbata* divides to form two or four spore mother cells.[2] The resultant small number of spores (8 or 16) within the sporangium of this species is not characteristic of all species, since the theoretical number of spores in sporangia of *C. medullaris* is 64. Mature sporangia are relatively small and are borne upon a stalk composed of four vertical rows of cells. The annulus is an obliquely vertical row that incompletely encircles the sporangium (Fig. 221*B*). One feature not found in previously

[1] Ogura, 1927. [2] Bower, 1899.

described families is the belt of thin-walled cells, the stomium, that predetermines the precise spot at which transverse dehiscence will take place.

A germinating spore divides into two cells, one functioning as the first prothallial cell and the other developing into the first rhizoid.[1] The first

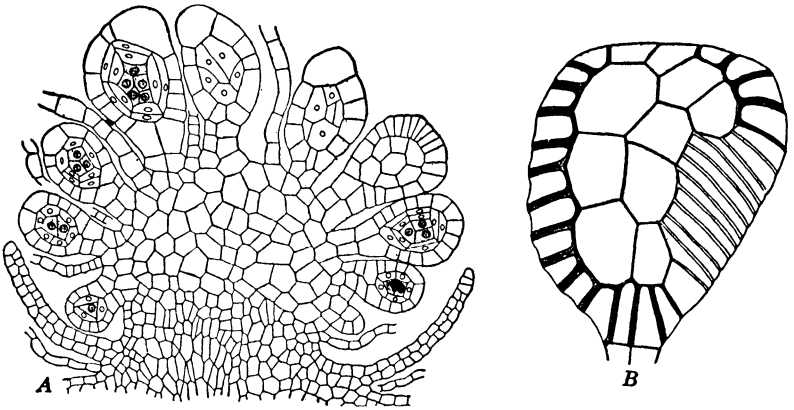

FIG. 221. *Cyathea medullaris* Sw. *A*, vertical section through a sorus. *B*, surface view of a mature sporangium.

prothallial cell divides and redivides transversely to form a filament of four to five cells which then divide longitudinally to form a small plate of cells (Fig. 222*A*). As the plate-like young gametophyte continues growth there is a differentiation of a single apical cell, but later this is replaced by a group of apical initials. A mature gametophyte (Fig. 222*B*)

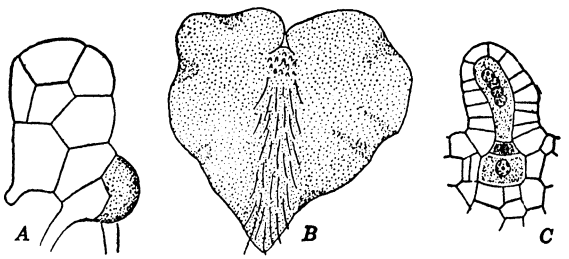

FIG. 222. *A*, *Cyathea muricata* Willd. Very early stage in development of gametophyte. *B*, *Cyathea tussacii* Desv. Mature gametophyte. *C*, *Cyathea medullaris* Sw. Archegonium. (*After Stokey*, 1930.)

is of the heart-shaped type found in gametophytes of polypodiaceous ferns, and as in them is more than one cell in thickness just back of the apical notch. Gametophytes of Cyatheaceae bear a distinctive scale-like type of hair not found on gametophytes of any other family of the Leptosporangiatae.[2]

[1] Stokey, 1930. [2] Stokey, 1930, 1951.

Antheridia are borne toward the posterior end of a gametophyte and are generally formed only on the ventral side, but a few may be produced on the dorsal side.[1] In development of an antheridium an antheridial initial divides unequally into a small wedge-shaped **stalk cell** and an **apical cell** (Fig. 223*A–B*). The apical cell divides transversely. Then, because of greater turgor in the upper daughter cell,[2] the cross wall between the two daughter cells is pushed toward the base of the lower daughter cell, the **first ring cell** (Fig. 223*C–D*). Next, the upper daughter cell divides transversely into a **dome cell** and a **primary androgonial cell** (Fig. 223*E*). Transverse division of the dome cell forms the **second ring cell** and the **primary cover cell** which eventually divides vertically into two cover cells, one of which is the **opercular cell** (Fig. 223*F–I*). The two ring cells

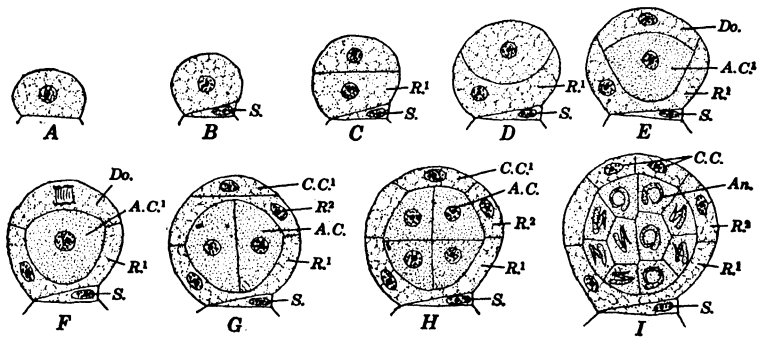

FIG. 223. *Cyathea*. Diagram showing stages in development of antheridium. (*A.C.*, androgonial cells; *A.C.*¹, primary androgonial cell; *An.*, androcytes; *C.C.*, cover cells; *C.C.*¹, primary cover cell; *Do*, dome cell; *R.*¹, first ring cell; *R.*², second ring cell; *S.*, stalk cell.) (*Based upon Davie*, 1951.)

and the two cover cells constitute the jacket portion of an antheridium. The primary androgonial cell that is differentiated at a relatively early stage in antheridial development divides and redivides to form androgonial cells the last cell generation of which are the **androcytes** that metamorphose into antherozoids (Fig. 223*I*).

Development of archegonia takes place in the manner typical of leptosporangiate ferns.[1] The primary canal cell usually has two nuclei, but sometimes it has four. The neck of an archegonium resembles that of Osmundaceae and Gleicheniaceae in being long and only slightly curved (Fig. 222*C*).

The demonstration[1] of the remains of antherozoids within the open neck of an archegonium containing a two-celled embryo shows that embryonal development may be initiated by gametic union. In other cases it is equally clear that the sporophyte is formed apogamously.[3] Apoga-

[1] Stokey, 1930. [2] Davie, 1951. [3] Stokey, 1948.

mously formed sporophytes are generally developed from a single cell adjoining the axial row of an archegonium (Fig. 94*E–F*, page 152). Sometimes there is also a parthenogenetic development of an egg into a sporophyte.

The scanty observations on development of the embryo show[1] that division of the zygote is vertical. It is very probable that the next division is also vertical and that the four organs of the embryo are established by the transverse divisions producing the octant stage. Somewhat older embryos show the typical leptosporangiate condition of a cotyledon and stem in the half embryo facing the apex of a gametophyte, and a root and foot in the other half.[2] During subsequent growth there is the usual more rapid development of cotyledon and primary root.

FAMILY 8. DICKSONIACEAE

The Dicksoniaceae have a gradate sorus bearing sporangia that dehisce transversely by means of an obliquely vertical annulus. The sori are borne marginally on the leaves and are usually surrounded by a two-lipped involucral indusium. Sporophytes are either erect and arborescent, or have prostrate rhizomes.

The family is mainly tropical and southern in distribution. Certain fossil genera of the Jurassic are thought to be members of the family.[3]

The arborescent habit, the structure of sori, and structure of sporangia are so much like that of Cyatheaceae that the Dicksoniaceae were placed[4] as a subfamily (Dicksonieae) of that family. Later the subfamily was elevated[5] to the rank of a family because the marginal position of the sori was thought to be a feature of fundamental significance. The difference in position of sori also correlates with other differences between Cyatheaceae and Dicksoniaceae. Stems of Cyatheaceae are clothed with scales and have numerous vascular strands running through the pith; whereas those of Dicksoniaceae are clothed with hairs and lack vascular strands in the pith. Gametophytes of Cyatheaceae have a unique type of scale-like hairs; whereas those of Dicksoniaceae are without hairs. Those[6] who recognize the family as distinct from Cyatheaceae are in agreement in assigning *Dicksonia*, *Cibotium*, *Cystodium*, and *Thrysopteris* to it; but disagree as to whether or not the family should include *Dennestedtia* and certain genera closely related to it.

Cibotium, which is here taken as illustrative of the family, has about a dozen species and is found in Central America, the Hawaiian Islands, and East Asia. Sporophytes of most species are arborescent and with a crown of leaves at the apex; but those of certain species, as *C. barometz*

[1] Stephenson, 1907; Stokey, 1930. [2] Stephenson, 1907. [3] Bower, 1926.
[4] Christ, 1897; Diels, 1898. [5] Bower, 1899.
[6] Bower, 1928; Christensen, 1938; Holttum, 1949.

(L.) J. Sm., have prostrate massive stems. Leaves are borne spirally on the stem, even in those species where it grows prostrate. The surface of a stem is densely clothed with unbranched filamentous hairs that may attain a length of 3 cm. or more. The stems are solenostelic, with the vascular cylinder amphiphloic, and with an endodermis both external and internal to the solenostele. The region internal to the solenostele lacks the vascular strands that are present in Cyatheaceae. Cortical portions of a stem are usually sclerenchymatous beneath the epidermis but sometimes, as in *C. barometz*, the cortex is wholly parenchymatous. Nodes of a stem are generally so close together that successive leaf bases give the stem an irregular instead of a circular outline when it is seen in cross section. The lower part of a departing leaf trace[1] is a solid arc but it becomes divided into several meristeles before it emerges from the cortex (Fig. 224).

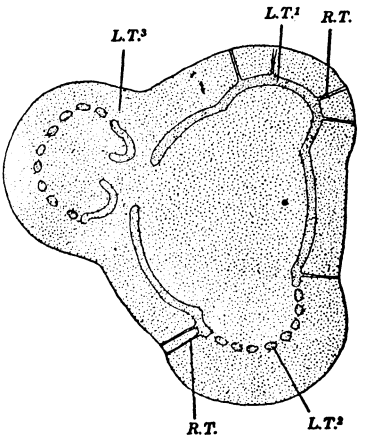

FIG. 224. *Cibotium barometz* (L.) J. Sm. Diagram of a cross section of a stem and passing through three leaf traces. Two of the leaf traces (*L.T.*¹, *L.T.*²) are cut below the leaf gap and at the level where there are root traces (*R.T.*); the third leaf trace (*L.T.*³) is cut at the level of the leaf gap. (*Based upon Ogura*, 1927.)

Adventitious roots are formed in abundance at the base of a leaf trace and a cross section of a stem shows numerous root traces extending radially from the base of each leaf trace and out through the cortex.

Although mature sori may seem to be borne somewhat inward from the leaf margin, early stages in their development show that they are borne marginally[2] The sorus is gradate and with the sporangia developing in basipetalous succession. Each sorus is overarched by a two-lipped involucrous indusium (Fig. 225), one lip developing from the abaxial face of the leaf and the other developing from the adaxial face. Sporangia develop according to the usual leptosporangiate sequence and typically have a spore output of 64 spores. Mature sporangia are relatively large and are borne on fairly long stalks. The annulus is diagonally vertical

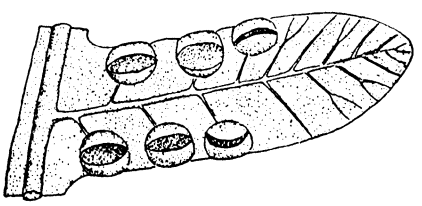

FIG. 225. Fertile pinnule of *Cibotium chamissoi* Kalf. (× 8.)

[1] Gwynne-Vaughan, 1903; Ogura, 1927. [2] Bower, 1899; Glück, 1895.

and there is a definite stomium associated with transverse rupture of the sporangium.

Early stages in development of gametophytes[1] are similar to those in *Cyathea* and, except for the absence of hairs, the mature gametophytes are also similar (Fig. 226*A–C*). Archegonia have somewhat longer necks than those of *Cyathea* and the neck shows a greater tendency to curve toward the posterior end of the gametophyte (Fig. 226*E*). Antheridia (Fig. 226*D*) have a jacket layer composed of four cells and there is a strong presumption that development is as in *Cyathea* because this has been shown[2] to be the case in another member of the family (*Dicksonia*).

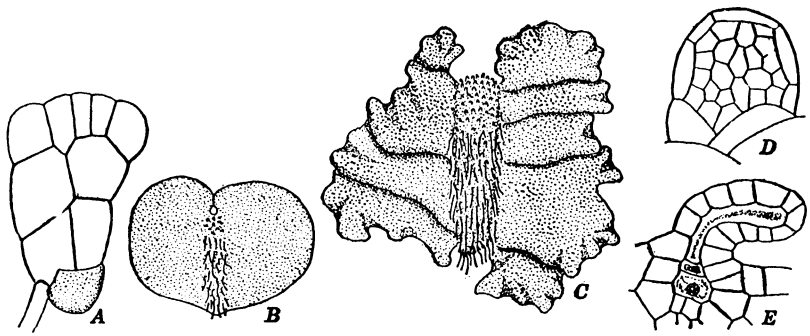

FIG. 226. *A*, *Cibotium barometz* (L.) J. Sm. Very young gametophyte. *B–C*, *Cibotium schiedii* Schlect. and Cham. Mature and very old gametophytes. *D*, *Cibotium menziesii* Hook. Antheridium. *E*, *Cibotium schiedii*. Archegonium. (*After Stokey*, 1930.)

Sporophytes may be formed by a union of gametes or may be formed apogamously.[1]

FAMILY 9. POLYPODIACEAE

The Polypodiaceae (*sensu lato*) are the only family in which the sorus is of a mixed type. The sporangia differ from those of other ferns in having a vertical annulus. Sporangia have a definite stomium in the region of dehiscence, and usually contain 32 or 64 spores. Early stages in development of gametophytes are filamentous instead of plate-like, and mature gametophytes are heart-shaped. Antheridia usually have a jacket layer composed of two ring cells and a single cap cell, and contain relatively few antherozoids.

Some 200 genera (with approximately 5,000 species) are of the type known as polypodiaceous ferns. In the United States about 85 per cent of all ferns native to the country are of the polypodiaceous type and even in Florida, which has a subtropical climate favorable for growth of a wide variety of ferns, they outnumber other ferns three to one. The oldest

[1] Stokey, 1930. [2] Davie, 1951.

known polypodiaceous ferns are from the Jurassic, but since the great majority of fossil ferns of this type are found in the Coenozoic[1] the group may be considered the most modern of all ferns.

The traditional treatment[2] of polypodiaceous ferns is to place them in a single family (Polypodiaceae), divided into a number of subfamilies on the basis of such characters as position of sorus, shape of sorus, structure of indusium if present, structure of receptacle, spore shape, smooth or clothed rhizomes, and leaf shape. The modern tendency is to divide the polypodiaceous ferns into a number of families; but the division of them into five,[3] seven,[4] and thirty-three[5] families shows the diversity of opinion as to how this should be done.

Although the structure of its stem is more complex than in most other members of the family, the bracken fern (*Pteridium*) is the fern most frequently studied as a representative of the family. It is a cosmopolitan genus with about half a dozen species. *Pteridium* is a "sun fern" that grows in open spaces or in wooded areas where there is relatively little shade, and when conditions are favorable it grows in profusion. It is one of the pioneer colonizers of cutover forest lands and here it grows in abundance until overtopped by a dense canopy of second-growth trees. Brackens frequently invade abandoned cultivated fields and when once established are extremely difficult to eradicate.

The stem of a sporophyte of *Pteridium* grows horizontally a few centimeters beneath the surface of the soil (Fig. 227). It is long and slender, has numerous dichotomous forkings, and is capable of indefinite growth. When progressive death and decay of older parts of a rhizome extend to a dichotomous forking, the two forks continue growth as separate plants. Increase in number of individuals in a field is generally due to this vegetative multiplication instead of due to a formation of new sporophytes as a result of gametic union. Small, slender, sparingly branched adventitious roots are borne at irregular intervals along a rhizome. Leaves are borne alternately on the upper side of a rhizome and are separated from one another by long internodes. The leaves may be up to a height of 3 meters or more. The blade, which is about equal in length to the petiole, is triangular in outline and is generally tripinnately divided in the lower portion. Sporangia are borne along the margin of a pinnule and lie in a continuous sorus surrounded by a two-lipped indusium, one lip being the recurved margin of the pinnule, the other being a sheet one cell in thickness that is borne adjacent to the receptacle (Fig. 229*B*).

Unlike most other ferns, the apical cell of a stem, at least in *P. latiusculum* (Desv.) Hieron., has two cutting faces that alternately cut off ventral and dorsal segments.[6] The first-formed portion of a stem has a

[1] Hirmer, 1927; Seward, 1910. [2] Christ, 1897; Christensen, 1938; Diels, 1898.
[3] Holttum, 1947, 1949. [4] Copeland, 1947. [5] Ching, 1940. [6] Chang, 1927.

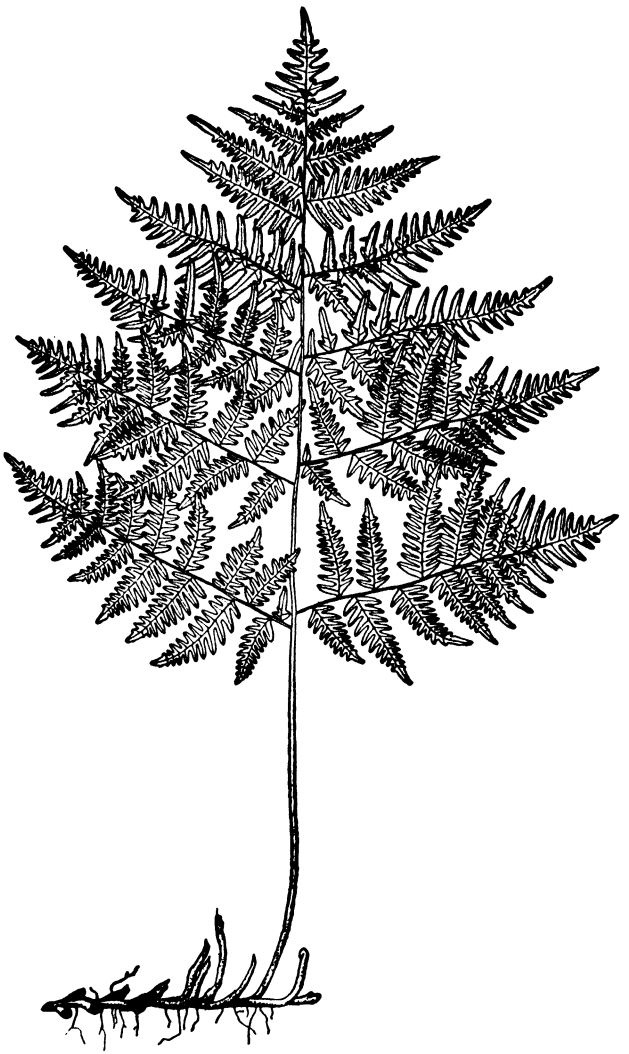

FIG. 227. Sporophyte of *Pteridium aquilinum* var. *pubescens* Underw. (× ⅓.)

siphonostelic central cylinder,[1] but later-formed portions are polycyclic and with two concentric cylinders of vascular tissue.[2] Different from the polycyclic stele of *Matonia* (see page 325), the outer cylinder in *Pteridium* is a much dissected dictyostele and the inner cylinder is dissected into two or more arcuate strips (Fig. 228*A*). As in most other polycyclic stems, both cylinders contribute to the trace supply departing to each leaf.[2]

[1] Jeffrey, 1917. [2] Tansley and Lulham, 1904.

Meristeles in both cylinders are completely encircled by an endodermis and have a pericyclic layer one to two cells in thickness internal to the endodermis. Abutting on the inner face of the endodermis is a layer of protophloem, one cell in thickness, and composed of small sieve tubes and somewhat larger phloem parenchyma cells.[1] The endodermis, pericycle, and protophloem arise from a common cell layer.[1] Internal to the protophloem is the metaphloem which is composed of large sieve tubes. At the center of the xylem mass are one or two small strands of protoxylem. External to the protoxylem and more or less completely separated from it by small parenchymatous cells are large scalariform elements, the metaxylem. These are generally called tracheids, but they are

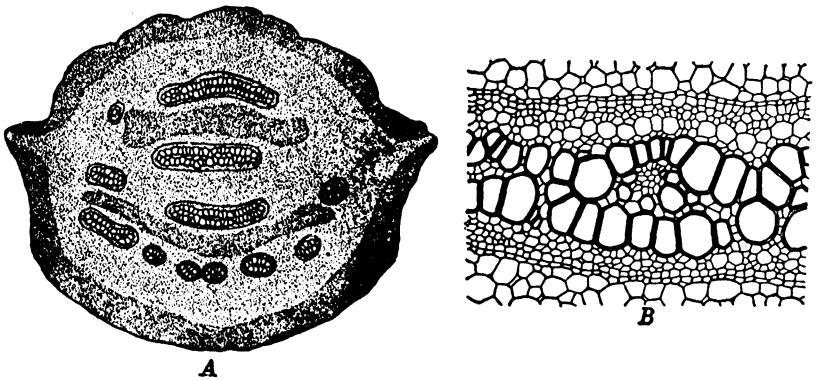

FIG. 228. *Pteridium latiusculum* (Desv.) Hieron. *A*, transverse section of a rhizome. *B*, transverse section of a portion of a meristele of Fig. *A*. (*A*, × 9; *B*, × 65.)

comparable to vessels since there are no closing membranes in pits on the end walls. The outermost portion of the xylem consists of small parenchymatous cells. The portion of the pith internal to the inner cylinder is wholly parenchymatous; that between outer and inner cylinders is partly parenchymatous and partly sclerenchymatous. The sclerenchymatous portion may more or less completely encircle the inner cylinder (*P. aquilinum*), or it may lie in two strips, one flattened, the other arcuate (*P. latiusculum*). The cortex consists of an inner parenchymatous region encircled by a broad band of sclerenchymatous tissue. The band of sclerenchyma is not continuous. Instead, it is interrupted on either flank by a tongue of parenchyma, continuous with that of the inner cortical region. The parenchymatous portion of the sclerotic band is generally interpreted as an aerating region (pneumatophore).

Adventitious roots are developed from an apical cell differentiated in the mother-cell layer giving rise to endodermis and pericycle.[2] This cell

[1] Ching, 1940. [2] Chang, 1927.

is of the usual pyramidal type found in roots. The stele in mature portions of a root is generally diarch.

Primordia of leaves are formed close to the growing point of a rhizome. Growth of embryonic leaves is at a slow rate, and in most cases they do not unfold until two years after their inception. During the first year there is the formation of an embryonic petiole that becomes 2 to 4 cm. long. During the second year there is the formation of an embryonic, spirally coiled blade at the apex of the petiole. At the beginning of the third year, elongation of the petiole pushes the coiled upper portion

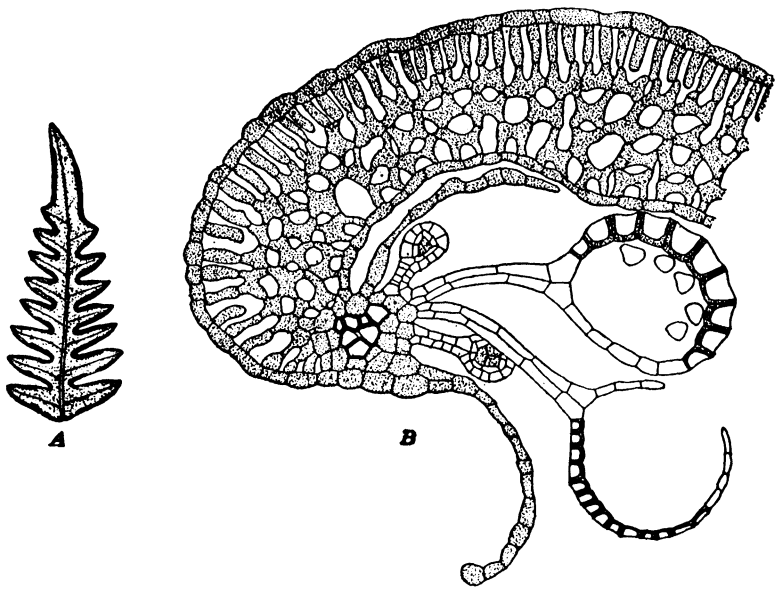

FIG. 229. *Pteridium aquilinum* var. *pubescens* Underw. *A*, a fertile pinnule. *B*, semidiagrammatic transverse section of a pinnule bearing a sorus. (*A*, × 1½; *B*, × 160.)

through the soil, and the rapidly elongating above-ground portion then uncoils from base to apex.

Petioles of mature leaves have several vascular bundles. Pinnules of the blade (Fig. 229*B*) have a structure resembling that of a dicotyledonous leaf blade. Just beneath the upper epidermis is a palisade layer, one to three cells in thickness. Below this is a spongy parenchyma with conspicuous intercellular spaces. Stomata are present in the lower epidermis only.

The position and general appearance of a sorus have been described above. Sori are strictly marginal in origin (Fig. 229*A*), and the outer and inner indusial flaps arise lateral to a very young receptacle.[1] Most

[1] Bower, 1918.

sori (Fig. 229*B*) are of the mixed type, but those on certain pinnules may show a tendency toward a basipetalous gradate organization. Stalk and capsule of a sporangium are derived from a single initial, a superficial cell of the receptacle. Development of a sporangium is strictly leptosporangiate. After elongating somewhat above the surface of the receptacle, the sporangial initial divides transversely into an inner and an outer cell. The inner cell may or may not divide. In either case, it or its daughter

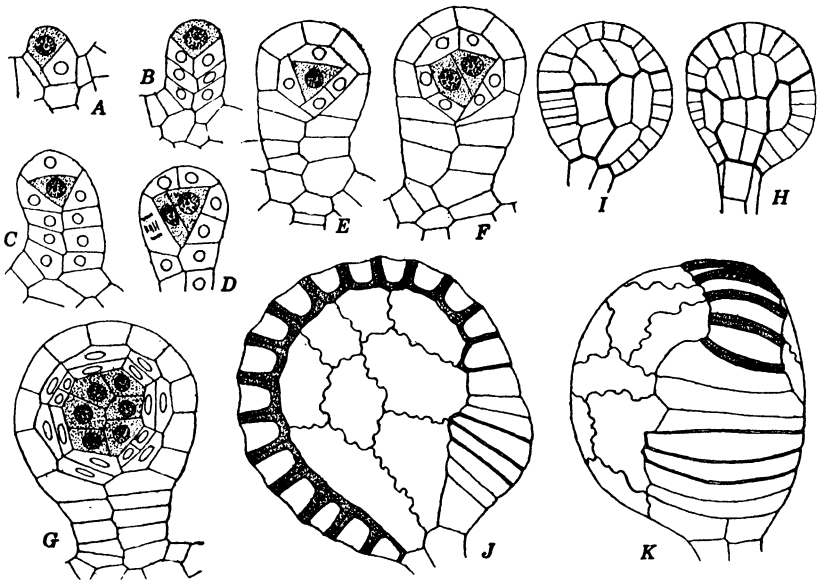

FIG. 230. *A–G*, *Pteris* sp. Stages in development of a sporangium. *H–I*, *Dryopteris filix-mas* (L.) Schott. Diagrams of the two sides of a young sporangium in which the portion derived from each of the four jacket initials is outlined with a heavy line. *J–K*, *Pteridium aquilinum* var. *pubescens* Underw. Side and front views of a mature sporangium. (*H–I*, *based upon Müller*, 1893.) (*A–G*, × 325; *J–K*, × 215.)

cells eventually become indistinguishable from other cells of the receptacle. The outer cell, by three successive diagonal divisions, gives rise to a pyramidal apical cell that cuts off four to five segments from each of its three lateral cutting faces (Fig. 230*A–B*). The last three segments cut off contribute to the sporangial jacket; those cut off previously go to form the stalk. After this the apical cell divides periclinally into a flat outer cell (a jacket initial) and an inner pyramidal cell, the archesporial cell (Fig. 230*C*). This latter cell functions as an internal apical cell that successively cuts off a tabular tapetal initial from each of its four cutting faces (Fig. 230*D*). By anticlinal and periclinal division the tapetal initials develop into a tapetal layer two cells in thickness (Fig. 230*F–G*). The cell remaining after cutting off of the tapetal initials is the primary

sporogenous cell. Theoretically, this undergoes four successive divisions to form 16 spore mother cells. Sometimes, either because of an abortion of certain spore mother cells or a failure to form a full complement of them, there is not the expected output of 64 spores.[1] Meanwhile there has been an anticlinal division and redivision of the four jacket initials. In the case of certain other Polypodiaceae[2] it has been shown that the last-formed initial develops into the upper half of the sporangial jacket and the other three initials into the lower half (Fig. 230*H–I*). Development of each initial into a portion of the jacket is according to a regular, although complicated, succession. The sequence of division is such that the two flattened faces of the jacket layer have a different cellular arrangement. The annulus is a vertical row of cells that starts at the sporangial base and encircles about three-fourths of the sporangium. It is derived in part from the first initial and in part from the fourth. Immediately below the free end of the annulus and derived from the third initial is a vertical strip of four cells that develops into the stomium. Mature stomial cells are thin-walled; mature cells of the annulus have a thickening of their radial and inner tangential walls (Fig. 230*J–K*).

Similar to other Polypodiaceae, the spores of *Pteridium* remain viable for some time after they are shed. Spores of many Polypodiaceae may remain viable for more than a year. One of the longest well-authenticated records for retention of viability is the germination of spores of *Asplenium serra* Langsd.-Fisch. from herbarium material forty-eight years old.[3] It is very probable that under natural conditions the spores of *P. aquilinum* do not germinate until the spring after they are shed.[4] Other Polypodiaceae may have the spores germinating the year they are shed and the gametophytes developing from them producing embryos the same year.

Different from most other families of Leptosporangiatae, germinating spores of most Polypodiaceae (including *Pteridium*) give rise to a short filament of three to six cells which remain undivided except for the terminal cell that, by two obliquely vertical divisions, gives rise to an apical cell alternately cutting off segments right and left.[4] Eventually the apical cell is replaced by a transverse row of apical initials. If conditions for growth are favorable and it is not crowded by neighboring ones, the gametophyte becomes heart-shaped because of a more rapid growth of portions lateral to the apical initials (Fig. 231). At first the gametophyte is one cell in thickness; later it becomes more than one cell in thickness in the region posterior to the apical notch. The first rhizoid is developed at the two-celled stage and with further growth additional ones are produced near the posterior end and on the ventral side. Formation of antheridia generally begins before that of archegonia, and the antheridia

[1] Bower, 1899. [2] Müller, 1893. [3] Fischer, 1911. [4] Lagerberg, 1906.

are borne marginally and ventrally on the posterior portion of a gametophyte. Formation of archegonia is restricted to the portion of a gametophyte immediately posterior to the apical notch and these are restricted to the ventral side. Gametophytes growing under unfavorable conditions may develop into branched filaments or irregularly branched straps that produce antheridia only. However, if such gametophytes are transferred to a favorable environment, the subsequently developed portion is heart-shaped and bears both antheridia and archegonia.

An antheridial initial originates by a vegetative cell sending out a papillate protusion that soon becomes separated from it by a cross wall.

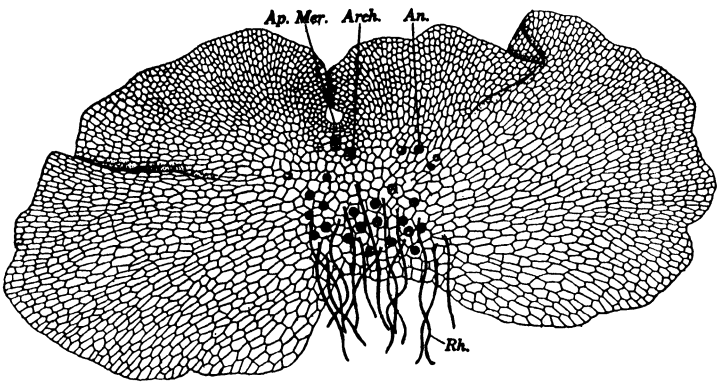

FIG. 231. *Nephrolepis* sp. Ventral view of a mature gametophyte. (*An*, antheridia; *Ap. Mer.*, apical meristem; *Arch.*, archegonia; *Rh.*, rhizoids.) (× 17.)

Most Polypodiaceae have the antheridial initial developing directly into an antheridium without first cutting off a stalk cell. When there is no formation of a stalk cell the antheridial initial divides transversely. Then, because of greater turgor in the upper daughter cell,[1] the cross wall between the two daughter cells is pushed toward the base of the lower daughter cell, the **first ring cell** (Fig. 232). Next, the upper daughter cell divides transversely into a **dome cell** and a **primary androgonial cell.** Transverse division of the dome cell forms the **second ring cell** and the **cover cell.** In a few Polypodiaceae the cover cell divides vertically to form two cover cells.[2] The two ring cells and the cover cell (or the two cover cells) constitute the jacket portion of an antheridium. The primary androgonial cell differentiated at a relatively early stage in antheridial development divides and redivides to form androgonial cells in which those of the last cell generation are **androcytes.** There are 30 to 50 androcytes, and the antheridium is mature after metamorphosis of them into antherozoids.

[1] Davie, 1951. [2] Hartman, 1931.

When external conditions are favorable, antheridia liberate their antherozoids immediately after becoming mature; but if conditions are unfavorable the antherozoids are not liberated. The essential condition for opening of antheridia is an external supply of water. Intake of this water results in a considerable swelling of the two ring cells and the resultant internal pressure on the antheridial contents causes a lid-like tilting or a shedding of the cover cell. If an antheridium has two cover cells, there is a tilting or shedding of only one of them.[1] Antherozoids swimming out from an antheridium are spirally coiled and with 20 to 30 flagella at the anterior end.

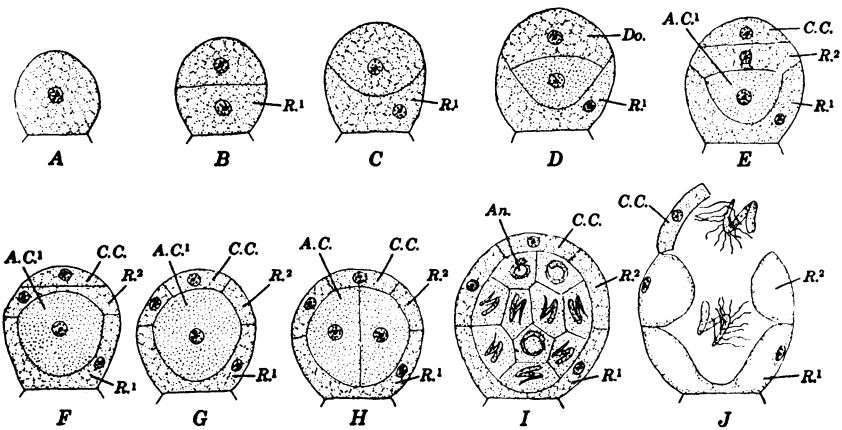

FIG. 232. Diagram showing stages in development of archegonia of Polypodiaceae. (*A.C.*, androgonial cells; *A.C.*[1], primary androgonial cell; *An.*, androcytes; *C.C.*, cover cell; *Do.*, dome cell; *R.*[1], first ring cell; *R.*[2], second ring cell.) (*Based upon Davie*, 1951.)

Development of archegonia in Polypodiaceae is not markedly different from that in other Filicales. By transverse division an archegonial initial gives rise to a basal cell, a central cell, and a primary cover cell (Fig. 233*A*). The primary cover cell divides vertically to form four neck initials, and by transverse division these develop into a neck five to seven cells in height (Fig. 233*B–D*). Polypodiaceae differ from most other Leptosporangiatae in having the necks of archegonia strongly curved toward the posterior end of a gametophyte. The central cell gives rise to a uni- or binucleate primary canal cell, a venter canal cell, and an egg (Fig. 233*C–D*). The primary canal cell and venter canal cell disintegrate into a gelatinous mass that is partially extruded when the archegonial neck opens by a spreading apart or a disintegration of its uppermost cells.

Free-swimming antherozoids respond positively to certain chemotactic stimuli,[2] and entrance of antherozoids into an archegonium is undoubt-

[1] Hartman, 1931. [2] Pfeffer, 1884; Shibata, 1911.

edly due to a chemotactic response. Many antherozoids frequently enter the gelatinous mass protruding from the archegonial neck (Fig. 233*E*). Several antherozoids may reach the base of a neck, but usually only one of them enters the egg.[1]

Development of the embryo (Fig. 213) is much the same from genus to genus among the Polypodiaceae. Division of the zygote is vertical and in a plane perpendicular to the long axis of the archegonium. The daughter cell toward the apex of the gametophyte is the anterior cell; its sister is the posterior cell. These two cells divide vertically in a plane perpendicular to the preceding plane of division. Each of the four cells next divides transversely. The four organs of a young sporophyte (cotyledon, primary root, stem, and foot) may each be referred to a definite portion

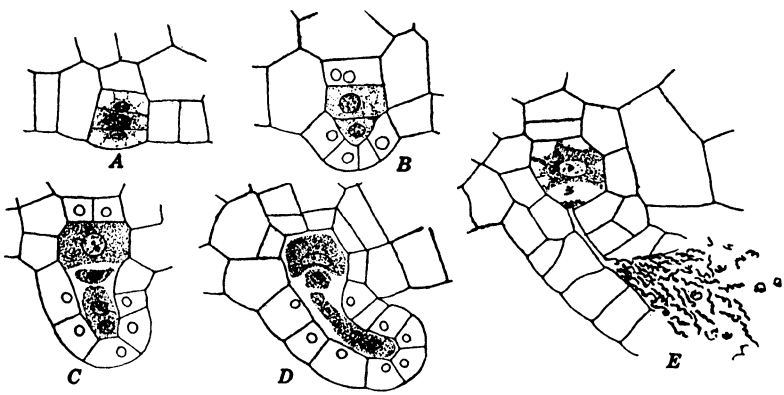

FIG. 233. *Onoclea sensibilis* L. Stages in development of archegonia. The thallus apex is toward the left. (× 325.)

of the eight-celled embryo. The two anterior cells nearest the archegonial neck produce the cotyledon, and the two other anterior cells produce the stem. The two posterior cells nearest the archegonial neck produce the primary root, and the two remaining posterior cells give rise to the foot. There is an approximately simultaneous division of each cell at the 8-celled stage and a similar simultaneous division at the 16-celled stage. The apical cells of cotyledon and primary root are clearly recognizable at approximately the 32-celled stage of embryonal development (Fig. 234*C*). Further growth of the cotyledonary quadrant is due in large part to derivatives cut off by its apical cell, and the same is true of the root quadrant. Growth of cotyledonary and root quadrants is at a more rapid rate than that of foot and stem quadrants. For a while enlargement of an embryo is accompanied by a compensatory enlargement of the surrounding archegonium, but eventually enlargement of the cotyledon

[1] Shaw, 1898; Yamanouchi, 1908.

and primary root ruptures the ensheathing archegonia tissue (calyptra). After this the cotyledon grows horizontally forward beneath the gametophyte and then grows vertically upward past the apical notch. The primary root also grows parallel to the under surface of the gametophyte for a time, but it soon bends downward and grows into the soil. Growth of the stem quadrant of a young embryo is at a very slow rate until the cotyledon is fully developed: then the apical cell of the stem quadrant functions more actively and a young sporophyte may form half a dozen

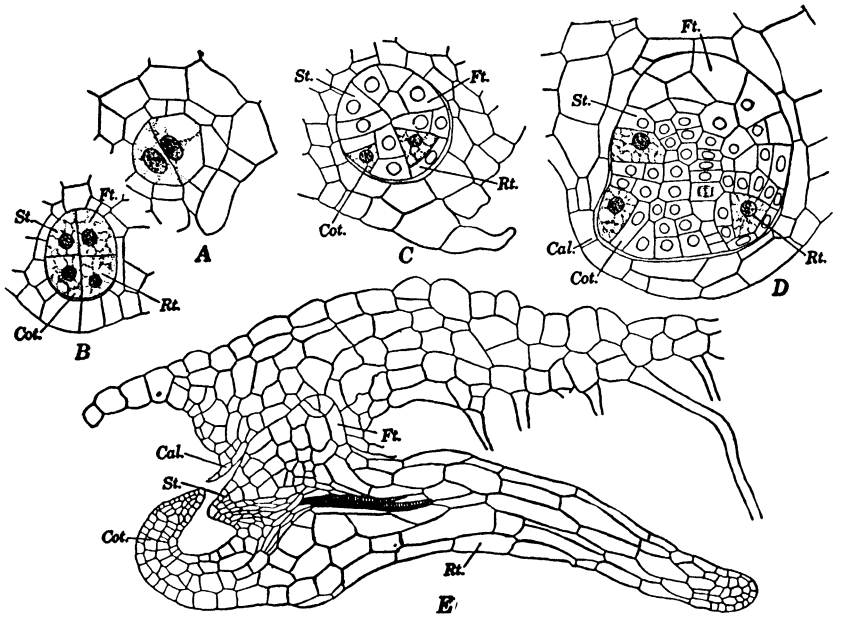

FIG. 234. *Onoclea sensibilis* L. *A–D*, stages in development of embryo. *E*, a young sporophyte after bursting through the calyptra. (*Cal.*, calyptra; *Cot.*, cotyledon; *Ft.*, foot; *Rt.*, root; *St.*, stem.) (*A–D*, × 215; *E*, × 80.)

leaves during its first year of growth. Leaves produced during the first year are generally simpler in structure than are those produced during the second or succeeding years. The foot is a haustorial organ which absorbs food from the gametophyte during early stages in development of a sporophyte. The gametophyte persists until a young sporophyte has two or more leaves, but the gametophyte does not appear to contribute much to the nutrition of a sporophyte after the cotyledon is mature.

Apogamy has been found in a number of Polypodiaceae.[1] Apogamous gametophytes may be those developed from spores or they may be those formed aposporously.

[1] Steil, 1939.

FAMILY 10. PARKERIACEAE

The Parkeriaceae differ ecologically from other homosporous Filicales in being hydrophytic. The sporangia are borne remote from one another and abaxially on the leaves. They have a vertical annulus and are without an evident stomium. Antheridia are borne marginally on a gametophyte and are not emergent.

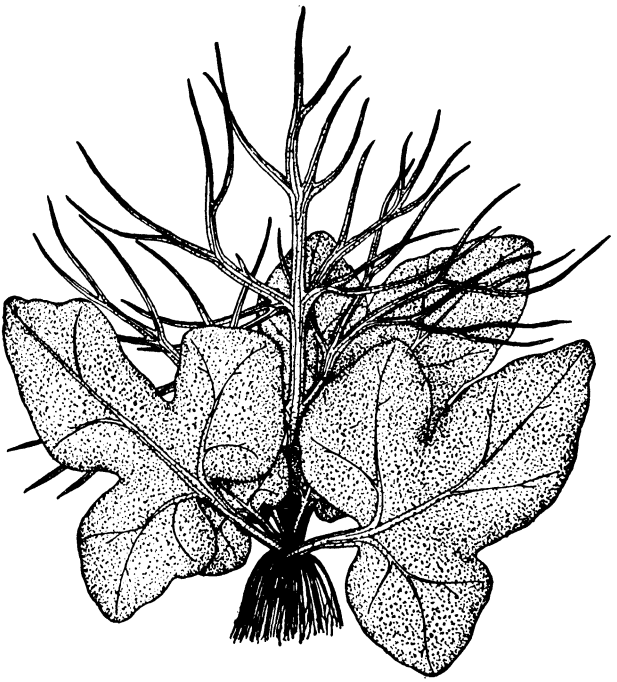

FIG. 235. Sporophyte of *Ceratopteris pterioides* (Hook.) Hieron. (× ⅓.)

There is but one genus, *Ceratopteris*. Some botanists[1] think that it should be placed among the polypodiaceous ferns instead of being segregated in a separate family. *Ceratopteris* is a hydrophyte of world-wide distribution throughout tropical and subtropical regions. Sometimes it grows on damp soil, but generally it is a true aquatic and either free-floating or rooted in mud. *Ceratopteris* is the only fern that has ever been grown as a food crop. It has been cultivated in rice paddies by transplanting young plants developing from dormant adventitious buds in the axils of old leaves.[2] The leaves of *Ceratopteris* are used both as a cooked vegetable and for the making of salads.

[1] Bower, 1928; Christensen, 1938; Holttum, 1949. [2] Copeland, 1942.

The sporophyte is an annual. New sporophytes may develop as a result of gametic union or may develop from adventitious buds persisting from leaves of plants of the previous year. A sporophyte has a short prostrate or erect stem (Fig. 235). The leaves, which are of two kinds, are borne alternately on a stem. The sterile leaves are erect or spreading and have a broad, two- to four-times divided, pinnate or trifoliate blade. Petioles of plants rooted in mud run horizontally for a short distance and then bend abruptly upward; those of free-floating plants do not have this elbow-like bending in the lower portion. At the base of the petiole of each sterile leaf is a complete or incomplete whorl of adventitious roots. Fertile leaves are always taller than sterile ones and two to five times divided into narrow strap-like segments. The sporangia are subsessile and lie in one or two rows parallel to, and some distance inward from, the margin of a segment. According to the species,[1] a sporangium has a vertical annulus of 4 to 10 cells that causes an irregular dehiscence, or a vertical annulus of 20 to 70 cells that causes a transverse dehiscence (Fig. 236*C*). Sporangia of one species contain 16 spores; those of other species contain 32.

The small stem of *Ceratopteris* is fleshy in texture. The first-formed portion of it has a protostelic central cylinder.[2] Above this there is a dictyostelic siphonostele. Later-formed portions of a stem may have medullary vascular strands that are connected with the trace supply of leaves.[3] It is very probable that such portions of a stem have a polycyclic organization more or less like that in *Cyathea* (page 340). Meristeles in a stem of *Ceratopteris* are each surrounded by an endodermal layer[2] that appears to have originated from the same mother-cell layer as the pericycle internal to it.

Adventitious roots arise endogenously from the endodermal layer of a leaf bundle.[2] Roots of *Ceratopteris* are similar in structure to those of *Schizaea* (page 315) and *Azolla* (page 374). The pericycle, endodermis, and innermost cortical layer are each six cells in perimeter, and the three arise from a common mother-cell layer. The cortex also resembles that of *Azolla* in its six intercellular spaces.

Sporangial initials are differentiated some distance inward from a leaf margin.[3] Sporangial development is strictly leptosporangiate.[4] An initial first cuts off three to four stalk cells from each of its three cutting faces.[5] Unlike most other ferns there is no subsequent elongation of these stalk cells. Development of a capsule[6] takes place in the usual manner and has a formation of a tapetum two cells in thickness (Fig. 236*A–B*). The archesporial cell may give rise to four or eight sporocytes.

[1] Benedict, 1909. [2] Ford, 1902. [3] Bower, 1928. [4] Kny, 1875.
[5] Bower, 1928; Kny, 1875. [6] Ford, 1902; Kny, 1875.

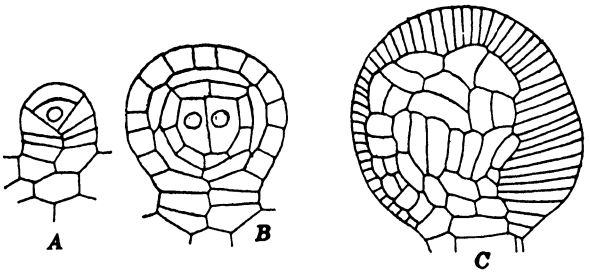

FIG. 236. *Ceratopteris pterioides* (Hook.) Hieron. *A–B*, vertical sections of young sporangia. *C*, surface view of an old sporangium. (*After Kny*, 1875.) (*A–B*, × 200; *C*, × 100.)

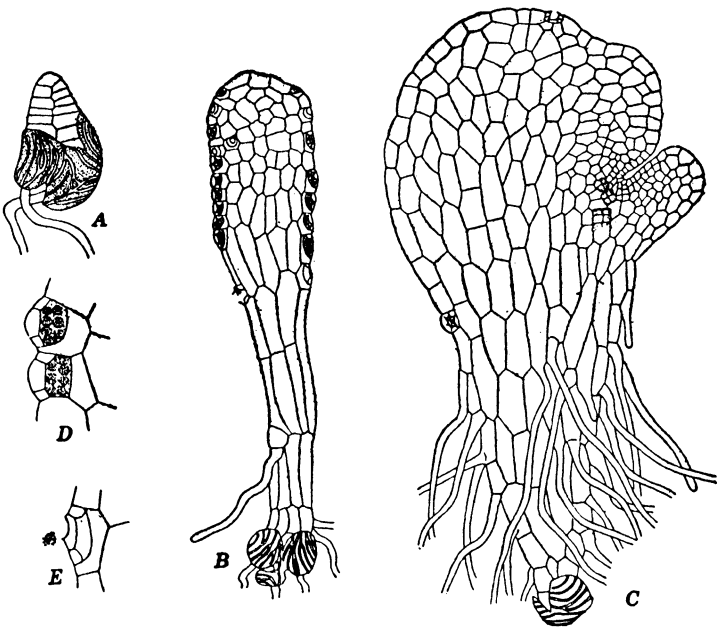

FIG. 237. *Ceratopteris pterioides* (Hook.) Hieron. *A*, germination of spore. *B*, gametophyte with antheridia. *C*, gametophyte with antheridia and archegonia. *D–E*, antheridia before and after discharge of antherozoids. (*After Kny*, 1875.) (*A*, × 75; *B*, × 40; *C*, × 50; *D–E*, × 160.)

Spore germination begins with a rupture of the outer spore-wall layer and a protrusion of the protoplast, still surrounded by the inner spore-wall layer. There is next a formation of one or two rhizoids.[1] Following this there may or may not be an immediate differentiation of an apical cell (Fig. 237*A*). In the latter case a gametophyte may even develop to a stage where it bears antheridia without establishing an apical cell.

[1] Kny, 1875.

Fully developed gametophytes are heart-shaped but at times with the two lateral lobes of unequal size.[1]

Antheridia (Fig. 237*B*, *D–E*) are produced only at the margin of a gametophyte[2] and rarely protrude beyond the margin. These antheridia are not of the embedded type found in Eusporangiatae. Instead, they appear to be a modification of the polypodiaceous type and one in which the antheridial initial does not protrude beyond the gametophyte as in most other Leptosporangiatae. Archegonia are produced in the region posterior to the apical notch where the gametophyte is more than one cell in thickness. A mature archegonium has the usual leptosporangiate axial row of three cells and the neck is usually five cells in height.

Differentiation into cotyledon, primary root, stem, and foot occurs very early in development of an embryo[1] and presumably at the eight-celled stage. One unusual feature is that of the primary root differentiating endogenous apical cells of secondary roots long before it grows out through the overlying gametophytic tissue.[1]

ORDER 2. MARSILEALES

The Marsileales are heterosporous and produce their sporangia within sporocarps. Each sporocarp contains numerous gradate sori in which each sorus produces both macro- and microsporangia. The wall of a sporocarp is a modified blade of a pinna.

It has been argued[3] that the Marsileales are an offshoot from the Schizaeaceae. This view is based upon similarity in vegetative structure of the two, the enfolding of fertile pinnae so that the fertile sides face each other, and resemblance of the vestigial annulus of certain Marsileales to the distinctive type of annulus found in Schizaeaceae. One major difficulty in relating the Marsileales to the Schizaeaceae is the structure of the sorus. In Schizaeaceae the sporangia are borne singly and develop simultaneously; in Marsileales the sporangia are borne in sori of a gradate type in which sporangia at the apex of a receptacle develop before those at the base of the receptacle. On this account the relationships of the Marsileales appear to be more with the homosporous leptosporangiate ferns with gradate sori that are borne abaxially on the leaves and are surrounded by an involucroid indusium.

There is but one family, the Marsileaceae. This family includes three living genera, *Marsilea* with about 65 species, *Pilularia* with 6 species, and the monotypic *Regnellidium*. All three genera are hydrophytes that grow rooted in the mud of marshes and shallow pools. Certain fossil ferns have been assigned to the family, but their relationship to it is of so ques-

[1] Mahabelé, 1948. [2] Kny, 1876; Mahabelé, 1948. [3] Bower, 1908, 1926.

tionable a nature that the geological record of the family should be considered a blank.

At least six species of *Marsilea* are known to occur in the United States. Five of them are native to this country and found chiefly in the Gulf and Pacific Coast States. The sixth species (*M. quadrifolia* L.) is an introduced one that has escaped from cultivation and become established in certain ponds in New England. The sporophyte of *Marsilea* (Fig. 238) looks like an aquatic four-leaf clover. It has a creeping dichotomously branched rhizome capable of indefinite growth. In *M. vestita* Hook. and Grev. a single plant may grow in all directions until it covers an area 25 meters or more in diameter. The leaves are borne alternately along

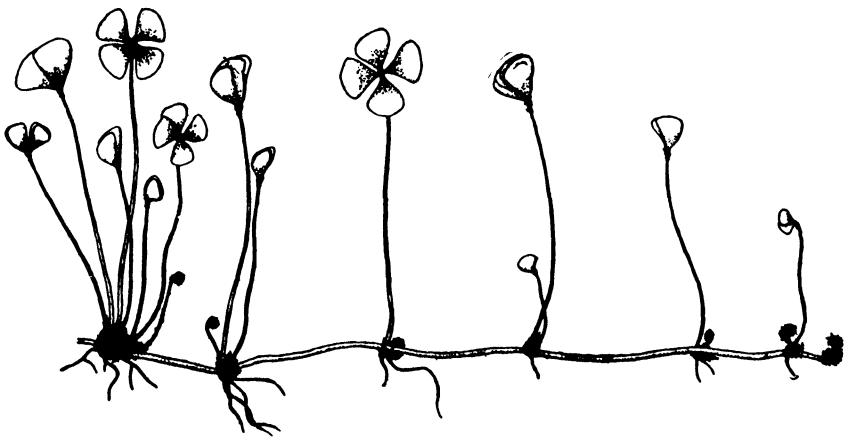

FIG. 238. Sporophyte of *Marsilea vestita* Hook. and Grev. (*Natural size.*)

the upper side of a rhizome. Internodes between successive leaves may be long or short. There are one or more adventitious roots at each node and on the underside of the rhizome. Elongating leaves posterior to a branch or stem apex have the circinate vernation typical of most Filicales. Leaves of submerged individuals have long flexible petioles and leaf blades that float on the surface of the water. When the same species grows on mud or damp soil, the leaves have short rigid petioles. In either case, the blade is divided into four obovate to obcuneate pinnae. Division of a blade into four pinnae results from two dichotomies arising in close succession to each other. The veins of each pinna are dichotomously branched and have numerous cross connections that unite the vein system in a closed reticulum. Most species resemble *M. vestita* in that sporocarps develop to maturity only on individuals that are not submerged. The sporocarps are borne on short or long stalks (peduncles) inserted a short distance above the base of the petiole (Fig. 240*A*). In most species

the peduncle is unbranched and has a single sporocarp at its apex. Some species have a dichotomously branched peduncle that bears 2 to 5 sporocarps (*M. quadrifolia*) or 6 to 26 of them (*M. polycarpa* Hook. and Grev.).

Rhizomes of *Marsilea* have an amphiphloic, solenostelic, vascular cylinder (Fig. 239). Some species, including *M. vestita*, have conspicuous protoxylem masses that are exarch in position; other species, including *M. quadrifolia*, lack conspicuous protoxylem elements. All species have the siphonostele externally and internally limited by an endodermal layer.

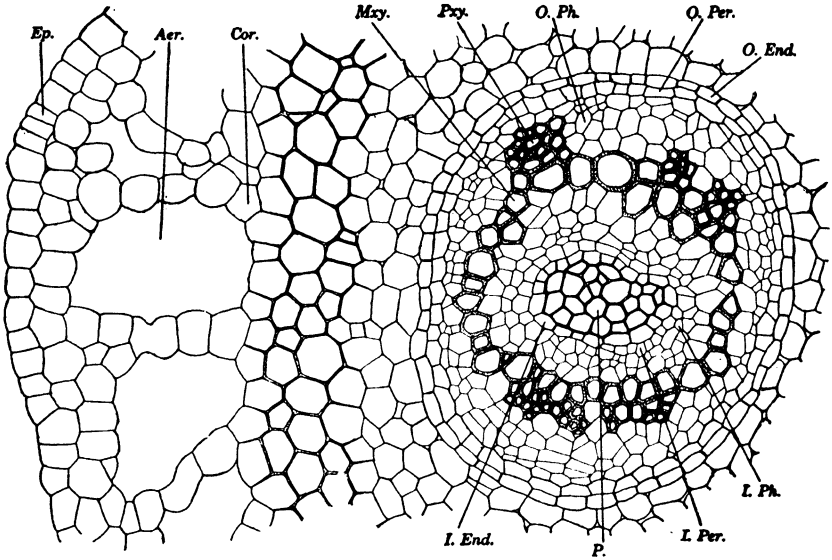

FIG. 239. *Marsilea vestita* Hook. and Grev. Transverse section through internode of a rhizome. (*Aer.*, aerenchyma; *Cor.*, cortex; *Ep.*, epidermis; *I. End.*, inner endodermis; *I. Per.*, inner pericycle; *I. Ph.*, inner phloem; *Mxy.*, metaxylem; *O. End.*, outer endodermis; *O. Per.*, outer pericycle; *O. Ph.*, outer phloem; *P.*, pith; *Pxy.*, protoxylem.) (× 215.)

Just within the outer endodermis is a pericyclic layer one cell in thickness. The structure of the pith depends upon environmental conditions. Rhizomes of submerged plants generally have a parenchymatous pith; those of plants growing on mud have a more or less sclerotic pith. The inner portion of the cortex is a solid tissue of thin-walled or sclerotic parenchyma. External to this is an air-storage tissue (**aerenchyma**) with a single ring of air chambers. The outermost portion of the cortex is a parenchymatous tissue, one to several cells in thickness. An undivided leaf trace departs from the stele at each node. It is similar in structure to the single vascular bundle in a petiole. The latter has a V-shaped mass of xylem with the protoxylem exarch in position. The xylem is succes-

sively surrounded by a band of phloem and an endodermal layer. The portion of the petiole external to the endodermal layer is generally aerenchymatous.

The sporocarp of *Marsilea* is bean-shaped, with a main vein along the narrow side facing the peduncle and with numerous lateral veins perpendicular to the main vein (Fig. 240). The lateral veins are given off alternately right and left, and each of them forks dichotomously about midway between its base and apex (Fig. 243*B*). On the inner face of the two halves (valves) of the sporocarp wall, and at the region where each lateral vein forks, there is a development of a receptacle. Receptacles on one valve of the sporocarp alternate with those on the opposite valve.

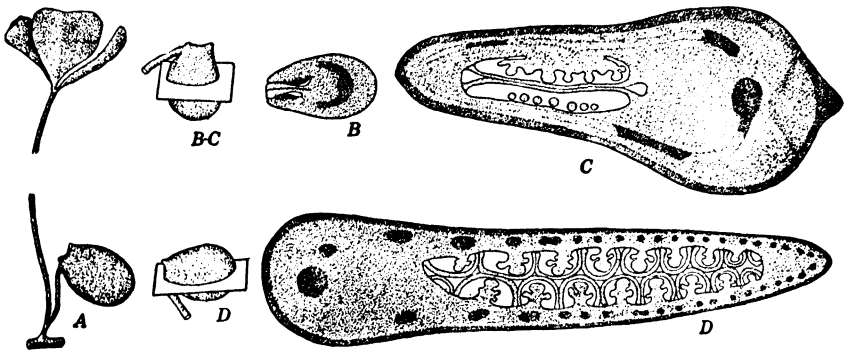

FIG. 240. *Marsilea vestita* Hook. and Grev. *A*, leaf bearing a sporocarp. *B*, transverse section of a young sporocarp. *C*, transverse section of an older sporocarp. *D*, longitudinal section of an older sporocarp cut in the plane perpendicular to the flat surface. (*A*, × 2; *B–D*, × 30.)

Axillary to each receptacle is a flap-like outgrowth, two cells in thickness, that extends in a hood-like manner over the entire receptacle and has the free end adjoining the inner face of the sporocarp wall (Fig. 240*C–D*). Each receptacle projects inward from the sporocarp wall and soon differentiates a row of sporangial initials along its summit. Other sporangia are differentiated in basipetalous succession along the flanks of a receptacle. The result is a typical gradate sorus in which sporangia at the summit are well along toward maturity before the lowermost ones begin to develop (Fig. 241*A*).

Sporangial initials at the apex of a receptacle develop into macrosporangia; those lower down develop into microsporangia. Both types of sporangia are strictly leptosporangiate in development.[1] Development in the two is alike up to the stage where each has a jacket one cell in thickness, a tapetal layer two cells in thickness, and 32 or 64 young spores (Fig. 241*A–E*). Only one of the spores in a macrosporangium matures. The

[1] Marschall, 1925.

others disintegrate and contribute to the multinucleate plasmodium formed by disintegration of the tapetum. All young spores in a microsporangium generally mature. The jacket layer of macrosporangia and microsporangia of *Marsilea* is a thin-walled homogeneous structure and

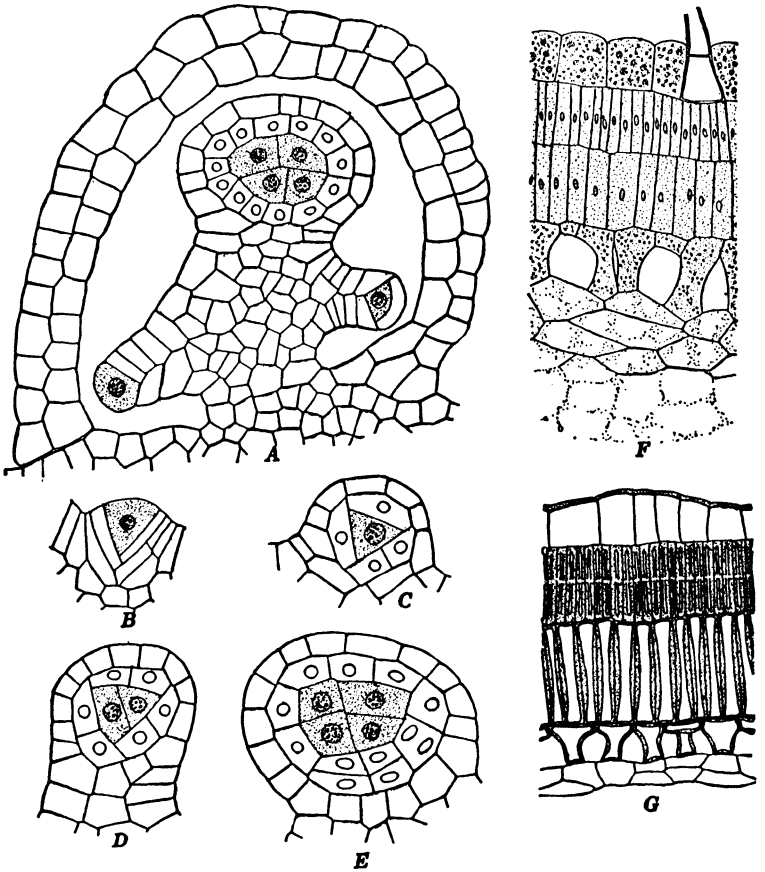

FIG. 241. *Marsilea vestita* Hook. and Grev. *A*, vertical section of a receptacle and indusium. *B–E*, stages in development of macrosporangia. *F–G*, transverse sections of young and old walls of sporocarps. (*A–E*, × 485; *F–G*, × 215.)

has no indication of an annulus. In another member of the family (*Pilularia*) the arrangement of thin-walled cells at the jacket apex is suggestive of the annulus of Schizaeaceae.[1]

As the sporangia are developing, there is a differentiation of a stony layer of cells at the outer face of a sporocarp. In *M. vestita* Hook. and Grev. this begins with a periclinal division of cells in the layer imme-

[1] Campbell, 1904.

diately beneath the epidermis. This is followed by an anticlinal division of each cell in the outer of the two layers, and a considerable elongation, in the anticlinal axis, of the cells in both layers (Fig. 241*F*). There is then a thickening of cell walls in both layers (Fig. 241*G*). Coincident with differentiation of the stony tissue there is, except for sporangia and indusia, a gelatinization of the receptacles and of the inner half of the sporocarp wall.

The sporocarp of Marsileales has been interpreted both as homologous with a modified fertile segment from the lower part of a leaf[1] and as

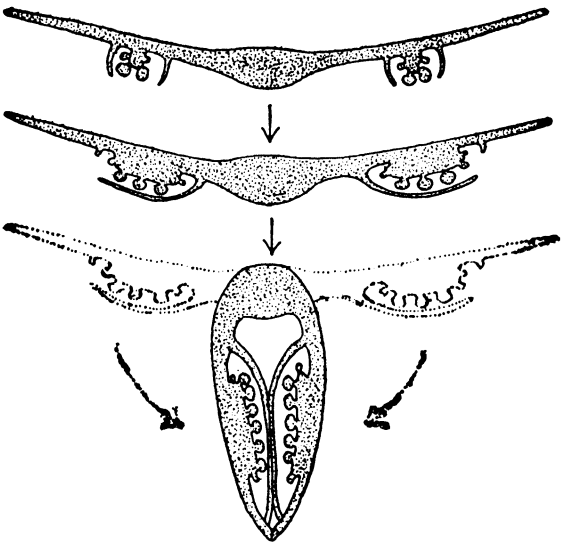

FIG. 242. Diagrams showing suggested evolution of the sporocarp of Marsileaceae by an enfolding of a pinnule with abaxial sori with an involucroid indusium. The sori are drawn as if opposite each other.

homologous with an entire leaf.[2] The chief argument for the latter interpretation is the resemblance of apical growth of a sporocarp to that of an entire leaf rather than to that of a pinna. However, both the vascular supply to the peduncle and the vascular supply within the sporocarp seem to show that it is a modification of a leaf segment instead of a modification of an entire leaf. Adherents of the leaf-segment theory variously interpret the sporocarp as resulting from the apposition of two pinnae,[3] from enfolding of a single pinna,[4] or from the enfolding of a pinna with several pinnules each with a marginal sorus.[5] The single bun-

[1] Bower, 1926; Busgen, 1890; Campbell, 1905. [2] Johnson, 1898, 1933.
[3] Busgen, 1890. [4] Bower, 1926; Campbell, 1905. [5] Puri and Garg, 1953.

dle in the peduncle and the single main vein in the sporocarp indicate quite clearly that the sporocarp is derived from a single pinna. As already suggested (see page 360) it seems more probable that the ancestors of Marsileales were ferns with a gradate sorus surrounded by an involucroid indusium rather than ferns of a type belonging to the Schizaeaceae. The first step in evolution of a sporocarp would be an unequal growth on opposite sides of a cup-like indusium to produce a hood-like indusium growing out from the adaxial side of the receptacle (Fig. 242), as is found in certain Polypodiaceae. The next step in evolution of the sporocarp would be an apposition of the two lateral margins of the abaxial side of the pinna. There is no evidence showing whether the heterospory characteristic of Marsileales arose before or after evolution of the sporocarp, but the homospory of all ferns without sporocarps suggests that the appearance of heterospory was correlated with the evolution of the sporocarp.

The spores of *Marsilea* are capable of developing into gametophytes as soon as a sporocarp is mature, but it is very probable that under natural conditions sporocarps do not open until the second or third year after they are formed. It is also very probable that opening is due to a partial decay of the stony layer of the sporocarp wall. A long delay in opening of a sporocarp is immaterial because the spores within it remain viable for many years, as is shown by the germination of spores from sporocarps that have been stored in the laboratory for 20 or 30 years. At any time after it is mature, there is an immediate opening of a sporocarp if it is placed in water and a small piece of the stony layer is cut away. Within 15 to 20 minutes the gelatinous material within the sporocarp begins to swell because of an imbibition of water. This swelling causes the two valves of the sporocarp wall to spread apart. As more water is imbibed the gelatinized inner half of the sporocarp wall (the **sorophore**) begins to project beyond the opened valves. Since the sori are attached to the sorophore, they are gradually pulled out as the sorophore elongates. A fully elongated sorophore is a long gelatinous cylinder with a length 15 to 20 times that of the sporocarp (Fig. 243*A*). On either side of an expanded sorophore is a row of sori, alternate with one another. At the tip of a sorophore are a few small mammilate gelatinous projections, also alternate with one another. These are rudimentary sori that failed to develop. The indusia are intact, and the contained sporangia have an evident jacket when the sori are first freed from the sporocarp wall (Fig. 243*C*). There is, however, a gelatinization of the indusia and the sporangial jackets five to six hours after extrusion. The developing gametophytes generally remain embedded in this watery gelatinous matrix until they are mature.

A microspore is globose in shape with a small pyramidate apex, the

result of mutual pressure with sister spores in the tetrad. It has a relatively large, centrally located nucleus and numerous small starch grains scattered throughout the cytoplasm (Fig. 244*A*). Development of a microspore into a fully mature microgametophyte takes but 12 to 20 hours at ordinary room temperature. The first evident change in germination of a spore is a migration of the starch grains to the periphery of the cytoplasm. The nucleus then moves to one side of the spore, generally that opposite the pyramidate apex (Fig. 244*B*). Following a division of the nucleus, there is an asymmetrical division of the spore into a small lenticular cell (the prothallial cell) and a large apical cell (Fig.

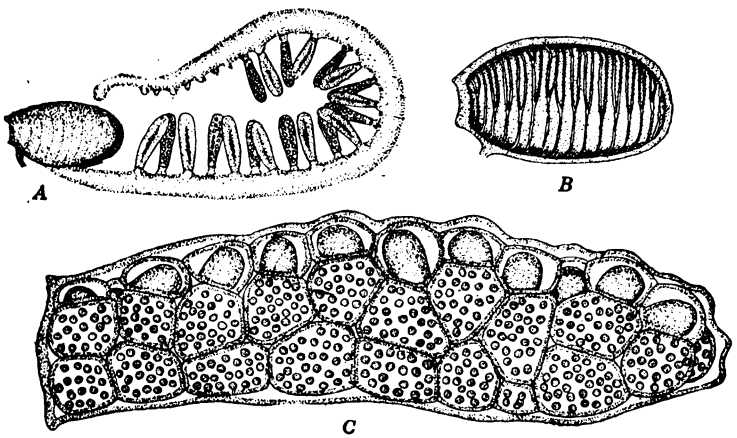

FIG. 243. *Marsilea vestita* Hook. and Grev. *A*, extrusion of sorophore and receptacles from an opened sporocarp. *B*, empty half of a sporocarp wall, viewed from the concave side. *C*, a receptacle shortly after extrusion from a sporocarp. (*A*, × 2½; *B*, × 6; *C*, × 21.)

244*C*). The apical cell has been described as next cutting off a basal cell,[1] but this is very doubtful, and all the evidence seems to show that it immediately divides into two antheridial initials in a plane diagonal to the prothallial cell (Fig. 244*D*). Both initials then cut off the first jacket cell by means of a curving wall diagonal to the previous plane of division.[2] The jacket cell in each antheridium does not divide again (Fig. 244*E*). The wedge-shaped sister cell divides periclinally into a small inner cell (the second jacket cell) and a large outer cell (Fig. 244*F*). Periclinal division of the outer cell forms the third jacket cell and the primary androgonial cell (Fig. 244*G*). The primary androgonial cell in each antheridium, by four series of simultaneous divisions, forms 16 androcytes (Fig. 244*H–I*). This is accompanied by a disintegration of the prothallial and a partial disintegration of the jacket cells. Metamorphosis of the androcytes into antherozoids is much the same as in other pteridophytes.[2] Up

[1] Belajeff, 1898; Campbell, 1892. [2] Sharp, 1914.

to this point the developing gametophyte is enclosed by the old spore wall. Shortly before the antherozoids are mature, there is a bursting of the spore wall and a protrusion of the antheridia beyond it. The antherozoids are liberated by a separation of the jacket cells from one another. Antherozoids of *Marsilea* differ from those of other ferns in that they have many more coils, sometimes a dozen or more. They are also unusual in that the flagella are attached only to the broad posterior coils.

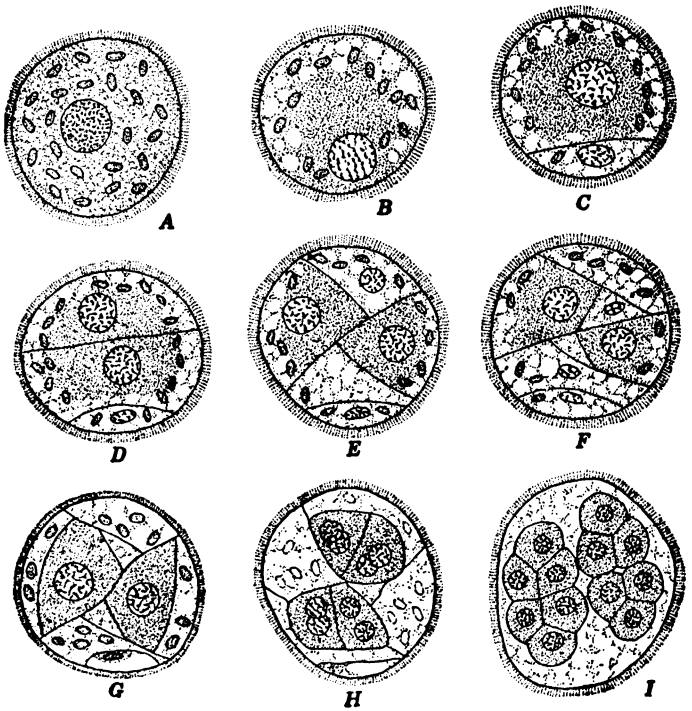

FIG. 244. *Marsilea vestita* Hook. and Grev. Stages in development of microgametophytes.

Macrospores of *Marsilea* are ellipsoidal with a small hemispherical protruberance at the anterior pole (Fig. 245*A*). The spore wall about the protuberant portion is relatively thin and has three radiating ridges. Elsewhere the middle spore-wall layer is much thicker and radially fibrillar. The protuberant anterior portion of the protoplast consists of densely granular cytoplasm and a small lenticular nucleus; the remainder of the protoplast contains numerous large starch grains embedded in a watery cytoplasm. Development of a macrogametophyte to maturity is slightly slower than that of a microgametophyte and takes 14 to 22 hours. At the beginning of spore germination in *M. vestita* Hook. and Grev., there is some increase in the amount of granular cytoplasm at the

anterior end, and the nucleus becomes spherical. Two or three hours after the inception of germination, there is a division of the nucleus,[1] and this is soon followed by a transverse cell division along the line of juncture between the densely granular and the watery portions of the cytoplasm (Fig. 245*B*). Although there is no further nuclear division in the large cell derived from the watery portion of the protoplast, there is a repeated

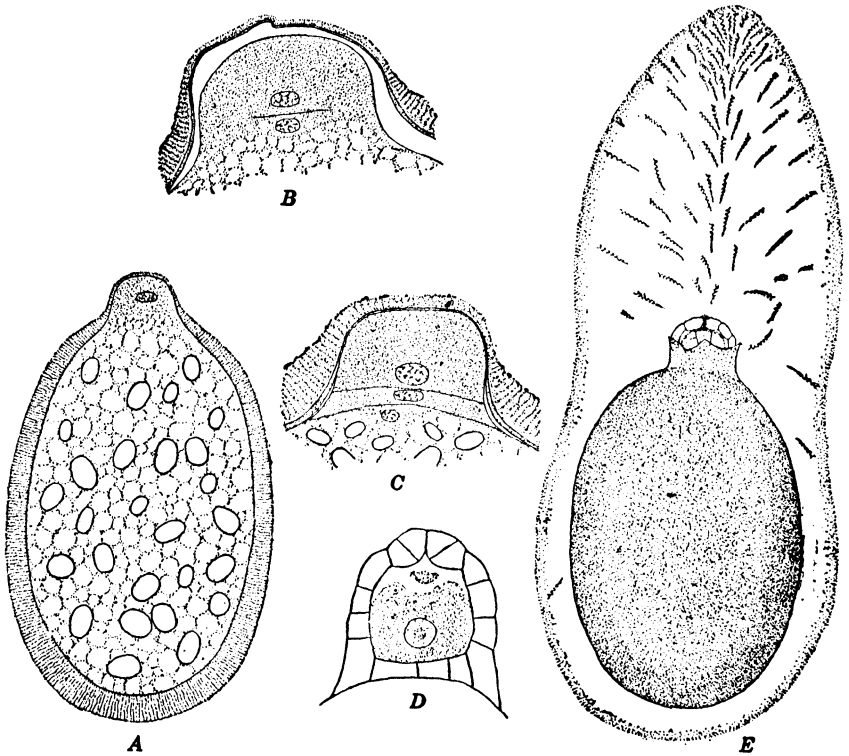

FIG. 245. *Marsilea vestita* Hook. and Grev. *A*, longitudinal section of a macrospore. *B–D*, stages in development of sterile tissue and archegonium of a macrogametophyte. *E*, surface view of a macrogametophyte after fertilization and with many residual antherozoids embedded in the surrounding gelatinous envelope. (*A*, × 120; *B–D*, × 215; *E*, × 80.)

division of the small cell formed from the papillate portion of the spore. The nature of this latter cell is somewhat doubtful. If it is interpreted as an archegonial initial, it is one unlike that of other pteridophytes since it gives rise to both neck and venter of the single archegonium. It is much more probable that it is an apical cell with four cutting faces, three lateral and one basal, which cuts off a single segment at each face before functioning as an archegonial initial. In *M. vestita* segments are not

[1] Campbell, 1892.

cut off in a regular sequence by the apical cell. Sometimes the first segment is cut off on the basal face (Fig. 245*C*). At other times, one, two, or three lateral segments are cut off before the basal one. Repeated anticlinal division in all four segments results in a vegetative tissue one cell in thickness. Development of an archegonial initial into an archegonium is the same as in other ferns.[1] It begins with a periclinal division of the initial into a primary cover cell and a central cell. Two successive anticlinal divisions of the primary cover cell result in four quadrately arranged neck initials. An oblique division of each neck initial results in a short neck composed of two tiers of four cells each (Fig. 245*D*). Simultaneous with development of the neck, there is a division of the central cell into a small lenticular primary canal cell and a large globose primary venter cell. In some species, including *M. drummondii* A. Br., the primary canal cell divides to form two small canal cells.[2] In all species there is a division of the primary venter cell into a small lens-shaped venter canal cell and a large globose egg. The last step in archegonial development is a disintegration of the canal cell (or cells) and venter canal cell, and an opening of the archegonial neck.

A mature macrogametophyte is surrounded by a broad, ovoid, gelatinous envelope in which there is a more watery funnel-shaped portion extending upward from the archegonium. When gametophytes are grown in the laboratory, hundreds of antherozoids swarm about the archegonial end of the gelatinous envelope surrounding each macrogametophyte. Many of them enter the gelatinous envelope, some reaching the neck of the archegonium, others failing to do so. The body of an actively swarming antherozoid is coiled in a conical helix, but as swarming continues the coiling becomes laxer and laxer (Fig. 245*E*), and the gelatinous envelope surrounding a macrogametophyte contains many of these laxly coiled antherozoids after swarming ceases.

At the time of fertilization an antherozoid enters the egg's cytoplasm anterior end forward, but later its orientation becomes reversed so that it penetrates the egg nucleus posterior end forward.[3] Embryonal development is generally initiated by a union of gametes, but it may also be due to parthenogenesis.[2] The demonstration of intact canal and venter canal cells in archegonia with young embryos (Fig. 94*G*, page 152) demonstrates parthenogenesis beyond all doubt. Because of abnormalities in division of sporocytes into spores, macrospores of parthenogenetic individuals have a diploid number of chromosomes.[2]

Division of the zygote of *M. vestita* takes place two or three hours after fertilization and usually in a vertical plane. Vertical division of a zygote takes place when a gametophyte lies on its side. That the plane of division is affected by gravity is shown by the transverse division of zygotes

[1] Campbell, 1892; Strasburger, 1907. [2] Strasburger, 1907. [3] Atkinson, 1943.

in macrogametophytes so oriented that the long axis stands vertical to the force of gravity.[1] If division of the zygote is vertical the two daughter cells of it also divide vertically, but in a plane perpendicular to that of the first division.[2] Two sister cells formed by this division develop, respectively, into cotyledon and stem of an embryo; the other two develop into its foot and root. The embryo half developing into cotyledon and stem is generally called the anterior (epibasal) half, but there is no justification for this since the macrogametophyte is radially symmetrical and without anterior-posterior differentiation. Embryonal development beyond the quadrant stage is in the manner typical of leptosporangiate

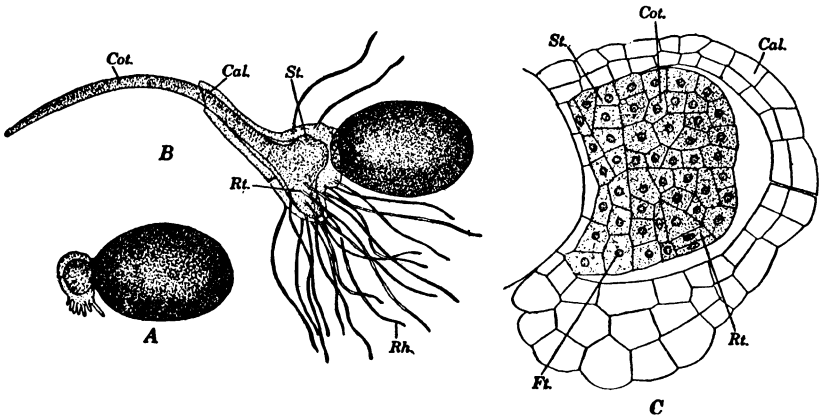

FIG. 246. *Marsilea vestita* Hook. and Grev. *A*, surface view of a macrogametophyte with a two-day-old sporophyte. *B*, surface view of a macrogametophyte with a six-day-old sporophyte. *C*, semidiagrammatic vertical section through a young sporophyte. (*Cal.*, calyptra; *Cot.*, cotyledon; *Ft.*, foot; *Rh.*, rhizoids, *Rt.*, root; *St.*, stem.) (*A–B*, × 30; *C*, × 325.)

ferns. Development proceeds with great rapidity in *M. vestita* and embryos three days old consist of many cells (Fig. 246*C*). Embryonal development is accompanied by a periclinal division of the adjoining gametophytic cells to form a calyptra two to three cells in thickness and one in which many of the superficial cells on the side of the calyptra facing the earth send out long rhizoidal projections (Fig. 246*A*). All cells of the calyptra, including the rhizoids, contain numerous small chloroplasts. Growth of the calyptra keeps pace with that of the embryo for the first four or five days; after this the cotyledon and primary root grow at a more rapid rate and burst through the calyptra (Fig. 246*B*).

ORDER 3. SALVINIALES

The Salviniales are heterosporous and produce their sporangia within sporocarps. A sporocarp contains either a single macrosporangium or nu-

[1] Leitgeb, 1878. [2] Campbell, 1892.

merous microsporangia, never both kinds of sporangia. The wall of a sporocarp is a modification of an indusium and so is of an entirely different nature from that in Marsileales.

There are two living genera, *Salvinia* and *Azolla*. These are generally placed in a single family, the Salviniaceae, but the two have also been segregated in separate families.[1] *Salvinia* has 10 species and at least one of them is native to the United States. *Azolla* has five species and two of them are native to this country; *A. caroliniana* Willd. in the eastern part, and *A. filiculoides* Lam. in the western part. Both genera are known in the fossil condition but neither from earlier than the Lower Coenozoic.[2]

The mode of sporangial development shows that the order is to be referred to the Leptosporangiatae. Adaptation of the sporophyte to a free-floating habit has resulted in such specialization that structural relationships with other ferns have been obscured; and enclosure of the sporangia within a sporocarp has obliterated one of the most distinctive phylogenetic indices, the annulus. The indusial nature of the sporocarp wall and the elevated column on which the sporangia are borne have been cited[3] to show a relationship to the Hymenophyllaceae. The gradate basipetalous receptacle of a sporocarp also resembles the receptacle of Hymenophyllaceae, but the history of its development shows that it is dissimilar since the whole receptacle in Salviniales is derived from a single sporangial initial. Because of this, it is better to consider the Salviniales an order of uncertain position among the Leptosporangiatae.

Sporophytes of *Azolla* (Fig. 247) resemble gametophytes of leafy Jungermanniales. They grow free-floating on the surface of permanent pools and backwaters of sluggish streams. Repeated vegetative multiplication by progressive growth and death and by abscission of lateral branches often results in a carpet of plantlets dense enough to conceal the water. Such free-floating masses of *Azolla* can frequently be recognized from a considerable distance because of their distinctive reddish color.

The pinnately branched, horizontally floating stem bears a long adventitious root here and there along the underside. A stem and its branches are densely clothed with small, alternately arranged, overlapping leaves. Each leaf is divided into two lobes of approximately equal size. The thick upper (dorsal) lobe is aerial and green; the thin lower (ventral) lobe is submerged and nearly colorless. It is thought that intake of water is through the ventral leaf lobes rather than through the roots. The space enclosed by an overarching of juvenile leaves at each branch apex always contains a blue-green alga, *Anabaena azollae* Strasb. One or more hormogones of the imprisoned *Anabaena* always move into

[1] Christensen, 1938. [2] Arnold, 1947; Hirmer, 1927; Seward, 1910. Bower, 1928; Campbell, 1918.

a special chamber formed within the dorsal lobe of a young leaf. The alga multiplies within the chamber and persists within it as long as a leaf remains alive. The relationship between alga and host is not merely that of a space parasitism. Experiments[1] seem to show that there is a true symbiosis in which the *Anabaena* fixes free nitrogen for the host. The universal occurrence of the same species of *Anabaena* within *Azolla* indicates that dispersal of the latter is effected by a transportation of vegetative portions rather than by a dissemination of spores. It is very probable that aquatic birds are the chief agency in dispersing the *Azolla*.

Growth of a stem is by means of a three-sided apical cell that successively cuts off a segment from each cutting face. The embryonic region of a stem is upwardly recurved. The mature region, which is close

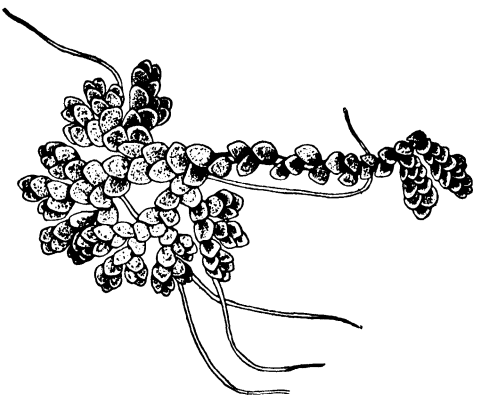

FIG. 247. Sporophyte of *Azolla filiculoides* Lam. (× 4.)

to the growing point, has a small central cylinder. In *A. filiculoides* Lam. it is impossible to draw a sharp distinction between central cylinder and cortex because the pericycle, endodermis, and innermost cortical layer are derived from a common mother-cell layer. The endodermal and pericyclic layers are each one cell in thickness and nine cells in perimeter (Fig. 248*A*). When seen in transverse section, the region internal to the pericycle contains about six xylem elements and about twice as many phloem elements. The central cylinder seems to be protostelic in organization, but adaptation to an aquatic life has been accompanied by so great a reduction of the vascular tissues that it is impossible to determine this with certainty. The cortical region is five to eight cells in thickness and composed of thin-walled parenchymatous cells without intercellular spaces.

Each adventitious root is formed from a single cell of the mother layer giving rise to pericycle, endodermis, and innermost cortical layer. This

[1] Oes, 1913.

cell soon gives rise to a pyramidal apical cell with four cutting faces, one toward the outer side and three lateral (Fig. 248*B*). Segments from the external face contribute to a root cap that ensheaths tissues of the root proper long after they are mature. Eventually, however, older tannin-filled portions of the cap are sloughed off. Segments cut off from the

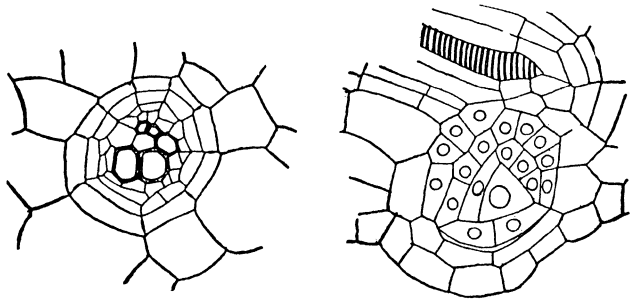

FIG. 248. *Azolla filiculoides* Lam. *A*, transverse section of stele and a portion of the cortex of a stem. *B*, longitudinal section of a portion of a stem containing the primordium of a root. (*A*, × 325; *B*, × 650.)

three lateral faces of an apical cell contribute to the remainder of the root. As seen in transverse section, tissues of maturing (Fig. 249*A*) and mature regions (Fig. 249*B*) in roots of *A. filiculoides* Lam. are diagrammatically arranged. At the outside is an epidermal layer of many cells. Internal

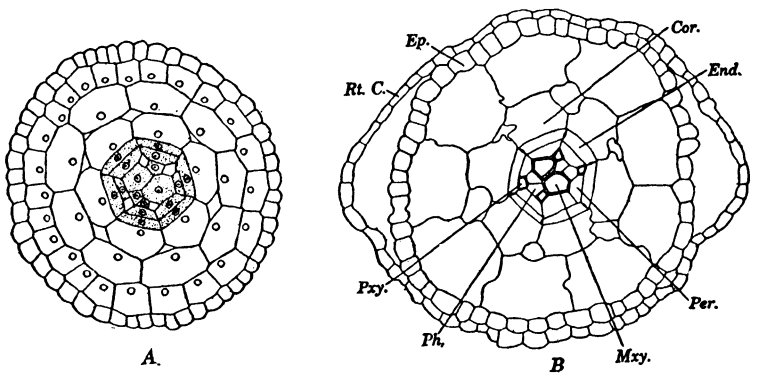

FIG. 249. *Azolla filiculoides* Lam. Transverse sections through immature (*A*) and mature (*B*) portions of a root. (*Cor.*, cortex; *End.*, endodermis; *Ep.*, epidermis; *Mxy.*, metaxylem; *Per.*, pericycle; *Ph.*, phloem; *Pxy.*, protoxylem; *Rt. C.*, root cap.) (× 325.)

to this are two layers of cortical cells; the outer with nine cells, the inner with six. Successively within the inner cortical layer and derived from the same mother-cell layer are a six-celled endodermal layer and a six-celled pericyclic layer. Mature portions of a stele contain four small protoxylem elements (Fig. 249*B*). In addition, there are two large metaxy-

lem and four phloem elements. Root hairs are not formed until a root has attained about half its ultimate length. They are formed in transverse belts and from embryonic epidermal cells near the growing point that are still ensheathed by the root cap. The embryonic epidermal cell divides diagonally into two daughter cells, one of which matures into a root hair, the other into an ordinary epidermal cell. As long as growth continues there is a formation of root hairs just back of the growing point. After the apical cell ceases to function, it may divide into a number of cells each of which elongates into a root hair.[1]

A young leaf soon becomes differentiated into a dorsal and a ventral lobe. The distal half of a mature ventral lobe is one cell in thickness; the

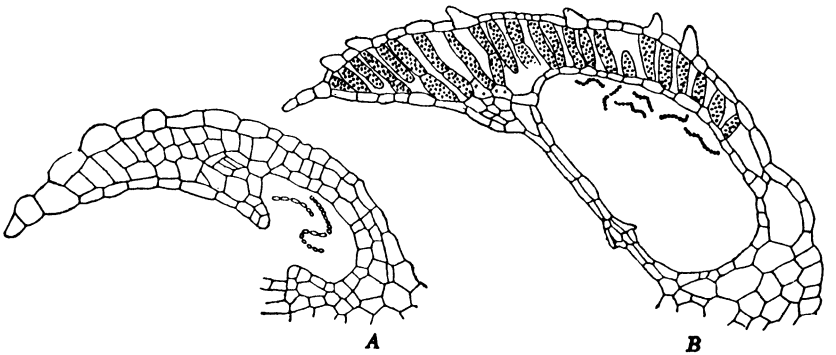

FIG. 250. *Azolla filiculoides* Lam. Longitudinal sections through the dorsal lobe of an immature (*A*) and a mature (*B*) leaf. (*A*, × 215; *B*, × 80.)

proximal half is more than one cell in thickness and has a single layer of large chambers. This portion of the ventral lobe may contain a few chloroplasts. Early in development of the dorsal lobe, there is the formation of a cavity on the adaxial face and near the leaf base (Fig. 250*A*). The cavity opens externally by a large circular pore. One or more hormogones of *Anabaena* migrate into this cavity and eventually become permanently imprisoned within it by a development of proliferous outgrowths from the margin of the pore. A mature dorsal lobe (Fig. 250*B*) has an upper and a lower epidermis, the former with numerous one- or two-celled hairs. Except for a small vein, the remaining tissue is a palisade parenchyma with large intercellular spaces.

Only the lowermost leaf of a branch is fertile. According to the species this forms two or four sporocarps in the axil of the dorsal lobe.[2]

In the youngest stage at which a sporocarp can be recognized, there is a macrosporangial initial that has cut off one or two stalk segments at its inner face.[3] At the same time a ring of cells, the beginning of the

[1] Leavitt, 1902. [2] Strasburger, 1873. [3] Pfeiffer, 1907.

indusium, is recognizable at the base of the young stalk (Fig. 251*A*). Development of an indusium is more rapid than that of a sporangium, and it soon becomes a cup-like sheath, two cells in thickness, that projects beyond the developing sporangium. Indusia overarching sporangia always contain one or more hormogones of *Anabaena*. Eventually the

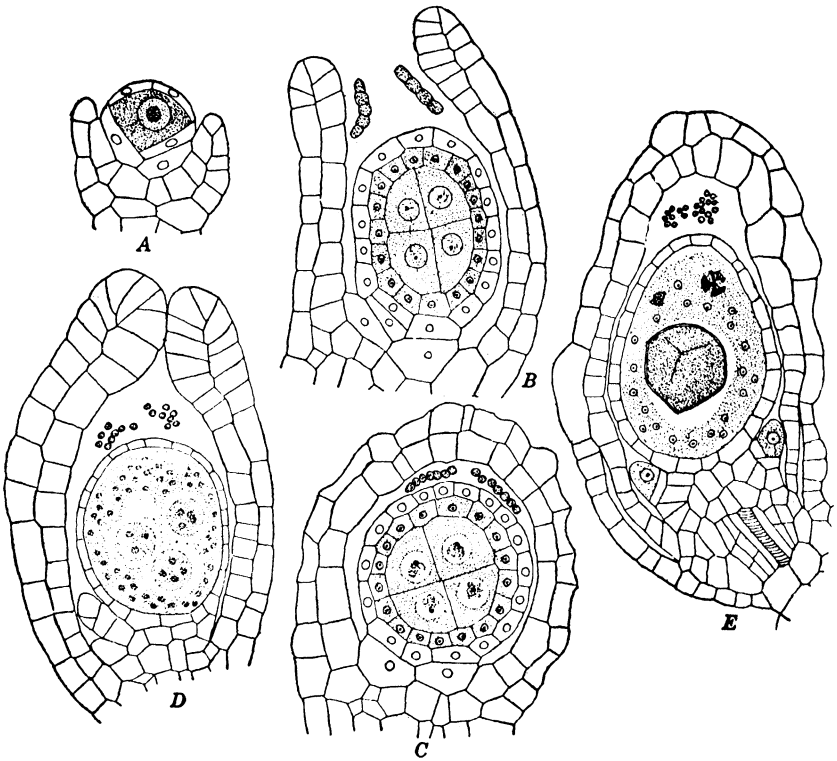

FIG. 251. *Azolla filiculoides* Lam. Stages in development of macrosporangia and the surrounding sporocarp wall (indusium). (*A–C*, × 650; *D–E*, × 325.)

opening at the distal end of an indusial cup becomes closed by an approximation of the free margins (Fig. 251*B*, *D*). Development of the macrosporangial initial into a macrosporangium (Fig. 251*B–E*) takes place in a typically leptosporangiate manner.[1] A macrosporangium has a tapetal layer one cell in thickness and eight macrospore mother cells. During meiosis the tapetum breaks down into a multinucleate plasmodium in which the number of nuclei may continue to increase. Each of the 32 young macrospores forms a thin spore wall.

[1] Campbell, 1893; Pfeiffer, 1907.

One conspicuous difference between development of this macrosporangium and sporangia of other Leptosporangiatae is the repeated division of the stalk cells to form a massive columnar stalk. An even more striking difference is the functioning of certain superficial stalk cells as initials of additional sporangia (Fig. 251*E*). Sporangial initials differentiated in stalks of macrosporangia are always microsporangial.

Irrespective of their nature, all sporocarps have a similar ontogeny up to this stage of development. Their subsequent history depends upon the behavior of the macrosporangium. One young macrospore in a macrosporangium may begin enlargement to form a functional macrospore (Fig. 251*E*). In such a case there is no further development of the juvenile microsporangia below the macrosporangium. Enlargement of the functional macrospore is accompanied by a formation of four quadrately arranged alveolar bodies (**massulae**) by the plasmodial tapetum. The functional macrospore lies in the large massula at the base of a sporangium. The three massulae in the upper portion may contain one or more small nonfunctional macrospores. When the macrospore is mature, there is a transverse rupture of the surrounding macrosporangium and indusium. The distal portion of indusium and macrosporangium, as well as the three massulae with nonfunctional spores, remains attached to the massula containing the macrospore (Fig. 253*A*). The portions attached to the macrospore and its massula have been called the "swimming apparatus"[1] because they were thought to be filled with air and thus to give buoyancy. Repeated observations on ripe spores after indusial rupture show that they never float but always sink.[2]

A macrosporangium may have a disintegration of all spores within it instead of a development of one of them into a functional macrospore.[3] When this takes place, the microsporangial initials on its stalk develop into mature microsporangia and additional microsporangial initials are differentiated in basipetalous succession (Fig. 252*A*). Thus, depending on the fate of the macrosporangium, all sporocarps on a leaf may be macrosporocarps, all may be microsporocarps, or there may be both kinds. Development of microsporangia is leptosporangiate and has the formation of a long narrow stalk (Fig. 252*B–D, G*). Similar to a macrosporangium there are eight spore mother cells and a tapetal layer one cell in thickness. There is also a breaking down of the tapetum into a multinucleate plasmodium during meiosis (Fig. 252*C*). All 32 microspores are functional. When first formed, they are evenly distributed throughout the plasmodium; later on they move to the periphery of the plasmodium (Fig. 252*D*). Following this, the plasmodium gives rise to four or more quadrately arranged alveolar massulae, each of which contains several micro-

[1] Strasburger, 1873. [2] Campbell, 1893.
[3] Goebel, 1905; Pfeiffer, 1907; Strasburger, 1889.

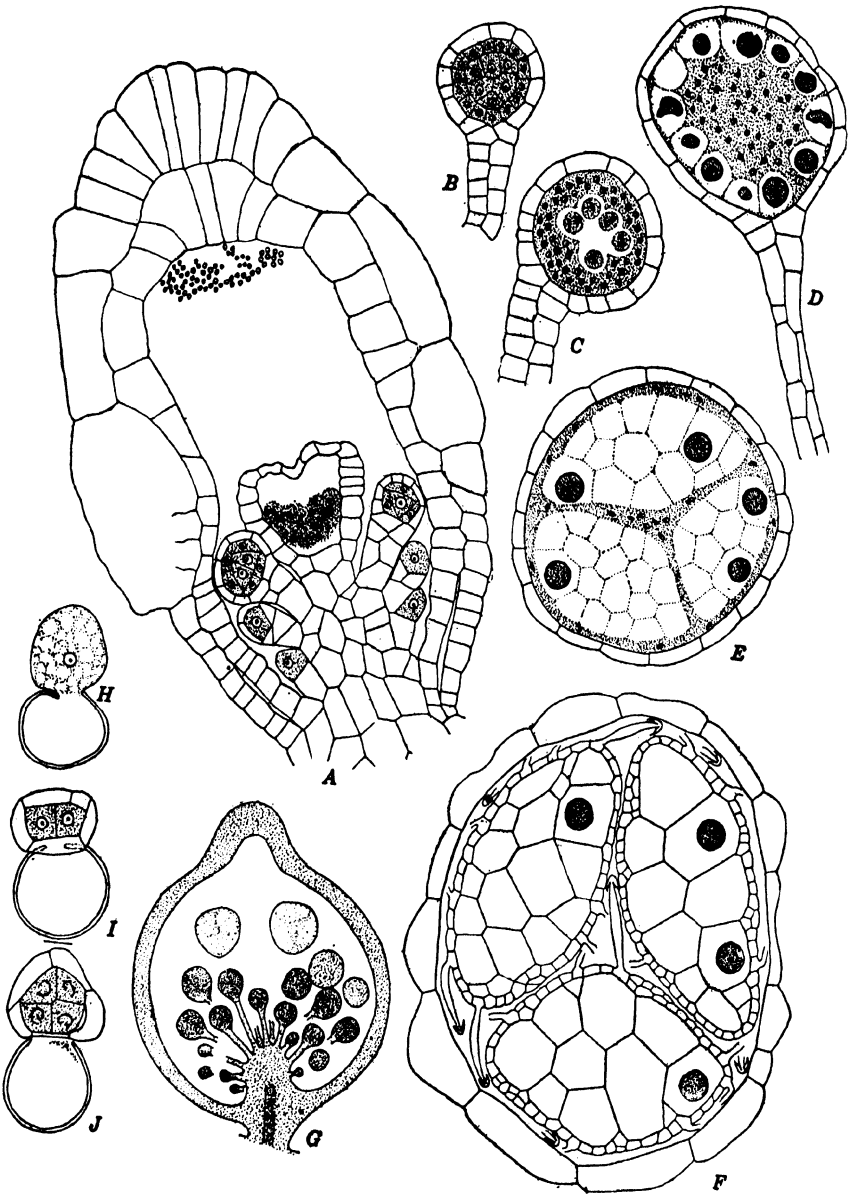

FIG. 252. *Azolla filiculoides* Lam. *A*, longitudinal section of a young microsporangial sporocarp. *B*, microsporangium at a late stage in development of sporogenous tissue. *C–F*, stages in development of massulae within microsporangia. *G*, longitudinal section of a nearly mature microsporangial sporocarp. *H–J*, stages in development of microgametophytes. (*A–F*, × 325: *G*, × 60; *H–J*, × 650.)

spores embedded in the peripheral portion (Fig. 252*E*). Massulae of species belonging to the section *Euazolla*, which includes *A. filiculoides* Lam., develop numerous elongate hooked processes (**glochidia**) on their surfaces (Fig. 252*F*). Massulae of species belonging to the section *Rhizosperma* lack glochidia. When a microsporocarp is ripe, there is a breaking of the indusium and a rupture of each sporangial jacket. The liberated massulae float away. In the case of *A. filiculoides* several microsporic massulae may become attached to a macrosporic massula by means of their glochidia (Fig. 253*B*). Neither macrospore nor microspore has begun development into a gametophyte at the time this attachment takes place.

A microspore remains embedded within a massula during the entire course of its development into a gametophyte. The time interval between spore germination and full development of a microgametophyte is much the same as with a macrogametophyte, that is, a week or so. Germination begins with a bursting of the outer spore-wall layer and a protrusion of the cytoplasm and nucleus, still surrounded by the inner wall layer (Fig. 252*H*). The protuberant portion becomes the single antheridial initial by formation of a cross wall near the apex of the spore cavity.[1] The large vegetative cell within the spore cavity cuts off a small lenticular cell and then divides no further.[2] The antheridial initial develops into an antheridium with eight androcytes and a jacket layer of a few cells (Fig. 252*I–J*). It is very probable that the mature antherozoids escape from the surrounding massula by a gelatinization of the latter.

Development of a macrospore into a mature gametophyte takes about a week.[1] The first indication of germination is an increase in size of the macrospore nucleus. Following a division of the nucleus there is a cutting off of a small lenticular cell at the upper end of the macrospore. The large sister cell, which contains numerous starch grains, does not divide again, but it does become multinucleate. The lenticular cell divides vertically into two daughter cells of unequal size.[1] The larger of these may divide either vertically or horizontally. In either case the young macrogametophyte soon becomes a lenticular disk two cells in thickness (Fig. 253*B*). It is at this stage that one of the median cells in the upper layer functions as the first archegonial initial. Up to this time the macrospore wall has remained intact. Shortly after this, it ruptures, and the developing gametophyte protrudes through the opening. The macrogametophyte eventually becomes a protuberant hemispherical mass five to eight cells in thickness. At first it has but one archegonium, that formed from the first initial. If there is no fertilization of the egg in this archegonium, additional archegonial initials are differentiated lateral to it. If these fail to function, further archegonia are produced until a

[1] Campbell, 1893. [2] Belajeff, 1898; Campbell, 1893.

dozen or more have been formed (Fig. 253*C*). Archegonial development is much the same as in other ferns. An initial divides periclinally into a central cell and a primary cover cell (Fig. 254*A*). Two successive anticlinal divisions of the cover cell produce four quadrately arranged neck initials (Fig. 254*B*). The neck initials, by oblique and transverse division, give rise to a short neck three to four cells in height. Meanwhile, there

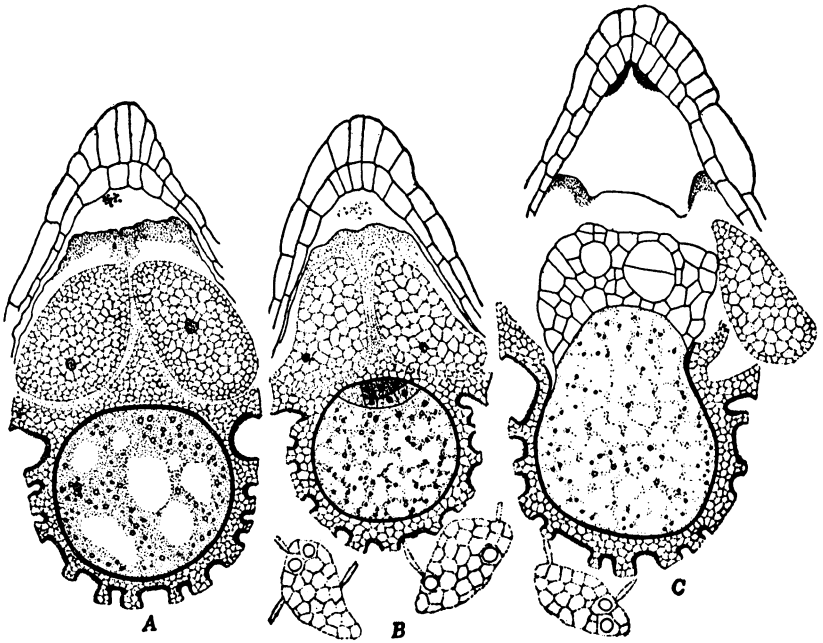

FIG. 253. *Azolla filiculoides* Lam. *A*, macrospore within a massula and adjoined by other macrosporic massulae and the apical portion of the sporocarp wall (indusium). *B*, an early stage in development of a macrogametophyte. *C*, a mature macrogametophyte with a two-celled embryo. In *B* and *C* microsporic massulae are attached to a macrosporic massula by their glochidia. (× 160.)

has been a division of the central cell into a small lenticular primary canal cell and a large primary venter cell (Fig. 254*D*). The primary canal cell pushes up into the developing neck. It may remain undivided or may divide to form two neck cells (Fig. 254*E*). Sometimes the primary venter cell divides into a small lenticular venter canal cell and a large egg.[1] In other cases it appears to function directly as the egg. Opening of the archegonium probably takes place in the usual manner.

A zygote of *Azolla* elongates vertically and then divides transversely (Fig. 254*F*). Each daughter cell then divides in a plane perpendicular to that of the preceding division.[1] As in most other Leptosporangiatae,

[1] Campbell, 1893.

each of the four parts of an embryo can be traced back to a cell of the quadrant stage. The two cells nearest the neck give rise to the cotyledon and stem; the two inner ones produce the foot and primary root (Fig. 254*G*). Cotyledon, stem, and primary root each grow by means of an apical cell. The chief difference between embryonal development in *Azolla* and that in other leptosporangiates is the relative rate at which the various organs develop. In *Azolla*, development of the stem is almost as rapid as that of the cotyledon (Fig. 254*H*). On the other hand the primary root develops at a very slow rate. The slow development of the

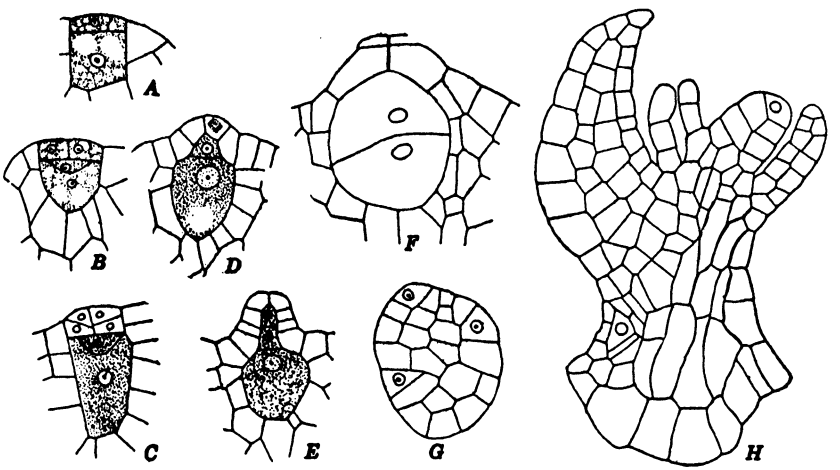

FIG. 254. *Azolla filiculoides* Lam. *A–E*, stages in development of archegonia. *F*, two-celled embryo. *G*, young embryo. *H*, embryo at an advanced stage of development. (× 325.)

root, as compared with that in other leptosporangiates, cannot be ascribed to the hydrophytic habit of the plant because other hydrophytic ferns, as *Marsilia*, have a rapid development of the primary root. It is very probable that retardation of root development is due to the fact that the cotyledon and first-formed leaves function as water-absorbing organs.

Bibliography

Arber, E. A. N. **1906.** *Ann. Bot.* **20**: 215–232. [Primofilices.]

Armour, Helen M. **1907.** *New Phytol.* **6**: 238–244. 4 figs. [Sporangia, *Dipteris.*]

Arnold, C. A. **1939.** *Contr. Mus. Paleont. Univ. Michigan* **5**: 271–314. 10 pl. 1 fig. [*Archaeopteris.*]

1940. *Amer. Jour. Bot.* **27**: 57–63. 7 figs. [*Iridopteris.*]

1947. An introduction to paleobotany. New York. 433 pp. 187 figs.

1952. *Palaeonographica* **92**, Abt. B: 63–73. 3 pl. 5 figs. [Fossil Osmundaceae.]

Atkinson, Lenette R. **1943.** *Amer. Jour. Bot.* **30**: 401–404. 9 figs. [Fertilization, *Marsilea.*]

Bartoo, D. R. **1929.** *Bot. Gaz.* **87**: 642–652. 12 figs. [Root, *Schizaea.*]
1929A. *Ibid.* **88**: 322–331. 20 figs. [Sporangia, *Schizaea.*]
1930. *Ibid.* **89**: 137–153. 27 figs. [Anatomy, *Schizaea.*]
Bauke, H. **1876.** *Jahrb. Wiss. Bot.* **10**: 49–116. 5 pl. [Gametophyte, *Cyathea.*]
Belajeff, W. **1898.** *Bot. Zeitg.* **56**: 141–194. 2 pl. [Microgametophyte, *Azolla, Marsilea.*]
Benedict, R. C. **1909.** *Bull. Torrey Bot. Club* **36**: 463–476. 3 figs. [*Ceratopteris.*]
Benson, Margaret. **1911.** *Ann. Bot.* **25**: 1045–1057. 3 pl. 3 figs. [*Botryopteris.*]
Bertrand, C. E., and F. Cornaille. **1904.** *Compt. Rend. Acad. Sci. Paris* **139**: 346–348. [Primofilices.]
Bertrand, P. **1913.** *Progr. Rei Bot.* **4**: 182–302. 59 figs. [Primofilices.]
1933. *Bull. Soc. Bot. France* **80**: 527–537. 12 figs. [Primofilices.]
Boodle, L. A. **1899.** *Ann. Bot.* **13**: 377–394. 1 pl. [Anatomy, *Ophioglossum.*]
1900. *Ibid.* **14**: 455–496. 3 pl. [Anatomy, Hymenophyllaceae.]
1901. *Ibid.* **15**: 359–421. 3 pl. [Anatomy, Schizaeaceae.]
1901A. *Ibid.* **15**: 703–747. 2 pl. [Anatomy, *Gleichenia.*]
1903. *Ibid.* **17**: 511–537. 3 figs. [Anatomy, *Schizaea.*]
Boodle, L. A., and W. E. Hiley. **1909.** *Ibid.* **23**: 419–432. 1 pl. 3 figs. [Anatomy, *Gleichenia.*]
Bower, F. O. **1888.** *Ibid.* **1**: 269–305. 3 pl. [Apogamy, *Trichomanes.*]
1889. *Ibid.* **3**: 305–392. 5 pl. [Sporangia, *Osmunda.*]
1896. Studies in the morphology of spore-producing members. II. Ophioglossaceae. London. 86 pp. 9 pl. 3 figs.
1897. *Phil. Trans. Roy. Soc. London B* **189**: 35–81. 5 pl. [Sporangia, Marattiales.]
1899. *Ibid.* **192**: 29–138. 6 pl. [Sporangia, Leptosporangiatae.]
1908. The origin of a land flora. London. 727 pp. 361 figs.
1911. *Ann. Bot.* **25**: 537–553. 2 pl. [Anatomy, *Ophioglossum.*]
1911A. *Ibid.* **25**: 277–298. 3 pl. [Anatomy, *Ophioglossum.*]
1912. *Ibid.* **26**: 269–323. 7 pl. [Morphology, various ferns.]
1913. *Ibid.* **27**: 443–477. 3 pl. 2 figs. [Morphology, various ferns.]
1915. *Ibid.* **29**: 495–529. 2 pl. 19 figs. [Anatomy, *Dipteris.*]
1918. *Ibid.* **32**: 1–68. 43 figs. [Sporangia, *Schizaea.*]
1923. The ferns. Vol. 1. Cambridge. 359 pp. 309 figs.
1926. *Ibid.* Vol. 2. Cambridge. 344 pp. 271 figs.
1928. *Ibid.* Vol. 3. Cambridge. 306 pp. 175 figs.
1935. Primitive land plants. London. 658 pp. 449 figs.
Brebner, G. **1902.** *Ann. Bot.* **16**: 517–552. 2 pl. 2 figs. [Anatomy, Marattiales.]
Britton, Elizabeth G., and Alexandria Taylor. **1901.** *Bull. Torrey Bot. Club* **28**: 1–19. 6 pl. [Gametophyte, *Schizaea.*]
Brown, Dorothy W. **1920.** *Ibid.* **47**: 339–345. 10 figs. [Apogamy, *Osmunda.*]
Browne, Isabel M. P. **1935.** *Bot. Rev.* **1**: 427–447. [Evolution of sporophyte.]
Bruchmann, H. **1904.** *Bot. Zeitg.* **62**: 227–247. 2 pl. [Gametophyte, *Ophioglossum.*]
Bruyn, Helena de. **1911.** *Ann. Bot.* **25**: 761–772. 2 pl. [Anatomy, *Dipteris.*]
Burlingame, L. L. **1907.** *Bot. Gaz.* **44**: 34–56. 2 pl. [Sporangium, Ophioglossales.]
Busgen, M. **1890.** *Flora* **73**: 169–182. 1 pl. [Sporocarp, *Marsilea.*]
Campbell, D. H. **1892.** *Proc. California Acad. Sci.* **2** ser. **3**: 183–205. 2 pl. [Gametophytes and embryo, *Marsilea.*]
1892A. *Ann. Bot.* **6**: 49–94. 4 pl. [Gametophyte and embryo, *Osmunda.*]
1893. *Ibid.* **7**: 155–187. 3 pl. [Gametophyte and embryo, *Azolla.*]
1894. *Ibid.* **8**: 1–20. 2 pl. [Gametophyte, *Marattia.*]
1895. The structure and development of mosses and ferns. 1st ed. London. 544 pp. 266 figs.
1904. *Amer. Nat.* **38**: 761–775. 9 figs. [Relationships, Marsileales.]

1905. The structure and development of mosses and ferns. 2d ed. New York. 657 pp. 322 figs.

1907. *Ann. Jard. Bot. Buitenzorg.* 2 ser. **6**: 138–194. 11 pl. [Gametophyte, *Ophioglossum.*]

1908. *Ibid.* **8**: 69–102. 8 pl. [Gametophytes, Marattiales, *Gleichenia.*]

1911. The Eusporangiatae. *Carnegie Inst. Washington Publ.* **140**: 1–229. 13 pl. 192 figs.

1918. The structure and development of mosses and ferns. 3d ed. New York. 708 pp. 322 figs.

Chang, C. Y. **1927.** *Bot. Gaz.* **83**: 288–306. 18 figs. [Anatomy, *Pteridium.*]

Charles, Grace M. **1911.** *Ibid.* **51**: 81–101. 4 pl. 3 figs. [Anatomy of young sporophyte, *Marattia.*]

Cheeseman, T. F. **1925.** Manual of New Zealand flora. Wellington. 1163 pp.

Ching, R. C. **1940.** *Sunyatsenia* **6**: 201–270. [Classification.]

Christ, H. **1897.** Die Farnkräuter der Erde. Jena. 388 pp. 293 figs.

Christensen, C. **1938.** Filicinae. In F. Verdoorn, Manual of pteridology. The Hague. Pp. 522–550.

Chrysler, M. A. **1910.** *Ann. Bot.* **24**: 1–18. 2 pl. 16 figs. [Fertile spike, Ophioglossales.]

1925. *Bull. Torrey Bot. Club* **52**: 126–132. 1 pl. [Fertile spike, Ophioglossales.]

Clausen, R. T. **1938.** *Mem. Torrey Bot. Club* **19**, No. 2: 1–177. 33 figs. [Ophioglossaceae.]

Copeland, E. B. **1942.** *Amer. Fern Jour.* **32**: 121–126. 1 fig. [Edible ferns.]

1947. Genera filicorum. Waltham, Mass. 247 pp. 10 pl.

Cross, G. L. **1931.** *Bot. Gaz.* **92**: 210–217. 8 figs. [Embryo, *Osmunda.*]

Darrah, W. C. **1939.** *Harvard Univ. Bot. Mus. Leaflets* **7**: 157–168. 6 pl. [*Botryopteris.*]

1941. *Amer. Midland Nat.* **25**: 233–269. 11 pl. [Coenopterid ferns.]

Davie, J. H. **1951.** *Amer. Jour. Bot.* **38**: 612–628. 26 figs. [Antheridia, various Leptosporangiatae.]

Diels, L. **1898.** Cyatheaceae, Polypodiaceae, Parkeriaceae, Schizaeaceae. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. Teil. 1. Abt. 4. Pp. 113–371. 121 figs.

Duncan, R. E. **1940.** *Bull. Torrey Bot. Club* **67**: 391–412. 30 figs. [Sporangium, *Azolla.*]

Faull, J. H. **1901.** *Bot. Gaz.* **32**: 381–420. 4 pl. [Anatomy, *Osmunda.*]

Fischer, H. **1911.** *Beih. Bot. Centralbl.* **27**: Abt. 1: 54–59. [Gametophytes, Polypodiaceae.]

Ford, Sibille O. **1902.** *Ann. Bot.* **16**: 95–121. 1 pl. 8 figs. [Anatomy, *Ceratopteris.*]

Georgevitch, P. **1910.** *Jahrb. Wiss. Bot.* **48**: 155–170. 30 figs. [Apogamy and apospory, *Trichomanes.*]

Glück, H. **1895.** *Flora* **80**: 303–387. 1 pl. 40 figs. [Sorus, *Cibotium.*]

Godwin, H. **1932.** *New Phytol.* **31**: 254–264. 7 figs. [Anatomy, *Cyathea.*]

Goebel, K. **1880–1881.** *Bot. Zeitg.* **38**: 545–552, 561–571. 1 pl. **39**: 697–706, 713–720. 1 pl. [Development of sporangia.]

1905. Organography of plants. English ed. Translated by I. B. Balfour. Part 2. Oxford. 707 pp. 417 figs.

1915. Organographie der Pflanzen. 2 Aufl. 2d Teil. Jena. 694 pp. 730 figs.

1930. *Ibid.* 3 Aufl. 2d Teil. Jena. 736 pp. 850 figs.

Gwynne-Vaughan, D. T. **1903.** *Ann. Bot.* **17**: 689–742. 3 pl. [Anatomy, Dicksoniaceae.]

1911. *Ibid.* **25**: 525–536. 1 pl. 5 figs. [Anatomy, *Osmunda.*]

Halle, T. G. **1936.** *Palaeont. Sinica* Ser. A. **1**, fasc. 4: 1–38. 5 pl. 2 figs. [*Protopteridium.*]

Hartman, M. Elizabeth. **1931.** *Bot. Gaz.* **91**: 252–276. 27 figs. [Antheridia, Polypodiaceae.]

Haupt, A. W. **1940.** *Bull. Torrey Bot. Club* **67**: 125–129. 16 figs. [Sex organs, Marattiales.]

Hirmer, M. **1927.** Handbuch der Paläobotanik. Bd. 1. Munich, 708 pp. 817 figs.
1938. Geographie und seitliche Verbreitung der fossilen Pteridophyten. In F. Verdoorn, Manual of pteridology. The Hague. Pp. 474–495.
Høeg, O. A. **1942.** The Downtownian and Devonian flora of Spitzenberg. Norges Svalbard. og Ishaus-Unders. No. **83**: 1–228. 62 pl. 35 figs.
Holloway, J. E. **1923.** *Trans. New Zealand Inst.* **54**: 577–618. 21 pl. [Ecology, Hymenophyllaceae.]
1944. *Trans. Roy. Soc. New Zealand* **74**, pt. 2: 196–206. 47 figs. [Gametophyte, embryo, Hymenophyllaceae.]
Holttum, R. E. **1938.** Ecology of tropical ferns. In F. Verdoorn, Manual of pteridology. The Hague. Pp. 420–450. 18 figs.
1947. *Jour. Linn. Soc. Bot. London* **53**: 123–158 [Classification, Leptosporangiatae.]
1949. *Biol. Rev.* **24**: 267–296. [Classification, Leptosporangiatae.]
Jeffrey, E. C. **1917.** The anatomy of woody plants. Chicago. 478 pp. 306 figs.
Johnson, D. S. **1898.** *Ann. Bot.* **12**: 119–145. 3 pl. [Sporocarp, *Marsilea.*]
1933. *Bull. Torrey Bot. Club* **60**: 555–564. 1 pl. [Sporocarps, Marsileales.]
Johnson, T. **1911.** *Sci. Proc. Roy. Dublin Soc.* N.S. **13**: 114–136. 3 pl. 8 figs. [*Archaeopteris.*]
Jonkman, H. F. **1880.** *Arch. Néerland. Sci. Exactes et Nat.* **15**: 199–224. 3 pl. [Gametophytes, Marattiales.]
Kidston, R., and D. T. Gwynne-Vaughan. **1907.** *Trans. Roy. Soc. Edinburgh* **45**: 759–780. 6 pl. [Fossil Osmundaceae.]
Kny, L. **1875.** *Nova Acta K. Leop.-Carol. Deutsch. Ak. d. Naturf.* **37**, No. 4: 1–66. 8 pl. [*Ceratopteris.*]
Kräusel, R. **1938.** Psilophytinae. In F. Verdoorn, Manual of pteridology. The Hague. Pp. 496–499.
Kräusel, R., and H. Weyland. **1926.** *Abhandl. Senckenbergischen Naturf. Ges. Frankfurt a/M.* **40**: 115–155. 15 pl. 46 figs. [*Cladoxylon.*]
Kubärt, B. **1917.** *Denkschr. Akad. Wiss. Wien* (Math.-Nat. Kl.) **93**: 551–584. 7 pl. 26 figs. [*Anachoropteris.*]
Lagerberg, T. **1906.** *Ark. Bot.* **6**, No. 5: 1–28. 5 pl. [Gametophyte, *Pteridium.*]
Lang, W. H. **1902.** *Ann. Bot.* **16**: 23–56. 3 pl. [Gametophyte, *Ophioglossum.*]
Leavitt, R. G. **1902.** *Bot. Gaz.* **34**: 414–419. 1 pl. [Root hairs, *Azolla.*]
Leitgeb, H. **1878.** *Sitzungsber. Akad. Wiss. Wien* (Math.-Nat. Kl.) **77**[1]: 222–242. 1 pl. [Embryology, *Marsilea.*]
Mahabelé, T. S. **1948.** *Bot. Gaz.* **109**: 349–354. 19 figs. [Gametophyte, *Ceratopteris.*]
Maheshwari, P., and B. Singh. **1934.** *Jour. Indian Bot. Soc.* **13**: 103–123. 3 pl. 44 figs. [Anatomy, *Ophioglossum.*]
Manton, Irene. **1932.** *Jour. Genetics* **25**: 423–430. 4 figs. [Apospory, *Osmunda.*]
Marschall, Cornella C. **1925.** *Bot. Gaz.* **79**: 85–94. 9 figs. [Sporangia, *Marsilea.*]
Maxon, W. R. **1909.** Cyatheaceae. In North American flora. Vol. 16. Part 1. New York. Pp. 65–88.
1925. *Nation. Geogr. Mag.* **47**: 541–586. 45 figs. [Ferns.]
Müller, C. **1893.** *Ber. Deutsch. Bot. Ges.* **11**: 54–72. 1 pl. 2 figs. [Sporangia, Polypodiaceae.]
Oes, A. **1913.** *Zeitschr. Bot.* **5**: 145–163. 1 fig. [*Anabaena* in leaves of *Azolla.*]
Ogura, Y. **1927.** *Jour. Faculty Sci. Imp. Univ. Tokyo.* Sect. 3. *Botany* **1**: 141–350. 74 figs. [Anatomy, Cyatheaceae, Dicksoniaceae.]
Petry, L. C. **1914.** *Bot. Gaz.* **57**: 169–192. 16 figs. [Anatomy, *Ophioglossum.*]
1915. *Ibid.* **59**: 345–365. 2 pl. 6 figs. [Apical cell, *Ophioglossum.*]
Pfeffer, W. **1884.** *Unters. Bot. Inst. Tübingen* **1**: 363–482. [Chemotaxis, antherozoids.]
Pfeiffer, Wanda M. **1907.** *Bot. Gaz.* **44**: 445–454. 2 pl. [Sporocarps, *Azolla.*]

Posthumus, O. **1925.** *Rec. Trav. Bot. Neérland* **21**: 111–296. 20 figs. [Anatomy, Coenopteridales.]
Puri, V., and M. L. Garg. **1953.** *Phytomorphology* **3**: 190–209. 63 figs. [Sporocarp of *Marsilea.*]
Renault, B. **1875.** *Ann. Sci. Nat. Bot.* 6 ser. **1**: 220–240. 6 pl. [*Botryopteris.*]
1876. *Ibid.* **3**: 1–29. 4 pl. [Sporangia, *Botryopteris, Etapteris.*]
Robinove, J. J., and C. D. LaRue. **1929.** *Papers Michigan Acad. Sci. Arts and Lett.* **9**: 273–286. [Ecology.]
Rogers, Lenette M. **1923.** *Bot. Gaz.* **75**: 75–85. 3 pl. [Gametophyte, *Lygodium.*]
1927. *Cellule* **37**: 327–352. 3 pl. [Gametophyte, *Lygodium.*]
Rostowzew, S. **1891.** *Overs. K. Danske Selsk. Föhr.* **1891**: 54–83. 2 pl. [*Ophioglossum.*]
Sadebeck, R. **1898.** Hymenophyllaceae. In A. Engler and K. Prantl, Die natürlichen Pflanzenfamilien. Teil 1, Abt. 4. Pp. 91–112. 11 figs.
Sahni, B. **1933.** *Trans. Roy. Soc. London B* **222**: 29–44. 3 pl. 7 figs. [*Zygopteris.*]
Sarbadhikari, P. C. **1939.** *Ann. Bot.* N.S. **3**: 137–147. 1 pl. 4 figs. [Apogamy, *Osmunda.*]
Schimper, W. P. **1869.** Traité de paléontologie végétale. Vol. 1. Paris. 738 pp. 110 pl.
Schmelzeisen, W. **1933.** *Flora* **127**: 46–80. 5 pl. 5 figs. [Gametophyte, *Cyathea.*]
Scott, D. H. **1920.** Studies in fossil botany. 3d ed. Vol. 1. London. 434 pp. 190 figs.
Seward, A. C. **1899.** *Phil. Trans. Roy. Soc. London B* **191**: 171–209. 4 pl. [*Matonia.*]
1910. Fossil plants. Vol. 2. Cambridge. 624 pp. 265 figs.
Seward, A. C., and Elizabeth Dale. **1901.** *Phil. Trans. Roy. Soc. London B* **194**: 487–513. 3 pl. [Anatomy, *Dipteris.*]
Sharp, L. W. **1914.** *Bot. Gaz.* **58**: 419–431. 2 pl. [Microgametophyte, *Marsilea.*]
Shaw, W. R. **1898.** *Ann. Bot.* **12**: 261–285. 1 pl. [Fertilization, Polypodiaceae.]
Shibata, K. **1911.** *Jahrb. Wiss. Bot.* **49**: 1–60. 3 figs. [Chemotaxis, antherozoids.]
Shreve, F. **1911.** *Bot. Gaz.* **51**: 184–209. 8 figs. [Ecology, Hymenophyllaceae.]
Steil, W. N. **1919.** *Trans. Amer. Microsc. Soc.* **38**: 271–273. 2 figs. [Gametophytes, Polypodiaceae.]
1939. *Bot. Rev.* **5**: 433–453. [Apogamy and apospory.]
Stephenson, G. B. **1907.** *Trans. and Proc. New Zealand Inst.* **40**: 1–16. 5 pl. [Embryo, *Cyathea.*]
Stokey, Alma G. **1918.** *Bot. Gaz.* **65**: 97–102. 10 figs. [Apogamy, Cyatheaceae.]
1930. *Ibid.* **90**: 1–45. 186 figs. [Gametophyte, *Cyathea.*]
1940. *Ibid.* **101**: 759–790. 35 figs. [Gametophytes, Hymenophyllaceae.]
1942. *Ibid.* **103**: 559–569. 30 figs. [Gametophyte, *Marattia.*]
1945. *Ibid.* **106**: 402–411. 53 figs. [Gametophyte, *Dipteris.*]
1948. *Ibid.* **109**: 363–380. 90 figs. [Sex organs, Hymenophyllaceae.]
1950. *Bull. Torrey Bot. Club* **77**: 323–339. 81 figs. [Gametophytes, Gleicheniaceae.]
1951. *Phytomorphology* **1**: 39–58. 30 figs. [Gametophytes and classification.]
Stokey, Alma G., and Lenette R. Atkinson. **1952.** *Ibid.* **2**: 138–150. 82 figs. [Gametophyte, *Matonia.*]
Strasburger, E. **1873.** Ueber Azolla. Leipzig. 86 pp. 7 pl.
1889. Histologische Beiträge. Heft 2. Jena. 186 pp. 4 pl.
1907. *Flora* **97**: 123–191. 6 pl. [Apogamy, *Marsilea.*]
Tansley, A. G., and Edith Chick. **1903.** *Ann. Bot.* **17**: 493–510. 2 pl. 1 fig. [Anatomy, *Schizea.*]
Tansley, A. G., and R. B. Lulham. **1904.** *New Phytol.* **3**: 1–17. 59 figs. [Anatomy, *Pteridium.*]
1905. *Ann. Bot.* **19**: 475–519. 3 pl. 5 figs. [Anatomy, *Matonia.*]
Thomas, A. P. W. **1902.** *Ibid.* **16**: 165–170. [Gametophyte, *Schizaea.*]
Thompson, J. M. **1920.** *Trans. Roy. Soc. Edinburgh* **52**: 715–735. 4 pl. 9 figs. [Anatomy, *Schizaea.*]

Twiss, Edith M. **1910.** *Bot. Gaz.* **49**: 168–181. 2 pl. [Gametophytes, Schizaeaceae.]
Underwood, L. M., and R. C. Benedict. **1909.** Marattiales. In North American flora. Vol. 16. pt. 1. New York. Pp. 15–23.
Wagner, W. H. **1953.** *Amer. Jour. Bot.* **40**: 34–40. [Phylogenetic indices.]
West, C. **1915.** *Ann. Bot.* **29**: 409–422. 1 pl. 14 figs. [Anatomy, Marattiales.]
1917. *Ibid.* **31**: 77–99. 1 pl. 9 figs. [Mycorrhiza, Marattiales.]
1917A. *Ibid.* **31**: 361–414. 2 pl. 33 figs. [Anatomy, Marattiales.]
Wettstein, R. von. **1933–1935.** Handbuch der systematischen Botanik. 4th ed. Leipzig. 1149 pp. 709 figs.
Wherry, E. T. **1920.** *Amer. Fern. Jour.* **10**: 15–22, 45–52. [Ecology.]
1921. *Ibid.* **11**: 5–16. [Ecology.]
1922. *Ann. Rept. Smithsonian Inst.* **1920**: 247–268. [Ecology.]
Williams, S. **1928.** *Trans. Roy. Soc. Edinburgh* **55**: 795–805. 7 figs. [Sporangia, *Osmunda*.]
Yamanouchi, S. **1908.** *Bot. Gaz.* **45**: 145–175. 3 pl. [Gametophytes, Polypodiaceae.]
Zimmermann, W. **1930.** Die Phylogenie der Pflanzen. Jena. 452 pp. 250 pp.
1938. Phylogenie. In F. Verdoorn, Manual of pteridology. The Hague. Pp. 558–618. 20 figs.

INDEX

Numbers in **boldface** type refer to pages on which the subject is illustrated or especially described.

A

Acrogyny, nature of, 61
Actinostele, **143, 148, 170, 187,** 243, 275, **298**
  exarch, 222
  mesarch, **167, 272**
  nature of, 144
Aerenchyma, **362**
Air chamber, **30, 38, 41, 48, 53, 228**
  formation of, 40
Aitchinsoniella, 40
Alternation of generations, 150
  in algae, 6
  antithetic theory of, 9
  heteromorphic, 9
  homologous theory of, 9
  intercalation theory of, 9
  isomorphic, 9
  modification theory of, 9
  origin of, **6, 9–10**
Amblystegium riparium, **110, 113**
Amphithecium, **24, 35, 43,** 56, **91,** 92, 102, 106, **120,** 121
  nature of, 24
Anabaena, 372, 373, **375, 376**
  azollae, 372
  role of, 373
Anachoropteridaceae, **278–279**
Anachoropteris, **279**
  involuta, **274**
  pulchra, **279**
Anacrogyny, 45
  nature of, 45, 61
Andreaea, 104–107
  rupestris, 105, 106
Andreaeaceae, **104–107**
Andreaeales, **104–107**
Andreaeobrya, 96, **104–107**
  nature of, 104
  relationships of, **10**
Androcyte, **21, 42,** 58, 90, 117, 193, 204, 229, **230,** 260, 291, **343, 354,** 367, **368,** 379
  nature of, 21
Androcyte mother cell, 21, 58, 117, 260
Androgonial cells, **20,** 21, 100, **101, 116, 175,** 260, **291, 309,** 310, **343, 354**
  primary, **20,** 21, 58, **80,** 81, 90, 100, **101, 116,** 117, **175,** 192, **204,** 229, **230,** 260, 290, **309,** 310, **343, 354,** 367, **368**
Anemia, 312, 317
Aneura, 16, 63
Aneurophyton, 271
Annularia radiata, 247
Annulus, **121, 124,** 125, 257, 276, **277,** 278, 279, **308, 316, 321, 327,** 329, **330, 336, 342,** 345, **350, 351,** 352
Antheridial cell, primary, **20,** 58, **80,** 81, 90, **204**
Antheridial chamber, **33, 45, 52,** 64, **65, 89**
Antheridiophore, 46, **47, 52**
  development of, **51**
  nature of, 46
Antheridium, of bryophytes, **27,** 38, 41, **42, 45, 52, 65, 68, 76, 105**
  development of, **20, 33, 57–58,** 64, **68,** 69, **80, 89,** 90, 100, **101, 116**
  initial of, **20,** 32, 58
  origin of, 8
  of pteridophytes, **193,** 317, **330, 337, 346, 353, 359,** 360
  development of, **175, 192–193, 260, 290–291, 300, 309, 310, 322, 343, 353–354**
  initial of, 260, 353, 367, **368,** 379
  origin of, **134, 135**
Antherozoid, **21,** 58, 100, 117, 205, 229, 260
  discharge of, 52, 59, 354
  formation of, 291
Anthoceros fusiformis, **87, 89**
  halli, 88
  hawaiensis, 92
  laevis, **92**
  pearsoni, 92
Anthocerotaceae, **87–95**
Anthocerotae, 3, **87–95**
  nature of, 12, 87
  relationships of, **10**
Anthocerotales, **87–95**
Aphlebiae, 275

Apical cell, **20**, 25, **31**, **41**, 47, 57, 61, 68, 79, 88, 97, **99**, 105, **113**, 170, 176, **208**, **255**, 256, 284, 290, 347, 349, 352, 373
of antheridium, **116**
of archegonium, **118**
differentiation of, 25, 74, 128, 192
division of, 64, 71, 88
division of derivatives, **99**, **110**, **255**
growth and, 19
Apogamy, 151, **152**, **153**, 207, 311, **330**, 331, 338, 343, 346, 356
nature of, 6
Apophysis, **121**
Apospory, 114, **151–152**, 311, 338
nature of, 6
Archaeocalamites, **239**
Archaeopteridales, 270, **279–281**
Archaeopteris, **279–281**
hibernica, 280, **281**
latifolia, **280**, **281**
Archegoniophore, 46, **47**, **53**, **337**
development of, 50, **51**
nature of, 46
Archegonium, of bryophytes, **27**, **34**, **35**, 38, **41**, 45, 50, **53**, **54**, **65**, **69**, **76**, **105**
abnormal, **8**, 119
development of, **22**, **34**, 50, **59–60**, 65, **69**, 81, **82**, 90, **91**, **101**, **117–118**
initial of, 33
origin of, **8**
primary, 101
secondary, 101
of pteridophytes, **193**, **215**, **261**, **300**, **309**, 310, 318, **330**, **337**, **342**, 343, **346**, **353**, **359**, 360, **369**
development of, **175–176**, **193–194**, **206**, **230–231**, 260, **291–292**, **322**, **323**, **354–355**, 380, **381**
initial of, 322, 370
origin of, **134**
Archesporial cell, 65, **173**, **202**, 307, **308**, 316, 322, 341, **351**, **384**
Archesporium, 36, 56, 92, **121**
Archidium, 122, 125
Arthrostigma, 137
Asplenium serra, 352
Asterella, 50, 51, 53
californica, **47**
Asteroxylaceae, **166–168**
Asteroxylon, 137, **166–168**
elberfeldense, 166
mackiei, **166**, **167**
Athalamia, 50
pusilla, **47**
Autoecism, 75
nature of, 75, 114
Axial cell, 90, **101**, **118**
primary, **22**
Azolla, 358, **372–381**
carolinia, 372
filiculoides, **140**, 372, **373–376**, **378**, 379, **380**, **381**

B

Baragwanthia, 179, **182**
longifolia, 182
Barbula convoluta, **128**
Blasia, 57
Blepharoplast, **21**, 58, 291
Bogs, creeping, 97
quaking, 97
Bothrodendraceae, **217–219**
relationships of, **180**
Bothrodendron, **217–219**
minutifolium, **218**
mundum, 218, **219**
Botrychioxylon, 275
Botrychium, 142, 282, 289
silaifolium, **283**
Botryopteridaceae, **276–278**
Botryopteris, **276–278**
americana, **274**
ramosa, **278**
Bract, 139, 242, 245, **246**
perichaetial, **73**, **75**
nature of, 75
perigonial, **75**, **76**
nature of, 75
Branch, aerial, **247**, 252, **353**
primordia of, **113**, 252
Branch gap, 146
nature of, 144
Branch trace, 144, **239**, **255**
nature of, 144
Bryophyta, **5–130**
classes of, 3
classification of, **11–12**
evolution among, **10–11**
interrelationships among, **10**
life cycle of, **5–6**
nature of primitive, **7**
origin of, **6–7**
origin, of antheridium, **8**
of archegonium, **8**
of gametophyte, **7–8**
of sporophyte, **9–10**
position in natural system, **1–2**
Bulbil, 113, 176
Buxbaumia aphylla, **115**
indusiata, **115**

C

Calamitaceae, 240, **246–251**
relationships of, **240**

Calamites, **247–251**
ramosus, **247**
Calamophyta, 3, **237–263**
classes of, 3
evolution of, **155**
geological range, **240**
interrelationships among, **240**
nature of, 154
Calamophyton, 139, **241–242**
primaevum, **241**
Calamostachys, 238, **250**
binneyana, 251
casheana, 251
ramosa, 247
Calobryaceae, 79
Calobryales, 11, 28, **78–82**
relationships of, **10**
Calobryum, 58, **79–82**
blumei, **79, 80, 82**
Calyptra, 39, **45**, 52, **54**, 67, **77**, 81, 94, **106**, 119, **232, 261, 371, 356**
nature of, 39
Cambium, 142, 212, **224**, 225, 243
Canal, carinal, 248, **249**, 254, **255**
central, 252, **255**
vallecular, 248, 252, **255**
Canal cells, **22**, 23, **101, 118**, 194, 207, 260, 292
primary, 90, **101, 118**, 176, 193, 207, 231, 260, **292**, 322, 354, **355**, 370
Capsule, **24, 27, 54, 55, 63, 77, 82, 93, 161, 162**
dehiscence of, 44, 56, **63**, 67, 70, **87**, 93, 103, **105**, 107
development of, **120–125**
Cardiomanes, 331, 335
reniforme, 337
Carpocephalum, 46
Casparian strip, 144, **198**, 199
nature of, 144
Central cell, **22**, 23, **118**, 175, 193, 207, 230, **231, 292**, 354
Central cylinder, **99**, 112
(*See also* Stele)
Cephalozia, 77
pleniceps, **75**
Cephaloziella rubella, **75**
Ceratopteris, **357–360**
pteroides, **357, 359**
Chemotaxis, 23, 60, 355
Chiloscyphus rivularis, **72**
Chloronema, 127
Chlorophyceae, relation to Bryophyta, 6, **10**
Cibotium, **344–346**
barometz, **345, 346**
chamissoi, **345**
menziesii, **346**
Cibotium, scheidii, **346**
Circinate vernation, 163, 315, 338
Cladode, 136
Cladoxylaceae, **272–274**
Cladoxylon, **273–274**
scoparium, **272, 273**
Coenopteridales, **274–275**
Coenopterideae, 269
Columella, **91**, 92, **93**, 102, **103, 106, 121, 122**
Commissural strand, 296, **297**
Compensating tongue, 326
Conocephalum, 29, 52, 53
Cork cambium, 245
(*See also* Phellogen)
Corsinia, 29, **37–40**
coriandrina, **38, 39**
Corsiniaceae, 17, **37–40**
Cortex, 112, 161, **162, 167, 170, 171**, 186, 197, **198, 256**, 284, **285, 286, 315, 320**, 332, **362, 374**
initials of, **71, 213**
inner, **213**
middle, **213**
outer, **213, 219**
primary, **224**, 225
secondary, **224**, 225
Cotyledon, 194, **195, 208**, 231, **232, 293, 301**, 337, 344, **356, 371, 381**
initial of, **232**, 318, 355, **356**, 371, 381
Cotyledonary sheath, **232**
Cotyledonary trace, **297**
Cover cells, **343**, 353, **354**
primary, **22**, 23, 90, **91, 118**, 175, 193, 207, **230**, 231, 260, **292, 343**
shedding of, 354
Cryptomitrium, 56
Cupule, 48
Cyathea, **338–344**, 358
dealbata, 341
medullaris, 338, **339, 341, 342**
muricata, **342**
tussacii, **152, 342**
Cyatheaceae, 156, 304, **338–344**
relationships of, **266**
Cyathodium, **40**, 110
Cyathophorum bulbosum, **109, 118**
Cystodium, 344

D

Danaea, 296
alata, **297**
elliptica, **300**
Dendroceros, 88
Dennestedtia, 344
Dicksonia, 344, 346

Dicksoniaceae, **344–346**
relationships of, **266**
Dictyostele, **143, 285, 297,** 305, **306**
nature of, 147
polycyclic, **143, 340, 349**
nature of, 147
Dineuron pteroides, **274**
Diplolabis roemeri, **274**
Dipteridaceae, 156, **327–331**
relationships of, **266**
Dipteris, 327, **328–331**
conjugata, 264, 328, **329, 330**
lobbiana, **329, 330**
Dome cell, **343,** 353, **354**
Dryopteris filix-mas, **351**
Dumortiera, 28, 44

E

Ectocarpus, 7
Egg, **22,** 23, **34,** 60, 90, **91, 101,** 102, **118,** 194, 207, 231, 260, **292,** 354, 370
Elater, **43,** 46, **55,** 61, **66,** 70, **77, 82, 258**
primitive, 38
Elaterophore, 61, **66,** 70
nature of, 61
Embryo, of bryophytes, **24, 35, 39, 43, 54, 76, 91, 106**
development of, **35, 70, 91,** 102
filamentous type, 53
foot of (*see* Foot, of bryophitic embryo)
quadrant type, 53
of pteridophytes, **176–177, 194–195, 207–209, 231–233, 261–262, 292–294, 301–302, 310–311, 323, 337–338, 355–356, 360, 370–371, 380–381**
foot of (*see* Foot, of pteridophytic embryo)
polarity of, **232–233**
Enation theory, **137**
Enations, **137, 138**
nature of, 137
Endodermis, 144, **170,** 187, **198, 255,** 256, 278, 284, **286, 306, 314, 315, 320, 334, 349, 374**
formation of, 373
inner, **326,** 328, **362**
nature of, 143
outer, **326,** 328, **362**
Endophelloderm, **213**
Endospore, 126
Endosporium, 37
Endothecium, **24, 35,** 36, **43,** 56, **91,** 92, 102, 106, **120,** 121
nature of, 24
Ephemerum, **128**
serratum, **115**
Epibasal cell, 29, 35, 38, 60, 65, 69, 176, 301
Epidermis, 112, **162, 170, 171, 193,** 254, **256, 286, 287, 350, 362, 374**
Equisetaceae, 240, **251–263**
relationships of, **240**
Equisetales, **246–263**
relationships of, **240**
Equisetinae, 3, **240–263**
nature of, 240
Equisetites, 251
Equisetum, 149, 238, **239,** 246, 247, **251–263**
arvense, 252, 261
debile, **259,** 260, **261,** 262
giganteum, 251, 252, 254
palustre, 252, **253**
telmateia, **140, 253, 255, 256, 258, 261**
Etapteris, 275, 276, **277**
bertrandi, **274**
diupsilon, 276
lacattei, 276, **277**
Euazolla, 379
Eubrya, **107–128**
acrocarpous, 114, **115**
nature of, 114
autoicous, nature of, 114
cleistocarpous, nature of, 125
development, of capsule, **120–126**
of sex organs, **116–119**
embryos of, **119–120**
nature of, 107
occurrence of, **108**
paroicous, nature of, 114
pleurocarpous, nature of, 114
relationships of, **10**
stegocarpous, 123, 125
nature of, 123
synoicous, nature of, 114
vegetative multiplication, **113–114**
vegetative structure, **109–113**
Eusporangiatae, 269, **281–302**
nature of, 281
relationships of, **266**
Exophelloderm, **213**
Exospore, 126
Exosporium, 36, 258

F

Ferns, annual, 358
coenopterid, 270
edible, 357
sun, 265
(*See also* Filicinae)

Fertile spike, 281, **283**
development of, **287–289**
morphological nature, **288–289**
Fertilization, 23, 34, **35**, 60, 69, 119, 205, 207, 260, **369**, 370
Filicales, **303–360**
Filicinae, 3, **269–381**
nature of, 269
Flagella, 21
Foot, of bryophytic sporophyte, **24**, 25, **27, 43, 54, 55, 77, 93, 103**
of pteridophytic embryo, 176, 194, **195, 208, 232, 261**, 293, 301, 310, 338, 344, **356, 371, 381**
initial of, **232**, 318, 323, 355, **356**, 371, 381
Fossombronia, 60–63, **67–71**
angulosa, **68, 69**
intestinalis, **67**
longiseta, **67**
pusilla, **70**
Fritschiella, 7
Frullania, 60, 77
armitiana, **73**
Funaria, 119, 124, 127
hygrometrica, **111, 116, 120–124**
Funicularia, 38

G

Gametophore, 96, **98**, 103, **105**
dimorphic, **115–116**
early development of, **128**
initial of, **126**
nature of, 96
sexuality of, **114–116**
structure of, **109–113**
Gametophyte, of bryophytes, **19–24, 26–27, 29–34, 38, 40–42, 44–52, 57–61, 64–65, 67–69, 71–77, 79–81, 87–91, 96–102, 104–106, 109–119**
of pteridophytes, **149–150, 174–177, 192–194, 204–207, 210, 215, 219, 229–233, 258–263, 289–294, 297–302, 308–311, 317–318, 322–323, 327, 329–331, 335–338, 342–344, 346, 352–357, 359–360, 366–371, 379–382**
filamentous type, **317**
hairs of, 342
primitive type, 149
tracheids in, 174
Gemma, 26, 32, **49**, 113, **128, 186**
development of, 49
endogenous, 64
Gemmaling, 26
Geothallus, 19
Germinal disk, **25**
Germinal tube, 25, 37
Gleichenia, 149, 265, **319–323**, 327
dichotoma, **320, 322**
flabellata, **321**
pectinata, **319, 321–323**
Gleicheniaceae, 304, **318–323**, 331
relationships of, **266**
Glochidium, **378, 380**
nature of, 379
Glossopodium, **200**
Grimaldia, 50, 53
indica, **47**

H

Haplomitriaceae, **79–82**
Haplomitrium, 79, 81
Haplostele, **143, 148**
nature of, 144
Helminthostachys, 282
Hepaticae, 3, 11, **14–84**
classification of, **18**
fossil, **15–16**
gametophytes, evolution among, **16–17**
primitive, **16**
geographical distribution of, **15**
nature of, 12, 14
occurrence of, **14–15**
relationships of, **10**
sporophytes, evolution among, **17**
nutrition of, **17–18**
primitive, **17**
Herbertia adunca, **73**
Heterophyllum, 196
Heterophylly, 242, **243**
Heterospory, 115, 195, **215**, 222, 246, 251, **281**
evolution of, 150
Heterothallism, 20, 26, 32, 45, 49, 75, **80**, 89, 100
Homoeophyllum, 196
Homospory, 246, 251, 303
Homothallism, 26, 32, 49, 75, 100, **105**
Hornea, 162
Hyaline cells, **99**
Hydroids, 112
Hydropteridae, 303
Hyenia, 241
Hyeniales, 238, 239, **241–242**
relationships of, **240**
Hymenophyllaceae, 304, **331–338**, 372
relationships of, **266**
Hymenophyllites, 331
Hymenophyllum, 331, **332–338**
acanthoides, **337**
australe, **333, 334**
cruentum, 332, 334
demissum, 333

Hymenophyllum, dilatatum, 335
fucoides, 334
javanicum, 264
kurzii, **337**
pulcherrimum, 332
scabrum, 333
Hyphal tissue, **193**
Hypobasal cell, 24, 29, 35, 38, 60, 65, 69, 176, 301

I

Indusium, **327**, 335, **336, 342, 345, 350, 364, 376**
Internode, 252
Inversicatenales, 269
Involucre, **19, 20, 22, 38**, 39, **41, 45**, 46, 51
Iridopteris, **272**
eriensis, **271**
Isoetaceae, 181, **223–233**
relationships of, **180**
Isoetales, 181, **221–233**
relationships of, **180**
Isoetes, 142, 150, 180, 210, 211, 215, 221, 222, **223–233**
bolanderi, **223**
braunii, **231, 232**
lithophylla, **232, 233**
nuttallii, **224, 227, 228**
Isoetites, 221, 223

J

Jacket, of antheridium, **20, 42, 80**, 100, **101, 116, 175**, 192, 229, **230, 309**, 310, 367, **368**, 379
initials of, **20**, 21, 58, **80**, 81, 90, 100, **101, 116**, 117, **118, 175**, 192, 260, 310
of capsule, **24, 39, 43, 54, 55, 66, 77, 82**, 92, **93, 103, 106**
of sporangium, **173, 201, 202, 216**, 276, 278, **288**, 307, **308, 316**, 351, **352, 376**
initials of, **173, 191, 202**, 290, 307, 335, **351**
Jungermanniales, 11, 25, 44, 46, **57–78**, 120
relationships of, **10**
Jungermannineae, 59, 62, **71–78**

L

Lastrea pseudo-mas, 152
Leaf, of bryophytes, **75, 79**, 98, **105, 109**, 111, **128**
development of, 98, **99, 110–111**
dorsal, **73**
Leaf, of bryophytes, evolution of, 74
incubous, nature of, **72**
initial of, **71**
lateral, **72, 73**
perichaetial, nature of, **111**
structure of, **111, 113**
succubous, nature of, **72**
under, **72**
ventral, **73**
of pteridophytes, **166, 183**, 238, **241, 261, 280, 319, 324, 333, 348, 361**
dimorphic, 196, **197**
macrophyllous, 146, 238, 267, **273**
nature of, 136
origin of, **136**
microphyllous, 146, 181, 238
nature of, 137
origin of, **137, 138**
primordia of, 189, 350
structure of, 172, **189**, 199, **200, 226–227**, 249, **297, 334–335, 350, 375**
Leaf gap, **145**, 146, **306, 330, 345**
nature of, 144
Leaf sheath, primary, **261**
Leaf supply, 144
Leaf trace, **167, 171**, 183, **213, 219, 224, 239, 255, 278, 285**, 287, **297**, 305, 307, 320, 329, **330, 345**
nature of, 144
Lepidocarpaceae, 210, **216–217**
relationships of, **180**
Lepidocarpales, 181
Lepidocarpon, **216–217**
lomaxi, **216**
Lepidodendraceae, **211–216**
relations of, **180**
Lepidodendrales, 181, **210–221**
relationships of, **180**
Lepidodendron, **211–216**, 220
aculeatum, **213**, 214
obovatum, **212**
vasculare, **213**, 214
Lepidophlois, 216
Lepidophyta, 3, **179–236**, 266
antiquity of, **180**
classes of, **3**
classification of, **181**
evolution of, **153–155**
geological range, **180**
nature of, 179
relationships of, **154**
"seeds" of, **209**, 210, **217**
Lepidospermae, 181
Lepidostrobus, 214, **215**, 222
veltheimianus, 215
Leptopteris, 304, 331
Leptosporangiatae, 269, **302–381**
classification of, **303**

Leptosporangiatae, nature of, 302
relationships of, **266**
Leskea pulvinata, **109**
Ligule, 179, 199, **201, 208, 209, 213,** 214, **215, 219, 220, 232**
structure of, **200**
Lunularia, 48
Lycopodiaceae, **184–195**
relationships of, **180**
Lycopodiales, 181, **182–195**
relationships of, **180**
Lycopodinae, 3, 166, **181–233**
Lycopodites, 184
Lycopodium, 149, 155, 174, **184–195,** 214, 312, 313, 317
annotinum, **193**
cernuum, 141, **191**
clavatum, **193**
complanatum, **193**
inundatum, **185**
phlegmaria, 184, **185, 195**
selago, 184, 190
serratum, **189**
volubile, **185, 189**
Lycopsida, as division, **2**
nature of, 2
steles of, **146**
as subdivision, 2

M

Macrogametophyte, **209, 215,** 216, **219,** 221, **371,** 379, **380**
development of, **205–207, 230–231, 368–370, 379–380**
Macrosporangium, **201,** 210, **215, 219, 220, 281**
dehiscence of, 204
development of, **202–204,** 228, **363–364, 376**
Macrospore, **201, 215, 219, 220, 281, 367**
number of, 203, 215, 220, 229, 363, 376, 377
Macrosporophyll, **201, 209, 215, 219, 220,** 223
Marattia, **295–302**
alata, **295, 297–299**
douglasii, **300, 301**
fraxina, **297, 299, 300**
Marattiaceae, 294, **295–302**
relationships of, **266**
Marattiales, 285, **294–302**
Marchantia, 17, 23, 29, 46
polymorpha, 46, **47–49, 51–55**
Marchantiaceae, 17, 28, **46–56**
primitiveness of, **28**
Marchantiales, **27–56,** 60, 64
evolution among, **28–29**
relationships of, **10**
Marsilea, 150, 360, **361–371**
drummondii, **152,** 370
polycarpa, 362
quadrifolia, 361, 362
vestita, **140, 361–364, 367–369,** 370, **371**
Marsileaceae, 303, **360–371**
relationships of, **266**
Marsileales, 303, **360–371**
sporocarp of, **363–364**
dehiscence of, **366–367**
nature of, **365–366**
Marsupia, **78**
Massulae, **377**
macrosporic, 377, **380**
development of, **377**
microsporic, **380**
development of, **378**
Matonia, **325–327,** 328, 340, 348
pectinata, 147, **324–326**
Matoniaceae, 156, 304, **323–327**
relationships of, **266**
Mazocarpon, 220
oedipternum, **220**
Meristele, **285, 306, 340, 349,** 358
nature of, 147
Meristem, **93,** 174, **193,** 197, 225
Merophyte, formation of, **71**
nature of, 71
Mesome, **136, 137, 138**
nature of, 136
Mesophyll, 298
Mesosporium, 36
Metaphloem, 349
nature of, 142
Metaxylem, **170, 171,** 183, **187, 189, 198, 213, 244,** 248, **249,** 254–**256,** 284, **285, 286, 298, 306, 320, 334, 362, 374**
nature of, 140
Metzgeria, 57
Metzgerineae, **62–70**
Miadesmia, **209–210**
membranacea, **209**
Miadesmiaceae, 181, **209–210**
relationships of, **180**
Microgametophyte, development of, **204, 229–230, 367–368, 378**
liberation of, 203
Micromitrium, 115
salakanum, **115**
Micropyle, **216**
Microsporangium, **201, 215, 219, 281**
dehiscence of, 203
development of, **202–203, 228, 363, 377–379**
initial of, 377, **378**
Microspore, **201, 215, 219, 281, 367, 368**
number of, 363
Microsporophyll, **201, 215, 219,** 223

Mnium, 8
orthorhynchum, **109**
Mohria, 312, 313
Monoclea, 28, **44–46**
forsteri, **44**
gottschei, 44, **45**
Monocleaceae, **44–46**
Monoselenium, 28, 44
Monostele, nature of, 143
Musci, 3, **76–130**
nature of, 12, 76
relationships of, **10**
Mycorhiza, **174**, 177, 192, 285, 290, **296**, 300

N

Naiaditia, 15, 16
Nathorstia, 221
Neck canal cells, **22**, 23, **118**, **292**
primary, 260
Neck initials, **22**, 23, 59, 175, 194, 207, 231, **292**, 354, 370
Nephrodium filix-mas, 141
molle, **152**
Nephrolepis, **353**
Neuroloma, 104
Nitrogen fixation, 373
Nostoc, 88
Notothylaceae, 87
Notothylas, 87, 92
Nurse cells, **24**, 25, 27, **35**, 36

O

Onoclea sensibilis, **355**, **356**
Opercular cell, **175**, 192, 260, **291**, 310, 331
Operculum, of antheridium, **116**, 117
of capsule, 102, **103**, **121**, **122**
development of, **123–125**
shedding of, 103, 125
Ophioglossaceae, 141, **282–294**
relationships of, **266**
Ophioglossales, **282–294**
Ophioglossum, 142, **282–294**, 301
moluccanum, **283**, 290, 292, **293**, **297**
palmatum, 283, 284
pendulum, 284, 289, **290–293**
reticulatum, 287
vulgatum, **285**, **286**, **288**, **289**, 292, 293
Osmunda, **304–311**, 313, 322
cinnamomea, 306, **309**, 310
claytoniana, **305**, **306**, 307, **308**, **309**, 310, **311**
regalis, **306**, **308**
Osmundaceae, **304–311**, 331
relationships of, **266**

P

Palaeopteridales, 269
Palaeostachys, 238, **250**
Palisade tissue, **193**, **350**
Pallavicinia, 61
Paraphyses, **116**
Parichnos, **213**, 214, **216**
function of, **214**
structure of, **214**
Parkeriaceae, **357–360**
relationships of, **266**
Paroecism, nature of, 76
Parthenogenesis, **152**, 344
nature of, 152
Peat, **97**
Pellia, 61
Perforations, **239**
Perianth, **73**, **75**
Pericycle, 187, **198**, **255**, **306**, **314**, **315**, **320**, **334**, **349**, **394**
formation of, 313, 373
inner, **326**, **362**
outer, **326**, **362**
Periderm, 222, 245, 284
Peripheral cells, 59
Peripheral initials, **22**
Peristome, **121**, 122, 123
teeth of, 123, **124**, 125
Peristomial layer, inner, **124**
outer, **124**
Phanerosorus, 325
Phellogen, 222, 284
Phloem, 139, **141-142**, **167**, **170**, **171**, **187**, **189**, **198**, **213**, **219**, **256**, **278**, 284, **298**, **314**, **315**, **320**, **334**, **374**
inner, **326**, **362**
outer, **326**, **462**
primary, **224**
secondary, 142, 244
Phloem parenchyma, 141, 254
Phylloglossum, 155, 184
Phyllogonium, 110
fulgens, **109**
Phyllophore, **274–275**, **277**
nature of, 275
xylem of, **274**
Physcomitrium sphaericum, **125**
Pilularia, 360, 384
Pinna, fertile, **324**
Pinnule, fertile, **281**, **305**, **341**, **345**, **350**
sterile, **280**, **281**
Pith, 284, **306**, **314**, **349**, **362**
tracheids of, **314**
Plagiochasma, 17, 29
adiantoides, **76**
asplenioides, **73**
Plasmodesmen, 142

Plectostele, **143**
nature of, 144
Pleuromeia, 221, 222–**223**, **225**
sternbergii, **222**
Pleuromiaceae, 181, **221–223**
relationships of, **180**
Pleurozia, 71
Polypodiaceae, 156, 304, **346–357**
relationships of, **266**
Polyspermy, 23, 60
Polystele, **143**, 181, **198**
nature of, 143
Polytrichum, 112, 122
juniperum, **112**
Porella, 10
bolanderi, **76**, **77**
platyphylloides, 14
Pottia, 127
Preissia, 50, 53
Primofilices, **269–281**
nature of, 269
relationships of, **266**
Prismatic layer, **224**
structure of, 225
Progressive sterilization, 10, 17
Propagula, **128**
Prothallial cell, **204**, 229, **230**, 367, **368**
Protobryophytes, relationships of, **10**
Protocorm, 186, **195**
nature of, 195
Protolepidodendraceae, **182–184**
relationships of, **180**
Protolepidodendron, **182–183**
scharyanum, 182, **183**
Protonema, 76, 103, 109, 126
filamentous, **126–129**
rate of growth, 127
size of, 127
perennial, 115
primary, 114
secondary, 114
thallose, 103, **104**, 127
Protophloem, 349
nature of, 142
Protophyll, nature of, **195**
Protopteridales, **270–274**
Protopteridiaceae, **271–272**
Protopteridium, **271–272**
minutum, **271**
Protostele, **143**, 144, 161, **162**, **183**, **213**, 238, 296, 305, 313, **320**, 325, 340, 358, 373
nature of, 144
(*See also* Actinostele; Haplostele; Plectostele)
Protoxylem, **167**, **170**, **198**, 248, 254, **255**, **256**, 349, **362**, **374**
endarch, 144, 284, **285**, **334**
Protoxylem, endarch, nature of, 144
exarch, 144, **187**, **189**, 213, 220, 222, 243, **286**, **298**
nature of, 144
mesarch, 144, **171**, **306**, **320**
nature of, 144
nature of, 140
polyarch, 220
Pseudobornia, 240
Pseudoelater, **93**
Pseudoperianth, **52**, **54**, **55**
Pseudopodium, **103**, **106**, 107
nature of, 103
Pseudosporochnaceae, **164**
Pseudosporochnus, **164**
krejcii, **164**
Psilophyta, 3, **159–178**
classes of, 3
nature of, 159
relationships of, **10**, **154**, **180**, **240**, **266**
Psilophytaceae, **163–164**
Psilophytales, 155, 159, **160–168**, 267, 270
Psilophytinae, 3
Psilophyton, 137, 159, **163–164**
princeps, 163
Psilopsida as subdivision, 2
Psilotales, 160, **168–177**
Psilotum, 160, 168, 172, 174
flaccidum, 168, 169
triquetrum, 148, 168, **169**, **170**, **173**
Pteridium, **347–357**
aquilinum, 141, **142**, 265, **348–351**, 352
latiusculum, 347, **349**
Pteridophyta, 2
validity of, **2–3**
Pteridophytes, **131–386**
evolution among, **153–156**
sporophylls, **138–139**
sporophytes, **134–138**
gametophytes of, **149–150**
life cycle of, **150–153**
nature of, 131
origin of, **131–134**
position in natural system, **1–2**
vascular system, **139–149**
elements of, **139–142**
evolution of, **142–149**
Pteris, 187, **351**
Pterophyta, 3, **264–386**
classes of, **3**
ecology of, **264–266**
evolution of, **155–156**
evolution of leaf, **267**
evolution of stem, **267**
geological range, **266**
interrelationships among, **266**

Pterophyta, nature of, 264
occurrence of, **264**
phylogenetic indices in, **267–269**
relationships of, **154**
Pteropsida, as division, 2
nature of, 2
steles of, 147
as subdivision, 2
Pteropsiella, 74
frondiformis, **73**
Pyrenoid of Anthocerotales, 88

R

Rachis, 275
structure of, **274**, 276, 278, 279
Reboulia, 47, 53, 56
hemisphaerica, **48**
Receptacle, of bryophytes, **38**, 45
nature of, 29
of pteridophytes, **321**, **327**, **336**, 341, **342**, **350**, **364**, **367**
Regnellidium, 360
Rhizocarpae, 303
Rhizoid, **19**, **30**, **48**, **52**, **53**, 127, **128**, **161**, **259**, 290, **300**, **309**, **342**, **353**, **359**, **371**
Rhizoidal cell, 192
Rhizome, **79**, **161**, **163**, **166**, 168, 177, **247**, 252, **324**, **333**, **348**, **361**
Rhizophore, 195, 196, **197**, **208**, **212**, **218**, **222**, 223, **224**
nature of, 199
structure of, 226
Rhizosperma, 379
Rhopalostachya, 184
Rhynia, **160–163**, 167
gwynne-vaughani, **162**
major, **161**
Rhyniaceae, **160–163**
Riccardia, 61, 62, **63–67**, 299
pinguis, **63**, 64, **65**, **66**
thaxteri, 63
Riccia, 14, 17, **29–37**, 51
bischoffi, 32
curtisii, 32, 36
glauca, **30**, **31**, **33**, **34**, **36**
trichocarpa, **30**
Ricciaceae, 17, **29–37**
primitiveness of, **28**
Riella, 14, 18, **25–27**
affinis, 26, **27**
americana, 25, **26**
Riellaceae, **25–27**
Ring cell, first, **343**, 353, **354**
second, **343**, 353, **354**
Root hair, 188
Root trace, **224**, **278**, **285**, **297**, **345**
Roots, adventitious, 188, 244, 263, 296, 306, 314, 321, 332, **340**, 345, 349, **357**, 358, 361, **373**
diarch, 278
monarch, 334
origin of, 267
primary, 194, 231, **232**, **261**, **293**, **301**, 310, 337, 344, **356**, **371**, **381**
initial of, **232**, 318, 323, 355, **356**, 371, 381
structure of, **188–189**, 199, 226, **227**, **245**, **256–257**, 286, 296, **314**, **315**, 334, 358, **373–375**

S

Salvinia, 372
Salviniaceae, 303, **372–381**
relationships of, **266**
Salviniales, 303, **371–381**
relationships of, 372
Scales, **30**, **41**, **48**, **52**, **53**
Scapina nemorosa, **73**
Schiffneria, 74
hyalina, **73**
Schizaea, 145, **312–318**, 358
bifida, **316**
dichotoma, 313
elegans, **313**
molucceana, **314**
pusilla, 312, **313**, **316**, **317**
rupestris, 312, **316**
Schizaeaceae, 304, **312–318**
relationships of, **266**
Sclerenchyma, **170**
Secretory zone, **213**
Seftenbergia, 312
Selaginella, 145, 155, 180, 186, 187, **196–209**, 210, 211, 214, 215, 221, 226
kraussiana, 197, **198**, 202, **204**, 205, **206**
martensii, 207, **208**
oregana, **201**
wallichii, 199
wildenovii, 197
Selaginellaceae, **196–209**
relationships of, **180**
Selaginellales, 181, **195–210**
relationships of, **180**
Selaginellites, 196
Seta, **24**, 25, **27**, **43**, **54**, **55**, **63**, **77**
Sex chromosomes, 20, 32, 49
Sexual dimorphism, **115–116**
Sheath, **200**
Sieve plate, 142
Sieve tube, 141, **142**, 254, 349
Sieve-tube segment, 142
Sigillaria, **212**, **220–221**

Sigillariaceae, **219–221**
relationships of, **180**
Sigillariostrobus, 220
Silicification, 254
Siphonostele, **143**, 213, 238, 241, 248, 254, 296, 340
amphiphloic, 146
ectophloic, 146
evolution of, **145**
nature of, 145
(*See also* Dictyostele; Solenostele)
Solenostele, **330**
amphiphloic, **143**, **326**, **362**
ectophloic, **143**, 313, **314**
lycopsidan, **145**
nature of, 147
polycyclic, **143**
pteropsidan, **145**
Sorophore, 366, **367**
nature of, 366
Sorus, gradate, 304, 335, **336**, 341, **342**, 363, **364**
nature of, 303
mixed, 304, 346, **350**
nature of, 303
simple, 304, 307, **316**, 321, **326**, 329, **330**
nature of, 303
Sphaerocarpaceae, **18–25**
Sphaerocarpales, 11, **18–27**
relationships of, **10**
Sphaerocarpos, 18, **19–25**, 27, 33, 34
californicus, **19**
cristatus, 19, **20**, **22**, **24**, 25
donnellii, 19, **21**, 25
Sphagnaceae, **97–104**
Sphagnales, **97–104**
Sphagnobrya, **96–104**
nature of, 96
relationships of, **10**
Sphagnum, **97–104**, 106, 107, 127
cymbifolium, **104**
recurvum, **98**
subsecundum, **99**, **101**, **103**
Sphenophyllales, **242–246**
relationships of, **240**
Sphenophyllum, 137, **242–246**
cuneifolium, **243**
dawsonii, **246**
emarginatum, **243**
majus, **243**
plurifoliatum, **244**
Sphenopsida, as division, 2
as subdivision, 2
Splachnum, 127
ovatum, **126**, **128**
Spongy tissue, **350**
Sporangiogenic band, **287**, **288**
Sporangiophore, **169**, 172, **173**, **241**, 242, 245, **246**, **250**, **258**
development of, **173**
evolution of, **138**, **139**
nature of, 237
primitive, **241**
Sporangium, 153
eusporangiate type, **163**, **165**, 168, 172, **173**, **190**, **241**, 246, **250**, **271**, **273**, 274, **277–279**
dehiscence of, 165, 168, 198, 283, 288, 299
development of, **173**, **190–191**, **258**
nature of, 269
leptosporangiate type, 302, **316–317**, 321, **327**, **330**, 336, **342**, 345, **350**
dehiscence of, **308**, 322
development of, **307**, **308**, **316–317**, **321**, 329, **336**, 341, **342**, **351**, 358, **363–365**, **376–378**
nature of, 269
Spore sac, inner, **121**, **122**
outer, **121**, **122**
Spores, **24**, 25, **36**, **55**, **66**, **77**, **82**, **106**, **258**
germination of, 25, 37, 61, 107, **126**, 192, 299, 308, 329, 336, **337**, 342, 352, 359
liberation of, 37
longevity of, 103, 264, 352
number of, 56, 299, 307, 317, 329, 341, 346, 352
Sporocarp, 303, 362
dehiscence of, **366–367**
development of, **363–365**, **375–379**
macrosporangial, **376**, **380**
microsporangial, **378**
nature of, 303
structure of, **363**, **376**, **378**
wall structure, **364**, **376**, **378**
Sporocyte, 24, **27**, **35**, 36, 38, 46, 56, 61, 107, 203
Sporogenous cells, **24**, 173, **174**, **288**
primary, **66**, 307, **308**, **316**, 317
Sporogenous layer, primary, 92, **93**
Sporogenous tissue, **24**, **35**, 38, **39**, **54**, **66**, 107, **191**, **202**, 257
Sporophyll, **183**, **190**, **222**
evolution of, **138–139**
(*See also* Macrosporophyll; Microsporophyll)
Sporophyte, of bryophytes, **24–25**, **27**, **34–39**, **43–46**, **53–56**, **60–61**, **66–67**, **69–70**, **77–78**, **81**, **91–95**, **102–104**, **106–107**, **109**, **119–126**
nutrition of, 55, 94, 107, 119

Sporophyte, of pteridophytes, **160–168, 182–191, 209–215, 217–229, 241–258, 271–278, 282–289, 295–297, 304–308, 312–317, 319–322, 325–329, 332–335, 338–342, 346–347, 347–352, 358–359, 361–366, 372–379**
Stalk, **20**
Stalk cell, **343**
primary, **20**, 58, **80**, 81, 90
Stauropteris, **274**
Stelar theory, **142–149**
Stele, **142–147**
diarch, 188, **189, 286**, 306
nature of, 188
hexarch, 256
monarch, nature of, 188
polyarch, **298**
polycyclic, 147, **325**
tetrarch, **256**
triarch, 188, 256, 306
nature of, 188
tricyclic, **325**
(*See also* Actinostele; Dictyostele; Haplostele; Monostele; Plectostele; Polystele; Siphonostele; Solenostele)
Stem, of bryophytes, **72, 73**, 75, **76**, 98, **105, 109**, 110, **116**
initial of, **71**
structure of, **99, 111, 112**
of pteridophytes, **195, 208, 261**
embryonic, **293**, 301, 310, 338, 344, **356, 371**
initial of, 318, 323, 355, **356**, 371, **381**
hypocotyledonary, 209
initial of, **232**
structure of, **162, 167, 170, 171, 186–188, 197–199, 210–214, 219–226, 242–245, 247–249, 251–256, 273, 275–276, 278, 283–284, 296, 304–306, 313, 314, 320–321, 325–329, 332–334, 338–340, 345, 347–349, 358, 373, 374**
Stereids, 112
Sterilization, progressive, 10, 17
Stigeosporium marattiaceum, 285, 296
Stigmaria, 210
Stigmarian root system, 211
Stigmarian rootlets, 211
Stoma, 92, **162, 170, 171, 287**
Stomium, 191, 346, **351**
Strobilus, **190, 201, 219**, 220, 237, 245, **250**, 257, **258**
Suspensor, 194, **195**, 207, **208**
Svalbardia, 280
Symphyogyna, **61**
Synangium, 172, **173, 279, 299**
development of, **298–299**
nature of, 298

T

Tapetum, **191, 202**, 203, **228**, 257, **288, 316**, 341, **351, 376, 384**
formation of, 203, 307, **308**
initials of, 316, 321, **351**, 364
nature of, 191
Targionia, **40–44**
hypophylla, **40–43**
Targioniaceae, **40–44**
Telome, **136–138**
nature of, 136
Telome theory, **135–138**
Telome truss, **136–138**
nature of, 136
Tentacle, **209**
Tetraphis, 127
Thrysipteris, 344
Thurstophyton, 137
Tmesipteris, 160, 168, 173
tannensis, 168, **169, 171**, 172, **174, 175, 177**
Todea, 304
Trabecula, of sporangium, 215, **228**
of stem, 197, **198**
Tracheids, **139–141**, 161, 165
annular, **140**
pitted, 244
reticulate, 225, 284
scalariform, **140**, 141, 241, 248, 254
spiral, **140**, 225
Tracheophyta, 2
Treubia, 61, 62
Trichomanes, 331, 332, 335
bilabiatum, **337**
reniforme, 337

U

Urostachya, 184, 186

V

Velum, **209**, 227, **228**
development of, **228**
nature of, 227
Venter, **22**, 23, **53**
initials of, **22**, 23, 59
Venter canal cell, **22**, 23, 60, **91, 101**, 102, **118**, 207, 231, 260, **292**, 354, 370
Venter cell, primary, 90, **91, 101, 118**, 176, 193, 207, 260, **292**, 354, 355, 370
Vessel, 141

W

Water conduction, 72
Water sac, **73**, 74
Wood ray, **213**, 214, **244**

X

Xylem, **139–141**, 161, **167, 219, 278, 285, 314, 315, 326**
primary, 210, **213, 224**, 241, 243, **244, 245**, 275
Xylem, secondary, 142, 170, **213**, 243, **244, 245**, 248, **249**, 275
dimorphic, 243, **244**
(*See also* Metaxylem; Protoxylem)
Xylem parenchyma, 244

Z

Zosterophyllaceae, **165**
Zosterophyllum, 139, **165**
myretonianum, **165**
Zygopteridaceae, **275–276**
Zygopteris, **275–276**
primaria, 275, **276**