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Introduction

Extant ferns comprise a group of about 12 000 species of plants widely distributed throughout the world in many habitats and niches. As wide as their distribution is their range in size, with extremes such as the small water ferns with leaves less than 1 cm long and the giant tree ferns which attain heights of almost 25 m and bear crowns of leaves 30 cm or more in diameter. In many contemporary systems of classification with which developmental botanists will feel comfortable, ferns are assigned to the group Pteropsida or Filicopsida. Members of this group along with those of Psilopsida, Lycopsidea and Sphenopsida constitute a major division of the plant kingdom known as Pteridophyta (pteridophytes). A distinctive anatomical feature of pteridophytes, which they share with gymnosperms and angiosperms, is the presence of a vascular system in the plant body, but pteridophytes differ from the latter two divisions in lacking the seed habit (hence the name, seedless vascular plants, for the division). During their evolutionary past, pteridophytes have stabilized and almost perfected the vascular system for a seedless plant so much so that they are also designated as vascular cryptogams. Most pteridophytes, including ferns, are trapped into a life cycle in which they are constrained by some primitive features such as the production of motile sperm and the requirement for free water for fertilization.

The life cycle of a fern, like that of other sexually reproducing plants, involves an alternation between a sporophytic and a gametophytic generation. Both the sporophyte and gametophyte are free-living multicellular plants, the former representing the asexual and the latter the sexual phase. The macroscopic fern plant is a sporophyte with a diploid number of chromosomes in each cell. It has its origin in the zygote, the product of fertilization of the egg by a sperm. The sporophyte possesses an underground stem or rhizome from which leaves and adventitious roots are produced at regular intervals. The most prominent feature of the sporophyte is its leaf, which is known as the frond, both in science and in common parlance. Ferns are unique among vascular cryptogams in possessing large leaves or megaphylls. The hallmarks of a megaphyll are its branched venation system and the frequent association of the leaf trace

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with one or more leaf gaps in the vascular cylinder of the stem. The fern frond may be a simple expanded lamina with a petiole or stipe or, more commonly, the lamina is cut up into leaflets or pinnae to give it the appearance of a compound leaf. Owing to the absence of an expanded blade on the pinnate leaf, the petiole continues as the main axis or rachis of the frond bearing the pinnae. In most ferns, the meristematic young leaves are rolled into tight spirals (fiddleheads) in a bud typifying circinate vernation. Coiling of the young leaf and its subsequent unwinding result from differential growth on its upper and lower surfaces and are mediated by changes in the concentration of endogenous auxin. The external morphological features of the typical fern leaf are not seen in the leaves of water ferns, which are in a class by themselves.

The reproductive structure of the sporophyte is the sporangium, which is a multicellular container for the spores. The fruiting dots on the margins and undersurfaces of fern leaves are indeed familiar to the casual observer; each dot represents a cluster of sporangia called the sorus, which is usually overlaid by a protective covering, the indusium. However, the sporangia are not restricted to leaves. In some ferns, they occur on highly differentiated leaf-like structures whose only function is to bear sporangia; in still others, some leaves become differentiated into sporangia, while the rest remain green and photosynthetic.

The young sporangium is filled with sporogenous cells which give rise to sporocytes (spore mother cells). The most fundamental process initiating the gametophytic generation occurs in the sporangium by meiosis in the sporocytes, yielding spores with the haploid or gametic number of chromosomes. From the moment it is liberated from the restraining wall of the tetrad, the spore generates new levels of organizational complexity as it prepares for sexual recombination by way of formation of a multicellular gametophyte, sex organs and gametes. Genetic information is decoded and utilized as the spore unfolds its developmental program. Thus, a spore born out of reduction division of the sporocyte is the single-celled progenitor of the gametophyte and all essential properties of interactions occurring in the adult gametophyte emanate from the information pool of this cell. (The word 'gametophyte' is used in this book loosely to designate any stage of the haploid generation, although, strictly speaking, it means a gamete-producing plant.)

This book is about how the spore achieves the basic body plan of the gametophyte, how the gametophyte grows and reproduces and, finally, how it is set on track to initiate the sporophytic phase. The objective is to provide an account of those aspects of the developmental biology of the gametophyte, beginning with the single-celled spore, that impinge on the morphological, cytological, physiological, biochemical and molecular

changes in the cell population. It is important to realize that the progressive evolution of form and function of the gametophyte is specified by a series of developmental decisions. To understand how the spore discharges its genetically determined functions through the developmental landscape requires a study of the mechanism of these decisions.

For convenience, the book is divided into four parts. Chapters 2 to 5 deal with the structure, cytology and physiology of spores and their germination. The primary thrust of the discussion in these chapters is on the changing biochemical potential of the spore from a dormant cell to one undergoing metabolic fluxes as it germinates to form cells destined for different fates and functions. The next four chapters (Chapters 6 to 9) review the mechanisms of growth of the protonema initial of the germinated spore. This includes its growth as a filamentous structure, attainment of planar morphology and growth of the planar gametophyte. Chapters 10 and 11 ask what sort of mechanisms have evolved to account for the induction of sexuality in the gametophytes and to preserve genetic diversity in the population. The third chapter of this part (Chapter 12) examines the cellular and subcellular aspects of gametogenesis and the events leading to fertilization and initiation of the sporophytic phase. In the final part of the book, two chapters (Chapters 13 and 14) examine the alternative developmental programs of the sporophyte and gametophyte, resulting, respectively, in the formation of the gametophyte without meiosis and sporophyte in the absence of fertilization. Most of the information that is presented in the various chapters concerns ferns, which is as it should be in a book whose title specifies this group of plants. The excuse for occasional references to works on pteridophytes other than ferns is that they are of historical importance in a particular context or that they illuminate the concepts under discussion further.

Classification of ferns and other pteridophytes

There is a great diversity of opinion on the taxonomic arrangement of pteridophytes, especially of the ferns. Since 1940, more than 10 separate schemes or modifications of existing schemes of classification of ferns have been proposed and even to this day there is no consensus on the phylogenetic position of certain genera and families which have provoked severe disagreement in the past. Although the subject matter of this book is not even remotely connected to phylogeny, it is important that the genera discussed be identified in a phylogenetic framework to reflect relationships. In reviewing the different schemes of classification of ferns and other pteridophytes, I have found that the one proposed by Crabbe, Jermy and Mickel (1975) has incorporated many features that make it useful to the systematic pteridologist as well as to the developmental

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botanist. These investigators have divided the pteridophyte genera into seven assemblages, identifying families and subfamilies within each assemblage, as follows (subfamilies omitted here):

1. Fern allies (includes Psilopsida, Lycopsida and Sphenopsida)
 - Lycopodiaceae
 - Selaginellaceae
 - Isoetaceae
 - Equisetaceae
2. Eusporangiate ferns and Plagiogyriaceae
 - Ophioglossaceae
 - Marattiaceae
 - Osmundaceae
 - Plagiogyriaceae
3. Schizaeoid ferns to adiantoid ferns
 - Schizaeaceae
 - Parkeriaceae
 - Platyzomataceae
 - Adiantaceae
4. Filmy ferns and related groups
 - Loxosomaceae
 - Hymenophyllaceae
 - Hymenophyllopsidaceae
5. Gleichenioid ferns to polypodioids and grammatid ferns, by way of *Matonia*, *Cheiropleuria* and *Dipteris*
 - Stromatopteridaceae
 - Gleicheniaceae
 - Matoniaceae
 - Cheiropleuriaceae
 - Dipteridaceae
 - Polypodiaceae
 - Grammitidaceae
6. Protocyatheoid and cyatheoid ferns to dennstaedtioid, to thelypterid, to asplenioid ferns, the 'Aspidiales' and the blechnoid ferns
 - Metaxyaceae
 - Lophosoriaceae
 - Cyatheaceae
 - Thyrsopteridaceae
 - Dennstaedtiaceae
 - Thelypteridaceae
 - Aspleniaceae
 - Davalliaceae
 - Blechnaceae
7. Hydropterides (water ferns)
 - Marsileaceae

Salviniaceae

Azollaceae

In an older classification scheme of extant ferns proposed by Bower (1923–28), the genera of Osmundaceae, Plagiogyriaceae and of assemblages 3 to 7 delimited by Crabbe *et al.* (1975) were incorporated into an order known as Filicales. Basic families recognized in this order are Osmundaceae, Schizaeaceae, Gleicheniaceae, Matoniaceae, Hymenophyllaceae, Loxosomaceae, Dicksoniaceae, Plagiogyriaceae, Protocyatheaceae, Cyatheaceae, Dipteridaceae, Polypodiaceae, Marsileaceae, and Salviniaceae. Later, Copeland (1947) introduced a system of classification in which several natural families were carved out of Bower's Polypodiaceae. The order Filicales proposed by Copeland includes Osmundaceae, Schizaeaceae, Gleicheniaceae, Loxosomaceae, Hymenophyllaceae, Pteridaceae, Parkeriaceae, Hymenophyllopsidaceae, Davalliaceae, Plagiogyriaceae, Cyatheaceae, Aspidiaceae, Blechnaceae, Aspleniaceae, Matoniaceae, Polypodiaceae, Vittariaceae, Marsileaceae, and Salviniaceae. Occasional references made in this book to filicalean ferns are to Filicales of Copeland's classification.

The following convention is adopted in the book in respect to plant names. With rare exceptions, plants have been identified only by their scientific names, even though a common or a vernacular name might exist. The first occasion a genus or species is mentioned in the book, its familial position in the classification of Crabbe *et al.* (1975) is indicated in parenthesis. In all instances, in the text as well as in the tables, binomials as used by the original author are given, even though they are not recognized now as the valid names; in such cases, the genus or species in which it is felt that a particular plant belongs, preceded by the sign =, is given in parenthesis. It is safe to say that, for a period of time, a lack of consensus on the phylogenetic position of certain families and genera of ferns was matched to an equal degree by ambiguity about the generic and specific status of some ferns. Fortunately, recent morphological, cytological, and taxonomic studies have helped to bring a much-needed order in the matter of identification of ferns, although a lot more remains to be done. As mentioned earlier, controversy about the phylogeny of ferns continues with no end in sight.

Cambridge University Press
0521017254 - Developmental Biology of Fern Gametophytes
V. Raghavan
Excerpt
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Part I

The beginning

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The spore – beginning of the gametophytic phase

It was noted in the introductory chapter that, in ferns, the genesis of a spore marks the beginning of the developmental process that produces a gametophyte. From the standpoint of understanding the evolution of the gametophyte in multicellularity, sexuality and functional competence, an understanding of the formation of the spore and of its structure is important. Therefore, in this chapter we focus on sporogenesis in ferns and on the normal course of morphogenesis of the spore to attain maturity. For the most part we will be concerned with description of events, with little emphasis on the underlying mechanisms. As we shall see later, some features of sporogenesis are surprisingly similar across the entire group of ferns, although the final products generated vary somewhat in their morphology.

Sporogenesis

Existing evidence suggests that the types of spores produced by ferns are of great significance in the evolution of the group. Although evolutionary considerations are not emphasized in this book, we shall nonetheless begin this part with an account of the two major spore types found in ferns.

Homosporous and heterosporous

One of the most important concepts generated from studies on sporogenesis in ferns is the recognition of homosporous and heterosporous plants (Fig. 2.1). Homosporous types produce only one kind of sporangium and just one kind of spore, as is characteristic of the vast majority of extant ferns. Exosporic gametophytes, that is, gametophytes that are free-living and not restricted within a spore wall, are common to homosporous ferns. In contrast, some ferns generate two kinds of sporangia and two kinds of spores, the large megaspores, produced in the megasporangium giving rise to female gametophytes, and the small microspores, encased in the microsporangium, yielding male types. This

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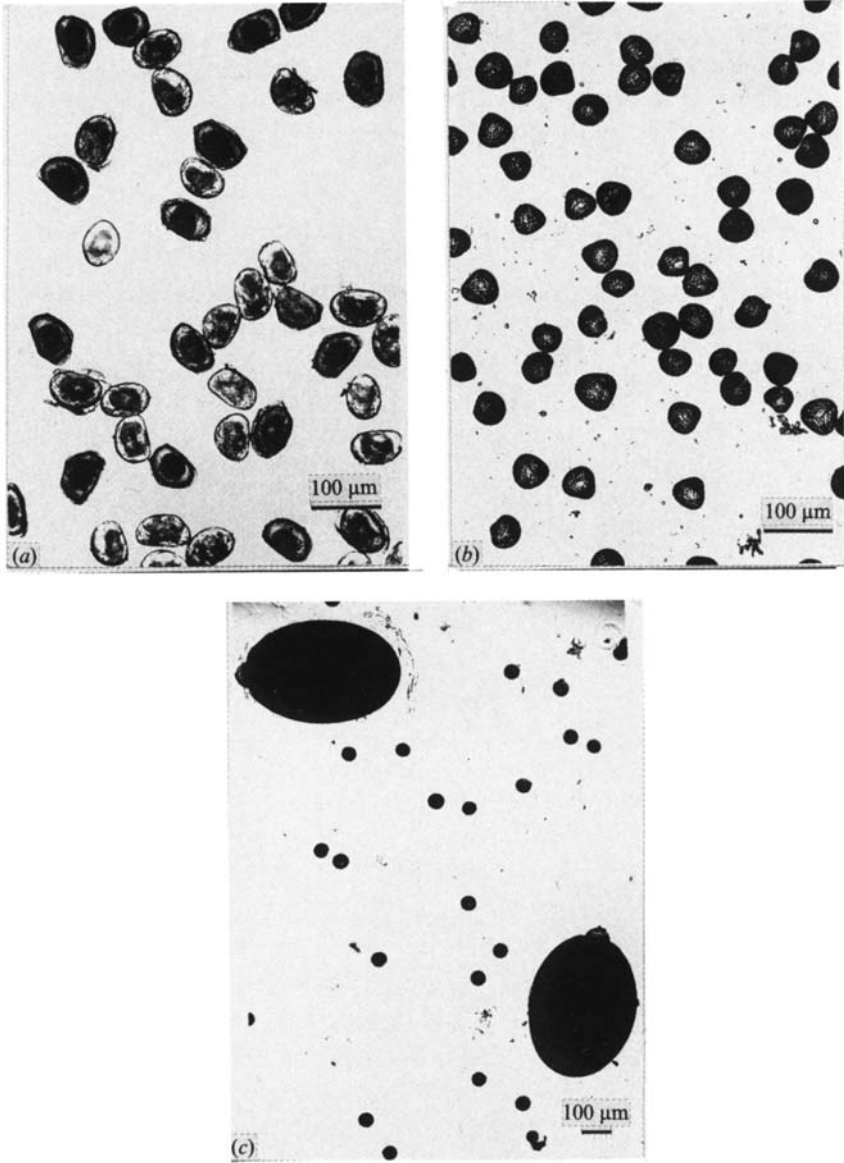


Figure 2.1. Whole mounts of spores of homosporous and heterosporous ferns. (a) *Onoclea sensibilis*. (b) *Ceratopteris thalictroides*. (c) *Marsilea vestita*. In c the small dark structures are microspores and the large ones are megaspores.

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is the heterosporous condition, well known in Marsileaceae, Azollaceae and Salviniaceae, among ferns and in Selaginellaceae and Isoetaceae, among other pteridophytes. Both macro- and microgametophytes are nonphotosynthetic and, being enclosed within the original spore wall for the most part of their life, are endosporic. A unique situation, characterized as ‘incipient heterospory’, is encountered in *Platyzoma microphyllum* (Platyzomataceae), which produces a limited number of small and large spores in morphologically different types of sporangia. The small spores are committed to maleness and the large spores yield females which subsequently turn bisexual. The deviations from typical heterospory are concerned with the photosynthetic and exosporic nature of gametophytes of both kinds (Tryon, 1964).

It is generally assumed that plants that produce spores of two kinds with different potentials are better adapted to a terrestrial existence than those that produce a single type of spore. Accordingly, heterospory has been interpreted as a major landmark in the evolution of vascular plants. From our perspective, an important question is: what causes heterospory? It is to be emphasized here that, while heterospory is often reflected in size differences in spores, it is actually defined on the basis of the sexual function of spores. In a thoughtful essay, Sussex (1966) has argued that spore dualism is an expression of the sex-determining process of the plant. This argument relegates the great majority of homosporous ferns to a group in which sex determination is delayed until spore germination and gametophyte development. In contrast, in heterosporous ferns sex determination is thought to occur somewhat early, at a specific stage in the sporophytic phase of the life cycle. On the whole, it appears from this that the strategy of ferns is one of flexibility, probably depending upon the selective activation and repression of genes concerned with the functioning of sex determinants.

Sporangial structure and ontogeny in homosporous ferns

Studies on sporogenesis in homosporous ferns have emphasized evolutionary comparisons and the number of initial cells that go into the formation of the sporangium. Typically, a mature fern sporangium is borne on a definite stalk and contains one or more spores enclosed within a protective wall. The wall becomes multilayered and massive, as in members of Ophioglossaceae and Marattiaceae, or is reduced to a single layer of cells, as in most filiclean ferns. The development of the wall has been widely studied as an adaptation for dehiscence of the sporangium. Undoubtedly, the most specialized and familiar dehiscence mechanism of the sporangium of many filiclean ferns is one implemented by a special layer of unevenly thick-walled cells, known as the annulus, and a few

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thin-walled cells constituting the stomium. On the other hand, in *Angiopteris* (Marattiaceae), an annulus as such is absent and the dehiscence mechanism of the sporangium is made up of a band of enlarged lignified cells. In most homosporous ferns, the sporangial wall is separated from the sporogenous tissue by one or two layers of thin-walled, densely cytoplasmic cells known as the tapetum. This is a short-lived tissue whose cells break down before or just after meiosis in the sporocytes. Despite the scanty evidence, it is widely presumed that the cytoplasm of tapetal cells is appropriated as nourishment by the developing sporocytes and spores (Bierhorst, 1971).

Ontogeny of the sporangium. Typically, as seen in *Phlebodium aureum* (Polypodiaceae), sporangial development is initiated by an oblique division of a single superficial initial cell (Wilson, 1958). The inner of the two cells formed is subsequently partitioned transversely to separate a basal cell from an upper pair of cells constituting the sporangium primordium. The basal cell virtually remains undivided as the sporangium is fabricated from the primordium. Three oblique divisions ensue in quick succession in the outer cell of the sporangium primordium to form a tetrahedral mother cell surrounded by three cells. These latter cells by further divisions contribute to the wall of the sporangium and part of the subtending stalk. The other part of the stalk is generated by divisions of the inner cell of the sporangium primordium. A critical stage in the development of the sporangium is the occurrence of one transverse and three oblique divisions, in that order, in the tetrahedral cell. The result is the formation of a central cell enclosed by four cells which separate it from the sporangial wall. Each of these four cells divides by anticlinal and periclinal walls to produce a two-layered tapetum. Concomitantly, the central cell divides in various planes to form the sporogenous tissue which in turn yields sporocytes.

As far as is known, details of the major division sequences leading to the establishment of the sporangium are very similar in the various genera of homosporous ferns, but the origin of the sporangium itself has been a point of contention. This has given rise to a widely accepted division of extant ferns into two unequal groups. In the smaller of the two groups, known as the eusporangiate type, the sporangium originates from several initial cells. Other characteristics which go with the eusporangiate ferns are the relatively large size of the sporangium, production of numerous spores and the development of a several-layered wall. In the second group, known as the leptosporangiate type, the sporangium arises from a single parent cell or initial cell and has a wall composed of but a single layer of cells. The number of spores produced per sporangium is also limited and is usually a multiple of two. The most common configuration is one in which a group of 16 sporocytes yield, by meiosis, a total of 64