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GAMETOPHYTES OF HOMOSPOROUS FERNS

B. K. NAYAR[1] AND S. KAUR[2]

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[1] Professor and Head of the Department of Botany, University of Calicut, Kerala (India).

[2] National Botanic Gardens, Lucknow (India).

INTRODUCTION

The pteridophytes have attracted the attention of botanists perhaps more than any other group of plants. This is mainly on account of the central position they occupy in the evolutionary history of the vegetable kingdom. Nevertheless they still remain one of the most controversial with respect to taxonomy and phylogeny. This is particularly so of the major group of pteridophytes, the ferns. This state of affairs is scarcely surprising when we consider that several major aspects of morphology and life history of most of the ferns are still little known, and that the ferns as a class do not offer any compact complex of characters (comparable for example to floral morphology in Angiosperms) with which to assess relationships and interpret evolutionary progression. The search for a suitable complex of characters in this group is still progressing, and in this endeavor attempts are continuously being made to find new comparative criteria.

Until recently (or perhaps even today) students of pteridophyte taxonomy and evolution were concerned only with the morphology of the sporophyte, the sporophyte being by far the dominant phase in the life history. The gametophyte of ferns has always been a neglected generation, ignored by morphologists and taxonomists alike. Even in the present century which has witnessed a tremendous upsurge in the study of morphology and taxonomy of the ferns, the gametophytic generation has scarcely been looked upon as one worth serious consideration. Perhaps the unencouraging appraisal of the fern gametophyte by the greatest fern morphologist of the present century, Prof. F. O. Bower, discouraged attempts to use characters of the gametophyte in comparative studies. Bower, though acknowledging that gametophytes of the vast majority of ferns were unknown in his times and those of most of the others only imperfectly known, dismissed the gametophyte as morphologically unstable and thus undependable for use "in comparison with a view to classification of the ferns." He concluded "that its vegetative characters are deficient in stability and in variety of detail and consequently . . . of minor importance for phyletic comparison" (Bower, 1923: 296). Though a wealth of information on the fern gametophyte has become available in the literature since Bower's days, no fern taxonomist has so far cared to re-examine the case of the fern gametophyte as an aid to comparative studies or paid much heed to the gametophyte. One reason for this lack of interest on the part of taxonomists could be that information on the gametophytes is too scattered in literature. Even as recently as 1949 the shadow of Bower's remarks could be detected in the assessment of the fern gametophyte by Prof. R. E. Holttum. Speaking of the gametophyte as an aid to taxonomy, he remarked: "Little has yet been published on the comparative morphology of the majority of ferns. There must be at least a considerable specialization to different habitats. In such a simple organism, such specialization may overshadow distinctive features that might indicate evolutionary lines." However, soon afterwards, Alma G. Stokey (1951), after a lifetime of work on fern gametophytes, most effectively presented a classical account dealing with the contribution of gametophyte morphology to the classification of the ferns. She proved beyond doubt that the fern gametophyte, though simple in structure when compared to the sporophyte, affords dependable criteria for taxonomic and phyletic studies. In the past 20 years since this publication, a vast amount of information has been added to our knowledge of the gametophytes of the ferns, more especially of the various groups of the advanced ferns, most of which were practically unknown to Stokey. This additional information serves materially to substantiate Stokey's conviction in the significance of gametophyte morphology for an understanding of the evolution and phylogeny of the ferns and in the characterization of the major taxonomic groups.

Despite the neglect it has suffered, the study of gametophyte morphology of ferns has a long history. As far back as 1561, Cordus noted that all ferns reproduced by means of "pulviuscules" borne on the lower surface of their fronds. Subsequently to the development of the microscope in the second half of the 17th Century, observations on the spores of ferns began to be recorded. The pioneers in the field are perhaps Grew (1672) and Malpighi (1675). The detailed structure of the fern spore was perhaps first noticed by Bischoff (1828), who pointed out that spores, unlike seeds, did not contain any part of the future plant. The credit of making the fern spore germinate goes to Morison (1699). The raising of ferns by germinating the spores was achieved nearly a century later by Lindsay (1794). Lindsay was the first to give a detailed account of spore germination in a fern; the first detailed description of prothallial development of a fern is given by Kaulfuss (1827). Fée (1852) was the first pteridologist to introduce characters of the spore as a criterion in the taxonomy and classification of ferns. Sachs (1868) for the first time classified pteridophytes according to the type of spores they possess (into homosporous and heterosporous pteridophytes), and soon afterwards Caruel (1881) elaborated on this scheme. Nearly all classifications to follow used this character of the spores. By the latter half of the 18th Century the fern gametophyte was well understood. The common, cordate, prostrate prothallus of the leptosporangiate ferns was described in detail by Kny (1869), the asymmetrical thallus of anemiaceous ferns by Burk (1875a, b) and Bauke (1878a, b), the ribbon-like thallus of the Hymenophyllaceae by Mettenius (1864) and deBary (1878), and the prothalli of several genera of ferns by Goebel (1877, 1887, 1888, 1898, 1912) and Campbell (1885, 1887, 1892, 1894, 1895, 1905, 1908, 1909, 1911, 1914, 1921, 1922). Several detailed accounts of fern gametophytes were published early in this century (Heim, 1896; Lampa, 1901; Britton & Taylor, 1902; Thomas, 1902; Twiss, 1910; Schlumberger, 1911; Waldemann, 1928). By far the largest contribution to the study of the gametophytic generation of ferns in later years has been that of Stokey.

THE FERN PROTHALLUS

The fern gametophyte is an autotrophic, free-growing entity with a definite form, pattern of growth, structure, and mode of reproduction. It is a prolonged phase in the life history of a fern, but is generally not a dominant one. The gametophytic generation starts with formation of spores in the fern sporangium; the spores germinate to form prothalli, which produce sex organs in which by union of gametes the second generation of sporophyte is initiated. Although the spore is the first phase of the gametophyte, the term gametophyte is commonly used in fern morphology to mean only the prothallus. (Study of spore morphology is a specialized and vast subject in itself. Spore morphology is, therefore, practically omitted from the present discussion.) Compared to the sporophyte, the fern prothallus is a relatively simple entity, very much smaller, thalloid, and undifferentiated into specialized organs. Also it has generally a shorter life span. In fact, few fern prothalli are perennial, the large majority being seasonal plants in contrast to the perennial sporophytes. Perennial prothalli are characteristic of the comparatively primitive groups of ferns like the Ophioglossidae and Marattiidae,[1] and there is a distinct shortening of the life span of the prothallus as we progress from the more primitive to the advanced groups. However, a tendency to have perennial prothalli is found in certain lines of evolution of the more advanced groups of ferns also, as in some of the Polypodiaceae (*Colysis*, *Kaulinia*, *Leptochilus*, etc.). More commonly the prothallus of the advanced ferns completes its life cycle in four to eight months, some of the fast-growing types like *Davallia*, *Pityrogramma*, and *Onychium* requiring only 60 to 90 days to attain full growth, and *Ceratopteris* requiring only 40 to 50 days. Some of the perennial ones, on the other hand, may grow for 10 to 15 years or more.

Ecologically, both the sporophyte and the gametophyte have nearly the same requirements, but being of a simpler organization and devoid of elaborate protectory devices, the gametophyte is more susceptible to lack of humidity in the substratum and in the atmosphere. Also, for sexual reproduction the fern prothallus is totally dependent on the avail-

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[1] The classification of ferns followed here is after Nayar (1970, 1971).

ability of free water. Morphologically the gametophyte has generally nothing in common with the sporophyte, its form, pattern of development, and structure being entirely different. However, like the sporophyte, it is often capable of indefinite vegetative propagation. In most cases it is by regeneration of fresh prothalli from older ones, but in some cases organized methods of vegetative multiplication (by means of gemmae, etc.) occur. It was long assumed by pteridologists that the fern prothallus is morphologically too plastic, to the extent that its morphology varies according to the ecological conditions under which it grows. Though unfavorable growing conditions variously affect the prothalli, the salient morphological characteristics, such as the sequence of cell divisions at spore germination, the sequence of developmental stages, the type of development, the gross form and structure of the adult thallus, the nature of trichomes borne on the thallus, and the morphology of sex organs, are little altered. The extent of such variation is not much wider than that exhibited by the sporophyte, so that it does not render the prothallus any less suitable for comparative studies as against the sporophyte.

SPORE GERMINATION

The fern spore, whether of the tetrahedral or bilateral type, is unicellular with a solitary, usually centrally placed nucleus surrounded by vacuolate cytoplasm in which are suspended chloroplastids or leucoplastids and food material, commonly in the form of oil globules. The protoplasmic contents are surrounded by a thin wall layer—the intine. A thick impervious outer layer, the exine (sometimes with an additional skin-like layer—the perine), forms a spore coat surrounding the intine. At the proximal pole of the spore (that end of the spore which faced the center of the spore-tetrad) the spore coat has a characteristic trilete or monolete aperture, a region where there is a fissure in the exine. In the majority of ferns the spores are shed from the sporangium in this one-celled condition and are capable of remaining dormant for some time. Rarely, as in *Christiopteris tricuspis* (Hk.) Christ (Nayar, 1967a), the spores are two- or three-celled at the time of shedding and may remain dormant at this stage for some period. In some ferns there is scarcely any dormant period, the spores germinating before they are shed (as in Hymenophyllaceae and Vittariaceae) or immediately on shedding (Osmundaceae). The homosporous ferns exhibit wide variations in the extent to which their spores retain viability. In some, like *Osmunda*, the viability is lost in a few days. However, several ferns are known to retain spore-viability for quite long periods. More commonly fern spores retain viability for two to three months, but the spores of some, such as *Onychium*, *Pityrogramma*, etc., remain viable for over a year. Several instances of long viability of fern spores are reported by Laage (1907), Hartt (1925), and Dopp (1927). Exceptionally long periods of viability (up to 20 years or more) are reported in some rare cases (Coleby & Druery, 1904; Anonymous, 1910; Fischer, 1911). Spores of *Plagiogyria* normally lose viability soon on storage but remain viable for several months when sown on a moist substratum (Stokey & Atkinson, 1956b; Nayar & Kazmi, 1962a, b).

For the fern spore to germinate there should be an adequate supply of moisture, a suitable temperature and pH range (pH 4-8), and availability of a sufficient light intensity of suitable quality. The various experimental aspects of germination were reviewed recently by Miller (1968) and so need not be repeated here. In most species the spores germinate soon after shedding, if suitable conditions are available. However, a definite dormancy period is reported in some species like *Alsophila australis* R. Br. (Life, 1907), *Notholaena* spp. (Hevly, 1963), and *Drymoglossum* spp. (Nayar, 1957). In the large majority of homosporous ferns, germination is preceded by swelling of the contents of spores by absorption of water; the intine expands, but the exine (which is practically inelastic, except rarely in some taxa) is pushed open at the laesura. However, in some genera of the Hymenophyllaceae the exine expands considerably as the spores swell. A series of cell divisions take place in a definite sequence resulting in the formation of the prothallus. The sequence of cell divisions and differentiation leading on to development of the characteristic adult form of the prothallus from the unicellular spore varies among the ferns. The uniformity exhibited by the different groups of genera in these respects has long been recognized. Commonly on germination the spore produces a primary rhizoid followed by an elongated uniseriate germ filament. Rarely, as in some of the more primitive ferns, a mass or a plate of cells is formed instead of a germ filament.

An attempt to classify the various known patterns of spore germination in homosporous ferns was made by Momose (1942). He described three types of spore germination: Centrifugal (thallus growing in a direction opposite to that of the primary rhizoid); Centripetal (thallus growing perpendicularly to the rhizoid, and rhizoid seated on the basal cell of the thallus); and Tangential (as in Centripetal, but rhizoid seated at the region of the cross wall between the basal cell and the cell next to it). Later, Nishida (1965) renamed the Centripetal and Tangential types as the Aspidioid- and Polypodioid- types respectively and added another, which he named the Tripolar-type, to accommodate the pattern described earlier by Atkinson & Stokey (1964) in the Hymenophyllaceae. He suggested that the Tangential type of germination is derived from the Tripolar-hymenophylloid pattern and the Centripetal type from the Tripolar-trichomanoid; the germination pattern found in *Ceratopteris* was cited as intermediate between the Tripolar-trichomanoid and the Centripetal types. Recently Nayar & Kaur (1968) pointed out that these interpretations of spore germination are incorrect inasmuch as they ignored the polarity of the germinating spore. Nayar & Kaur gave a detailed account of the patterns of spore germination, classifying them on the basis of the planes of cell division (in relation to the polarity of the spore) and directions of growth of the primary rhizoid and the prothallus. Thus, among

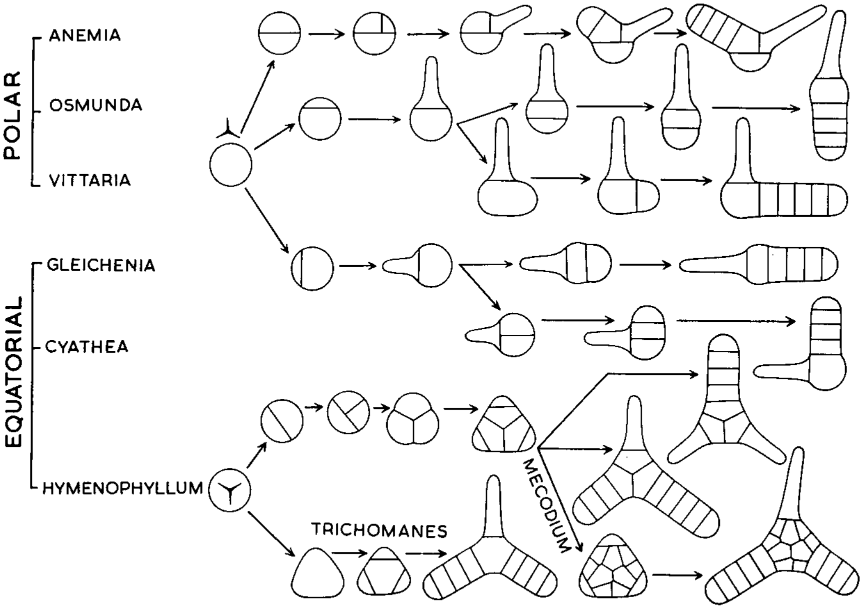


FIG. 1. Schematic representation of types of spore germination in homosporous ferns. [The triradiate mark in the drawing of spores on extreme left denotes the position of the proximal pole in all spores in that row. The arrows indicate successive steps in spore germination.]

homosporous ferns three distinct categories (Polar, Equatorial, and Amorphous) of germination are recognized. Three different types of Polar germination are described (Anemia-, Osmunda-, and Vittaria- types) and six of Equatorial germination (Cyathea-, Christiopteris-, Gleichenia-, Hymenophyllum-, Mecodium-, and Trichomanes- types), all differing in the plane and sequence of cell divisions. A diagrammatic representation of the different types of spore germination is given in Fig. 1. In all types of Polar germination the first cell division (sometimes a few succeeding ones also) in the germinating spore is by a wall formed parallel to the equatorial plane of the spore; elongation of primary rhizoid and young thallus is parallel to the polar axis of the spore. In contrast, the first cell division (sometimes also a few succeeding ones) is by a wall formed parallel to the polar axis of the spore, and elongation of the thallus is in a plane parallel to the equatorial plane of the spore in all types of Equatorial germination. Amorphous germination is rather rare (restricted to some of the more primitive groups of ferns such as Angiopteridaceae, Marattiaceae, Matoniaceae, *Actinostachys*, and *Lophidium* of Schizaeaceae, and possibly also Ophioglossaceae and *Stromatopteris* of Gleicheniaceae) and exhibits no polarity either with regard to cell divisions or direction of growth. This results in a mass or a plate of cells in which a meristematic cell is differentiated at a later stage in one of the peripheral marginal cells; further elongation of the thallus is in the direction of the meristematic cell.

The simplest type of Polar germination is the Osmunda-type, characteristic of the Osmundaceae. At germination a small rhizoid initial is cut off at the proximal pole of the spore by a wall perpendicular to the polar axis, and this elongates parallel to the polar axis to form the primary rhizoid. A uniseriate germ filament is formed by one or two (sometimes more) divisions by walls parallel to the first wall and elongation of the daughter cells. The germ filament elongates in the same plane as the rhizoid but facing in the opposite direction. In the Anemia-type of germination the first division of the spore is as in the Osmunda-type but results in two equal daughter cells of which the distal one remains quiescent throughout. The proximal one, by a wall perpendicular to the first wall, cuts off a lateral rhizoid initial from a larger prothallial initial. The latter divides by a series of walls parallel to the first wall and develops into a germ filament. The germ filament elongates parallel to the polar axis of the spore (facing the proximal pole) while the primary rhizoid elongates perpendicularly to it (parallel to the equatorial axis of the spore). The Anemia-type of germination occurs in the Anemiaceae and Lygodiaceae. By far the most common type of germination pattern is the Vittaria-type. As in the Osmunda-type, a rhizoid initial is cut off at the proximal pole by a wall perpendicular to the polar axis. The distal cell (prothallial initial) then divides by a wall perpendicular to the first wall into two equal daughter cells one of which remains quiescent and the other, by a series of divisions by walls parallel to the second wall, grows into a germ filament. The second division may occur before the prothallial initial expands laterally or after it has expanded; in the latter case the second wall does not intersect the first. The primary rhizoid elongates parallel to the polar axis, while the germ filament elongates perpendicularly to it (along the equatorial plane).

The simplest type of Equatorial germination is the Gleichenia-type, found in the Gleicheniaceae, Dipteridaceae, Loxogrammaceae, and many of the Polypodiaceae. At germination a rhizoid initial is cut off laterally by a wall parallel to the polar axis of the spore. A series of divisions in the prothallial initial cell by walls parallel to the first resuts in a uniseriate germ filament. Both the germ filament and primary rhizoid elongate along the equatorial plane of the spore in opposite directions. A variation of this is found in *Christiopteris* (Polypodiaceae). The germ filament may develop as in the typical Gleichenia-type, but often it remains short and sometimes even ends in a rhizoid. Secondary germ filaments are formed as branches from any one or more of the cells of the filament; the branches are perpendicular to the primary filament and thus parallel to the polar axis of the spore. In the Cyatheaceae, Loxsomaceae, and Cheiropleuriaceae a rhizoid initial is formed laterally as in the Gleichenia-type; but the second division (in the prothallial initial cell) is perpendicular to the first division, and subsequent divisions are parallel to it (i.e., parallel to the equatorial plane of the spore). Thus, in the Cyathea-type of spore germination the germ filament grows along the polar axis, while the primary rhizoid elongates along the equatorial plane (perpendicular to germ filament). The Equatorial germination in the Hymenophyllaceae is characteristic in that growth is basically tripolar. In the *Hymenophyllum*-group of genera (Hymenophyllum-type of germination) all cell divisions at spore germination are by walls parallel to the polar axis of the spore. The first two walls are perpendicular to each other and divide the spore into an equatorially expanded plate of three equal cells. In each of these cells a lens-shaped daughter cell is cut off towards the center of the lateral peripheral wall. Each lens-shaped cell may grow out either into a rhizoid or a germ filament; in the latter case a series of divisions occur by walls parallel to the last-formed wall. In the *Trichomanes*-group of genera (Trichomanes-type of germination) the first two divisions of the typical Hymenophyllum-type of germination are omitted (so that three lens-shaped cells are formed simultaneously at the periphery of the triangular spore cell towards the equatorial periphery). In the genus *Mecodium*, on the other hand, extra divisions occur in each of the three cells of the primary plate formed as in the typical Hymenophyllum-type. This results in a large, triangular, one-cell-thick plate of 9 to 12 cells expanded along the equatorial plane of the germinating spore. Three lens-shaped peripheral cells are cut off, one at each corner of the plate afterwards, and these develop as in *Hymenophyllum*.

PROTHALLIAL DEVELOPMENT

The prothallus of the homosporous ferns follows a definite pattern of development leading ultimately to the characteristic adult form. This pattern is constant for each species and commonly to taxa of higher order under normal conditions of growth. Variations induced by abnormal and induced conditions were recently reviewed by Miller (1968). In general seven different patterns of development (Fig. 2) are recognized among homosporous ferns (Nayar & Kaur, 1969c), viz., Adiantum-type, Aspidium-type, Ceratopteris-type, Drynaria-type, Kaulinia-type, Marattia-type, and Osmunda-type. These differ in the sequence of cell divisions, in the stage of development and the region at which a meristem is established, and in the resultant form of the adult thallus. In all, except the Marattia- and Osmunda- types, spore germination results in a uniseriate, elongated, germ filament composed of barrel-shaped chlorophyllous cells and bearing one or more rhizoids at the basal end. All cell divisions are by cross walls perpendicular to the long axis of the filament. Commonly cell divisions are mostly restricted to the anterior cells, but in many taxa the intercalary cells are more active than the others. An abrupt change in the plane of cell divisions occurs usually when the germ filament becomes 2 to 10 cells long. However, in some taxa, such as the Grammitidaceae (Stokey & Atkinson, 1958), this change is often much delayed so that the uniseriate stage is more extensive. Also abnormal growing conditions often delay

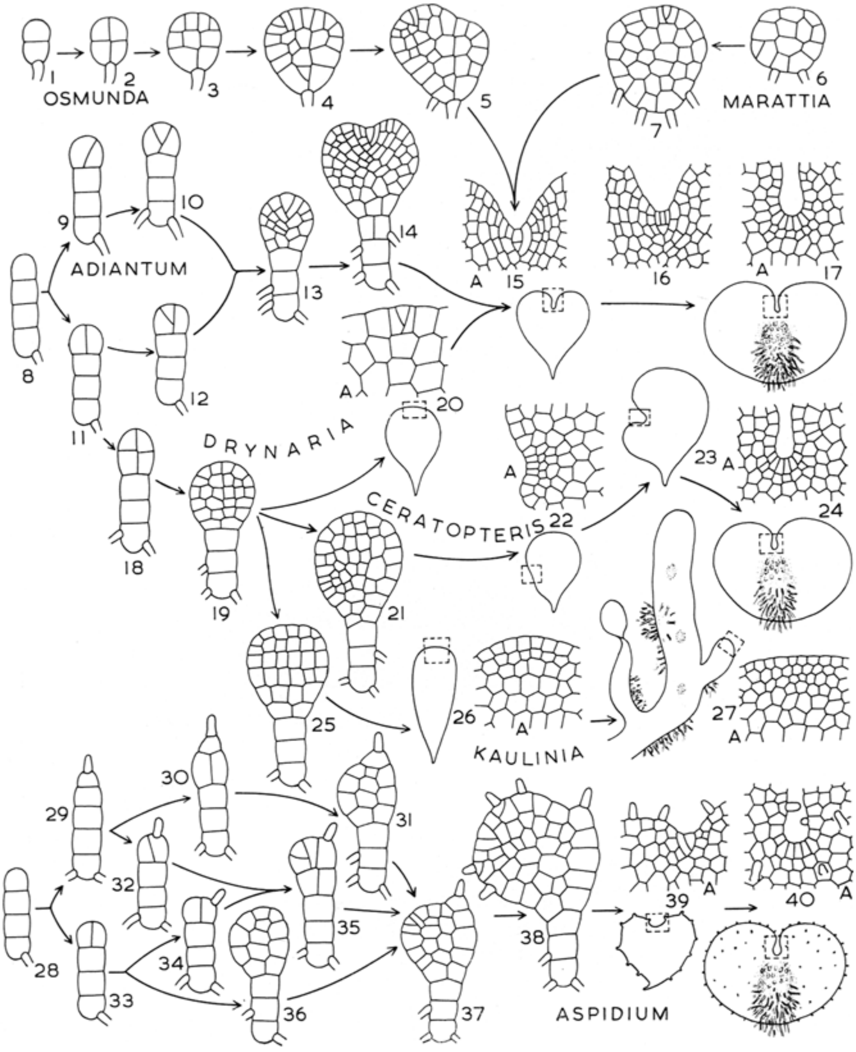


FIG. 2. Schematic representation of the types of prothallial development in homosporous ferns. The arrows indicate successive stages in each type of prothallial development as follows: numbers 1, 2, 3, 4, 5, 15, 16, 17—Osmunda-type; numbers 6, 7, 15, 16, 17—Marattia-type; numbers 8, 9, 10 (or 8, 11, 12), 13, 14, 15, 16, 17—Adiantum-type; numbers 8, 11, 18, 19, 20, 15, 16, 17—Drynaria-type; numbers 8, 11, 18, 19, 21, 22, 23, 24—Ceratopteris-type; numbers 8, 11, 18, 19, 25, 26, 27—Kaulinia-type; numbers 28, 29, 30, 31 (or 28, 29, 32, 35 or 28, 33, 34, 35 or 28, 33, 36), 37, 38, 39, 40—Aspidium-type. [In outline drawings of prothalli, the portion indicated by the hatched square is shown in detail at *A* next to each.]

the onset of this change. Exceptionally, in some genera like *Schizaea* and *Trichomanes* no change ever occurs in the plane of cell divisions, and the prothallus remains filamentous throughout.

In the Adiantum-type of development the terminal cell of the germ filament divides by a wall oblique to the long axis of the filament, and this is followed by another division by a wall at right angles to it (Fig. 2: 8–10). Thus, a transverse row of three daughter cells is formed, of which the middle one is wedge-shaped and acts as a meristematic cell. In some cases the first division in the terminal cell is by a wall parallel (instead of oblique) to the long axis of the filament. The second division is oblique to it, cutting off a wedge-shaped median cell in which another wall perpendicular to the second wall is formed (Fig. 2: 11, 12), cutting off a median meristematic cell. All cell divisions in the meristematic cell are by walls parallel to the oblique walls, each wall being perpendicular to the one preceding it. The daughter cells expand and, by repeated transverse and longitudinal divisions, form an expanded one-cell-thick obovate prothallial plate (Fig. 2: 13). The apex of the thallus at the region of the meristematic cell becomes notched and later cordate (Fig. 2: 13, 14). The obconical meristematic cell then divides by a transverse wall (Fig. 2: 15); the anterior daughter cell divides further by two or three walls parallel to each other and perpendicular to the basal wall. Thus a row of three or four narrow cells is formed, the cells elongated parallel to the long axis of the thallus (Fig. 2: 16). These cells constitute a pluricellular meristem in which the cells divide actively; all divisions are by walls parallel either to their lateral or basal walls. Soon a midrib is formed by cells behind the meristem in the median plane of thallus, and a symmetrically cordate prothallus results with a median midrib and semicircular lateral wings (Fig. 2: 17).

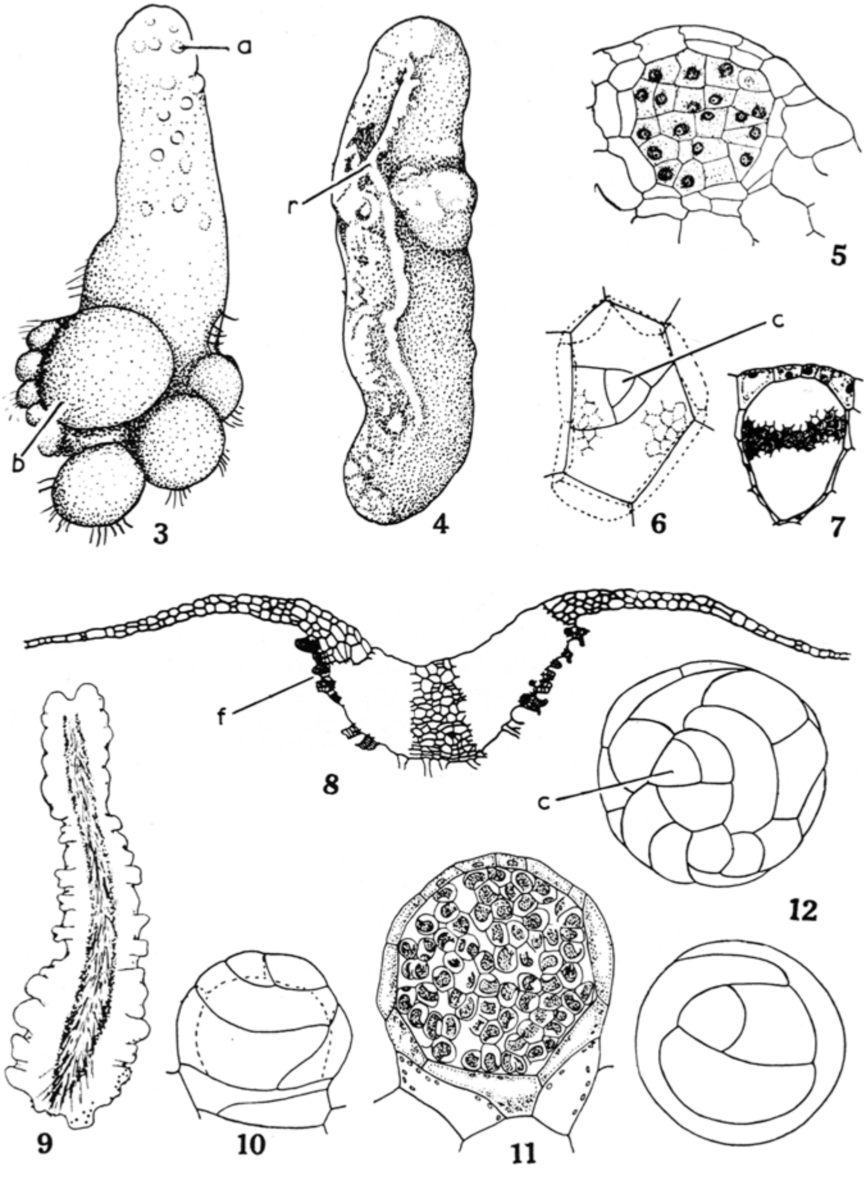
The Drynaria-type of development differs from the Adiantum-type in that the establishment of an apical meristematic cell is far delayed. A broad spatulate prothallial plate is formed (Fig. 2: 11, 18, 19) by division of the anterior cells (including the terminal cell) of the germ filament by walls parallel to the long axis, and by repeated longitudinal and transverse divisions in the daughter cells. An obconical meristematic cell is formed by two oblique divisions in one of the anterior marginal cells of the prothallial plate when it is 5 to 10 or sometimes more cells broad (Fig. 2: 20). Further growth is as in the Adiantum-type and results in a symmetrical cordate thallus. In the Kaulinia-type also a nonmeristic prothallial plate develops as in the Drynaria-type. However, no meristematic cell or meristem is ever established. No organized meristem is ever formed (Fig. 2: 26), cells of the entire anterior region of the thallus being actively meristematic. The thallus elongates and becomes ribbon-shaped (Fig. 2: 27), with its anterior end smoothly rounded (not notched). Branches may develop from groups of marginal cells. No midrib is ever formed, but towards maturity small, irregularly circular cushions two to four cells thick are developed scattered in the median plane of the thallus. The early stages of the Ceratopteris-type of development are also similar to the Drynaria-type, and a broad nonmeristic prothallial plate is formed. However, in some cases the anterior region of the germ filament may not take part in the formation of an expanded thallus, or may be sluggish. In such cases a prothallial plate is formed from the intercalary cells. No meristematic cell is ever differentiated, but as the prothallial plate grows, meristematic activity gradually becomes restricted to a group of marginal cells on one side of the plate, away from the apical region (Fig. 2: 21). This lateral meristematic region soon differentiates into a pluricellular meristem and becomes lodged at the bottom of a notch which progressively becomes more pronounced as growth proceeds (Fig. 2: 22, 23). A midrib is formed immediately behind the meristem. The young thallus is thus cordate but asymmetrical with one wing larger than the other (Fig. 2: 24); in some extreme cases only one wing is developed. On the other hand, the thallus may become nearly symmetrical by unilateral growth of the wings on either side, making the meristem nearly apical.

In the Osmunda-type of development, characteristic of the Osmundaceae, a plate of four cells is formed (Fig. 2: 1, 2) by longitudinal divisions in both the cells of a short (two cells long) germ filament, or the anterior pair of cells if the germ filament is longer. By repeated divisions in all the four cells and expansion of daughter cells, a nearly circular broad prothallial plate is formed (Fig. 2: 3). An obconical meristematic cell is established in the usual way in a marginal cell towards the middle of the group of cells developed from one of the anterior quadrants of the early four-celled plate (Fig. 2: 4). The quadrant that develops the meristematic cell grows faster than the others, and the thallus becomes asymmetrical (Fig. 2: 5). The young thallus elongates, becomes notched at the meristematic region, and develops into a symmetrically cordate structure as in the Adiantum-type. As in the Osmunda-type, the Marattia-type of development results in a symmetrical cordate adult prothallus. This type of development is restricted to ferns in which spore germination is of the Amorphous-type, resulting in a circular plate of cells (Fig. 2: 6) (Marattiidae), which may become more than one cell thick. An obconical meristematic cell is established in the usual way in one of the marginal cells as the plate grows (Fig. 2: 7). The meristematic region becomes notched, and subsequent growth is as in the Adiantum-type, but often resulting in a massive adult thallus.

The Aspidium-type differs from all others in that there is often a margin of variability in the process of development and that it is conditioned by early hair formation in the young prothalli. Commonly the terminal cell of the germ filament produces a unicellular papillate hair crowning it and becomes sluggish (Fig. 2: 29), taking little part in development. Sometimes one or two cells behind it may also remain sluggish. A broad plate is formed by cells behind the sluggish anterior region (Fig. 2: 30, 31), and it is usually lopsided, one side being broader than the other. An obconical meristematic cell is differentiated by two oblique divisions in one of the marginal cells on the more expanded side of the plate (Fig. 2: 37). It may either be formed early during plate formation or only after the plate becomes several cells broad. In some cases the terminal cell of the germ filament, though producing a hair, is not sluggish but takes part in plate formation; it divides longitudinally into a larger and a smaller daughter cell, the former bearing the hair and remaining sluggish, the latter actively dividing and contributing to the development of the prothiallial plate (Fig. 2: 32, 35). The plate is thus slightly lopsided at its anterior end. A meristematic cell is differentiated in one of the marginal cells formed from the active daughter cell of the terminal cell. Marginal unicellular hairs are produced continually, whether a meristematic cell is differentiated early or not. Another variation is one in which hair formation is delayed until after plate formation is initiated by longitudinal divisions in the anterior cells of the germ filament. One of the daughter cells of the terminal cell remains sluggish and may later bear a hair crowning it (Fig. 2: 33, 34); a meristematic cell is formed marginally in the plate developed from its sister cell. All these variations may occur together in the prothallial development of the same species. Development of the thallus after the establishment of a meristematic cell is as in the Adiantum-type (Fig. 2: 38, 39). Because the meristematic cell is formed laterally in the prothallial plate, the young thalli are lopsided, the asymmetry being more marked when the formation of a meristematic cell is more delayed. As the thalli grow, however, the asymmetry is lost and the adult thallus is symmetrically cordate (Fig. 2: 40). Marginal as well as superficial hairs are generally profuse on the thallus from early stages onwards.

MORPHOLOGY OF ADULT PROTHALLUS

Form of Adult Thallus. In ultimate shape when adult, there are five types of prothalli among homosporous ferns, viz., Tuberous, Filamentous, Cordate-thalloid, Strap-like, and Ribbon-like. Of these the Cordate-thalloid form (Fig. 33) is the most common. The thallus is dorsiventrally flattened, usually subcircular in outline but with a notched anterior end having a well differentiated meristem located at the bottom of the notch and consisting of a thick, median midrib and broad, one-cell-thick, flat, nearly semicircular wings on its either side. More commonly, the Cordate-thalloid prothalli are quick-growing seasonal plants, completing their life cycle in 4 to 8 months. Among the primitive homosporous ferns they are slow-growing and may live for several years. Sex organs and rhizoids are usually restricted to the midrib on its ventral surface. The wings are commonly spread out flat on the substratum but in some groups may be markedly curved up (Fig. 34) and raised above the substratum (as in Anemiaceae, Parkeriaceae). In some like the Dipteridaceae (Fig. 76) and Matoniaceae the wings are characteristically ruffled. Except in some of the comparatively primitive groups of ferns (Marattiidae, Osmundaceae), the wings are one cell thick throughout and sharply delimited from the thick midrib; in the primitive groups it



FIGS. 3–12. Prothallial morphology of Marattiaceae, Ophioglossaceae and Osmundaceae (*a*, antheridium; *b*, branch; *c*, opercular cell; *f*, archegonium; *r*, median longitudinal ridge). Fig. 3. Adult prothallus of *Helminthostachys zeylanica*. Fig. 4. Adult prothallus of *Botrychium virginianum*. Fig. 5. Longisection of a young antheridium of the same. Fig. 6. Surface view of embedded antheridium of *Macroglossum smithii*, showing triangular cap cell. Fig. 7. Longisection of antheridium of the same. Fig. 8. Transection of adult prothallus of *Todea barbara*. Fig. 9. A six-year-old pro-

is often several cells thick near the midrib and is one cell thick towards the margins only (Fig. 8). The midrib is massive and heavy (10 to 12, sometimes 18 to 24 cells thick) in the more primitive groups but in the advanced families four to eight cells thick only.

All the other types of prothalli are rather rare among the homosporous ferns and are restricted to certain specific taxa. By far the more common among them is the Ribbon-like type found in the Loxogrammaceae, Vittariaceae, and some of the Hymenophyllaceae (Fig. 60) and Polypodiaceae (Fig. 77). The thallus is slow growing, perennial, thin, one cell thick, flat, and dorsiventral. It grows indefinitely, often bearing profuse lateral branches. It is narrow, markedly elongate, with nearly parallel sides and a rounded apex devoid of any well-organized meristem. The pattern of prothallial development resulting in a Ribbon-like thallus is of the Kaulinia-type. There is no midrib; sex organs are borne on scattered, small, nearly circular cushions two to four cells thick (marginal in the Hymenophyllaceae; superficial in the others), and rhizoids are mostly borne in marginal clusters. The Grammitidaceae, and some of the Lomariopsidaceae (Figs. 39, 40) and Polypodiaceae, possess Strap-like adult prothalli, which are intermediate in form between the Ribbon-like and Cordate-thalloid types. The thallus is slow growing, several times longer than broad, with nearly parallel sides as in the Ribbon-like thalli, but is unbranched, possessing a cordate apex with a well defined pluricellular meristem and having a median, ill-differentiated, thin, often interrupted midrib. The thalli follow the Kaulinia-type of development pattern but ultimately develop a cordate apex with a definite apical meristem at the bottom of the notch. Sex organs and rhizoids are borne on the midrib region, but the latter are more profuse on the margins than on the midrib.

The Tuberous- as well as Filamentous- types of prothalli are perennial and are rare among ferns; the latter type is restricted to *Schizaea* (Fig. 22) and the trichomanoid genera of the Hymenophyllaceae, and the former to the Ophioglossaceae (Figs. 3, 4), *Actinostachys*, and *Lophidium* (Fig. 23) of Schizaeaceae and *Stromatopteris* of Gleicheniaceae. Filamentous prothalli are of indefinite growth and consist of branched uniseriate filaments bearing sex organs and rhizoids laterally. The Tuberous type of prothallus is usually subterranean, nearly cylindrical or irregular in shape, very slow growing, several cells thick, parenchymatous, and bearing sex organs all around or in restricted areas. It is devoid of an organized meristem in *Botrychium* and *Helminthostachys*, growing by the activity of a 4-sided apical meristematic cell in *Ophioglossum* and *Actinostachys*,

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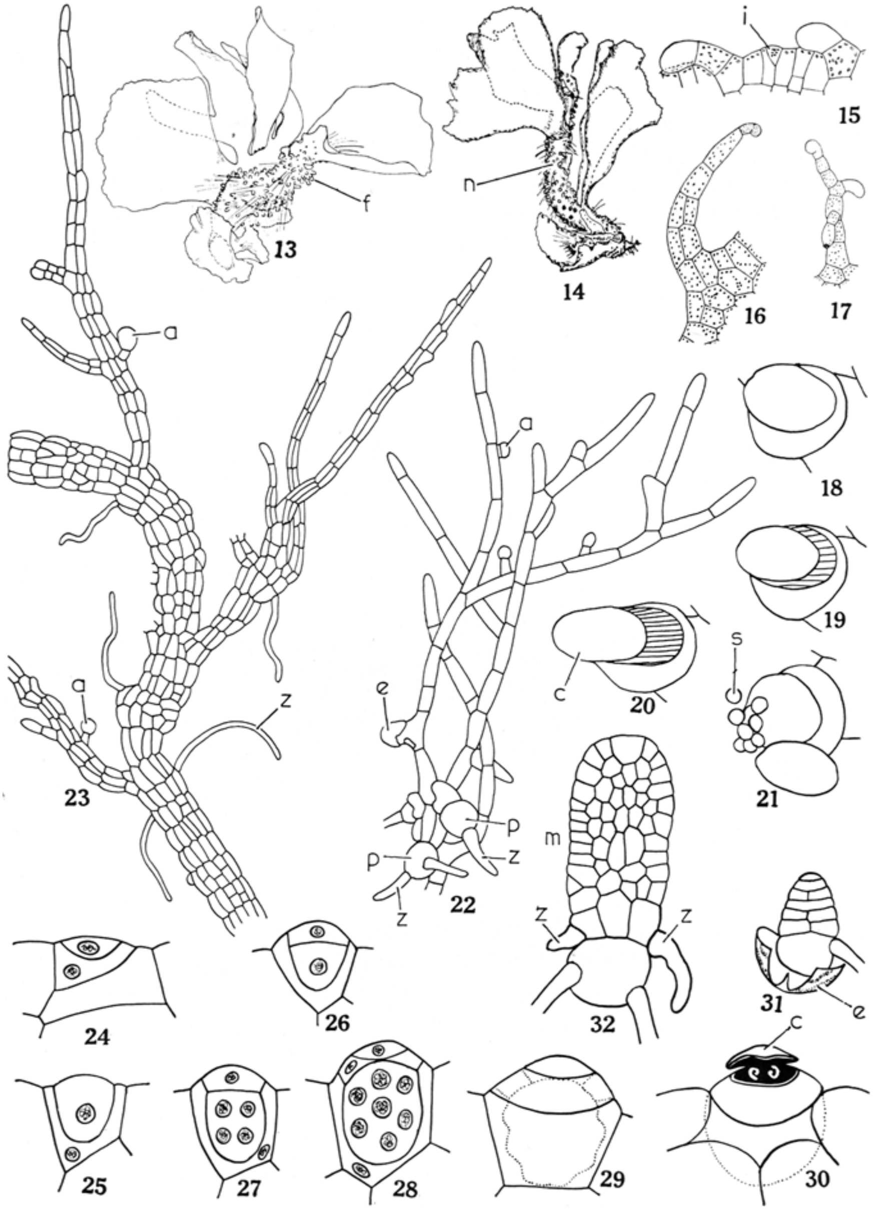
thallus of *Todea barbara*. Fig. 10. Lateral view of mature antheridium of the same. Fig. 11. Longisection of a large antheridium of the same. Fig. 12. Dorsal view of mature antheridia of *Osmunda javanica*, showing triangular opercular cell. [Fig. 3, after Lang, 1902; Fig. 4, after Jeffrey, 1896; Fig. 5, after Campbell, 1905; Figs. 6, 7, after Stokey, 1942; Figs. 8–12, after Stokey & Atkinson, 1950.]



FIGS. 13–32. Prothallial morphology of Anemiaceae, Parkeriaceae, and Schizaeaceae (*a*, antheridium; *c*, cap cell; *e*, spore coat; *m*, meristem; *n*, wingless region of midrib; *p*, rhizoidophore; *s*, spermatozoids; *z*, rhizoid). Figs. 13, 14. Adult prothalli of *Mohria caffrorum*. Fig. 15. Stages in the development of marginal hair of *Anemia underwoodiana*. Figs. 16, 17. Marginal hairs of *Anemia adiantifolia*, crowning prothallial protuberances. Figs. 18–21.

and having a uniseriate growing apex (growing in length by transverse divisions of cells) in *Lophidium.* The thallus is erect growing, except in *Botrychium.* Branching of the thallus is common in *Lophidium, Stromatopteris, Ophioglossum,* and *Helminthostachys.*

Prothallial Trichomes. The prothalli of a majority of ferns are naked, insofar as they do not bear any trichomes. However, the possession of specific types of prothallial trichomes is characteristic of a large number of genera of homosporous ferns, and related genera and groups have similar type of trichomes. There are exceptions like *Asplenium, Athyrium, Blechnum, Bolbitis, Diplazium, Egenolfia, Matteuccia,* and *Notholaena,* in all of which some species possess trichomes while others have naked prothalli. Rarely, as in *A. viride*-group of species of *Asplenium* (Nayar, Raza, & Lata, 1968), which have naked prothalli, papillate protrusions are found on the peripheral walls of the marginal cells, and these resemble trichomes found in related species. Among the more conspicuous groups of homosporous ferns possessing characteristic prothallial trichomes are Anemiaceae, Aspleniaceae, Blechnaceae, Cyatheoideae, Davalliaceae, Dryopteridaceae, Gleicheniaceae, Grammitidaceae, Loxsomaceae, Oleandraceae, Polypodiaceae, and Thelypteridaceae. Commonly prothallial trichomes of ferns are either simple, unicellular hairs or multicellular, branched or unbranched hairs; rarely multiseriate structures recalling sporophytic trichomes (Figs. 64, 75) are encountered (Cyatheoideae, Loxsomaceae, *Lepisorus normalis*). There is often some degree of similarity between sporophytic and gametophytic trichomes in the same genus, as pointed out by Nayar (1956b), the prothallial trichomes being similar but often simpler in structure than the sporophytic trichomes. Depending upon the taxa, prothallial trichomes are borne either all over the thallus, including margin and both the surfaces, or are restricted to either the margin or the surface. The stage of prothallial development at which trichomes appear on the thalli is also characteristic of individual taxa. In some, such as many genera of the Dryopteridaceae, Blechnaceae, and Davalliaceae, they are formed from very early stages of prothallial development, whereas in others such as the Polypodiaceae they are developed only after the thallus has become spatulate or even cordate. In

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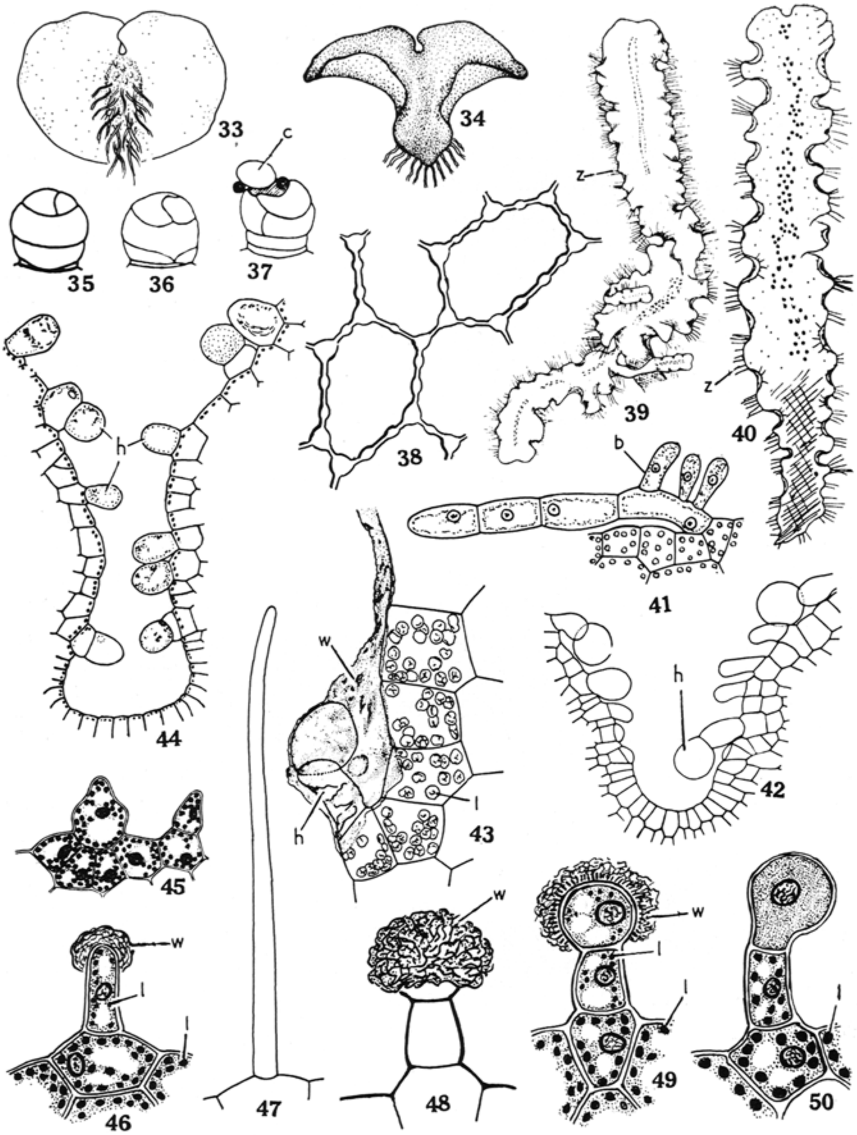
Stages in antheridial dehiscence of *Anemia.* Fig. 22. Adult prothallus of *Schizaea pusilla.* Fig. 23. Portion of adult prothallus of *Lophidium dichotomum.* Figs. 24–28. Longisection of antheridia of *Ceratopteris thalictroides,* showing stages in development. Fig. 29. Lateral view of mature antheridium of the same. Fig. 30. Same, showing dehiscence. Fig. 31. Germ filament of *Ceratopteris thalictroides.* Fig. 32. Young prothallus of the same, showing lateral meristem. [Figs. 13, 14, after Atkinson, 1960; Figs. 15–21, after Atkinson, 1962; Fig. 22, after Atkinson & Stokey, 1964; Fig. 23, reconstructed drawing based on photographs from Bierhorst, 1967.]



FIGS. 33–50. Prothallial morphology of Adiantaceae, Aspleniaceae, Cheilanthaceae, Cyatheaceae, Dryopteridaceae, Lomariopsidaceae, Oleandraceae and Pteridaceae (*b*, branch; *c*, cap cell; *h*, hair; *l*, chloroplast; *w*, extracellular secretion; *z*, rhizoid). Fig. 33. Ventral view of adult prothallus of *Adiantum caudatum*. Fig. 34. Dorsal view of adult prothallus of *Pityrogramma chrysophylla*. Figs. 35, 36. Antheridia of *Hemitelia horrida* (35) and *Alsophila cooperi* (36). Fig. 37. Antheridial dehiscence in *Alsophila excelsa*. Fig. 38. Wing cells of *Doryopteris concolor*. Figs. 39, 40. Adult prothallus of *Rhipidopteris peltata* (39) and *Elaphoglos-*

extreme cases, as in the Cyatheoideae, they are formed only towards maturity of the thallus.

The most common type of prothallial trichomes among homosporous ferns are unicellular hairs. These are either papillate or acicular and develop from small lens-shaped initial cells formed towards the middle of the peripheral wall of the prothallial cells. Papillate hairs are borne both marginally and superficially on the prothallus and are widely distributed in the more advanced groups belonging to the Cyatheoid-Dryopteroid line of evolution (Aspleniaceae, Blechnaceae, Dryopteridaceae, Davalliaceae, Oleandraceae, Thelypteridaceae) and the Gleichenioid-Polypodioid line (Polypodiaceae), and are found either mixed with other types of trichomes or alone on the prothallus. Papillate prothallial hairs (Fig. 46) are short, cylindrical, with a rounded anterior end, thin-walled and with vacuolated protoplasmic contents including several chloroplasts. The chloroplasts are generally smaller in size compared to those of other prothallial cells, but in some like *Oleandra* and *Asplenium* they are nearly of the same size (Fig. 45). Commonly the papillate hairs are secretory, secreting an extracellular, often yellowish, waxy substance, which often forms a cap crowning the hair. The secretion may in some cases be scanty as in the Davalliaceae, Oleandraceae, and most of the Polypodiaceae. Commonly it forms a tough cap, which retains its shape when dislodged but may rarely be of a fluid consistency so as to drain off the hair. The apical region of the hair is swollen in some genera like *Polystichum*; the base of the hair is markedly and characteristically dilated in some species of *Asplenium* (Fig. 45), so that the hair is mammillate. In size the papillate hair varies widely in different taxa; in some species of *Blechnum* (Nayar, Bajpai, & Raza, 1966) they are very short and nearly as long as broad, while in most taxa they are four to six times longer than broad. An extreme case is the hairs found on the adult prothallus of *Hypodematium crenatum* (Forsk.) Kuhn; these are much elongated and slender, recalling rhizoids (Fig. 47). Papillate hairs on the surface of the prothallus are generally larger in size compared to those borne on the margin of the same thallus. Occasional division of the hair by a transverse septum

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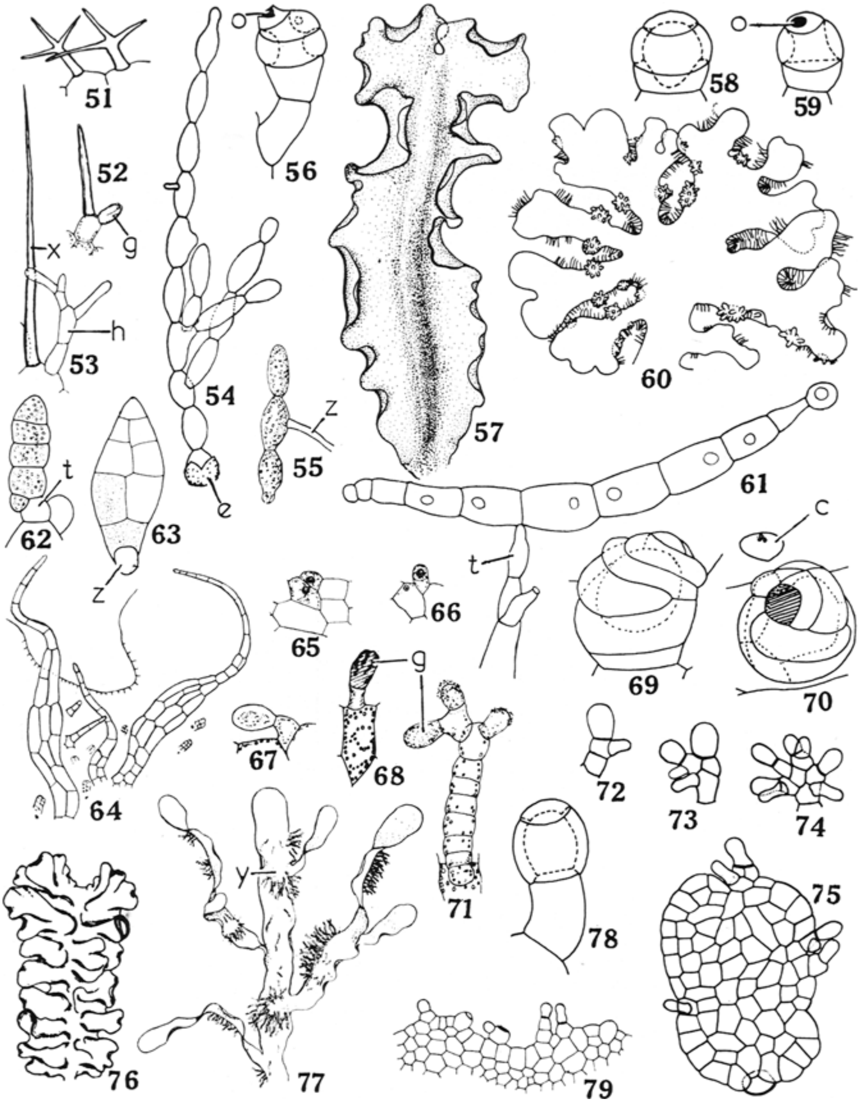
sum stenophyllum (40). Fig. 41. Branched prothallial hair of *Arthropteris tenella*. Fig. 42. Apical region of adult prothallus of *Diellia erecta*, showing hairs. Fig. 43. Full grown prothallial hair of *D. erecta*, showing extracellular secretion. Fig. 44. Apical region of adult prothallus of *Diplazium stellato-pilosum*, showing hairs. Figs. 45, 46. Longisection of marginal prothallial hairs of *Asplenium adiantum-nigrum* (45) and *Hypodematium crenatum* (46). Fig. 47. Marginal rhizoid-like hair of *H. crenatum*. Fig. 48. Marginal glandular hair of *Notholaena aschenborniana*. Fig. 49. Longisection of the same. Fig. 50. Longisection of a glandular hair of *Bolbitis subcrenata*. [Figs. 35–37, after Stokey, 1930; Figs. 39, 40, after Stokey & Atkinson, 1957; Fig. 41, redrawn from Stokey, 1950; Figs. 42, 43, after Wagner, 1952; Fig. 44, after Atkinson, 1967; Fig. 45, after Nayar, Raza, & Lata, 1969; Fig. 50, after Nayar, 1960.]



FIGS. 51–79. Prothallial morphology of Blechnaceae, Cheiropleuriaceae, Dipteridaceae, Gleicheniaceae, Grammitidaceae, Hymenophyllaceae, Loxsomaceae, Polypodiaceae and Thelypteridaceae (*c*, cap cell; *e*, spore coat; *g*, glandular cell; *h*, glandular hair; *o*, pore-like opening in cap cell; *t*, sterigma; *x*, acicular hair; *y*, archegonial cushion; *z*, rhizoid). Fig. 51. Prothallial hair of *Goniopteris biollyei*. Figs. 52, 53. Marginal hairs of *Xiphopteris deletescens* (52) and *Ctenopteris suspensa* (53). Fig. 54. Germ filament of *C. mollissima*. Fig. 56. Antheridium of *C. suspensa*, showing pore-like opening in cap cell. Fig. 57. Dorsal view of a three-year-old prothallus of *Blechnum brasiliense*. Fig. 58. Mature antheridium of *Woodwardia orientalis*. Fig. 59. Antheridial dehiscence in

(often near the base) is reported in many species. The hair-bearing prothallial cell may form a conical protuberance subtending the hair, and rarely the protruded portion gets cut off from the mother cell. In some taxa, in which the prothallia are profusely hairy, the hair-bearing prothallial cell may grow out as a uniseriate filament subtending the hair. This tendency is more marked in the marginal hair-bearing cells as in some species of *Blechnum* and *Asplenium*. In contrast to the papillate hairs, the acicular hairs are rather uncommon among ferns; they are restricted to the Grammitidaceae and the Thelypteridaceae. Acicular hairs (Fig. 53, *x*) are nonglandular, slender, elongated (usually 15 to 20 times longer than broad), needle-like (tapered to a pointed apex), devoid of contents when fully developed, and with nearly hyaline, thickened walls. Commonly they are produced only towards the maturity of the prothallus. In *Thelypteris (Goniopteris) biollyi* (Christ in Pitt.) Proctor the acicular hairs are forked or variously branched (Fig. 51), but this is a rare condition. As in the case of papillate hairs, occasionally the acicular hairs may be divided by one or two transverse septae, commonly in their basal half.

Among multicellular prothallial trichomes the more common is the club-shaped hair (Fig. 50), commonly composed of a swollen, glandular cell with dense cytoplasmic contents and a slender, uniseriate stalk, one to several cells long. Rarely the terminal cell is transversely divided as in some of the Lomariopsidaceae. Club-shaped hairs are thin-walled and chlorophyllous like the papillate hairs, and like them are developed from superficial lens-shaped initial cells. As in the Polypodiaceae, Davalliaceae, and the Tectarioideae, some or all the stalk cells bear a lateral unicellular branch resembling the papillate hair (Figs. 41, 53 *h*, 71, 72); club-shaped

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Stenochlaena tenuifolia. Fig. 60. Portion of adult prothallus of *Mecodium flabellatum.* Fig. 61. Gemma of *Polyphlebium venosum* attached laterally to sterigma. Fig. 62. Gemma of *Mecodium australe* attached basally to sterigma. Fig. 63. A detached gemma of the same, showing basal rhizoid initial. Fig. 64. Trichomes of *Loxsoma cunninghami.* Figs. 65–67. Stages in the development of gleicheniaceous hair in *Sticherus bifidus.* Fig. 68. Fully developed gleicheniaceous hair of *Hicriopteris glauca.* Figs. 69, 70. Lateral (69) and apical (70) views of antheridia of *Cheiropleuria bicuspis.* Fig. 71. Multicellular hair of *Platycerium alicorne.* Figs. 72–74, Multicellular glandular hairs of *Lepisorus normalis.* Fig. 75. Palea-like hair of the same. Fig. 76. Dorsal view of an old prothallus of *Dipteris conjugata.* Fig. 77. Portion of adult prothallus of *Paraleptochilus decurrens.* Fig. 78. Pendulous antheridium of *Polypodium amoenum.* Fig. 79. Apex of a branch of the prothallus of *Kaulinia pteropus,* showing formation of gemmae. [Fig. 51, after Stokey, 1960; Figs. 52–56, after Stokey & Atkinson, 1958; Figs. 60, 62, 63, after Stone, 1965; Fig. 61, after Stone, 1958; Fig. 64, after Stokey & Atkinson, 1956; Figs. 65–68, after Stokey, 1950; Figs. 69, 70, after Stokey & Atkinson, 1954; Fig. 71, after Stokey, 1960; Figs. 72–75, after Nayar, 1962; Fig. 76, after Stokey, 1945; Fig. 77, after Nayar, 1963b; Fig. 79, after Nayar, 1963a.]

hairs devoid of branches are characteristic of the Anemiaceae and Aspleniaceae. In the Grammitidaceae the stalk cells often bear unicellular branches resembling acicular hairs (Fig. 52). In some taxa, the stalk of the club-shaped hair is branched (Figs. 73, 74), each branch bearing a swollen terminal cell. In rare cases the stalk cells may divide longitudinally and become multiseriate, and in some extreme cases [*Lepisorus normalis* (D. Don) Ching] the stalk forms a flat, expanded, palea-like structure (Fig. 75). Club-shaped hairs are found in most genera of the Polypodiaceae, Grammitidaceae, Anemiaceae, and Tectarioideae and in some genera of the Oleandraceae, Davalliaceae, and Lomariopsidaceae. They are almost always found mixed with unicellular hairs, are produced only towards maturity of the prothallus, and are commonly superficial on the thallus (rarely as in *Arthropteris, Bolbitis, Egenolfia,* and *Merinthosorus,* they are marginal also). The terminal glandular cell of the club-shaped hairs is nonsecretory in most cases; the papillate branches borne on the stalk cells often have an extracellular secretion. The terminal glandular cells of the club-shaped hairs in some of the Aspleniaceae and Oleandraceae are secretory, though often the secretion is very scanty. The club-shaped hairs of *Diellia* (Wagner, 1952) and *Notholaena* are exceptional in that they have copious extracellular secretion; the secretion is of a fluid nature in *Diellia* (Fig. 43), while it is waxy and in the form of slender, tortuous, solid rods that form a dense tangled mass surrounding the terminal cell in *Notholaena* (Figs. 48, 49).

A characteristic type of club-shaped hair is found in the Gleicheniaceae. These develop from special wedge-shaped initial cells (Figs. 65–67) cut off towards the anterior end of the prothallial cells (formed by a wall oblique to the lateral wall of the mother cell, on the side facing the prothallial meristem) and consist of a swollen glandular terminal cell and a slender stalk (Fig. 68), which is commonly one or two cells long (rarely longer). When young these gleicheniaceous hairs are chlorophyllous, but the chloroplasts disintegrate towards maturity. The terminal cell contains tannin deposits. Another rare and characteristic type of prothallial trichome is the "bristle-like" hair (Fig. 64) found on the adult prothalli of the Loxsomaceae and the Cyatheoideae. These are large, pluricellular, thin-walled, chlorophyllous trichomes two to several cells wide, several cells long, tapered to a uniseriate apex and commonly bristle-like or palea-like. They are restricted to the lower surface of the prothalli in the midrib region and are produced only towards maturity of the prothallus. Like the gleicheniaceous hairs, they develop from special wedge-shaped initials formed at the anterior face of the prothallial cells.

Sex Organs. Except in some specialized cases, the prothalli of homosporous ferns reproduce sexually by producing characteristic antheridia and archegonia on the same thallus. A tendency towards dioecism is occasionally reported, but it is quite doubtful whether any of the homosporous ferns are truely dioecious. Small, irregularly shaped, stunted prothalli bearing solely antheridia are found mixed with bisexual prothalli in many ferns. Unfavorable growth conditions tend to increase the percentage of male thalli in a population. Under certain extremely favorable growth conditions, particularly in cultures, strictly archegoniate thalli (producing no antheridia at all) are sometimes produced; however the same species grown under less favorable conditions produces bisexual prothalli. In general, conditions that induce vigorous and rapid growth of the prothallus also favor femaleness, while those that induce weak slow growth favor maleness. The physiology of formation of sex organs by fern prothalli is not yet well understood. Nutritional status of the substratum has been shown to affect sexuality (Reed, 1907; Nagai, 1914, 1915; Sossountzov, 1954, 1957a, b), as also availability of light (Twiss, 1910; Nagai, 1914; Hurel-Py, 1950; Schraudolf, 1967). It is demonstrated that antheridial formation in fern prothalli is specifically controlled by naturally occurring substances commonly termed antheridiogens. Different types of antheridiogens specific to certain groups of species (not necessarily related) but inactive in others are demonstrated (Dopp, 1950, 1959; Naf, 1956, 1959, 1960, 1961, 1965; Voeller, 1964). It is believed that these specific substances are produced by the prothalli at specific periods in their developmental history, and these substances diffuse into the substratum. Extremely small concentrations (e.g., 10^{-4} μ g./ml.) in the substratum have been shown to induce antheridial formation (Naf, 1956; Pringle, 1961) in species sensitive to the particular antheridiogen. The nature of antheridiogens and the mechanism of their action are not yet well understood. (A review of the work in this field has been given recently by Miller, 1968.)

The prothalli of homosporous ferns produce antheridia earlier in their life history than archegonia. Antheridial formation is commonly initiated well before midrib formation (sometimes even before development of the prothallial plate), while archegonia are formed only after a midrib (cushions on the thalli, in the case of Ribbon-like prothalli) is developed. Antheridia are often borne all over the young thallus (including margins), while archegonia are restricted to the midrib (or cushions, as the case may be). (The case of ferns with Filamentous-type of prothalli is exceptional; both types of sex organs are borne laterally on the filaments, but sometimes the archegonia are borne on special multicellular cushions.) On the thalloid prothalli antheridial formation often ceases partially or completely as archegonial formation is initiated. However, many ferns bear both types of sex organs together indefinitely. When both occur together on the Cordate-thalloid and Strap-like types of prothalli, they generally occupy different regions on the thallus. Antheridia are generally borne on the posterior half of the thallus (often restricted to the midrib region of the adult thallus), while archegonia occupy the anterior region of the midrib. In the thalloid dorsiventral types of fern prothalli, sex organs are restricted to the ventral surface (exceptional cases are reported of sex organs borne on the dorsal surface also, under certain growth conditions). Though on young bisexual thalli and stunted male prothalli marginal antheridia are common, among the thalloid forms of prothalli antheridia are not borne marginally on adult bisexual thalli (*Ceratopteris* is exceptional in this respect: in this genus marginal antheridia are very frequent on adult cordate prothalli). On the thalloid types of prothalli archegonia are borne scattered on the midrib towards the growing apex of the thallus, the progressively younger ones being nearer the apex. In the Osmundaceae young archegonia are found mixed with older ones. Also, archegonia are borne in distinct longitudinal rows on either lateral side of the midrib on the lower surface. Recently Momose (1958a) has suggested that the distribution of sex organs, particularly the antheridia, on the Cordate-thalloid prothallus is characteristic of specific taxa. How far this is true of the majority of ferns having cordate prothalli is not known.

Antheridium. The antheridium of the homosporous ferns is a simple structure consisting of a globose mass of spermatozoids sheathed all round by a wall, one cell thick. In the two primitive groups, Ophioglossidae and Marattiidae (Figs. 5–7) the antheridium is embedded in the prothallial tissue, only the anterior end being exposed. Among the others all except *Ceratopteris* have the antheridium fully exposed, protruding as a subglobose structure attached by a flat base. In *Ceratopteris* the antheridium (Figs. 28–30) is embedded but, being borne on the one-cell-thick wings of the prothallus, is only partially surrounded by prothallial tissue. Basically two types of antheridia are met with among homosporous ferns, the Eusporangiate-type characteristic of the relatively primitive groups and the Leptosporangiate-type of the more advanced genera. The Eusporangiate-type (Figs. 10–12, 69, 70) is comparatively more massive, each producing over 100 spermatozoids sheathed by a wall consisting of 10 to 20 (up to 25 to 30) narrow, elongated cells (from one of which an operculum consisting of one or two small triangular to ovate cap cells is differentiated towards the anterior end of the antheridium). It is attached to the prothallus by two or three thin, flat, wedge-shaped, basal cells. At dehiscence the cap cell is thrown off intact to release the spermatozoids (Fig. 70). The Eusporangiate-type of antheridium originates as a wedge-shaped initial cell formed towards one end of a superficial prothallial cell. There is no regular sequence of cell divisions, but ultimately a large central androgonial cell (which produces the mass of spermatozoids) is separated from a many-celled wall.

The Leptosporangiate-type of antheridium is comparatively much smaller and simpler in structure, commonly producing only 16 to 32 spermatozoids. Its wall consists of three cells, of which the one at the anterior end is the cap cell (operculum), that at the posterior end the basal cell with which the antheridium is attached to the prothallus, and the middle one (the ring cell) annular, surrounding the central mass of spermatozoids. Abnormal divisions of any one of these cells may occur but are not frequent or characteristic of any taxon. The basal cell of the Leptosporangiate antheridium is commonly funnel-shaped (Fig. 58), but in some taxa it is barrel-shaped or disk-shaped (Figs. 56, 59, 78). At antheridial dehiscence the cap cell is thrown off (Hartman, 1931); it often collapses in the process. However, in some like the Cheilanthaceae and Parkeriaceae it opens up like a hinged lid (Fig. 30), while in several other taxa a pore-like opening is formed in the cap cell to release the sperms (Figs. 56, 59); in the Anemiaceae the cap cell is detached all around and slips off sideways (Figs. 18–21), opening up the antheridium (Atkinson, 1960, 1962). In contrast to the Eusporangiate-type, the Leptosporangiate-type of antheridium develops as a superficial, thick, papilla-like initial cell formed towards the middle of the peripheral wall of the mother cell. A transverse division by a flat (or nearly flat) wall followed by a periclinal division by a dome-shaped wall (with its rim touching the first wall all around, a little away from the peripheral wall) cuts off a central androgonial cell from a basal cell and a peripheral wall cell. A third flat or saucer-shaped transverse wall (with its middle portion touching the anterior end of the dome-shaped wall) divides the wall cell into a smaller, anterior, disk-shaped, cap cell and a larger, annular, ring cell encircling the androgonial cell. Initially the androgonial cell is often shaped like a biconvex lens, but it soon enlarges so that the anterior wall becomes dome-shaped and the basal wall commonly funnel-shaped. However, in many taxa the lower wall remains flat or nearly so throughout.

For long it was believed that the Leptosporangiate-type of antheridium develops from the unicellular initial cell by three successive divisions by funnel-shaped walls, the first and last of which are with the narrower end facing the basal end and the second in the opposite direction (Strasburger, 1869; Campbell, 1886, 1905; Atkinson, 1894; Lagerberg, 1908). Davie (1951) maintained that all the three walls are flat and transverse when first formed, the successive walls being formed only after the previous wall has become curved, resulting in the characteristic shape and configuration of the wall cells in the mature antheridium. Another version of antheridial development is presented by Stone (1958, 1961, 1962, 1969). According to her, the first wall formed in the antheridial initial is flat as described by Davie, but the second wall is dome-shaped and the third wall funnel-shaped as described by the early workers. Verma & Khuller (1966) recently undertook a detailed study of antheridial development in some species of *Adiantum*, *Pteris*, and *Onychium*, and concluded: "The differentiation of the polypodiaceous fern antheridium from the antheridial initial does not follow a rigid course. . . . The first wall is transverse (flat or concave to varying degrees), which very often gets displaced downward resulting in a funnel-shaped wall and first ring cell. . . . The second wall is invariably hemispherical, lying over the first wall like an inverted saucer or cup, whose convexity lies generally parallel to the outer bounding wall of the antheridium (and then periclinal). The third wall is transverse, and generally concave" (Verma & Khuller, 1966: 313).

The form and ontogeny of the embedded antheridia as found in Ophioglossidae, Marattiidae, and *Ceratopteris*, differ from those of both the Eusporangiate- and Leptosporangiate- types described above. In the Ophioglossidae and Marittiidae the antheridium is basically of the massive Eusporangiate-type. A superficial cell of the prothallus acts as an antheridial initial, and it does not protrude beyond the surface of the thallus. During development it divides by a transverse wall into a lower androgonial cell and an upper (peripheral) cover initial. The latter divides three or four times by vertical, often intersecting walls to form a row of cover cells of which a centrally placed one constitutes an opercular (cap) cell. In most of the Ophioglossidae the cover initial divides also by transverse walls so that the cover is more than one cell thick (Fig. 5). The androgonial cell meanwhile enlarges markedly, pushing against the prothallial cells, which surround it, and divides repeatedly to produce a mass of spermatozoids. As the spermatozoids are formed, a jacket composed of radially flattened cells is developed around the androgonial cell, enveloping it on all the sides except at the region of the cover cells (Fig. 7). This jacket layer is cut off from the surrounding prothallial cells. In the Ophioglossidae the jacket is two or three cells thick. The embedded antheridium of *Ceratopteris* is basically of the Leptosporangiate-type (Nayar & Kaur, 1969b). It differs in that the antheridial initial is cut off from the mother cell by a wall obliquely extending from the middle of the peripheral wall to the middle of one of the lateral walls, and thus is wedge-shaped. The first wall formed in the initial cell is very markedly curved downwards and is basket-shaped, with its rim touching the peripheral wall of the mother cell all around (Fig. 24). The anterior cell is thus nearly cylindrical with a dome-like base and a flat anterior end: the basal cell is deeply cup-shaped (Fig. 25) and surrounds the anterior cell on all sides except the peripheral (flat) side. The second wall is formed close to the peripheral flat wall of the anterior cell. It is flat, touches the basket-like wall all around, and appears like a lid fitting into the peripheral end of the anterior cell a little below the rim of the basket-shaped first wall (Figs. 26, 27). This division separates a large central androgonial cell from a discoid peripheral wall cell. The third wall is formed in the wall cell and is similar to the third wall of the typical Leptosporangiate-type antheridium (Fig. 28). It is concave, touches the upper wall of the androgonial cell, and cuts off a circular cap cell.

Archegonium. Compared to the antheridium, the archegonium of the homosporous ferns is a more uniform structure. It is shaped like a round-bottomed flask and consists of an axial row of three cells (a large basal egg; an ephemeral, small, ventral canal cell; an anterior, elongated, neck canal cell) surrounded by a jacket of one layer of cells. The jacket consists of an embedded (exposed in the case of some ferns with Filamentous-type of adult prothallus, e.g., *Schizaea*) venter surrounding the egg and an elongated, protruding neck (generally of four rows of cells). In the Ophioglossidae and Marattiidae the neck is also embedded in the prothallial tissue and is short. Except in these two groups the archegonial neck is comparatively longer (7 to 12 cells long) in the more primitive families like the Chieropleuriaceae, Cyatheaceae, Dipteridaceae, Gleicheniaceae, Matoniaceae, and Osmundaceae. In the more advanced ferns it is usually only four or five cells long. The neck of the archegonium is curved towards the growing apex of the prothallus in the primitive homosporous ferns (Anemiaceae, Chieropleuriaceae, Matoniaceae, and Gleicheniaceae); in the others it is curved away from the apex. The neck canal cell is binucleate and generally swollen towards the apex at maturity. In some of the more primitive groups like the Gleicheniaceae, Schizaeaceae, Cyatheoideae, and Dicksonioideae the neck canal cell is sometimes 4-nucleate; it is divided into a row of four cells in the Plagiogyriaceae. Recently Nishida & Sakuma (1961) have pointed out that aberrant archegonia with multinucleate or divided neck canal cells, or sometimes with two ventral canal cells, are common in the more primitive groups of homosporous ferns (except the Ophioglossidae).

The fern archegonium develops from a superficial cell of the prothallus, which divides by two transverse walls, forming a tier of three cells. The upper cell divides into a rosette of four daughter cells (neck initials) by walls perpendicular to its basal wall; these by repeated transverse divisions develop into an elongated neck. Meanwhile the middle cell of the row of three enlarges and protrudes between the rows of neck cells. Its nucleus divides, and one of the daughter nuclei enters the protruded anterior end. The anterior end is cut off as the neck canal cell, which later becomes binucleate. The basal cell cuts off a small ventral canal cell next to the neck canal cell and develops into the egg. The lowermost cell of the row of three generally divides vertically once or twice and forms a set of basal cells that are generally indistinguishable from the other prothallial cells. Nishida & Sakuma (1961) have pointed out that there exists some characteristic regularity in the sequence of nuclear divisions in the axial row of the fern archegonium. According to them a ventral canal cell is formed before the nucleus of the neck canal cell divides in Marattiidae, Anemiaceae, Cyatheaceae, Gleicheniaceae, Grammitidaceae, Hymenophyllaceae, Loxsomaceae, Osmundaceae, Parkeriaceae, Plagiogyriaceae, and Polypodiaceae. In the Ophioglossidae, Adiantaceae, Cheilanthaceae, Dennstaedtiaceae, Dryopteridaceae, Lindsaeaceae, and Pteridaceae the ventral canal cell is differentiated only after the neck canal cell has completed its nuclear divisions. Both conditions occur in the Blechnaceae and Matoniaceae. This character is regarded by them as of some significance in the study of the phylogeny of the ferns.

VEGETATIVE PROPAGATION

Vegetative propagation by means of proliferations that develop on old prothalli is fairly widespread among homosporous ferns. Regeneration by branches arising from superficial or marginal cells and developing into daughter prothalli probably occurs in all ferns under certain conditions. In the case of the Ribbon-like type of prothalli, progressive degeneration of the older regions occurs regularly, resulting in the separation of the branches as independent prothalli. Other than these common methods of vegetative propagation, a few groups of ferns exhibit well organized methods of vegetative multiplication characteristic of each group. For example, in the Grammitidaceae there is a prolonged filamentous stage during early development of the prothalli. The germ filaments are moniliform (Fig. 54) and easily break into fragments. Each fragment (Fig. 55) then develops into an independent prothallus. The Hymenophyllaceae, Vittariaceae, and some of the Polypodiaceae that possess Ribbon-like perennial prothalli produce special prothallial gemmae which, when shed, develop into fresh prothalli. Gemmae are produced marginally at the anterior end of branches of the prothalli and are borne on short, usually unicellular, papilla-like sterigmata. Among the Polypodiaceae, genera like *Colysis, Kaulinia* (Fig. 79), *Leptochilus,* and *Paraleptochilus* produce gemmae. In all these genera the gemmae are unicellular, dumbbell-shaped, densely chlorophyllous structures borne singly on the sterigmata. Fresh gemmae are produced on the same sterigmata when the older ones are shed. In the Vittariaceae and Hymenophyllaceae (Figs. 61–63) the gemmae are larger and are filamentous structures, usually three or four (often two to six) cells long. In the *Hymenophyllum*-group of genera the gemmae become multiseriate by longitudinal divisions in the intercalary cells (Fig. 63). The gemmae of the Vittariaceae and *Hymenophyllum*-group are spindle-shaped and are borne vertically on the sterigmata (attached by an end cell). In the *Trichomanes*-group the gemmae are borne perpendicular to the sterigmata (attached by one of the middle cells) and may become 10 to 12 cells long (Fig. 61). On shedding, one or both ends of the gemma produce a germ filament, or one end may produce a rhizoid. Sometimes both ends may produce rhizoids, and the intercalary cells produce perpendicular branches that develop into germ filaments. Vegetative multiplication by gemmae often results in the formation of extensive colonies of prothalli and in some cases wide distribution of fern taxa represented by their prothalli alone, as reported in the case of *Grammitis nimbata, Hymenophyllum tunbridgense, Vittaria lineata,* and *Trichomanes* spp. (Farrar, 1967). An extreme case is the Appalachian prothallus covering extensive patches (several metres across) and identified as the prothallus of a vittariaceous fern (Wagner & Sharp, 1963), which by reduction has lost the sporophytic stage and is now represented only by the gametophyte propagating itself by vegetative means.

APOGAMY

Apogamous development of sporophytes from prothalli is found in several groups of ferns. In some cases as in *Pelleaea glabella* apogamous as well as sexual races are found in the same species and then the geographical range of the apogamous race is comparatively greater (Tryon, 1968). Also, many apogamous species are able to thrive in comparatively more xeric habitats (Klekowski, 1969; Tryon, 1968). This is possibly because the sexual species are dependent upon the availability of free water for reproduction while the apogamous ones are not. As mentioned earlier, apogamy in fern gametophytes was known for long from the descriptions of Farlow (1874a, b), deBary (1878), Leitgeb (1885), and Lang (1898). Many species of homosporous ferns exhibit obligate apogamy. In these, sex organs are either not produced or are generally nonfunctional (particularly the archegonia). Also, the sporophyte and the gametophyte, then, have the same chromosome number, because of apomixis in the sporangium, resulting in the formation of spores with the same chromosome number as the sporophyte (Farmer & Digby, 1907; Heilbronn, 1910; Dopp, 1932; Manton, 1950; Bell, 1960; Mehra & Bir, 1960; Braithwaite, 1964). The cytological mechanisms of apogamy have been reviewed by Steil (1939, 1951) and more recently by Miller (1968). In many ferns (in which apogamy is not obligate) apogamy is induced when fertilization is prevented, because of unsuitable physical or physiological environment. The mechanism involved in this type of apogamy is not known. Gametophytes of some species like *Pteridium aquilinum* (L.) Kuhn, which under ordinary conditions of growth reproduce sexually, become apogamous when grown in a culture medium containing sugars (Whittier & Steeves, 1960, 1962). Apogamy is widespread in certain groups of ferns like the Adiantaceae, Cheilanthaceae, and Pteridaceae. It is comparatively rare among the primitive families of homosporous ferns. In general, the prothalli of apogamous species are reported to grow and mature faster than those of related sexual species and the adult thalli are comparatively smaller in size (Whittier, 1968, 1970).

TAXONOMY

As mentioned above, the fern prothallus is characteristic of each major taxonomic group in its structure, form, and development. The salient features of gametophyte morphology of the different families of homosporous ferns are summarized below; the Hymenophyllopsidaceae, Kaulfussiaceae, and Metaxyoideae are omitted since their prothalli are totally unknown. The classification adopted here is one proposed recently by one of us (Nayar, 1970, 1971).

OPHIOGLOSSIDAE (OPHIOGLOSSACEAE)

Details regarding the early development of the prothallus are unknown in the group, but the morphology of the adult prothallus of *Botrychium* (Hoffmeister, 1862; Jeffrey, 1896; Bruchmann, 1906; Campbell, 1921, 1922; Nozu, 1954; Nishida, 1955), *Helminthostachys* (Lang, 1902, 1914; Nozu, 1958, 1961), and *Ophioglossum* (Bruchmann, 1904; Campbell, 1911; Lang, 1902; Manton, 1950; Nishida, 1955; Nozu, 1961) is known in sufficient detail. The Ophioglossaceae differ markedly in their prothallial morphology from other ferns. The adult thallus is of the Tuberous-type, fleshy, naked, massive, subterranean, saprophytic, brownish, and bearing rhizoids all over. There is no well-organized meristem in *Botrychium* and *Helminthostachys*, but the prothalli of *Ophioglossum* grow by means of a 4-sided apical meristematic cell. The prothalli are very slow-growing and live for several years. An endophytic fungus is found in the prothallial tissue. In *Botrychium* (Fig. 4) the prothallus is dorsiventral having a dorsal longitudinal ridge bearing sex organs; antheridia are borne in two or three irregular rows on the upper part of the ridge and archegonia in several rows on the sides of the ridge, spreading on to the adjacent flat areas. Septate rhizoids are reported in *Botrychium virginianum* (L.) Sw. (Jeffrey, 1896). The prothallus of *Helminthostachys* is radially symmetrical (Fig. 3), irregularly ovoid or cylindrical (devoid of ridges as in *Botrychium*), and erect-growing, with the sex organs borne on the distal regions of both the main axis and the lobes. The prothallus of *Ophioglossum* is also cylindrical and often branched. Rhizoids are profuse except probably in some species (Bruchmann, 1904), and sex organs are restricted to the apical end.

The spores in the family are of the tetrahedral type (usually with a tendency to be globose), devoid of any perine and ca. 20–35 × 30–35 μ in size (Devi & Nayar, 1969). The exine bears characteristic depressions all over; the depressed areas may either be small and scattered (pitted exine) or large and crowded, sometimes elongated and rarely forming a regular reticulate pattern. The spores have dense opaque contents that include many albuminous and starch granules. On germination the spore swells considerably and divides into two equal daughter cells by a wall perpendicular to its polar axis. No chlorophyll is usually seen in the prothallial cells. The next division occurs in the lower cell (the cell away from the laesural end of the spore) and is by a wall parallel to the polar axis of the spore, dividing the celll into two equal parts. Details of further growth of the prothallus are imperfectly known. The thallus develops into a nearly circular mass before the adult form is attained. Sex organs are embedded in the prothallial tissue. The antheridium (Fig. 5) is massive and either completely or partially embedded. The antheridial wall, contrary to the condition in other ferns, is two- or three-layered. The anterior exposed end of the antheridial wall usually consists of two or three layers of cover cells; the cover is only one layer thick in some species of *Ophioglossum*. The wall cells are small and radially flattened. The opercular cell is small and triangular to pentagonal in outline. The archegonial neck has six to eight tiers of four discoid cells each and is vertical. The neck canal cell is binucleate, but may sometimes be divided in *Helminthostachys* (Nozu, 1961). The neck protrudes partially out of the prothallial tissue in *Botrychium* and *Helminthostachys*.

MARATTIIDAE (ANGIOPTERIDACEAE, DANEACEAE, AND MARATTIACEAE)

Prothallial morphology of the Marattiidae has long attracted the attention of pteridologists, and the prothallus of most genera has been investigated. Detailed accounts of prothallial morphology are available of *Marattia* (Campbell, 1894; Stokey, 1942) and *Macroglossum* (Campbell, 1914; Stokey, 1942); some details of the prothallial morphology are known of *Angiopteris* (Luerssen, 1875; Jonkman, 1878, 1880; Farmer, 1892; Haupt, 1940; Nozu, 1956), *Archangiopteris* (Sasaki, 1928), and *Danaea* (Brebner, 1896). The adult prothallus is Cordate-thalloid, naked, massive, fleshy, and dark green in color. The midrib is broad and heavy and merges gradually with the wings on either side, the wings being four or more cells thick near the midrib and gradually tapered towards the margin. The prothallus is large (over 2 cm long), slightly elongated, and slow-growing; the midrib is occasionally branched. An endophytic fungus is found in the midrib region. The rhizoids may often be septate.

The spores of the Marattiidae (Nayar, 1964a; Devi, 1966; Devi & Nayar, 1969) are either of the tetrahedral type (*Angiopteris*, *Archangiopteris*, and *Macroglossum*) or of the bilateral type (*Christensenia*, *Danaea*); both the types occur in *Marattia* (Mettenius, 1856a, b; Selling, 1946). A distinct perine is found in some, but in the others a perine is not so evident. The spore coat is granulose (*Angiopteris*, *Macroglossum*) to spinulose (*Archangiopteris*) or even spinose (*Christensenia*, *Danaea*). In general, the spores are quite small in size (15–22 × 25–35 μ) in the group. Spore germination is of the Amorphous-type. On germination the spore coat opens at the laesura, and the contents enlarge considerably to form a globose, densely chlorophyllous cell. This cell divides irregularly to form a small plate of cells that soon becomes a mass by cell divisions in the third plane. Division in the third plane may be initiated when the plate consists of only four cells or may occur only later. A rhizoid may be formed early or is formed only after a plate or mass is developed. In *Angiopteris suboppositifolia* de Vries, Nozu (1956) reports the formation of a row of two or three cells on spore germination; these cells soon form a plate and later a mass. Prothallial development is of the characteristic Marattia-type. Sex organs are of the Eusporangiate-type and, contrary to the condition in the higher ferns, are embedded in the prothallial tissue. The antheridial wall is one cell thick (Fig. 7), and the cap cell divides to form a triangular operculum (Fig. 6). The archegonial neck is short and consists of four rows of three or four short cells each; the anterior set of neck cells protrude slightly out of the prothallial tissue. The egg is small and the ventral canal cell very conspicuous. The neck canal cell is sometimes divided by a transverse wall. Some cases of apogamy are reported.

OSMUNDACEAE

Details of prothallial morphology are known of all the three genera of the family, viz., *Leptopteris* (Luerssen, 1874; Stokey & Atkinson, 1956a), Osmunda (Kny, 1872; Luerssen, 1874; Campbell, 1892; Jung, 1927; Gerhardt, 1927; Orth, 1936; Sarbadhikari, 1939; Stokey & Atkinson, 1956a), and *Todea* (Stokey & Atkinson, 1956a; de Maggio, 1961). The adult prothallus is Cordate-thalloid, often large and conspicuously elongated (Fig. 9) when old (usually four to six cm long, but sometimes two or three times as much), naked and with a heavy median midrib (10 to 20 cells thick). The wings merge imperceptibly with the midrib (up to four cells thick near the midrib but gradually one cell thick towards the margin; Fig. 8), flat and spread out in young thalli but ruffled in the older ones. The prothalli continue to grow for several years, and many of them often branch. Rhizoids borne on old thalli are firm in texture and reddish to orange or dark brown in color; those on young thalli are nearly hyaline and soft. On adult thalli the rhizoids are aggregated towards the center of the midrib (not the sides). Septation in the rhizoids is not uncommon.

The spores are large ($55–60 \times 60–75\ \mu$), conspicuously chlorophyllous, globose-tetrahedral, devoid of perine, and with the exine thin and prominently granulose (Erdtman, 1957; Nayar, 1964a; Devi, 1966; Devi & Nayar, 1969). Spore germination is characteristically of the Osmunda-type, but in some species minor variations are reported: in *Osmunda cinnamomea* Linn. a short uniseriate germ filament may be produced instead of the usual quadrant at spore germination (by the prothallial cell dividing transversely two or three times before any longitudinal division occurs); *O. claytoniana* L. exhibits a pronounced tendency to form germ filaments (up to 17 cells long) under insufficient light conditions; young prothallial plates give rise to uniseriate germ filaments under adverse conditions of growth in *O. claytoniana* Linn., *O. javanica* Bl. and *O. banksiifolia* (Pr.) Kuhn. Prothallial development is of the Osmunda-type. Young prothallial plates grow rather rapidly, producing an apical meristematic cell in about 10 days after spore germination. The meristematic cell maintains its identity for only a short period, after which it is replaced by a pluricellular meristem. In some cases a prothallial plate may develop two meristematic cells (instead of one), one in each of the anterior quadrants. A meristematic cell stage is omitted, and a marginal meristem is directly established in some prothalli. All rhizoids borne on young prothalli are chlorophyllous, the first rhizoid containing more chloroplasts than the later formed ones. Antheridia are commonly developed by the prothalli four to six weeks after spore germination, and archegonia two to three weeks later (i.e., when thallus is distinctly cordate), both types of sex organs being produced together. The antheridia of the Osmundaceae are of the Eusporangiate-type and massive, with the wall consisting of several (8 to 12, up to 20 to 25 in large antheridia) curved cells (Figs. 10–12). The archegonia are massive and restricted to the lateral (rhizoidless) sides of the midrib and are in one or two rows (3 to 7 rows on large old thalli) on either side, sometimes slightly extending on to the wings as in *Leptopteris superba* (Col.) Pr., but not on to the median plane of the midrib. The archegonial neck is straight and at right angles to the midrib. All cells of the archegonium, including the egg, contain starch deposits. The neck canal cell is usually binucleate at maturity. Regeneration from adult prothallus is frequent in all the genera.

PLAGIOGYRIACEAE

The adult prothallus of the solitary genus *Plagiogyria* is Cordate-thalloid (Bower, 1910; Stokey & Atkinson, 1956b; Nayar & Kazmi, 1962a, b) with large, spread out, thin-walled wings and a broad midrib (4 to 7 cells thick and composed of large cells) bearing profuse stout brownish rhizoids. The prothalli are naked, large (over 1 cm across), and longer than broad, often with a narrowed base.

The spores of *Plagiogyria* are of the tetrahedral type, devoid of perine, with the exine usually bearing deciduous verrucate ornamentation (Nayar, 1964a; Devi, 1966). On shedding, they lose viability rapidly when dry, but retain viability for long periods when sown on a wet substratum. Germination of the spores is irregular and belated, some spores germinating in about 30 to 90 days of sowing, while others take a far longer time, extending 200 to 300 days (Stokey & Atkinson, 1956b; Nayar & Kazmi, 1962a, b). Germination is of the Vittaria-type, producing a chlorophyllous rhizoid at the proximal end and a uniseriate germ filament (composed of short cells) lateral to the rhizoid. Formation of a prothallial plate is initiated by longitudinal division of the anterior cells when germ filaments are two to six cells long, and all cells (sometimes including the basal cell) divide longitudinally during the process. Prothallial development is of the Adiantum-type, but the apical meristematic cell is sluggish and often differentiated only after the prothallial plate becomes two or three cells broad; in many cases a meristematic cell stage is omitted and a pluricellular meristem is established directly. Prothalli reach maturity about six months after spore germination. The antheridia are of the Eusporangiate-type (subglobose with a central mass of sperms enveloped by a variable number of narrow curved cells) and are produced by prothalli from the early cordate stage onwards. On adult thalli they are found mostly on the wings and the lateral edges of the midrib. The cap cell is often lateral. Archegonia are restricted to the ventral anterior half of the midrib and have elongated necks curved away from the apex of the prothallus. The neck canal cell is septate and often divided into four (axial row of archegonium consisting of egg, ventral canal cell, and a row of four neck canal cells). Regeneration of prothallus is reportedly very frequent.

SCHIZAEACEAE

The family as construed here includes three genera, *Actinostachys*, *Lophidium*, and *Schizaea*. Information on the gametophytic generation was for a long time restricted to the descriptions of the filamentous prothalli of *Schizaea pusilla* Pursh (Britton & Taylor, 1901), *S. rupestris* R. Br. (Thomas, 1902) and *S. bifida* Willd. (Goebel, 1918). Recently Bierhorst (1965, 1966, 1967a, b, 1968a) brought to light a wealth of very interesting information regarding the prothalli of *Actinostachys* and *Lophidium* in addition to describing the prothalli of *Schizaea fistulosa* Labill. and S.

robusta Bak. in Hook. et Bak. The adult prothallus of *Schizaea* (Fig. 22) is of the branched, uniseriate Filamentous-type, devoid of any trichomes, and either subterranean (as in some species) or surface-living. The thallus is perennial and reported to live for over 13 years (Atkinson, 1965b). Rhizoids are borne on special bulbous cells (rhizoidophores) borne laterally on the creeping filaments and inhabited by a symbiotic fungus. Antheridia are borne on special short lateral branches and are of the common leptosporangiate type, but with the basal cell barrel-like or disk-like. Archegonia are produced in clusters either directly on the filaments or on small lateral cushions formed by the division of a short unicellular archegoniophore. The archegonium is entirely exposed as nowhere else in vascular plants; it has a bulbous venter with its wall composed of two layers of cells and a three-cells-long neck having the neck canal cell binucleate and narrow.

Both *Actinostachys* and *Lophidium* are unique in having subterranean, radially symmetrical, fleshy, tuberous, nonchlorophyllous prothalli composed of parenchymatous cells. In *Lophidium* the adult prothallus is a bushy, highly branched body apparently 1.0 cm in diameter, having a main axis bearing progressively thinner branch orders (Fig. 23). The ultimate ends are uniseriate, and growth in length is by transverse divisions of the terminal cell. The axis is strikingly jointed, each joint developing by longitudinal divisions in the cells of the uniseriate anterior region. Branches are borne at the acropetal ends of the joints. Slender, elongated, nonseptate rhizoids are borne on the thicker axes. Nearly all cells of the prothallus contain an endophytic fungus. The prothallus of *Actinostachys* is unbranched (or rarely branched) and tuberous with dense starch deposits in the cells. It is several cells thick throughout and grows in length by the activity of an obconical apical meristematic cell with three oblique cutting faces as occur in the sporophyte. Increase in girth is by secondary meristematic activity at the periphery. The thallus is mycorrhizal, its cells harboring an endophytic fungus. Rhizoids are borne in tufts on the surface and are one or two cells long (with a bulbous basal cell and an elongated anterior cell). Sporangia are sometimes borne on the tips of the rhizoids on old gametophytes of *A. oligostachys* Bierhorst. These sporangia are Gleicheniaceaeous in structure and not Schizaeaceous: the annular ring is uninterrupted and nearly vertical, with the stalk (rhizoid) attached lateral to the annulus at the base. The prothalli of all the known species are naked and apparently perennial; those of *A. oligostachys* are peculiar in being persistent and remaining attached permanently to the daughter sporophytes.

The spores of the Schizaeaceae are of the bilateral type, devoid of perine, with exine either smooth, pitted or costate (Selling, 1946; Harris, 1955; Devi & Nayar, 1969). Spore germination and details of development of the prothallus are imperfectly known in both *Actinostachys* and *Lophidium*. Available descriptions suggest that spore germination in *Actinostachys* results in a mass of cells (shaped like a tear drop) without any indication of a filamentous stage or rhizoid. The first rhizoid is produced when the cell mass consists of 3 to 10 cells. An obconical meristematic cell is differentiated when the cell mass is nearly five cells long and four cells across at its widest. By the activity of the meristematic cell a cylindrical thallus is produced, which is indistinguishable from an axis produced vegetatively from an older gametophyte. When the gametophyte is 1 to 3 mm long, peripheral thickening is initiated. At the cylindrical stage the prothalli are 0.3 to 1.5 mm in diameter and bear rhizoids and antheridia. Increase in thickness is effected by the development of a peripheral thickening meristem. This meristem appears at first towards the base (older end) of the prothallus and progressively spreads towards the apex, ultimately catching up with the apical meristem. The prothallus soon becomes tuberous by the activity of this meristem and often has an irregular surface, which is due to differential activity of the meristem at different regions. On the primary gametophyte axes, the rhizoids are uniformly distributed.

Antheridia of both *Actinostachys* and *Lophidium* are borne laterally on the gametophyte axes and are of the leptosporangiate type. However, eusporangiate type of antheridia, in which the cap cell is smaller than in the leptosporangiate type of antheridium and the annular cell is divided two or three times (producing a jacket of three to five cells), are found as abnormalities in *Actinostachys*. The cap cell of the normal antheridium is described as "nipple-shaped." The basal cell is disk-like, but occasionally it may become elongated, making the antheridium "stalked." Antheridial dehiscence is by the discharge of the cap cell. During antheridial development the central spermatogenous cell is reported to originate as a sister cell of the basal cell rather than of the jacket cell as common among ferns (Bierhorst, 1966); the basal cell protrudes into the upper cell at the two-cell stage of antheridium development, and the protruded region is then cut off by a flat wall at the base to constitute the central cell. Archegonia are also borne laterally on the axes and are of the common Leptosporangiate-type with the venter embedded in the prothallus tissue. The neck is short, erect, and composed of four rows of cells, each consisting of three or four cells. The neck canal cell is usually binucleate (occasionally three- or four-nucleate) and swollen towards the tip at maturity. A distinct archegonial jacket is formed by division of cells proximal to the venter and later by the basal cells of the neck. Gametophytes of *A. melanesica* (Selling) Reed and *A. oligostachys* reproduce vegetatively by producing superficial buds. The bud is formed by proliferation of a solitary superficial cell on the older region of the prothallus, and originates as a subglobose protrusion in which an apical meristematic cell becomes differentiated later. In *A. intermedia* (Mett.) Reed vegetative multiplication is effected by proliferation of the necks of mature archegonia.

ANEMIACEAE

The gametophytes of both the genera of the family, *Anemia* (Bauke, 1880; Momose, 1949; Twiss, 1910; Kaur, 1961; Atkinson, 1962; Schraudolf, 1963) and *Mohria* (Bauke, 1878a; Atkinson, 1960b), are known in some detail. The adult prothallus of both is Cordate-thalloid but often elongated, with heavy, massive midrib and uplifted wings (so that the thalli are cornucopia-shaped). The wings are ruffled and often voluminous, and frequently one wing is smaller than the other. The wing cells in many species possess collenchyma-like or band-like thickenings on the lateral walls. In *Mohria* the prothallus (Figs. 13, 14) is one-sided, the midrib bearing a wing only on one side; the meristem is then lateral on the midrib. Also, the wing may be interrupted in *Mohria*, and in places the midrib is devoid of any wing at all. The midrib is often uplifted and grows nearly erect, becoming columnar and nearly cylindrical, with the meristem located just below the rounded tip (Fig. 14). Also, small flaps of sterile photosynthetic tissue are often borne on the midrib. The prothalli of both *Anemia* and *Mohria* are hairy, bearing both marginal and superficial hairs. The hairs (Fig. 15) are mostly club-shaped with a swollen, nonsecretory, terminal cell and a slender stalk, commonly one or two cells long; a few unicellular papillate hairs often occur in addition on the prothalli. In some species of *Anemia* and *Mohria caffrorum* (L.) Desv. the hairs are sometimes branched, and occasionally the stalk of the hair is three or more cells long (Fig. 17); rarely the stalk may become biseriate (Fig. 16), and sometimes the hair-bearing prothallial cells grow out into pluricellular protuberances subtending the hair.

The spores of the Anemiaceae are of the tetrahedral type, large (50–70 × 75–120 μ), and with the exine bearing characteristic thick concentric ridges; the ridges may bear verrucate to spinose excrescences or may be granulose or even smooth (Nayar, 1968b; Devi & Nayar, 1969). Spore germination is of the Anemia-type and results in a uniseriate germ filament usually composed of two to seven short cells. Plate formation is initiated by longitudinal divisions in the intercalary cells, and a broad spatulate thallus is developed in which a pluricellular marginal meristem is established laterally. The terminal cell of the germ filament may remain undivided, but generally it divides once or twice as the prothallial plate expands. All cells of the germ filament may divide longitudinally during plate formation. Prothallial development is in general of the Ceratopteris-type but differs from the typical form in that formation of a prothallial plate is effected mainly by the activity of cells behind the terminal cell of the germ filament (the terminal portion being sluggish). An obconical meristematic cell is never formed. Though the meristem is formed laterally, the extent of asymmetry of the young thallus varies with the species, depending on how far away from the terminal cell the meristem is formed; in some species of *Anemia* [*A. adiantifolia* (L.) Sw.] the meristem is nearly terminal, and the two wings are equal or nearly so.

Generally the two wings are unequal, the wing developed by the side away from the one which develops the meristem being conspicuously larger than the other in young prothalli. Development of a midrib is initiated much after a meristem is established. Sex organs in the family are of the Leptosporangiate-type. The basal cell of the antheridium is narrow and discoid. At dehiscence the cap cell of the antheridium is loosened at its rim, slips sideways (Figs. 18–21), and is then thrown off bodily (Atkinson, 1960b, 1962). The neck of the archegonium is nearly straight; the neck canal cell is binucleate (abnormally 3- to 4-nucleate).

PARKERIACEAE

Prothallial morphology of *Ceratopteris*, the only genus included in the Parkeriaceae, has long been well known (Kny, 1875; Yabe & Yasui, 1913); detailed descriptions are given by many contemporary authors (Bussman, 1939; Mahabale, 1948; Mahabale & Javalgekar, 1950; Javalgekar, 1960; Nishida, 1962; Pal & Pal, 1963; Momose, 1964a; Nayar & Kaur, 1969b; Klekowski, 1970a). The adult prothallus is naked, Cordate-thalloid, with a thin (3- to 4-cells-thick) midrib and often with unequal wings (composed of uniformly thin-walled cells) one or both of which are lifted up from the substratum so that the thallus is cornucopia-shaped. Irregularly shaped, nonmeristic, small, antheridial thalli occur mixed with cordate bisexual thalli. An endophytic fungus is reported by Mahabale (1948) and Javalgekar (1960) in the cells of the midrib region in thalli collected from nature; however, our observations and those of other workers (Pal & Pal, 1963) contradict this, a fungus being not normally present in the prothalli.

The spores of *Ceratopteris* are some of the largest among homosporous ferns (100–140 × 125–165 μ) and are tetrahedral, devoid of perine, with the exine bearing characteristic thick closely placed costate ridges forming concentric circles on each face of the spore (Erdtman, 1957; Nayar, 1964a, 1968b). Spore germination is of the Vittaria-type, producing a short germ filament composed of three to five short cells within two or three days of sowing of the spore (Nayar & Kaur, 1969b). The basal region of the germ filament is exceptionally stout, and the filaments are rather tapered upwards (Fig. 31). During development of a prothallial plate the anterior cells expand laterally and divide several times longitudinally so that the thallus assumes a Strap-like appearance; it has a large basal cell and next to it a row of three to five narrow elongated cells (Fig. 32). Sometimes all cells of the germ filament, including the basal cell, may divide longitudinally during plate formation. Usually the basal cell remains short and broad, while the cell next to it divides into two to four or sometimes more small daughter cells arranged in a row. Prothallial development is of the Ceratopteris-type (Pal & Pal, 1963; Nayar & Kaur, 1969b). A meristem is differentiated only after the prothallial plate is 6 to 12 cells broad, and the meristem is more towards the lower end of the plate than the apical end (Fig. 32 *m*). Consequently the young prothalli are markedly lopsided. The asymmetry of the wings persists to some extent to the adult stage. A wedge-shaped meristematic cell is not formed as reported by some workers (Mahabale, 1948; Javalgekar, 1960). The prothallus of *Ceratopteris* is fast-growing, taking scarcely a month to reach maturity.

Antheridia are produced by prothalli both marginally and superficially on the lower surface of the wings. They are characteristic in being embedded in the prothallial tissue and are basically of the common Leptosporangiate-type with the central mass of sperms surrounded by a deeply cup-shaped to basket-shaped basal cell, a short ring cell, and an undivided cap cell (Figs. 24–29). The basal cell is thin and encircles more than half of the central sperm mass. Antheridial dehiscence is by the cap cell that opens like a hinged lid on one side (Fig. 30) and is finally pushed off the antheridium. During development the antheridium may sometimes protrude slightly out of the prothallial surface so that the outer wall is conspicuously convex. In some rare cases the antheridium may protrude conspicuously out and appear hemispherical; then the ring cell is markedly broader and the basal cell less deeply basket-like. Archegonia are borne on the midrib and are of the usual Leptosporangiate-type, with the neck curved away from the apex of the prothallus and the neck canal cell swollen and binucleate at maturity. Apogamy is not infrequent and is possibly common in some cases. Regeneration from old as well as young thalli occurs, though not frequently.

LYGODIACEAE

The prothallus of the solitary genus *Lygodium* is Cordate-thalloid, symmetrical, and naked (Bauke, 1878b, 1880; Heim, 1896; Twiss, 1910; Rogers, 1923; Mahabale & Kulkarni, 1949, 1950; Chandra, 1963). Rogers (1923) recorded two cases in her cultures of *L. palmatum* (Bernh.) Sw., where the prothallus had hairs close to its meristem (a single hair in one case and two in another). She commented that "the two cases . . . should hardly be considered significant." Later, Mahabale & Kulkarni (1949) reported the occurrence of a few club-shaped hairs on the prothallus of *L. flexuosum* (L.) Sw. collected from nature. The presence of hairs in the species also requires confirmation. The prothallus in the genus is quick-growing (taking ca. 2 months to reach maturity), with a heavy (8–12 cells thick) midrib and one-cell-thick, spread out wings.

Spores of *Lygodium* are of the tetrahedral type, large (55–85 × 70–115 μ), devoid of perine, often having a prominently ornamented exine (Holttum, 1959; Devi, 1966). Spore germination is of the characteristic Anemia-type, producing a uniseriate germ filament three to five cells long. Formation of a prothallial plate is sometimes initiated very early by a longitudinal or oblique division in the sister cell of the first rhizoid mother cell as in *L. palmatum* (Rogers, 1923): thus at spore germination a plate of cells instead of a filament results. This plate, however, develops as does the prothallial plate developed from the elongated uniseriate germ filament. Prothallial development is of the Adiantum-type. The apical meristematic cell persists till the thallus is cordate. Sex organs are of the common Leptosporangiate-type.

PTERIDACEAE

The gametophytes of only four genera (out of nearly a dozen included in the family), viz., *Actiniopteris* (Stokey, 1948b; Nayar, 1963d), *Onychium* (Momose, 1964b), *Pityrogramma* (Nayar, 1964c), and *Pteris* (Farlow, 1874a; Goebel, 1930; Steil, 1933; Mehra, 1938b), are known in any detail. The present account includes many details of our own observations (unpublished) on the prothalli of several species of *Pteris* and *Onychium*. The adult prothallus in these genera is naked, Cordate-thalloid, with a distinct (sometimes massive) midrib and broad wings that become uplifted so that the prothallus has a funnel-like form (Fig. 34). The prothallus is quick-growing, reaching maturity in three to six months. Rhizoids are restricted to the lower surface of the midrib, are thin-walled, nearly hyaline or very pale brown in color, nonchlorophyllous, and with slightly dilated base (like an inverted funnel).

The spores of the family are of the tetrahedral type, 35–45 × 50–66 μ in size, with a granulose to rugulose exine and a characteristic collar-like equatorial ridge; a perine is absent but a skin-like outer layer of the exine often cracks and peels off in the mature spores (Nayar & Devi, 1966). The spores of the Pteridaceae retain viability long after shedding and germinate readily when sown. Spore germination is of the Vittaria-type, resulting in a uniseriate germ filament that develops a prothallial plate at its anterior end when three to eight cells long. Prothallial development is of the Ceratopteris-type. The stage in development at which a meristem is established differs slightly among the various species, as also the distance behind the apex where the meristem develops. In some species of *Pteris* a meristem is formed rather early and is more towards the apical region of the spatulate prothallial plate than towards the base of the expanded region. Also, in some cases an ephemeral wedge-shaped meristematic cell may sometimes precede the characteristic pluricellular meristem. On the other hand, in *Actiniopteris, Onychium, Pityrogramma,* and many species of *Pteris* a pluricellular meristem is formed directly from the marginal cells, and the meristem is nearer to the basal end of the expanded region of the prothallial plate than to its apex. Depending on the position of the meristem when it is established, the young prothallus is asymmetric (lopsided) for a longer or shorter period during its development; when the meristem is formed farther away from the apex, the thallus remains distinctly lopsided longer and vice-versa. In some, like *Actiniopteris,* the prothallus often remains more or less lopsided throughout.

Sex organs are of the common Leptosporangiate-type in the family. Antheridia are produced from early stages of development of the prothallus: some of the antheridia-bearing young prothalli exhibit arrested growth, remaining small, nonmeristic and irregularly shaped. During antheridial dehiscence the cap cell becomes loose and is pushed off, exposing the spermatozoids. The basal cell of the antheridium is funnel-shaped or saucer-shaped. The archegonial neck is elongated and curved away from the apex of the prothallus. It has a binucleate neck canal cell that is swollen towards the apex at maturity. Apogamy is frequent in the family, some genera like *Actiniopteris* being strictly apogamous with no sexual reproduction at all; in the other genera some species are apogamous, while some others reproduce sexually. Antheridia are produced, often profusely, on the apogamous prothalli and in most cases develop mobile spermatozoids. In many cases the apogamous thalli may bear archegonia also, but these do not develop to maturity and remain unopened and poorly developed. However, many species of *Pteris* exhibit apogamy as well as sexual reproduction in the same species. In such cases apogamous sporophytes are found on prothalli bearing normal sex organs.

CHEILANTHACEAEAE

Prothallial morphology is known of only six (out of nearly 16) genera, viz., *Aleuritopteris* (Mahabale & Shah, 1949; Panigrahi, 1955; Pray, 1961; Nayar, 1962f, 1963c), *Cheilanthes* (Pray, 1961; Nayar, 1962f, 1963c), *Doryopteris* (Nayar, 1960c), *Hemionitis* (Rao, 1949; Nayar, 1956a, 1962e), *Notholaena* (Tryon, 1947; Giaque, 1949; Nayar & Bajpai, 1964), and *Pellaea* (Pickett & Manuel, 1925; Pickett & Thayer, 1927; Steil, 1934; Nayar & Bajpai, 1964; Pray, 1968). In addition to published information, the present account includes details from our own observations on *Gymnopteris vestita* (Wall.) Und., and over two dozen species of *Cheilanthes* and *Notholaena*, particularly from the New World. The adult prothallus is Cordate-thalloid, with a prominent median midrib and broadly extended wings. As in the Pteridaceae the rhizoids possess slightly dilated bases. Collenchyma-like thickenings at the corners of the wing cells occur in many species; in some, like *Doryopteris*, band-like thickenings are found on the radial walls of the wing cells (Fig. 38). The prothalli of all genera, except *Notholaena*, are naked; glandular hairs, often secreting a waxy substance, occur on the prothallus of *Notholaena*. In some species (*N. incana* Pr. and *N. sinuata* Brack.) hairs are few, large, several cells long, sometimes more than one cell broad, and restricted to the anterior region of the mature prothallus; in some others (*N. aschenborniana* Kl., *N. galeottii* Fée, and *N. rigida* Dav.) hairs are profuse all over the margin, two cells long, and with swollen terminal glandular cell (Figs. 48, 49), and the hairs are produced from early stages in prothallial development.

Spores of the Cheilanthaceae are of the tetrahedral type, tending to be globose, 30 × 45 to 55 × 70 μ in size, and either with a smooth exine and a distinct perine or with an ornamented exine and devoid of a perine (Harris, 1955; Erdtman, 1957; Nayar & Devi, 1967; Knobloch, 1969). Spore germination is of the Vittaria-type, producing a uniseriate germ filament, three to eight cells long. Prothallial development is of the

Adiantum-type in *Aleuritopteris*, *Doryopteris*, and some species of *Cheilanthes*. However, there is often a strong tendency for the prothalli to omit the meristematic cell stage and establish a pluricellular meristem directly from the apical marginal cells of the spatulate prothallial plate. In many cases, even though an obconical meristematic cell is formed, it is differentiated rather late in prothallial development (only after a broad spatulate thallus is formed). In *Hemionitis*, *Notholaena*, several species of *Pellaea*, and some species of *Cheilanthes*, prothallial development is of the Ceratopteris-type. In some the terminal region of the germ filament is sluggish, and the prothallial plate is developed from intercalary cells of the germ filament. However, except in *Notholaena*, the young prothallus is often not lopsided, since during plate formation the terminal region is pushed to one side by more rapid expansion of the prothallial plate on the opposite side before a meristem is differentiated (on the more expanded side, and thus apparently terminal in position). In some species the sluggish terminal region of the germ filament may also take part in the expansion of the prothallial plate, though pushed away during development to a lateral position. Sometimes the products of the terminal cell of the germ filament remain as a protruded ameristic lobe as in *Hemionitis arifolia* (Burm.) Moore, *Notholaena sinuata*, and *Pellaea viridis* (Forsk.) Prantl. In general, there is much variation among the different species of *Pellaea* and *Cheilanthes* as well as in *Gymnopteris vestita* in the mode of development of the prothallus. Typical Adiantum-type of development is rare and typical Ceratopteris-type infrequent; the majority of the species exhibit an intermediate condition. A meristematic cell stage is omitted in most cases, the prothallial plate becoming several cells broad when a pluricellular meristem is formed directly from marginal cells at or near the apex of the plate. However, in some, such as *Pellaea atropurpurea* (L.) Link, *P. doniana* Bak., *P. falcata* (R. Br.) Fée, and *P. rotundifolia* (Forst.) Hook., an apical meristematic cell often precedes the establishment of a pluricellular meristem in most thalli. In others, such as *P. macrophylla* Fée, *P. viridis*, and some species of *Cheilanthes*, though the majority of thalli omit a meristematic cell stage, some do develop an obconical meristematic cell which functions for a short while. The meristem is formed either from the products of one of the daughter cells of the terminal cell of the germ filament (the other being sluggish) as in *Cheilanthes aemula* Maxon, *C. leucopoda* Link, *C. meifolia* D. C. Eat. in Watson and *Pellaea wrightiana* Hook., or from the products of the penultimate cell (behind the sluggish terminal cell of the germ filament) which forms the anterior region of the prothallial plate. In both cases the meristem is apparently 'apical,' being medianly placed at the anterior end of the broad prothallial plate; however, ontogenetically it is 'lateral.' In *Gymnopteris vestita* some prothalli follow the Adiantum-type of development while most others follow a nearly Ceratopteris-type.

Sex organs are of the common Leptosporangiate-type. Small, irregularly shaped, antheridial prothalli occur in most species. At antheridial dehiscence the cap cell either becomes loosened on one side and opens up like a hinged lid (many species of *Cheilanthes, Doryopteris, Hemionitis*), or opens by a lateral pore-like aperture developed in the cap cell (some species of *Notholaena,* and some of *Cheilanthes*) to release the spermatozoids. Apogamy is frequent and some species are totally apogamous. Some of the apogamous species develop antheridia with viable spermatozoids. Archegonia are rare on the apogamous prothalli, and where found are nonfunctional. Apogamy is more frequent in *Pellaea* and *Notholaena* than in the others, though several species of *Cheilanthes* (particularly of the New World) and *Aleuritopteris* are also apogamous. In most cases the apogamous gametophytes are highly reduced, irregularly shaped thalli.

ADIANTACEAE

The family Adiantaceae as construed here consists of six genera, of which gametophytes are known of *Acrostichum* (Schumann, 1915; Stokey & Atkinson, 1952c; Nayar & Kazmi, 1964), *Adiantum* (Mehra, 1932, 1938a; Kachroo & Nayar, 1952, 1953; Nayar, 1961b, 1962c), *Anogramma* (Taylor, 1846; Goebel, 1877; Proskauer, 1963), and *Coniogramma* (Nayar, 1962d). Some details of the gametophyte of *Syngramma* are reported in the literature (Heim, 1896; Atkinson, 1970); the present description gives details of our unpublished observations as well. The adult prothallus (Fig. 33) is Cordate-thalloid and naked, with a distinct median midrib and broad wings. Collenchyma-like thickenings occur at the corners of the wing cells in some species. Rhizoids are nearly hyaline and possess a slightly dilated basal region. The prothallus of *Anogramma leptophylla* (L.) Link is bryophytic in nature (Proskauer, 1963), being perennial and producing annual sporophytes, and bearing special tubers for storage of food material.

The spores are of the tetrahedral type, devoid of a perine (but sometimes having a tendency for an outer skin-like region of the exine to peel off in bits), and with a smooth or granulose to rugulose exine. Spore germination is of the Vittaria-type. There is much variation among the different genera in prothallial development. In *Adiantum* and *Coniogramma* the development is of the typical Adiantum-type. In *Acrostichum* it is of the Ceratopteris-type, with the terminal cell of the germ filament sluggish and prothallial plate developing from cells behind it. The young prothallus of *Acrostichum* is distinctly lopsided, and the asymmetry often persists till maturity. The meristem is established laterally, more towards the basal end of the prothallial plate than towards the apex. In *Syngramma* prothallial development is intermediate between the typical Adiantum- and Ceratopteris- types. An obconical meristematic cell is developed by some germ filaments but it is ephemeral and the prothallus soon becomes nonmeristic. Commonly the development of a prothallial plate is initiated by longitudinal divisions in the anterior cells, including the terminal cell of the germ filament, and the anterior end by repeated divisions forms an expanded plate in which a marginal pluricellular meristem is formed laterally near the apex. The asymmetry of the young prothallus is only transitory; soon the meristematic region becomes apical, and a symmetrical cordate thallus is formed. Sex organs are of the common Leptosporangiate-type in the family. The cap cell often opens like a lid before collapsing at antheridial dehiscence. Antheridial dehiscence is by a pore-like opening developed in the cap cell in *Acrostichum* and *Coniogramma*; the pore gradually widens till the cap cell collapses. The basal cell of the antheridium is often disk-shaped or saucer-shaped.

VITTARIACEAE

The morphology of the gametophyte of this small epiphytic family is only imperfectly known; gametophytes are known only of a few species of the two larger genera *Antrophyum* and *Vittaria* (Goebel, 1888; Britton & Taylor, 1902; Troll, 1932). Most of the details given here are based on our own unpublished observations on some species of *Vittaria* and *Antrophyum*. The adult prothallus is Ribbon-like, elongated, naked, branched, one cell thick, and devoid of a well-organized meristem. The spores (Copeland, 1947; Nayar, 1964a; Devi, 1966) in the majority of genera are of the tetrahedral type, but in *Vittaria* and *Antrophyum* some species possess bilateral spores. The spores possess a thin, smooth, or granulose exine and are devoid of perine. Spore germination is of the Vittaria-type. The germ filament develops into a flat, Ribbon-like thallus or may produce lateral branches from the intercalary cells, and these branches develop into broad thalli. The germ filament is usually much elongated and often branched. In some cases the germ filament stops terminal growth, and lateral branches are produced which continue growth. Prothallial development is of the Kaulinia-type. Sex organs are of the common Leptosporangiate-type. The antheridium has a barrel-shaped basal cell (often tapered to the base and with the upper wall flat) that is sometimes elongated and curved. Antheridia are produced from the early filamentous stage onwards and are sometimes profuse on young filaments developed from gemmae. On the adult thallus they are borne superficially on the lower surface. Archegonia are borne on irregular cushions two to four cells thick and scattered on the ventral surface of the prothallus towards the margins of the branches. Vegetative multiplication of the adult thallus is effected by fragmentation and by the production of gemmae. The gemmae are short-filamentous structures, two to four cells long, spindle-like, and borne vertically on short, unicellular, marginal sterigmata at the anterior end of the branches.

The occurrence of a branched, Ribbon-like prothallus multiplying vegetatively by means of gemmae in the Appalachian region of America, has recently been reported (Wagner & Sharp, 1963). It is ascribed to the Vittariaceae and is identified as a reduced form of *Vittaria lineata* (L.) Sm. The fern is remarkable in that it exists only as a gametophyte that propagates itself vegetatively by means of gemmae and by fragmentation. No sex organs are produced. The gemmae are spindle-shaped filamentous bodies 4 to 10 cells long. No naturally occurring sporophytes have ever been found, but abnormal apogamous buds are reported on cultured thalli. These buds bear clathrate paleae and rarely narrow simple leaves.

CYATHEACEAE

Subfamily Cyatheoideae

Our information on the gametophyte of the Cyatheoideae is restricted to the descriptions of the prothalli of *Lophosoria* (Stokey, 1930) and some species of *Cyathea* (including *Alsophila* and *Hemitelia*) (Bauke, 1876; Heim, 1896; Stephenson, 1907; Schlumberger, 1911; Stokey, 1918, 1930). The adult prothallus in both the genera is Cordate-thalloid (rather elongated and narrow), that of *Cyathea* being broader and shorter compared to those of *Alsophila* and *Hemitelia* (Stokey, 1930). The prothalli are long-lived (two to six years), and there is a tendency for the thalli to elongate slightly with age. The midrib is thin but often becomes heavy with age. In vigorous prothalli there is a tendency for the midrib to develop more strongly than the wings; in some such thalli the midrib extends as a heavy, flattened, or nearly cylindrical projection (sometimes prolonged and erect-growing) beyond the wings. The wings are rather thin, particularly in *Lophosoria*. Multicellular bristle-like hairs are borne on the prothalli towards maturity (only after midrib formation). Hairs occur on both the surfaces, but not on or near the margin. On the ventral surface they are along the sides of the midrib and adjacent area of the wings; on the dorsal they are mostly restricted to the midrib.

The spores of the cyatheoid ferns are of the tetrahedral type with the exine variously ornamented and often having a skin-like outer layer, which cracks and partially peels off. Spore germination is of the typical Cyathea-type. Prothallial development is of the Adiantum-type or nearly of the Drynaria-type, a meristematic cell often being established only when the thalli are four or five cells broad. Plate formation is initiated usually when the germ filament becomes three or four cells long (but sometimes when two cells long). The terminal cell divides by a wall perpendicular or nearly perpendicular to its basal wall to initiate formation of a prothallial plate. The thallus broadens rapidly and becomes broader than those of higher ferns at the same stage of growth. Both antheridia and archegonia are borne together on the prothalli, but some vigorous thalli are strictly archegonial. Antheridia are produced from the cordate stage in development of the prothallus. The antheridium (Figs. 35–37) is basically of the Eusporangiate-type but less massive than the typical form and with a simpler wall structure (wall commonly composed of five cells, i.e., a basal, usually wedge-shaped cell extending half to three-quarters across the base of antheridium; a narrow, lower ring cell attached longitudinally to the antheridial wall by a connecting wall; a broad, upper ring cell encircling the sperm mass; a crescent-shaped and an ellipsoid opercular cell formed by division of the primary cap cell). Many variations in wall structure occur in nearly all the species. In structure the antheridia of *Cyathea* (excluding *Alsophila* and *Hemitelia*) approach the Leptosporangiate-type more closely than those of the other taxa; the antheridia of *Lophosoria* are generally larger than those of the others, with a more complicated wall and often asymmetrical. During dehiscence the opercular cell is thrown off intact. Archegonia are produced only after the midrib becomes four or more cells thick. The archegonial neck is elongated (6 to 8 cells long), heavily cutinized on the outside, and only slightly curved (tilted in any direction). The neck canal cell is commonly binucleate but rather frequently 4-nucleate. Apogamy is reported in some species (Stokey, 1918).

Subfamily Dicksonioideae

Prothallial morphology of a few species of *Dicksonia* (Bauke, 1876; Stokey, 1930) and the monotypic genus *Cystodium* (Atkinson, 1965a) is known. The adult prothallus is Cordate-thalloid, often broader than long, with broad, ruffled wings and with the midrib becoming massive with age. The thalli are long-lived as in the Cyatheoideae but are naked. They are monoecious but show more tendency to dioecism than in the Cyatheoideae. Irregular, small, nonmeristic male thalli are often found. The spores of the Dicksonioideae are of the tetrahedral type, often with verrucoid (rarely striate) ornamentation on the exine, and are devoid of perine (Nayar & Devi, 1968). Spore germination and prothallial development are as in the Cyatheoideae, but the tendency to form an elongated germ filament is only very slight, plate formation often being initiated at the two-celled stage. The young thalli are broader and shorter than in the Cyatheoideae. The antheridia are of the type found in Cyatheoideae, but often have more complicated walls. The neck of the archegonium is longer than in the Cyatheoideae and either straight or more or less curved sideways. The neck canal cell is usually binucleate, but not infrequently 4-nucleate. Apogamy is reported in some species (Stokey, 1918).

Subfamily Cibotioideae

Prothallial morphology of *Cibotium schiedei* Schlecht. et Cham. is known from several early accounts (Kny, 1869; Bauke, 1876; Schlumberger, 1911), and that of this species as well as five others from the detailed account presented by Stokey (1930). The adult prothallus is Cordate-thalloid, broader than long, and with the wings flat when young but becoming ruffled with age. The midrib is broad and massive, and may occasionally be forked. The thalli are long-lived as in the Cyatheoideae and in some, like *C. barometz* (L.) J. Sm., become much elongated and branched when old. As in the Dicksonioideae the prothalli of the Cibotioideae are naked. The spores are of the tetrahedral type with the proximal side flat and possessing an equatorial collar-like ridge in some species; a perine is absent and the exine is granulose, rugulose, or tuberculate with the ornamentation markedly more prominent on the distal than on the proximal side. Spore germination and prothallial development are as in the Cyatheoideae. Formation of a prothallial plate is initiated early, but an elongated germ filament (four or five cells long) may occasionally be formed as in *C. regale* Linden. Sex organs are similar to those of the Dicksonioideae. Apogamy is reported in some species.

Subfamily Thyrsopteridoideae

Prothallial morphology of the monotypic genus *Thyrsopteris* and of *Culcita macrocarpa* Pr. (Stokey, 1930) is known. The adult prothallus is large (up to 2 cm long), Cordate-thalloid, but elongated, with wide thick (up to seven cells) midrib and narrow uplifted wings. In contrast to the Cyatheoideae, the prothalli are naked. Occasional forking of the midrib is reported in *Culcita*. The spores are of the tetrahedral type with an irregularly pitted exine (Erdtman, 1957). Spore germination and prothallial development are similar to those in the Cyatheoideae, but plate formation is initiated at the two-celled stage of the germ filament, and the plate is elongated (not rapidly broadening). The antheridia are of the typical Eusporangiate-type in *Thyrsopteris* but simpler in *Culcita* (intermediate between the *Thyrsopteris*- and *Cyathea*- types); rarely typically *Cyathea*-like antheridia with five wall cells occur in both. The opercular cell is thrown away at dehiscence. Archegonia are similar to those of the Dicksonioideae. There is a strong tendency for apogamy in *Thyrsopteris.*

DENNSTAEDTIACEAE

Gametophytes are known of both the major genera of the family, viz., *Dennstaedtia* (Conard, 1908; Kaur, 1962) and *Microlepia* (Kaur, 1962; Nayar & Kaur, 1963a, b). The adult prothallus is naked and Cordate-thalloid with a median light midrib, clearly demarkated from the broad flat wings. The rhizoids are nearly hyaline and restricted to the midrib. The spores are tetrahedral, devoid of perine, commonly ca. 25 × 35 μ in size, and with granulose to verrucate exine (Nayar & Devi, 1968). Spore germination is of the Vittaria-type, producing a slender uniseriate germ filament. Prothallial development is of the Adiantum-type. Sex organs are of the common Leptosporangiate-type. Antheridial dehiscence is by collapse of the cap cell. Apogamy is not common.

HYPOLEPIDACEAE

Details of gametophyte morphology are known of three major genera of the family, viz., *Histiopteris* (Nayar, Kaur, & Bajpai, 1967), *Hypolepis* (Nayar, Kaur, & Bajpai, 1967), and *Pteridium* (Farlow, 1889; Lagerberg, 1907; Conway, 1949; Wilkie, 1954, 1963; Steeves, Sussex, & Partanen, 1955; Davis, 1965; Davis & Postlethwait, 1966; Sobota & Partanen, 1967).

The adult prothallus is naked and Cordate-thalloid with spread-out broad wings. Both tetrahedral and bilateral spores occur in the family: some like *Pteridium* possess tetrahedral spores, others like *Histiopteris, Lonchitis,* and *Paesia* bilateral ones, and some like *Hypolepis* possess bilateral spores in some species and tetrahedral in others. The exine is commonly granulose but may be subverrucate to tuberculate in some. A perine is absent [except in *Paesia,* which is reported to possess perinate spores (Harris, 1955)]. Spore germination is of the Vittaria-type, and prothallial development is of the Adiantum-type. There is a tendency for some prothalli to omit the apical cell stage. Sex organs are of the common Leptosporangiate-type. The basal cell of the antheridium is commonly funnel-shaped or saucer-shaped, but in *Histiopteris* it is disk-like. The cap cell is thrown off at antheridial dehiscence.

LINDSAEACEAE

Though the family is geographically wide spread, little is known regarding their gametophyte. The present account is based on our own observations on a few species of *Lindsaea, Odontosoria retusa* (Cav.) J. Sm., *Sphenomeris chinensis* (L.) Maxon and *Schizoloma* (Nayar & Kaur, 1969a). The adult prothallus is naked, Cordate-thalloid, possessing a thin, median midrib and spread-out wings. The rhizoids are nearly hyaline in color and restricted to the midrib region. Both tetrahedral and bilateral spores occur in the family, different species of the same genus often having the different spore forms (Nayar & Devi, 1968). There is no distinct perine, but there is a poorly differentiated perinous layer outside the exine, and this is usually smooth or granulose. Spore germination is of the Vittaria-type, producing a slender uniseriate germ filament, which develops into a cordate prothallus in three to six months following the Adiantum-type of development pattern. Sex organs are of the common Leptosporangiate-type. During antheridial dehiscence the cap cell collapses to release the spermatozoids.

Some interesting observations on the gametophyte of the taxonomically ambiguous genus *Taenitis* are recently recorded by Atkinson (1970). The adult prothallus of *T. pinnata* (J. Sm.) Holttum and possibly also *T. blechnoides* (Willd.) Sw. is irregularly lobed with each lobe having a terminal meristem. The midrib is often asymmetrically placed and in some cases only one wing is found (so that the midrib is lateral). In old prothalli the midrib may branch. Adult prothalli are naked and are of various shapes due to lobing, but may occasionally be asymmetrically cordate. Spore germination appears to be of the Vittaria-type and a short germ filament is produced. Early development of the prothallial plate is of the Kaulinia-type, but one to several marginal pluricellular meristems are differentiated as the obovate plate expands. When only one meristem is formed, the thallus develops one large wing with a lateral midrib which may later form a second wing. When more than one meristem is formed the thallus becomes irregularly lobed. Sex organs are of the common

Leptosporangiate type. The basal cell of the antheridium is disk-shaped. Antheridial dehiscence is by formation of a lateral pore in the cap cell.

DRYOPTERIDACEAE

One of the largest of leptosporangiate families (ca. 1600 spp., 45 genera), the Dryopteridaceae includes five subfamilies, in all of which the adult prothallus is Cordate-thalloid, large (commonly 1 cm or more across), symmetrical, generally broader than long, and with a distinct, often not heavy (4 to 8 cells thick), median midrib and broad, spread out wings. Spores of the Dryopteridaceae are of the bilateral type and perinate (except rarely in the Athyrioideae), the perine commonly being characteristically wrinkled; both the exine and perine (or either one of them) are often ornamented, the ornamentation in most cases being granulose or spinulose. Spore germination is of the Vittaria-type. The more common pattern of prothallial development is of the typical Aspidium-type, but in some it is of the Adiantum-type. Sex organs in the family are of the typical Leptosporangiate-type.

Subfamily Onocleoideae

The adult prothallus of *Matteuccia* (Campbell, 1895; Lagerberg, 1908; Orth, 1936; Momose, 1958b; Gantt & Arnott, 1965; Nayar, 1968a) is naked, while those of *Onoclea* (Campbell, 1886, 1887; Momose, 1958b) and *Pentarhizidium* (Nayar, 1961e; Nayar & Kazmi, 1963) bear unicellular papillate secretory (secretion often profuse) hairs both on the surfaces and the margin. The prothallus is profusely hairy in *Onoclea,* and hair formation is initiated early during prothallial development; the young prothallus of *Pentarhizidium* is naked; hair formation is initiated only towards maturity, and hairs are comparatively sparse. The spores are very large in the subfamily (50×80 μ, exclusive of perine in *Pentarhizidium*), having smooth exine and loose granulose perine, which is wrinkled into a few blunt elongated folds. Prothallial development is of the Adiantum-type (with a tendency towards delayed formation of meristematic cell) in *Matteuccia* and *Pentarhizidium,* and of the Aspidium-type in *Onoclea.* Antheridial dehiscence is by collapse of the cap cell.

Subfamily Hypodematioideae

Prothallial morphology is known of only a single species [*Hypodematium crenatum* (Forsk.) Kuhn (Loyal, 1960; Nayar & Bajpai, 1970)] of this monotypic subfamily. The adult prothallus is profusely hairy, bearing unicellular papillate secretory hairs (Fig. 46) all over and in addition unicellular, much elongated, nonsecretory, rhizoid-like hairs (Fig. 47) at the anterior end (both superficial and marginal). Collenchyma-like thickenings occur at the corners of the wing cells. The spores are ca. 30×45 μ in size, with smooth exine and loose, granulose perine wrinkled into thin, short, sinuous, lobe-like folds. Prothallial development is of the typical

Aspidium-type, with the majority of the germ filaments terminating in a hair and developing a laterally placed meristematic cell marginally in a lopsided prothallial plate. Antheridial dehiscence is by collapse of the cap cell. Regeneration by proliferations developed on the midrib region is frequent.

Subfamily Athyrioideae

Little is known about the prothallial morphology of the Athyrioideae, and there is much variation in the prothallial morphology of the few genera of which the prothallus is known, viz., *Athyrium* (Druery, 1885; Lagerberg, 1908; Faegri, 1934; Nayar & Bajpai, unpublished data), *Cystopteris* (Blasdell, 1963; Kaur, 1963), *Diplazium* (Momose, 1938a; Mehra, 1949; Nayar, 1960d; Atkinson, 1967; Nayar & Bajpai, unpublished data), and *Hemidictyum* (Stokey & Atkinson, 1954c). The adult prothallus is either naked or hairy (depending on the species) in *Athyrium* and *Diplazium*; it is naked in *Hemidictyum* and hairy in *Cystopteris*. In some species of *Athyrium* and *Diplazium* the adult thallus continues apical elongation for a long time, and old prothalli are much elongated and Strap-like (up to ca. 3 cm long); occasionally such thalli may be branched also. Young prothalli are naked in all; hair formation is initiated only at a late stage in prothallial development. Hairs are commonly of the papillate secretory type, but one- or two-celled swollen glandular nonsecretory hairs (Fig. 44) are reported (Atkinson, 1967) on the adult prothallus of *Diplazium stellatopilosum* (Brause) Holtt. (papillate hairs are absent). Collenchyma-like thickenings occur at the corners of the wing cells in several species.

The spores of the Athyrioideae (Hagenah, 1961; Nayar & Devi, 1964) are commonly 25–35 × 30–55 μ in size and perinate in the majority of species, but several species possess nonperinate spores. The exine is commonly smooth in the perinate spores and granulose, rugulose, or spinulose, or even spinose (rarely smooth) in the nonperinate ones; the perine is smooth to granulose or rarely even spinulose, and often closely adherent to the exine and wrinkled into short ridge-like folds. Prothallial development is of the Adiantum-type (with a tendency for delayed development of meristematic cell) or nearly of the Drynaria-type. Antheridial dehiscence is by the formation of a pore-like opening in the cap cell in some species of *Diplazium*; in others the cap cell collapses at dehiscence. The neck canal cell of the archegonium is commonly binucleate at maturity but is trinucleate in some species of *Diplazium* (Atkinson, 1967).

Subfamily Dryopteridoideae

In this large subfamily prothallial morphology is known of a fairly large number of genera, viz., *Acrophorus* (Kaur, 1962; Nayar & Kaur, 1963c, 1966), *Arachniodes* (Kawasaki, 1956; Chandra, 1969; Chandra & Nayar, 1970), *Cyrtomium* (Kawasaki, 1956; Chandra, 1969; Chandra & Nayar, 1970), *Diacalpe* (Davie, 1912; Nayar & Kaur, 1963c, 1966), *Didy-*

mochlaena (Stokey & Atkinson, 1954c), *Dryopteris* (Kny, 1895; Momose, 1937, 1938b, 1939; Duncan, 1943; Nakazawa, 1960; Nakazawa & Ootaki, 1962), *Lithostegia* (Kaur, 1962; Nayar & Kaur, 1963c, 1966), *Peranema* (Davie, 1912, 1916; Nayar & Kaur, 1963c, 1966), *Polystichum* (Druery, 1887; Becquerel, 1931; Nayar, Kaur, & Chandra, 1968; Chandra & Nayar, 1970), and *Woodsia* (Brown, 1964). The adult prothallus is profusely hairy, bearing unicellular secretory papillate hairs all over, except in *Didymochlaena sinuata* Desv., the prothallus of which is naked. There is much variation among the various taxa in the incidence of hairs on the prothalli and in the stage of prothallial development at which hair formation is initiated. In the majority of taxa hairs are profuse, and hair formation is initiated very early during prothallial development. In several taxa septate papillate hairs are occasionally found, especially on the old thalli; in *Cyclopeltis* (Stokey, 1960) septate hairs are more abundant. Some species of *Polystichum* bear unicellular, swollen, nonsecretory hairs on the margin of the adult thalli, mixed with papillate secretory hairs.

The spores are ca. 25–35 × 40–50 μ in size, with a distinct loose perine that is wrinkled into characteristic crowded conical to subannular folds or elongated lobate folds. The exine is smooth (rarely granulose) and the perine smooth to granulose. Prothallial development is of the Aspidium-type, with the different variations occurring in various definite proportions in each taxa. More commonly a meristematic cell is formed laterally from a marginal cell of a lopsided prothallial plate developed after the terminal cell of the germ filament ends in a hair. The terminal cell itself may take part in plate formation or may remain sluggish, a prothallial plate developing through the activity of the penultimate cells. The young prothalli in both these cases are profusely hairy. In some taxa like *Didymochlaena*, *Woodsia*, and some species of *Polystichum*, prothallial development is nearly of the Drynaria-type. Hair formation is delayed till the young prothalli are cordate in *Woodsia* and *Polystichum*. Antheridial dehiscence is by collapse of the cap cell. Apogamy is rather frequent in the subfamily, and several taxa have obligate apogamy. So also, regeneration by proliferations of old thalli is frequent.

Subfamily Tectarioideae

In contrast to the Dryopteridoideae, prothallial morphology is more uniform in the two genera of Tectarioideae of which the prothallus is known, viz., *Tectaria* (Kachroo, 1956; Mahabale & Venkateswaran, 1959; Nayar & Kaur, 1964c; Srivastava, 1968) and *Quercifilix* (Nayar, 1960a). The adult prothallus is profusely hairy, bearing unicellular papillate secretory hairs all over. The hairs are rather elongated and frequently septate in *Quercifilix*; septate hairs are reported to be frequent on the old prothalli of *Pteridrys* also (Stokey, 1960). In addition to papillate hairs, multicellular club-shaped hairs (with a swollen, nonsecretory, glandular, terminal cell and one or two slender stalk cells), often bearing papillate unicellular branches on the stalk cells, are found on the lower surface, especially on the midrib region in both *Tectaria* and *Quercifilix*; such hairs are reported in *Pteridrys* and *Heterogonium* also (Stokey, 1960). Spores of the Tectarioideae are commonly 25–35 × 35–55 μ in size and distinctly perinate, though in some the perine is very closely adherent to the exine. Both the exine and perine are granulose to spinulose or even spinose, but both or either one may rarely be smooth. Prothallial development is of the Aspidium-type with the characteristic range of variations; a large majority of germ filaments terminate in a hair and develop a prothallial plate from the penultimate cells. Young prothalli are profusely hairy. Antheridial dehiscence is by collapse of the cap cell.

LOMARIOPSIDACEAE

Prothallial morphology is known of only four genera, *Bolbitis* (Nayar, 1960b; Nayar & Kaur, 1964a, 1965a), *Egenolfia* (Nayar & Kaur, 1964b, 1965a), *Elaphoglossum* (Stokey & Atkinson, 1957), and *Rhipidopteris* (Stokey & Atkinson, 1957). The adult prothallus is either Cordate-thalloid and then seasonal, or Strap-like and then long-lived (three to five years). In *Bolbitis* and *Egenolfia* it is Cordate-thalloid, generally broader than long, and large, with a heavy midrib and broad flat wings. There is a tendency in some species [*B. crispatula* (Wall.) Ching] for the thallus to elongate slightly with age, while in some others like *E. vivipara* (Ham.) C. Chr. the adult prothallus is distinctly elongated and with narrow wings. The prothallus of *Elaphoglossum* is of the latter type, elongated and Strap-like; in many species the thallus is very narrow and much elongated (Fig. 40), with nearly parallel sides and shallowly notched apex [*E. calaguala* (Klot.) Moore, *E. stenophyllum* (Sod.) C. Chr., *E. tectum* (H. B. Willd.) Moore, *E. villosum* (Sw.) J. Sm.]. In *Rhipidopteris* also the thalli are narrow, much elongated and Strap-like (Fig. 39) as in *E. tectum*, etc. There is profuse development of marginal rhizoids on the Strap-like thalli, and in many species the wings are crisped and curled; also the thalli may occasionally be branched. Collenchyma-like thickenings occur at the corners of the wing cells in some species of *Bolbitis* and *Egenolfia.* The midrib is heavy and often six to eight cells thick in the large cordate prothalli such as those of *Bolbitis*; it is comparatively thinner (often two to six cells thick) and sometimes discontinuous in *Elaphoglossum* and *Rhipidopteris. Rhizoids* are borne profusely over the midrib in all, and in *Elaphoglossum* and *Rhipidopteris* are reddish brown in color and firm in texture. The prothallus of *Rhipidopteris* and most species of *Bolbitis* and *Egenolfia* is naked throughout. In some species of *Bolbitis* [like *B. heteroclita* (Pr.) Ching] unicellular, papillate, secretory hairs occur sparsely on the margin of the adult prothallus. In some others [*B. semicordata* (Moore) Ching, *B. quoyana* (Gaud.) Ching, *B. subcrenata* (Hook. et Grev.) Ching] characteristic, club-shaped, multicellular, marginal hairs are found on the adult thallus towards the anterior end; the hairs are two or three (up to five or six) cells long, with a slender stalk and swollen anterior region (Fig. 50) and usually unbranched but sometimes bearing one or two unicellular lateral papillate branches on the stalk cells. The prothallus of *Elaphoglossum* is profusely hairy from early stages of development onwards; the hairs are unicellular, papillate, and secretory, and are both marginal and superficial.

The spores of the family are of the bilateral type and are perinate except in *Lomagramma* and *Thysanosoria* (Nayar & Kaur, 1963d, 1965b). The perine bears a delicate reticulate ornamentation in most genera, but may only be granulose or even smooth as in some species of *Bolbitis* and *Elaphoglossum*. The exine is usually smooth but sometimes granulose (*Lomagramma, Thysanosoria*) or even spinulose (*Lomariopsis* spp.). The spore size varies much in the family, some species of *Lomariopsis* possessing spores that are the largest among all the ferns possessing bilateral spores [*L. intermedia* (Holttum) Fée, ca. 200 μ across], whereas spores of some species of *Bolbitis* and *Elaphoglossum* are as small as 20 × 30 μ. Spore germination is of the Vittaria-type, resulting in a proximal rhizoid and a uniseriate germ filament lateral to it. Prothallial development is of the Drynaria-type (except in *Elaphoglossum*), an apical meristematic cell being established when the prothallial plate is four to six cells broad. In many cases a meristematic cell stage is omitted and a pluricellular meristem is developed directly from anterior marginal cells. In *Elaphoglossum*, prothallial development is of the Aspidium-type, the germ filament either ending in a hair and then a meristematic cell developing from the daughter cells of the penultimate cell, or the terminal cell itself dividing and the daughter cells later developing a meristematic cell either before or after hair formation (Stokey & Atkinson, 1957).

Sex organs are of the common Leptosporangiate-type. Irregularly shaped, small, nonmeristic, male thalli are reported in all the genera investigated. The basal cell of the antheridium is commonly disk-shaped or barrel-shaped (its upper wall nearly flat). During dehiscence a pore-like opening in the cap cell sheds the sperms in *Elaphoglossum*; in *Bolbitis* and *Egenolfia* the cap cell collapses to release the sperms. The archegonial neck is short, with the neck canal cell broad, binucleate, and conspicuously swollen towards the tip at maturity. Regeneration of prothallus is not uncommon.

OLEANDRACEAE

From the point of view of prothallial morphology, the family Oleandraceae is imperfectly known. Some details are available in the literature about the prothalli of *Nephrolepis* (Hurel-Py, 1943; Mahabale & Javalgekar, 1949, 1959; Steil, 1952; Javalgekar & Mahabale, 1959) and two species of *Oleandra* (Nayar, Bajpai, & Chandra, 1967). The following account includes details based on our own observations on some species of *Arthropteris* and *Nephrolepis* in addition. The adult prothallus in the family is Cordate-thalloid, with a well-differentiated midrib (five to eight cells thick) and broad flat wings. Unicellular papillate secretory hairs occur profusely on the margin and surfaces. The hairs are mostly rather elongated, slender, devoid of copious secretion, and sometimes septate. Multicellular club-shaped hairs occur in addition in *Arthropteris* usually restricted to the midrib, but in *A. macrocarpa* (Cordem.) C. Chr. (Stokey, 1960) unbranched, small, multicellular hairs occur on the margins, and large branched hairs on the ventral surface, and in *A. tenella* (Forst.) J. Sm. the margin bears profuse, unbranched, club-shaped hairs as well as much-elongated branched ones bearing many unicellular papillate branches on the stalk cells (Fig. 41).

The spores of the Oleandraceae are of the bilateral type 20–30 × 32–45 μ in size and provided with a distinct, wrinkled, often ornamented (granulose as in *Arthropteris* and spinose as in *Oleandra*) perine, except in some species of *Nephrolepis* in which the perine is not clearly differentiated (Nayar, 1964a; Devi, 1966). The exine is either smooth or variously spinulose. Spore germination is of the Vittaria-type. In *Oleandra* and most species of *Nephrolepis* prothallial development is of the Aspidium-type, with the germ filament usually terminating in a hair before plate formation is initiated. However, the common range of variation characteristic of the Aspidium-type of development occurs. In *Arthropteris* and some species of *Nephrolepis* the common pattern is one in which plate formation is initiated prior to hair formation. During plate formation the terminal cell of the germ filament divides and one of the daughter cells is more active than the other, producing a more expanded lobe; a meristematic cell is developed from a marginal cell of the expanded lobe, slightly away from the median position. Hairs are produced on such thalli only after a meristematic cell is well established (*Nephrolepis*) or much later in development (*Arthropteris*). Sex organs are of the common Leptosporangiate-type in all genera. The antheridium is small, subglobose, or oblong, with its basal cell barrel-shaped or sometimes slightly elongated. Antheridial dehiscence is by the formation of a pore-like opening in the cap cell.

DAVALLIACEAE

Little information is available in the literature on the prothallus of the Davalliaceae, but for the cursory accounts on *Davallia bullata* Wall. (Schmelzeisen, 1933), *D. fijiensis* Diels (Mahabale & d'Almeida, 1953), and *Leucostegia immersa* (Wall.) Pr. (Kachroo, 1955a). The following account is based mainly on our own observations (unpublished) on some species of *Araiostegia, Davallia, Davallodes, Humata, Leucostegia,* and *Scyphularia*. The adult prothallus is Cordate-thalloid with a well differentiated, rather light (four- to six-cells-thick) midrib and broad, flat wings. It is commonly broader than long and profusely hairy, bearing unicellular papillate hairs (generally devoid of any copious secretion) on the margin and surfaces; in *Humata* the hairs are conspicuously elongated and occasionally divided by one or rarely two transverse septae. In addition to the papillate hairs the prothalli of *Araiostegia, Davallia,* and *Humata* bear on the midrib (in some cases extending also to the wings) club-shaped multicellular hairs with swollen glandular terminal cell; in some species the terminal cell is scarcely specialized as a glandular structure. In some, the club-shaped hairs are unbranched, but in most species the stalk cells bear unicellular papillate branches.

The spores are of the bilateral type, 25–45 × 45–70 μ in size, devoid of perine and possessing a thick, commonly verrucate or tuberculate exine (Nayar, 1964a; Devi, 1966). Spore germination is of the Vittaria-type and prothallial development is of the Aspidium-type. In *Araiostegia* and *Davallia* the germ filament usually terminates in a hair before plate formation is initiated, and the hair-bearing terminal cell usually remains undivided during prothallial devolopment; the prothallial plate develops lateral to the terminal cell and develops a meristematic cell away from the terminal cell. Sometimes the terminal cell divides, so that the hair is seated on one of the daughter cells while the other daughter cell forms a prothallial plate. In *Davallodes, Humata, Leucostegia,* and *Scyphularia,* the common pattern is one in which a prothallial plate is developed much before a hair is formed. The terminal cell of the germ filament divides, and usually one of the daughter cells is more active in plate formation, forming a lobe in which a meristematic cell is differentiated from one of the marginal cells. Hairs are generally formed only towards maturity of the prothallus. Sex organs are of the common Leptosporangiate-type in the family. The antheridium is subglobose or oblong and small, and its basal cell is usually barrel-shaped (with flat or nearly flat upper wall) or sometimes elongated and curved so that the antheridium lies parallel to the surface of the prothallus. Antheridial dehiscence is by the formation of a pore-like opening in the cap cell.

ASPLENIACEAE

The family consists of one large genus *Asplenium* (over 700 spp.) and nine small genera. Prothallial morphology is known of *Asplenium* (Lagerberg, 1908; Freer, 1926; Karpowicz, 1927, 1963; Faegri, 1934; Wagner, 1952; Momose, 1941b, 1959–1962; Bir, 1962; Nayar, Raza, & Lata, 1968), *Camptosorus* (Pickett, 1914; Kawasaki, 1956, 1957), *Ceterach* (Dopp, 1927; Bir, 1962), *Diellia* (Wagner, 1952), *Pleurosorus,* and *Phyllitis* (Beck, 1878; Vladesco, 1931; Kawasaki, 1957; Armenise, 1959). The present description takes into account our own unpublished data on *Camptosorus rhizophyllus* (L.) Link, a few Indian species of *Asplenium* and *Ceterach officinarum* D. C. ex Lam., in addition. The prothalli of the asplenioid ferns are Cordate-thalloid, with a median light midrib and large spread out wings, and usually broader than long (but having a tendency in some cases to elongate slightly). The adult thallus is hairy except in some species of *Asplenium* (Euasplenium-, Sarelli-, and Boniniella- groups of species as well as *A. nidus* Linn., *A. pekinense* Hance, *A. tenuifolium* Don, *A. marinum* Linn., *A. unilaterale* Lam., and *A. dalhousiae* Hook.) in which the prothallus is naked throughout; the margin of the thallus is smooth in most species having naked prothalli, but in some like *A. trichomanes* Linn.

and *A. viride* Hudson (Euasplenium group) some of the marginal cells possess conspicuously protruded outer walls, the protrusions resembling stout hairs. In species which possess hairy prothalli the abundance of hairs varies with the species, some (*A. adiantum-nigrum* Linn. and *A. rutamuraria* Linn.) being very profusely hairy, nearly each marginal cell bearing a hair. The nature and form of the hair also vary, but in a large number of species the hairs are unicellular, slender, and papillate but most often devoid of any extracellular secretion. In some cases the papillate hairs are septate, either occasionally as in *A. adiantum-nigrum* or rather frequently as in *A. friesiorum* C. Chr., *A. septentrionale* (L.) Hoffm., *A. rutamuraria*, and *Pleurosorus rutifolius* (R. Br.) Fée. In some species the hairs are mammillate (Fig. 45) with a conspicuously swollen base and suddenly narrowed, short, subconical apex. Marginal hair-bearing cells of the prothalli sometimes grow out as short filamentous or broad protrusions (which makes the hair appear multicellular) in many species. In a few species like *Asplenium leucostegioides* Bak., *A. flabelliforme* Cav., *A. ritoense* Hayata, *Ceterach officinarum*, and *C. vulgare* Samp. hairs are sparse, club-shaped, two to five (up to eight) cells long, with a distinct glandular apical cell (often with an extracellular secretion around it). Similar but smaller (commonly two cells long) hairs with copious extracellular secretion occur marginally on the prothallus of *Diellia* (Figs. 42, 43).

The spores are of the bilateral type, ca. 20–40 × 30–60 μ in size, and perinate with the perine wrinkled characteristically and often having a distinct supralaesural fold. Commonly both the exine and perine bear granulose to spinulose ornamentation, and in many cases irregular areas on both are bare (Nayar & Devi, 1964b); in several species the ornamentation is of the spinose type, and in several others both or either layer of the spore coat are smooth. Spore germination is of the Vittaria-type, producing a proximal rhizoid and a uniseriate germ filament lateral to it. Abnormalities in germination resulting in a plate of cells instead of a germ filament are reported in *A. adiantum-nigrum* (Nayar, Raza, & Lata, 1968). Formation of a prothallial plate is usually initiated when the germ filaments are four to eight cells long; only the anterior cells of the germ filament take part. Prothallial development in most species of *Asplenium* and *Camptosorus* is mainly of the Aspidium-type, with most of the germ filaments developing an obconical meristematic cell in one of the daughter cells of the terminal cell and the terminal cell developing a hair before initiating plate formation. In such cases the prothalli are hairy from the early stages of development onwards. However, in several species of *Asplenium* the meristematic cell is distinctly lateral at origin, the terminal cell (and sometimes the penultimate cell) of the germ filament being sluggish and taking little part in the growth of the thallus. In species with naked prothalli and some others that develop hairs only towards maturity (*Diellia*), the prothallial development is more or less of the Adiantum-type. Even among these the common tendency is for the meristematic cell to be established only after the prothallial plate becomes three to five or more cells broad at the apex. Sometimes the meristematic cell is slightly away from the median plane of the prothallial plate when first differentiated.

Sex organs of the Aspleniaceae are of the common Leptosporangiate-type. Antheridia are produced from early stages of prothallial development onwards; on adult thalli they are restricted to the midrib and the nearby area on the lower surface. In *Asplenium* the distribution of antheridia (either restricted to the basal part or spread along the sides of the midrib) is regarded as a specific character by Momose (1959–1962). The basal cell of the antheridium in some species is distinctly barrel-shaped (its upper wall nearly flat) and in some cases markedly slender, elongated, and sometimes curved (as in *A. unilaterale* Lam.). Antheridial dehiscence is by a pore-like opening developed in the cap cell; the pore widens soon, and the cap cell ultimately is torn apart. However, in some cases (*A. normale* D. Don) the process of opening is rather sudden, and the development of a pore is not very obvious. Structure and development of the archegonium are of the common type in advanced ferns. The neck is slender and curved away from the apex of the prothallus. The neck canal cell is binucleate and swollen towards the apex at maturity. Apogamy is reported in some species (*A. unilaterale*) but is not common in the family. Regeneration of the prothalli is also not frequent.

THELYPTERIDACEAE

The thelypteridoid ferns are taxonomically a complicated group, the subdivision of the two larger genera, *Thelypteris (Lastrea)* and *Cyclosorus,* being highly controversial. Considering the large size of the family, little is known of its prothallial morphology; the prothallus of a few species of *Thelypteris* (Nayar & P. Chandra, 1965), *Cyclosorus, Abacopteris* (Schmelzeisen, 1933; Nayar & P. Chandra, 1963; Kachroo, 1963), and of *Ampelopteris prolifera* (Retz.) Copel. (Chandra & Nayar, 1968; Mittra & Sen, 1969), and some details of the prothallus of a few species of *Thelypteris (Goniopteris)* (Stokey, 1960; Atkinson & Stokey, 1964) only are known. The adult prothallus is Cordate-thalloid, usually broader than long, with a light midrib and spread-out broad wings. The thalli are profusely hairy, bearing simple, unicellular, papillate, secretory hairs all over the margin and both the surfaces. In some species (particularly of the *Cyclosorus*-group and *Ampelopteris*) elongated, acicular, nonglandular hairs are found sparsely along with unicellular papillate secretory hairs on the margins and on the lower surface. These hairs are usually unicellular but are sometimes septate as in *Cyclosorus parasiticus* (L.) Tardieu ex Tardieu et C. Chr., or stellately branched through unicellular (Stokey, 1960; Atkinson & Stokey, 1964) as in *Thelypteris (Goniopteris) biollyi* (Fig. 51).

The spores in the family are commonly of the bilateral type and perinate (Nayar & Devi, 1963, 1964a). Rarely some species, such as *Thelypteris ciliata* (Wall. ex Benth.) Ching, possess tetrahedral spores mixed with some of bilateral and intermediary forms (Nayar & P. Chandra, 1966). On an average the spores are 26 × 40 μ in size (ranging from ca. 20 × 30 μ to ca. 40 × 60 μ). The perine is distinct, rather adherent to the exine, granulose to spinulose, and characteristically wrinkled in most species; often a supralaesural fold, different from other folds, is present. However, a distinct perine is absent in some species (Nayar & Devi, 1963, 1964a; Devi, 1966). The exine is commonly smooth in the perinate species but usually bears spine-like excrescences in those species which lack a distinct perine. Spore germination is of the Vittaria-type, producing a proximal rhizoid and a uniseriate germ filament lateral to it. Prothallial development is more commonly of the Drynaria-type, an apical meristematic cell being differentiated after a spatulate nonmeristic thallus is formed by divisions of the anterior cell of the germ filament. However, in many species of *Thelypteris* a meristematic cell is differentiated rather early, sometimes even as early as when the plate is only two cells broad at the apex. Usually the thalli develop hairs only late in development, but in some species of *Thelypteris* hair formation may be initiated soon after the establishment of a meristematic cell. Sex organs are of the common Leptosporangiate-type. Antheridia are produced from the early filamentous stage onwards. Some irregularly developed, small, nonmeristic, male prothalli occur mixed with the cordate bisexual ones. The basal cell of the antheridium is commonly saucer-shaped or disk-shaped (its upper wall flat or curved slightly downwards) or sometimes funnel-shaped. The archegonial neck is elongated, slender, and curved away from the apex of the prothallus. The neck canal cell is binucleate at maturity. Profuse regeneration from old prothalli is reported in some species.

GRAMMITIDACEAE

Prothallial morphology of five of the larger genera of the family is known in some detail (Goebel, 1888; Copeland & Giaque, 1950; Stokey & Atkinson, 1958; Stone, 1960). The adult prothallus is Strap-like, elongated, often progressively broader towards the anterior end, unbranched, with a cordate apex having a well-defined pluricellular meristem and with a narrow, sometimes discontinuous, median midrib two to four cells thick. Rhizoids are borne over the midrib but are also marginal and submarginal. They are dark brown (often reddish brown) in color, firm, and more slender than is usual in other ferns. Hairs of various types are borne, but the common, simple, unicellular, papillate type of hair is rare. The most common type in the family is a branched, multicellular, club-shaped, glandular hair basically similar to the multicellular hairs of the Polypodiaceae, but often more complex (usually composed of up to ten cells). The simplest hair of this kind is typically of the polypodiaceous type, composed of a terminal swollen glandular cell and an elongated stalk cell which bears a slender, elongated, unicellular, papillate branch towards the anterior end. However, commonly the stalk is several cells long, each stalk cell (or nearly all) bearing one or sometimes two unicellular, elongated, large, club-shaped branches (Fig. 53*h*). Sometimes the stalk is branched, and then each branch bears a glandular cell at the tip. The lateral branches on the stalk cells may be glandular and possess a waxy extracellular secretion, or in some species these are nonchlorophyllous, elongated, thick-walled, acicular, and nonsecretory (Fig. 52). Many species bear elongated, often much prolonged, slender, nonchlorophyllous, acicular hairs (Fig. 53 *x*), basically similar to those found in the Thelypteridaceae, and with thickened, often yellowish walls. These are usually unicellular but may sometimes be septate. Hairs are commonly on the margin rather than on the surface of the thallus, and are often very abundant. The young thalli are naked; hairs are developed only as the apex of the thallus becomes cordate or even later.

Spores of the Grammitidaceae (Nayar, 1964a; Nayar & Devi, 1965; Devi, 1966) are usually chlorophyllous, devoid of perine, and commonly of the tetrahedral type; bilateral spores occur in some species and often they are found mixed with tetrahedral ones. The exine is granulose to verrucate, with the verrucae often deciduous. The spores often germinate before they are shed. On germination the first wall formed is generally parallel to the equatorial axis of the spore as is common in ferns, but the two cells are of equal size and function as prothallial cells; no rhizoid is developed early as in other ferns. There is considerable variation in the sequence of cell divisions at germination, and in some cases the first wall is nearly parallel to the polar axis of the spore. An elongated uniseriate germ filament is produced by successive divisions parallel to the first, or either both or one of the primary cells produce a germ filament elongated nearly at right angles to the long axis. (This probably occurs when the first division in the spore is by a wall parallel to the polar axis.) Sometimes, by irregular divisions of the two primary prothallial cells, a small plate of cells is formed first, and later uniseriate germ filaments grow out from some of the cells of this plate. Prothallial development is slow. Rhizoids are belated, the first rhizoid being formed only after a long germ filament is established or sometimes much afterwards. Rhizoids are produced by the basal cells and occasionally contain a few plastids. A prolonged and extensive development of the filamentous stage is characteristic of the grammitid ferns. The filamentous stage may continue indefinitely and persist for months or even years. The germ filaments are often extensively branched, and many species have a moniliform aspect resulting from the bulged sides of the cells (Fig. 54). Increase in length of the germ filament is brought about by division of the terminal cell (rarely by division of older cells), and the division is so unequal as to suggest "budding." Prothallial development appears to be of the Adiantum-type, but the apical meristematic cell is usually ephemeral and is soon replaced by a pluricellular meristem. Often the meristematic cell stage is omitted, the prothallial plates developing nonmeristically in the initial stages but producing an apical pluricellular meristem afterwards. Young prothalli continue to be spatulate in form for a long period (over six months), and the cordate stage appears rather slowly.

Both male and female sex organs are found together on the thalli and are usually formed only late in prothallial development. They are of the Leptosporangiate-type. The basal cell of the antheridium is barrel-shaped (its upper wall flat) and in some cases elongated and curved, making the antheridium pendulous. The cap cell may be divided. Antheridial dehiscence is by the formation of a lateral, pore-like opening in the cap cell. The archegonial neck is short, bulbous, and curved away from the apex of the prothallus. The neck canal cell is binucleate and swollen at the tip towards maturity. Apogamy occurs in some species (*Xiphopteris serrulata* Klf.). Vegetative multiplication by fragmentation of the germ filament (Fig. 55) is frequent and is apparently a common feature in the family.

BLECHNACEAE

The Blechnaceae consists of one predominantly large genus, *Blechnum*, and seven small genera closely allied to it. Though prothallial morphology of a few species of *Blechnum* is known in detail (Stubner, 1882; Lampa, 1901; Dopp, 1927; Karpowicz, 1927; Stokey & Atkinson, 1952b; Kachroo, 1955c; Stone, 1961; Nayar, 1962a; Nayar, Bajpai, & Raza, 1966) generalizations appear not to be of much value in taxonomic and phyletic studies, considering the large size of the genus (over 200 spp.) and the marked differences between the species. In addition to that of *Blechnum*, details of prothallial morphology are known of *Brainea* (Stone, 1969), *Doodia* (Sarbadhikari, 1927; Duncan, 1941; Nayar, Bajpai, & Raza, 1966; Stone, 1969), *Sadleria* (Stone, 1969), *Stenochlaena* (Stokey & Atkinson, 1952a; Nayar, Bajpai, & Raza, 1966; Klekowski, 1970b), and *Woodwardia* (Nayar, Bajpai, & Raza, 1966; Stone, 1969). The adult prothallus in all the genera is Cordate-thalloid, with a distinct tendency for the prothallus to continue growth after reaching maturity, often becoming much elongated (3 to 5 cm long), resembling a liverwort, particularly in *Blechnum*. The midrib of old, elongated prothalli is rather thick, and the wings are prominently ruffled and uplifted (Fig. 57). The adult prothallus of *Sadleria* is conspicuously longer than broad. Rhizoids are profuse and have a brownish (often reddish brown) color; in some, such as *Stenochlaena*, they may become septate. The prothallus is profusely hairy (except in some Australian species of *Blechnum*), bearing superficial and marginal, papillate, secretory, unicellular hairs. Hairs on old prothalli are sometimes septate; in *B. orientale* Linn. some of the marginal hairs on old prothalli are club-shaped, larger than the papillate hairs, and devoid of any secretion. The abundance of hairs on the thallus varies much with the species as also the stage of prothallial development at which hair formation is initiated. In some species such as *Blechnum orientale* and *B. gibbum* (Lab.) Mett. the young thalli are naked; hairs are formed only towards maturity. In others, such as *B. buchtienii* Rosenst., *B. brasiliense* Desv., *Doodia dives*

Kunze, etc., prothalli are profusely hairy from early stages of development and the thalli (even when young) possess jagged margins that are due to protruded hair-bearing cells. On the contrary, several Australian species of *Blechnum* [*B. minus* Ettingsh., *B. nudum* Mett., *B. patersoni* (R. Br.) Mett., *B. penna marina* (Poir.) Kuhn, *B. procerum* Sw.] are reported to possess naked prothalli (Stone, 1961).

The spores of the family are of the bilateral type. In all the genera except *Stenochlaena* the spores are perinate, but in some species of *Blechnum* the perine is often not clearly differentiated. The perine is loose and wrinkled in *Woodwardia* and *Lorinseria,* whereas in the other genera it is more or less adherent to the exine and scarcely wrinkled. Commonly both the exine and the perine are smooth (or rarely faintly granulose). In *Stenochlaena* and *Blechnum fraseri* (A. Cunn.) Luers. the exine is verrucate and a perine is absent. This is also the condition in the newly proposed genus *Pteridoblechnum* (Hennipman, 1966). Spore germination is of the Vittaria-type, producing a proximal rhizoid, lateral to which a slender uniseriate germ filament develops. Development of a prothallial plate is initiated generally when the filaments are 5–10 cells long. There is some variation in the pattern of prothallial development among the different species studied. Commonly the development is of the Aspidium-type, exhibiting the full range of plasticity that characterizes this type. Generally the meristematic cell is rather sluggish, and there is a strong tendency for the prothalli to omit the meristematic cell stage. In *Brainea, Doodia, Sadleria,* and several species of *Blechnum* (*B. gibbum, B. nudum, B. orientale*) the common pattern of development is nearly of the Adiantum-type; a meristematic cell is established in one of the daughter cells of the terminal cell of the germ filament, and no hairs are developed on the young prothalli. In most species of *Blechnum,* however, a hair is generally developed on the terminal cell prior to initiation of plate formation. A meristematic cell is commonly formed, as in *Blechnum orientale,* in one of the daughter cells of the terminal cell. However, occasionally it is formed later at the margin of a lobe developed by the activity of this daughter cell. In several species of *Woodwardia* a hair is formed by one of the daughter cells of the terminal cell, while the other develops an obconical meristematic cell (Stone, 1969). In *Stenochlaena* and some species of *Blechnum* (*B. elongatum* Gaud.), *Doodia* (*D. aspera* R. Br., *D. media* R. Br.) and *Woodwardia* (*W. orientalis* Sw.) the terminal cell (sometimes also the penultimate cell) often remains quiescent and does not take part in plate formation; the meristematic cell is formed laterally in a marginal cell of a one-sided plate as usual in the Aspidium-type of development pattern. Omission of a meristematic cell stage is frequent in most species of the family. In *Stenochlaena tenuifolia* (Desv.) Moore two or three (sometimes more) of the anterior cells of the germ filament often remain quiescent, and a prothallial plate is formed by the intercalary cells behind them; a terminal hair is developed prior to plate formation. A meristematic cell is often differentiated early (when the plate is only two cells broad). In S. *palustris* (Burm.) Bedd., on the other hand, the anterior cells of the germ filament often divide and take part in plate formation but are more sluggish than the cells behind them. A meristematic cell is differentiated laterally behind the sluggish apex (Stokey & Atkinson, 1952a), but more commonly the meristematic cell stage is omitted and a marginal pluricellular meristem is developed in a nonmeristically formed, often asymmetric, prothallial plate. The prothalli of the blechnoid ferns are quick-growing, reaching maturity in about two to three months after spore germination. However, in most cases the thalli exhibit prolonged growth, the thallus sometimes elongating considerably with age and sometimes branching.

Sex organs are of the common Leptosporangiate-type. Antheridia are commonly superficial and produced continually from early stages of development of the prothallus. The antheridium is usually oblong, sometimes with a slightly narrowed base. The basal cell is commonly short and disc-like or saucer-like, but in some species of *Blechnum* (*B. nudum*) and *Stenochlaena* it is elongated, barrel-shaped, and slender, while rarely it is funnel-like (Fig. 58). The opercular cell is commonly large and very conspicuous. At dehiscence a pore-like opening is formed in the opercular cell to release the sperms (Fig. 59); soon, however, it widens, tearing the cell apart. In *Doodia* and *Woodwardia* the opercular cell collapses at antheridial dehiscence. The archegonial neck is elongated (four or five cells long) and curved away from the apex of the thallus. The neck canal cell is binucleate and conspicuously swollen at the tip towards maturity. Obligate apogamy (Stone, 1969) is reported in some species of *Woodwardia* (*W. martinezii* Maxon ex Weath) and facultative apogamy (Duncan, 1941) in some species of *Doodia* [*D. caudata* (Cav.) R. Br.]. Regeneration of prothalli is not common.

HYMENOPHYLLACEAE

The family of filmy ferns, the Hymenophyllaceae, according to the current concepts (Copeland, 1938, 1947) consists of about three dozen genera (many of them monotypic) grouped together in two morphological groups commonly designated as the Hymenophyllum-group and the Trichomanes-group (with a few genera intermediate between the two). Though the gametophyte of the family has long been rather well known (Taschner, 1843; Presl, 1843; Mettenius, 1864; Prantl, 1875; Janczewski & Rostafinski, 1875; Goebel, 1888, 1892; Bower, 1888a, b, 1894; Giessenhagen, 1890; Georgevitch, 1910a, b; Holloway, 1923, 1930, 1944), exhaustive accounts of the gametophyte of any considerable number of species are comparatively recent (Stokey, 1940, 1948a; Stone, 1958, 1965; Atkinson, 1960a; Farrar & Wagner, 1968). Details regarding the prothalli of the following genera are known: *Amphipterum, Hymenophyllum, Mecodium,* and *Meringium* of the Hymenophyllum-group; *Crepidomanes, Crepidopteris, Didymoglossum, Macroglena, Polyphlebium, Selenodesmium, Sphaerocionium, Trichomanes,* and *Vandenboschia* of the Trichomanes-group; and *Apteropteris, Cardiomanes,* and *Microtrichomanes,* which are intermediate between the Hymenophyllum- and Trichomanes- groups. In all the genera, the prothalli are very slow-growing, often taking years to reach maturity, and capable of almost indefinite growth. Hymenophyllum- and Trichomanes- groups of genera are quite distinct with respect to the morphology of their adult prothalli. Three of the intermediate genera mentioned above agree with the Hymenophyllum-group, while the fourth one, *Microtrichomanes,* agrees with the Trichomanes-group in prothallial morphology.

The adult prothallus in the Hymenophyllum-group is naked, of the Ribbon-like type, and often profusely branched (Fig. 60); branching is terminal or subterminal. The prothallus is one cell thick, with discontinuous marginal archegonial cushions that are generally initiated close to the growing apex of the branches. The walls of the prothallial cells are usually markedly thickened and pitted. Rhizoids are short and found in marginal clusters. They are generally brownish or sometimes reddish brown in color (the characteristic coloration of the rhizoid wall is evident even in the first rhizoid produced during spore germination). Branched rhizoids are frequent. An endophytic fungus is reported in some of the rhizoids and rhizoid-bearing cells of the prothallus in cases where the thalli are collected from nature. However, the presence of the fungus is not obligatory for healthy growth of the prothallus. The adult prothallus in the Trichomanes-group is of the Filamentous-type, profusely branched and uniseriate (rarely longitudinal divisions occur in single cells or in sections of the filament in some species of *Microtrichomanes*; in some, such as several species of *Trichomanes,* auriculate, blade-like branches with the cells divided longitudinally and forminng a plate are seen; in *T. holopterum* Kze. the blade-like branches are profuse and often bear terminal gemmae). They are slow-growing and apparently of indefinite growth, devoid of prothallial trichomes and produce sex organs on short lateral branches. In *T. holopterum,* rhizoids on the filamentous portion of the prothallus are reduced to globose attachment organs secreting an adhesive substance (Farrar & Wagner, 1968); elongated rhizoids are borne only on the thalloid blade-like branches. In this species archegonia are borne on lateral globose multicellular cushions, which in addition bear erect thalloid branches.

The spores (both in the Hymenophyllum- and Trichomanes- groups) are of the tetrahedral type, devoid of any perine and often rather compressed along the polar axis. The exine is very thin, nearly transparent and smooth or faintly ornamented (granulose or spinulose, rarely tuberculate or spinose). They germinate before shedding and possibly there is no appreciable resting stage. In the Hymenophyllum-group of genera spore germination is typically of the characteristic Hymenophyllum-type (Fig. 1). Generally only one of the three peripheral lenticular cells formed at spore germination grows into a germ filament, but frequently two may develop. Growth is extremely slow in all cases; rhizoid development is late. In *Mecodium scabrum* (A. Rich.) Copel. and *M. sanguinolentum* (Forst.) Pr. ex Copel. the Mecodium-type of variation of the Hymenophyllum-type of germination is met with (Atkinson, 1960a). In these there is only slight expansion of the prothallus at the three-celled stage, so that the thallus remains within the spore coat even after a six-celled plate is formed. The spore coat generally opens at the 9 to 12-cell stage of development. Usually a 10 to 18-celled triangular plate having a lenticular cell at each corner is produced. Frequently divisions in the cells behind the lenticular cells in all the three arms continue, and a symmetrical triangular plate of several cells is formed. Also one or more lenticular cells often undergo an oblique division; one of the products of this division gives rise to a rhizoid, or both may enter into the formation of a Ribbon-shaped thallus two cells wide. Usually a uniseriate germ filament grows out from one of the lenticular cells; it may be formed when the plate is nine-celled, but often later. Sometimes all the three corner cells develop and produce full-grown thalli. Formation of additional cells in the primary plate is reported in *Mecodium rarum* (R. Br.) Copel. also (Stone, 1965). In contrast to this increase in the number of cells in the primary plate as found in the Mecodium-type, there are several variations in many species of the Hymenophyllum-group. In species of *Apteropteris*, *Mecodium*, *Meringium*, and *Sphaerocionium* the second division at spore germination is omitted. This leads to the formation of a two-celled "transverse" filament instead of a plate, but further development is as in the triangular plate. In *Mecodium pulcherrimum* (Col.) Copel. the first and second divisions are suppressed and two lenticular cells are developed at two corners of the solitary cell in the spore. One of these develops into a germ filament, while the other develops into a rhizoid. In *M. multifidum* (Ernst.) Copel., instead of a lenticular cell forming at each corner of the primary three-celled plate, cell divisions oblique to each other occur, and a two-cell-broad filament is often formed.

In the Trichomanes-group of genera spore germination is commonly of the Trichomanes-type. As in the Hymenophyllum-group, each of the lenticular cells develops independently and may form either a uniseriate germ filament or a rhizoid. Additional germ filaments and rhizoids may be formed from the central cell at a later stage of development as in *Vandenboschia*. Spore germination, however, is of the Hymenophyllum-type (producing first a three-celled plate before peripheral lenticular cells are formed) in *Cardiomanes reniforme* (Forst.) Pr. (Mettenius, 1864), *Microtrichomanes* [*M. digitatum* (Sw.) Copel., *M. nitidulum* (v.d. Bosch) Copel., *M. palmatifidum* (K. Mull.) Copel.], *Trichomanes crispum* Linn. (Mettenius, 1864; Goebel, 1888, 1892; Stokey, 1940) and *Vandenboschia draytoniana* (Brack.) Copel. (Campbell, 1905, 1918). However, development of the prothallus (after the formation of uniseriate germ filaments) does not follow the Hymenophyllum-type. In *Vandenboschia maxima* (Bl.) Copel. and *Polyphlebium*, though occasionally triradiate, development typical of the Trichomanes-type is found; commonly only two lenticular cells are formed, one of which develops into a rhizoid while the other develops into a germ filament. In extreme cases in this and some related species rhizoid development is belated, and then only one lenticular cell is formed. In the Trichomanes-group of genera the germ filaments continue uniseriate growth indefinitely and branch profusely, the branches being lateral in origin.

Development of the prothallus is typically of the Kaulinia-type in the Hymenophyllum-group of genera. The presence of a wedge-shaped apical meristematic cell, as found commonly in fern prothalli, is reported in *Mecodium australe* (Willd.) Copel., *M. flabellatum* (Lab.) Copel., *M. rarum*, and *Hymenophyllum cupressiforme* Lab. (Stone, 1965). This cell is reported as sluggish and soon replaced. However, in no case is a distinct, well-organized meristem observed, nor any tendency to form a notched apex. Though spore-germination is of the common Hymenophyllum-type, the development of the thallus in *Amphipterum fuscum* (Bl.) Pr. and *Mecodium javanicum* (Spreng.) Copel. is slightly different from that of others (Stokey, 1940). There is a prolonged filamentous stage with abundant branching. Though some of the branches become two cells wide and Ribbon-like, there is no pronounced apical activity. [The adult thalli of these species are unknown.]

In those genera which possess Ribbon-like prothalli (Hymenophyllum-group), antheridia are borne on the one-cell thick regions and are in marginal or submarginal groups, less frequently on the dorsal surface. In *Mecodium australe* the prothallus is very narrow and antheridia are borne on slender branches (Stone, 1965). The antheridium is of the Eusporangiate-type in all the taxa. The basal region of the mature antheridium consists of two or three wedge-shaped cells. Sometimes a few cells formed by intersecting walls make a short stalk, or a series of discoid cells may constitute an elongated stalk for the antheridium. The antheridial wall consists of several narrow, oblique cells and a small triangular apical or lateral opercular cell. In the Trichomanes-group of genera the antheridia are similar to those of the Hymenophyllum-group, but smaller in size and simpler in structure, with the wall composed of a smaller number of cells. In *Polyphlebium* (Stone, 1958) the antheridia are very small and with a barrel-shaped stalk cell bearing a globose head composed of a peripheral layer of four cells encircling a small number of spermatozoids. The antheridium of *Polyphlebium* originates as a papilla-like protuberance on a prothallial cell. The tip of the papilla becomes swollen and is cut off as an androgonial cell. The slender basal region is cut off from the parent prothallial cell, to constitute a stalk cell. In the androgonial cell a ring cell is cut off by an obliquely anticlinal wall, followed by a dome-shaped cell formed by a periclinal wall, thus producing a central spermatogenous cell. The dome-shaped cell divides to form another ring cell and a cap cell. The latter divides to form a small opercular cell. On the Ribbon-like prothalli of the Hymenophyllum-group, archegonia are borne on more or less erect branches or on branches spreading horizontally or obliquely above the substratum. They are restricted to small cushions two or three cells thick on the ventral surface. The cushions are marginal on the branches (superficial archegonial cushions occur sometimes in some species). Sometimes rhizoids and even antheridia may occur on the archegonial cushions. The archegonia are of the common type in ferns, but with a nearly straight elongated neck six to nine cells long. The neck canal cell is binucleate at maturity. On the filamentous prothalli of the Trichomanes-group archegonia are borne on specialized archegoniophores, which arise as short, stout branches on the filaments and develop into a globose to oblong mass of cells, each bearing a varying number of archegonia all around. The archegonia are of the common type with an axial row of three cells (egg, ventral canal cell, neck canal cell) and a short straight neck composed of four rows of four cells each (*Vandenboschia pyxidifera* (L.) Copel. and *Polyphlebium* are reported to have up to seven cells per row). The neck canal cell is binucleate.

Apogamy is frequent in the family. Regeneration from the marginal cells of old thalli is common in the Hymenophyllum-group, and vegetative multiplication by fragmentation in the Trichomanes-group. Aposporous development of gametophytes (with unreduced chromosome number) is reported in some members of the family (Bell, 1960). Vegetative multiplication by means of gemmae is reported in many species. In the Hymenophyllum-group the gemmae are elongated, multicellular structures produced as uniseriate short filaments (three to five cells long) in which the intercalary cells divide longitudinally (Figs. 62, 63). Sometimes the gemmae may develop basal rhizoid initials before they are shed (Goebel, 1905; Stone, 1965). Adverse conditions of growth (such as drying) are known to induce profuse formation of gemmae. Commonly the gemmae are barrel-shaped or spindle-shaped (Figs. 62, 63) and elongated parallel to the vertical axis of the sterigma. In the Trichomanes-group the gemmae, however, are different from those in the Hymenophyllum-group. Gemmae are produced terminally on intercalary cells and are borne on narrow elongated often flask-shaped sterigmata (Fig. 61). The gemmae are several (2–12) cells long, uniseriate, filamentous structures (usually tapered to either end) and oriented perpendicular to the sterigma (attached to the sterigma by a median cell). In *Trichomanes holopterum* gemmae are produced terminally on large, multiseriate, erect-growing, thalloid branches (Farrar & Wagner, 1968). On germination both ends may grow out into filamentous prothalli and branches may be borne on any of the cells. Extensive multiplication of prothalli resulting in formation of large colonies, resulting from vegetative multiplication by gemmae, is reported in some species (Wagner & Evers, 1963; Farrar & Wagner, 1968).

LOXSOMACEAE

The adult prothallus of both the genera of the family, *Loxsoma* (Goebel, 1912, 1930; Stokey & Atkinson, 1956c) and *Loxsomopsis* (Stokey & Atkinson, 1956c), is Cordate-thalloid with a shallow apical notch, usually longer than broad, becoming elongated with age, either with the wings uplifted as in *Loxsoma* or flat as in *Loxsomopsis*, and with a heavy midrib composed of 6 to 10 layers of large cells. Bristle-like cyatheaceous trichomes (Fig. 64) occur mixed with archegonia on the midrib; and very rarely trichomes occur also on the dorsal surface.

The spores of the Loxsomaceae are of the tetrahedral type with smooth or nearly smooth exine and devoid of perine. Spore germination appears to be of the Cyathea-type, the first wall formed being nearly parallel to the polar axis and separating a small laterally placed rhizoid initial. The prothallial cell develops into a short uniseriate germ filament (sometimes the basal cell is divided longitudinally); less frequently a plate is formed by the prothallial cell dividing transversely (parallel to the equatorial axis) first and each daughter cell soon afterwards dividing by a wall perpendicular to the transverse wall. Usually longitudinal divisions occur only when the germ filament is three or four cells long and the terminal cell divides first. Occasionally longer germ filaments are produced. In some cases both the daughter cells produced by the first division of the spore behave as prothallial cells, instead of one developing a rhizoid. A thallus two cells broad then develops by repeated divisions parallel to the equatorial axis in both the daughter cells. A rhizoid is developed much later by one of the basal cells cutting off a lateral rhizoid initial. Rarely the first division (by a wall parallel to the polar axis) is preceded by a division along the equatorial plane; the distal daughter cell then divides by a wall parallel to the polar axis, while the proximal one, by a series of divisions parallel to the first, develops into a uniseriate germ filament. Rhizoid formation is much delayed in such cases also. Prothallial development is of the Drynaria-type, an apical meristematic cell being differentiated from the products of one of the daughter cells of the terminal cell of the germ filament (generally away from the median plane of the prothallus). Branching of young thalli is not uncommon. Small, nonmeristic, irregularly shaped, antheridial thalli occur mixed with cordate bisexual thalli. A cordate prothallus is developed in about six to eight weeks after spore germination. Soon afterwards antheridia are formed, and archegonia are formed at three months. Thalli become full grown in approximately 10 to 12 months. Antheridia are of the Eusporangiate-type, with a large central mass of spermatogenous cells and the wall composed of many curved, narrow cells (variable in number and position) and a divided cap cell. One of the daughter cells of the cap cell is thrown off at antheridial dehiscence. The archegonia possess a large and long (especially in *Loxsomopsis*) neck composed of four tiers of four to six cells each. The neck is straight or slightly curved away from the apex of the prothallus. The neck canal cell is binucleate.

GLEICHENIACEAE

Details regarding the prothallus of *Dicranopteris, Hicriopteris, Gleichenia,* and *Sticherus* are known in the family. Some details regarding the prothallus of the queer genus *Stromatopteris* are recently mentioned by Bierhorst (1967b, 1968b), on the basis of which he believes that this genus "indicates a close relationship to the Psilotaceae, even closer than to the Gleicheniaceae." The prothallus in the family is slow-growing, perennial, and (except in *Stromatopteris*) Cordate-thalloid (Rauwenholf, 1890; Campbell, 1908; Stokey, 1950), with a heavy median midrib (18 to 24 cells thick) and uplifted wings having more or less irregular margins. There is a tendency for the prothalli to elongate rather markedly with age, and then the wings become ruffled. Rhizoids are characteristically abundant and colored brown (commonly reddish brown). Young rhizoids are chlorophyllous, but the plastids turn brown and disintegrate as the rhizoid matures. Two-celled (less frequently 3- or 4-celled), club-shaped, glandular hairs (Fig. 68) occur on both the surfaces of the midrib and sometimes also on the margins of the adult prothallus. The hairs develop from special wedge-shaped initials (Figs. 65–67). The terminal glandular cell is tannin-containing when mature. The hairs are never numerous in any species, and hair formation does not occur on old prothalli. The prothallus of *Stromatopteris* (Bierhorst, 1968b) is of the Tuberous-type; it is subterranean, nonchlorophyllous, mycorrhizal, cylindrical (0.1 to 0.5 mm in diameter), sparsely branched, and growing by means of a four-sided apical meristematic cell in the larger axes, but with a uniseriate apex and growing by means of transverse divisions in the terminal cell in the smaller axes. Rhizoids and sex organs are borne all over; the rhizoids are septate (2 to 4 cells long). The prothallus exhibits zonation, regions with short cells alternating with long-celled regions, as found in the underground rhizome.

Both tetrahedral and bilateral types of spores occur in the family, some genera like *Stromatopteris* being characterized by bilateral spores and others like *Dicranopteris* and *Sticherus* having tetrahedral spores in some species and bilateral ones in the others (Nayar, 1964a; Devi, 1966). However, the tetrahedral form is more common in the family. The spores are generally 20 to 35 × 30 to 55 μ in size, devoid of perine and usually with a smooth or faintly granulose exine. Spore germination is slow, taking two to three weeks or even more. It is typically of the Gleichenia-type, producing a short "transverse" germ filament composed of discoid cells. Frequently the formation of a prothallial plate is initiated soon after the filament becomes two cells long, the prothallial cell away from the first rhizoid dividing by a wall perpendicular to the long axis of the filament. Rarely divisions in the third plane occur, and then a mass of cells results. Longer germ filaments are formed under unfavorable conditions of growth. Prothallial development is of the Drynaria-type, an apical meristematic cell being formed rather late in the development of the plate. Hairs are absent on the young prothalli and are produced only towards maturity (i.e., after the sex organs are developed); formation of hairs ceases as the prothalli age. Hair formation may be initiated as early as when the prothalli are two months old [*Sticherus bifidus* (Willd.) Ching] or as late as when they are over six months old (*Gleichenia vulcanica* Bl.); hair formation may cease when the thalli are eight to nine months old as in *Sticherus bifidus* or continue for over four years as in some species of *Gleichenia.* Antheridia of the Gleicheniaceae are of the Eusporangiate-type, massive and with a complicated pluricellular wall composed of 6 to 10 narrow twisted cells and a triangular or oval small cap cell. The wall is occasionally two cells thick in *Stromatopteris.* Septate antheridia (in which sterile tissue forms a septum dividing the mass of spermatogenous cells and extends from top to bottom of the antheridium) are reported in *Sticherus flabellatus* (R. Br.) St. John (Stokey, 1950). Antheridia and archegonia occur together. Archegonia are massive with a long (8- to 10-cells-long) neck, which is straight or slightly curved forwards at the base. The neck canal cell is binucleate, but is sometimes divided by a cross wall between the two nuclei. The jacket layer of the venter is not conspicuous. The neck for the large part is frequently two cells thick in *Stromatopteris.* The walls of the neck cells in the basal region is thickened in this genus, and the archegonium dehisces by decapitation of the anterior thin-walled region of the neck. Regeneration of young prothalli from the margin and surfaces of old ones occur in all species.

MATONIACEAE

Prothallial morphology of only *Matonia pectinata* R. Br. is known (Bower, 1926; Stokey & Atkinson, 1952d), and that too incompletely. The adult prothallus is Cordate-thalloid, longer than broad, massive, and with a broad, heavy midrib and rather narrow, highly ruffled, uplifted wings which are more than one cell thick near the midrib. The thalli are naked throughout. Rhizoids are mostly restricted to the lower surface of the midrib, are chlorophyllous when young, and possess reddish or chestnut-brown, thickened walls when old.

The spores are large (ca. 55 × 65 μ), nonchlorophyllous, tetrahedral, devoid of any perine, with a thick (5 to 8 μ) granulose exine. Spore germination and early development are unknown, but Stokey & Atkinson (1952: 139, 140) infer "that on germination there is formed a mass . . . or a plate. . . . If conditions are less favorable, there is a filament formed on germination." Development of the prothallus is through the activity of a wedge-shaped apical meristematic cell, which is ultimately replaced by a multicellular meristem when the thallus becomes cordate. Sex organs are of the Eusporangiate-type. On young thalli, antheridia are borne on the lower surface of the wings, but on adult thalli they are borne on both the surfaces and are produced continuously throughout the life of the prothallus. The antheridium is subglobose, with a central mass of spermatozoids surrounded by a wall composed of many narrow, curved cells. The opercular cell is small, nearly triangular, and more or less towards one side at the apex; it is thrown off at dehiscence. Archegonia are abundant on the midrib. The neck is curved towards the apex of the prothallus, long (up to nine cells long), with the neck canal cell binucleate and swollen at the apex towards maturity.

CHEIROPLEURIACEAE

The adult prothallus of this monotypic family (Nakai, 1933; Stokey & Atkinson, 1954b) is Cordate-thalloid with a tendency to elongate and become massive (becoming 10 to 12 mm long at 18 months) with age. The wings are comparatively narrow. The prothallus is naked throughout. Rhizoids are dark reddish brown, heavy, and exceptionally stout. The first rhizoid, as well as some of the later ones, contain a few chloroplasts. Nakai (1933) reported the presence of an endophytic fungus in the prothallus of *Cheiropleuria*, but later Stokey & Atkinson (1954b), working with cultured prothalli, concluded that the presence of a fungus is facultative, not obligate.

Spores are of the tetrahedral type in *Cheiropleuria*, 30 × 38 μ in size, devoid of perine, and possessing a smooth exine bearing a triangular thick ridge around the laesura (Nayar & Devi, 1964c). Spore germination is of the Cyathea-type, and the germ filament is very short (often composed of three or four short, often discoid cells) when it broadens to form a prothallial plate; sometimes plate formation is initiated when the germ filament is only two cells long, so that spore germination apparently results in a plate of cells. The basal cell of the germ filament usually remains undivided but occasionally divides longitudinally along with the other cells during plate formation. As in the Polypodiaceae, development of the young prothallus is of the Drynaria-type, but the meristematic cell is often dominant, and the thalli remain naked. The prothallus of *Cheiropleuria* is comparatively slow-growing (reaching maturity in eight months but continuing growth much longer). Both antheridia and archegonia occur together on adult prothalli. The antheridium is of the Eusporangiate-type, with its wall composed of many narrow curved cells, and with a wedge-shaped basal cell (Figs. 69, 70). The wall cells, however, are more transversely placed than oblique as common in the Eusporangiate-type antheridium. The opercular cell is small, more or less lateral, and discharged intact at dehiscence. The archegonial neck is straight, having six to eight cells in each row, and usually pointed towards the apex of the prothallus (not away from the apex). The neck canal cell is often binucleate at maturity but is sometimes divided by a transverse wall between the two nuclei.

DIPTERIDACEAE

Of the two genera, *Dipteris* and *Holttumiella*, included in this family, the gametophyte is known only of the former; the prothallus of *D. conjugata* Reinw. is described by Stokey (1945). The present account includes in addition, our own observations on the prothallus of *D. wallichii* R. Br. The adult prothallus is naked and Cordate-thalloid, with a heavy median midrib and conspicuously ruffled narrow wings, which are often uplifted. The thalli are slow-growing and continue growth for several years after reaching maturity (up to seven years reported), elongating markedly and becoming nearly Strap-shaped (Fig. 76). The rhizoids are brownish and contain many chloroplasts especially on the young thalli.

The spores of *Dipteris* are chlorophyllous, of the bilateral type, devoid of perine, with a smooth, thin exine and approximately 25 × 30 μ in size (Nayar & Devi, 1964c; Devi, 1966). Spore germination is basically of the Gleichenia-type. The spore divides by a wall parallel to its polar axis, but later one of the daughter cells cuts off a rhizoid initial by a wall perpendicular to the first wall. Sometimes the first division is omitted and a rhizoid initial is cut off next to the laesura by a wall parallel to the equatorial axis of the spore. Soon after rhizoid formation, a plate of four cells is formed in either case; rarely the plate is larger. In some cases a short germ filament extended parallel to the equatorial axis of the germinating spore is formed instead of a plate, but soon divisions parallel to the equatorial axis set in and a plate of cells results. Further development is markedly slow and is of the Drynaria-type (but no hairs are ever produced). Antheridia and archegonia occur together on the prothalli. No nonmeristic male prothalli (as found in advanced families) are observed. Sex organs are borne on the dorsal surface of the prothallus in addition to the ventral surface. The antheridium is of the Eusporangiate-type and massive with its wall composed of many narrow, curved cells; the basal cell is wedge-shaped. The opercular cell is small, more or less lateral in position, and thrown off at dehiscence. The archegonium is massive, with a long, nearly straight neck composed of six to eight rows of cells; the neck is pointed towards the apex of the prothallus (or sideways when the archegonium is on the flanks of the midrib). The neck canal cell is binucleate at maturity. Apogamy is rather frequent, the apogamous sporophytes developing on normal sexually reproducing protholli.

LOXOGRAMMACEAE

The family is rather imperfectly known from the point of view of prothallial morphology, the only information being that published recently by Nayar (1967b) for two Indian species, *L. involuta* (D. Don) Pr. and *L. lanceolata* (Sw.) Pr. The gametophyte of *Anarthropteris*, the only fern genus recognized as a close relative of *Loxogramme*, is totally unknown. The adult prothallus of *Loxogramme* is of the Ribbon-like type, and often profusely branched so that the thallus appears as an irregular plate-like mass. Sex organs are borne on superficial, irregularly circular, scattered cushions. Rhizoids are short and reddish brown in color; they are mostly in marginal clusters. Multicellular hairs are reported on the adult prothallus of some species (Stokey, 1960), but the prothallus of *L. involuta* and *L. lanceolata* are naked, the hair-like protuberances occasionally found on the margin being sterigmata of gemmae.

Loxogramme is one of those rare genera of ferns which characteristically possess both tetrahedral and bilateral spores within the same sporangium (Nayar & Devi, 1965); a series of intermediate forms are also met with (Nayar, 1963e). However, some species of the genus (*L. involuta*) as well as *Anarthropteris* (Erdtman, 1957) possess only bilateral spores. The spores are perine-less and the exine bears granulose to sub-verrucate-areolate ornamentation. Spore germination is of the Gleichenia-type, the first wall formed in the spore being parallel to the polar axis and separating a lateral rhizoid initial. A uniseriate germ filament develops from the prothallial cell. In *L. lanceolata* the Christiopteris-type of germination is also encountered. The germ filament is often several cells long, and in *L. lanceolata* profusely branched. Prothallial development is of the Kaulinia-type, but young thalli have a marked tendency to be broader than long and later to branch irregularly before developing a Ribbon-like form. All rhizoids are reddish brown in color. Sex organs are of the common Leptosporangiate-type, and are borne on superficial irregularly circular cushions two to four cells thick, though antheridia may occur scattered on the one-cell-thick regions also. The archegonial neck is very short, three cells long and nearly straight. The prothalli are of indefinite growth, and vegetative multiplication is effected by progressive deterioration of the older regions, resulting in separation of the branches as independent prothalli. Vegetative multiplication is effected also by unicellular marginal gemmae as in some microsorioid ferns.

POLYPODIACEAE

Subfamily Platycerioideae

Gametophytes of all the three genera, *Drymoglossum* (Nayar, 1957), *Platycerium* (Bauke, 1878b; Straszewski, 1915; Schmelzeisen, 1933; Orth, 1936; Stokey & Atkinson, 1954a), and *Pyrrosia* (Schmelzeisen, 1933; Kachroo, 1955b; Nayar, 1961c; Nayar & S. Chandra, 1965, 1967), are known in detail. The adult prothallus is Cordate-thalloid, generally broader than long, with thin median midrib and broad spread-out wings, and reaching maturity in approximately 8 to 12 months. Collenchyma-like thickenings occur at the corners of the wing cells in many species. In all genera the prothallus bears unicellular, papillate, secretory hairs (both marginal and superficial) as well as club-shaped, multicellular, glandular hairs (superficial), which bear unicellular papillate branches on the stalk cells; the latter are sometimes several cells long as in *Platycerium* (Fig. 71) and some species of *Pyrrosia*. Rhizoids are mostly restricted to the lower surface of the midrib and its adjacent areas on the wings in the posterior region. They are colored, having a violet-brown tinge even when young. In some cases a few stray chloroplasts are found included in the young rhizoids, but these soon deteriorate and are lost.

Spores in the family are of the bilateral type, devoid of perine and with the exine smooth, granulose, verrucate, tuberculate or spinose. Spore germination is of the Gleichenia-type, producing a slender, uniseriate germ filament four to eight cells long. Prothallial development is of the Drynaria-type, but the meristematic cell stage is frequently omitted, a pluricellular meristem being established directly from the anterior marginal cells of broad spatulate young prothalli. Even when a meristematic cell is developed, it is usually sluggish and soon replaced by a pluricellular meristem. Sex organs are of the common Leptosporangiate-type. Irregularly shaped, small, nonmeristic male prothalli occur along with cordate bisexual ones. The antheridium is hemispherical to subglobose with the basal cell commonly short. Antheridial dehiscence is by collapse of the cap cell; in *Platycerium* a pore-like opening is formed prior to the collapse of the cap cell (Stokey & Atkinson, 1954a). The archegonial neck is slender, short, and curved away from the apex of the thallus. The neck canal cell is binucleate and swollen towards the tip at maturity. Regeneration of prothalli by branching of the germ filament occurs frequently; regeneration is not common in cordate thalli.

Subfamily Pleopeltidoideae

The gametophytes of five out of over a dozen genera of this subfamily are described in literature: *Lemmaphyllum, Lepisorus, Phlebodium, Pleopeltis,* and *Weatherbya* (Heilbronn, 1932; Nayar, 1961a, 1962b, 1964b; Nayar & Raza, 1970). The present account includes, in addition, our own observations on some species of *Lepisorus, Phlebodium aureum* J. Sm., and *Belvisia spicata* Mirbel. The adult prothallus is commonly Cordate-thalloid, generally broader than long and reaching maturity in about six to nine months. The thalli are generally small (ca. 5 mm across), with a light midrib (four to six cells thick) and spread out wings. In some species, such as *Lepisorus normalis* and *L. loriformis* (Wall. ex Mett.) Ching, the prothalli are elongated and Strap-like, with notched or cordate apex, narrow wings, and ill-differentiated (often interrupted) midrib; the thalli may occasionally be branched. In some others, such as *L. excavatus* (Bory) Ching, the prothallus is intermediate between the Cordate-thalloid and Strap-like types; it is Strap-like for a long time during early development, but the anterior region ultimately becomes broad and cordate. The adult prothallus, thus, has a broad cordate anterior region and a narrow, prolonged, strap-like, posterior region. The rhizoids are brownish (often with a reddish tinge) and mostly restricted to the midrib region. In the majority of the cases the prothalli of the pleopeltidoid ferns bear both unicellular, papillate, secretory hairs (both marginal and superficial) as well as club-shaped, multicellular, glandular hairs (superficial) bearing papillate unicellular branches on the stalk cells (Fig. 72). There is much variation among the different species in the incidence of the hairs. Some, such as *Lemmaphyllum, Lepisorus loriformis,* etc., bear only the papillate type of hairs, the multicellular type being absent. In some others, such as *Lepisorus normalis,* the multicellular hairs are much more complex (Figs. 73, 74), being often profusely branched (bearing more than one terminal glandular cell); also the stalk of these hairs often becomes multiseriate, broad, and palea-like. In extreme cases these hairs are large and resemble paleae (Fig. 75), being several cells broad, one cell thick, ovate or oblong in outline, bearing a terminal swollen glandular cell and sometimes one or two unicellular papillate hairs on the margin (Nayar, 1962b).

Spores of the pleopeltidoid ferns are of the bilateral type, devoid of perine and with the exine commonly verrucate to tuberculate, but sometimes granulose to smooth. Spore germination is either of the Gleichenia-type or the Vittaria-type, depending on the species. In both cases a slender, uniseriate, germ filament 5 to 10 cells long, is formed. Prothallial development is of the Drynaria-type; usually the establishment of a meristematic cell is delayed, and there is a strong tendency for the prothalli to omit the meristematic cell stage and to develop a pluricellular apical meristem directly. In nearly all cases the young prothalli are elongated and more or less Strap-like; broadening of the thallus occurs only after a cordate apex is developed. In those species which possess elongated or Strap-like adult prothalli, the meristematic cell stage is regularly omitted; a pluricellular meristem is established only towards maturity. In *Lepisorus loriformis* (Wall. ex Mett.) Ching prothallial development is of the Kaulinia-type, and the prothallus remains narrow and Ribbon-like for a long time; a pluricellular meristem is formed towards maturity, followed by the formation of an apical notch. Sex organs are of the common Leptosporangiate-type in all taxa. The antheridium is small, subglobose to hemispherical and characterized by a basal cell that is short and either saucer-shaped or funnel-shaped. At dehiscence the cap cell collapses to release the spermatozoids. The archegonial neck is short (three or four cells long) and curved away from the apex of the thallus. The neck canal cell is binucleate and prominently swollen towards the tip at maturity. Neither apogamy nor proliferation of the thalli is reported. However, the germ filaments may occasionally branch, and each branch develops into a separate prothallus.

Subfamily Polypodioideae

Little is known of the gametophytes of the Polypodioideae, our information being restricted to the descriptions of the prothalli of *Campyloneurum angustifolium* Fée (Nayar, 1962b) and a few species of *Polypodium* (Pickett & Thayer, 1927; Stokey, 1959; Nayar, 1962b; Nayar & Raza, 1970). Inasmuch as *Polypodium* is such a large genus (over 75 spp.), generalizations are not of much significance. The adult prothallus is Cordate-thalloid (ca. 7 mm across), usually nearly as broad as long, with a prominent midrib (5 to 10 cells thick) and broad spread-out wings. There is a tendency for the prothalli to become massive and to elongate slightly with age, becoming longer than broad (but not Strap-like). Unicellular, papillate, secretory hairs (both marginal and superficial) as well as club-shaped, multicellular, glandular hairs (superficial), bearing papillate unicellular branches on the stalk cells, are usually found on the prothalli. In some species hairs are rather sparse, and sometimes the multicellular hair is absent.

The spores of the polypodioid ferns are of the bilateral type devoid of a perine, and possess a thick exine commonly having a subverrucate-areolate ornamentation, but in some cases granulose and in others prominently verrucate. Spore germination is of the Gleichenia-type or sometimes Vittaria-type, producing a slender, elongated, uniseriate germ filament. Prothallial development is of the Drynaria-type. Sex organs are of the common Leptosporangiate-type. Small, irregularly shaped antheridial thalli occur mixed with the cordate ones. The antheridium is small and subglobose, commonly with the basal cell disk-shaped or barrel-shaped (with a flat upper wall). The basal cell is sometimes elongated, slender, and curved, making the antheridium "pendulous" (Fig. 78). The cap cell collapses at antheridial dehiscence. The archegonial neck is short (three to five cells long) and curved away from the apex of the prothallus. The neck canal cell is binucleate and swollen towards the tip at maturity.

Subfamily Microsorioideae

The gametophytes of the Microsorioideae are better known than those of any other of the polypodiaceous phyla. Details are known of the prothalli of *Aglaomorpha* (Nayar, 1965), *Christiopteris* (Nayar, 1967a), *Colysis* (Nayar, 1962b), *Dendroglossa* (Nayar, 1955, 1959), *Drynaria* (Nayar, 1958, 1961d, 1965; Nayar & Kachroo, 1953), *Drynariopsis* (Klein, 1881; Nayar, 1965), *Kaulinia* (Nayar, 1963a), *Leptochilus* (Mahabale, 1947; Nayar, 1963b), *Merinthosorus* (Bajpai, 1964; Nayar, 1965), *Microsorium* (Pal & Pal, 1960, 1962; Pal, 1962; Nayar, 1961f, 1963a), *Paraleptochilus* (Nayar, 1963b), *Photinopteris* (Nayar, 1965), *Pseudodrynaria* (Nayar, 1954, 1958, 1961d, 1965), and *Selliguea* (Atkinson & Stokey, 1964). The present account includes, in addition, our own unpublished observations on some Indian species of *Dendroglossa, Microsorium,* and *Selliguea.* Among the various genera in which the prothallus is known, the adult thallus is of the Ribbon-like type in *Christiopteris, Colysis, Dendroglossa, Kaulinia, Leptochilus,* and *Paraleptochilus* (Fig. 77). In *Selliguea* it is of the Strap-like type, whereas in the other genera it is Cordate-thalloid. The cordate prothalli are generally rather massive, large (7 to 10 mm across), with a heavy midrib (6 to 15 cells thick) and spread out broad wings; in some of the drynarioid ferns (*Drynaria*) it is comparatively smaller, with a thin midrib. They take about six to nine months to reach maturity and generally complete their life cycle in about a year. The thalli are generally broader than long, though in some like *Microsorium* the thallus is slightly longer than broad and exhibits a tendency to elongate slightly with age. Collenchyma-like thickenings occur at the corners of the wing cells in some species. Rhizoids are restricted to the midrib region and are brownish in color. In all genera that possess cordate prothalli, unicellular papillate secretory hairs occur on both the surfaces and margin. In addition club-shaped, multicellular, glandular hairs bearing unicellular papillate branches on the stalk cells occur on the surface; in some, such as *Aglaomorpha,* multicellular hairs occur on the margin also. There is much variation in the incidence of hairs on the prothalli, some such as *Microsorium*, being profusely hairy, while some species of *Drynaria* bear hairs only sparsely (some prothalli scarcely have any multicellular hair). Usually the multicellular hairs are two to three cells long, but in some (such as *Microsorium* spp.) they often possess prolonged stalks. Sometimes the hair-bearing prothallial cell divides, forming a columnar or conical protuberance subtending the hair. In those genera having Ribbon-like prothalli, the thallus is of indefinite growth, narrow with nearly parallel sides and rounded apex, and often branched; there is no well defined meristem as in the cordate prothalli. Rhizoids are brownish or reddish brown in color and produced profusely in marginal clusters as well as in small superficial groups on the lower surface. Generally the thalli are attached to the substratum by one margin, the other margin being slightly lifted up. The rhizoids of *Christiopteris* are characteristic in having a very broad base (several times broader than the body of the rhizoid) and suddenly narrowed upwards. The rhizoid initial is very broad, extending from end to end of the mother cell and completely covering one face of it; the rhizoid proper is produced as a papilla-like protrusion of the central region of its peripheral wall. On older thalli the dilated basal region is sometimes cut off by a cross-wall to form a hemispherical basal cell. No midrib is developed by the Ribbon-like prothalli, but small irregularly circular cushions (two to four cells thick) are formed here and there scattered irregularly towards the median plane of the thallus. These bear sex organs and rhizoids. The prothalli are profusely branched, bearing several Ribbon-like lateral branches which are developed secondarily by proliferation of one or a group of marginal cells of the main thallus. The prothalli grow for several years and the older regions progressively die and deteriorate, separating the branches as independent prothalli. In some cases, as in *Leptochilus* (Nayar, 1963b), prothalli over 100 mm long (2 to 3 mm broad) are reported. In several cases the thalli have alternating narrow and broad regions: the broad regions possibly represent growth during the favorable seasons. Cultured prothalli growing under uniform conditions are uniformly Ribbon-like. Unicellular, papillate hairs are found profusely on the margins and surface of the prothallus of *Christiopteris*; the cushions bear in addition two- to three-cell-long club-shaped hairs. In contrast, the prothalli of *Leptochilus* are naked. In *Paraleptochilus* a few sparse, inconspicuous, small, unicellular, papillate hairs are found on the margins and on the cushions. In all the other genera such hairs are found occasionally on the cushions on the lower side; otherwise the thallus is naked.

The spores in the Microsorioideae (Nayar & Devi, 1964c) are of the bilateral type devoid of perine, with the exine commonly bearing a subverrucate (sometimes spinulose) ornamentation. Spore germination is of the Vittaria-type or Gleichenia-type, depending on the species; some, such as *Christiopteris*, possess the characteristic variation of the Gleichenia-type, as described earlier (Nayar, 1967a; Nayar & Kaur, 1968). In both cases a slender uniseriate germ filament is produced; the germ filament is generally more slender than in other families, and is generally five to ten or more cells long when plate formation sets in. *Christiopteris* is exceptional in producing a transversely oriented (long axis parallel to the longest equatorial axis of the spore), elongated, primary germ filament at spore germination. The spores in this genus, when shed from the sporangium, are often already two- or three-celled, being divided by one or two cross walls parallel to the polar axis. As the spore coat ruptures, the filament elongates and may become three or four cells long. The two end cells may develop into rhizoids, or only one of them. One or two secondary germ filaments are produced as lateral branches (often perpendicular to the primary filament) from any of the cells of the primary filament other than the rhizoid initials. Prothallial development is of the Drynaria-type in species with Cordate-thalloid prothalli. There is a general tendency for many prothalli to omit the meristematic cell stage; even when a meristematic cell is formed, it is most often sluggish. The drynarioid fern *Merinthosorus* is exceptional in the family in possessing a prothallial development of the Aspidium-type. In this the terminal cell of the germ filament ends in a hair, and a lopsided prothallial plate is formed by intercalary cells behind the terminal cell. A wedge-shaped meristematic cell is then established laterally in one of the marginal cells on the more expanded side of the prothallial plate. Marginal hairs are produced continuously after the development of the terminal hair on the germ filament. In genera having Ribbon-like adult thalli, the prothallial development is of the Kaulinia-type.

Sex organs are of the Leptosporangiate-type in the subfamily. Irregularly developed, small, nonmeristic antheridial thalli are formed in many genera, along with normally developed bisexual prothalli. Antheridial dehiscence is by collapse of the cap cell. The basal cell of the antheridium is usually short and saucer-shaped; in some, like *Christiopteris*, it is elongated and barrel-shaped, often making the antheridium pendulous. The archegonial neck is short, slender, and curved away from the apex of the prothallus. The neck canal cell is binucleate and swollen towards its tip at maturity. Profuse vegetative multiplication of the prothalli by formation of unicellular, dumbbell-shaped, basally attached gemmae marginally at the anterior end of the branches (Fig. 79) is reported in all genera which possess Ribbon-like prothalli. The gemmae are produced directly on the protruded marginal cells (which thus form cylindrical sterigmata), which may bear successive crops of gemmae. On shedding, the gemma elongates and divides by wall perpendicular to its long axis and develops into a germ filament. In addition to development of gemmae, the Ribbon-like prothalli multiply by progressive death and deterioration of its older regions, separating the branches as independent thalli. Since the prothalli are perennial, they often form extensive colonies by this method. Vegetative propagation is rare in genera having Cordate-thalloid prothalli. Proliferation of the prothallus is uncommon but is

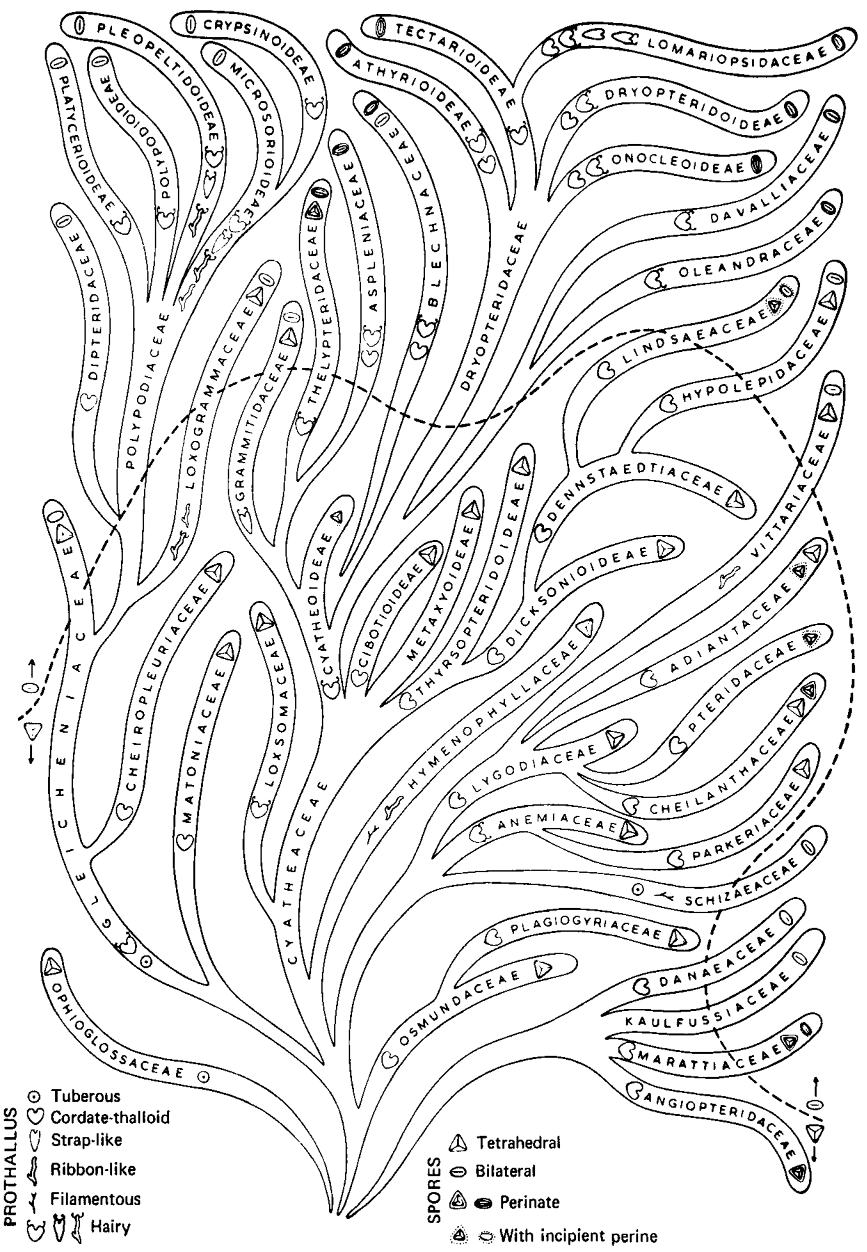

FIG. 80. Schematic representation of the interrelationships of the various families of homosporous ferns, showing the nature of spores and prothalli in each family.

induced by adverse conditions of growth. In many cases, branching of the germ filament leading on to the formation of more than one prothallus from a spore is reported in some genera. Apogamy is rare in the group.

Subfamily Crypsinoideae

Prothallial morphology of the only two genera *Arthromeris* (Nayar, 1962b) and *Crypsinus* (Nayar, 1962b) is known. The adult prothallus is Cordate-thalloid, with a thin midrib and broad, spread out wings. The thalli are small, quick-growing, and generally broader than long. Unicellular, papillate, secretory hairs are borne on both surfaces as well as the margin, and club-shaped, multicellular glandular hairs bearing unicellular branches on the stalk cells, occur on the surfaces (more commonly on the lower) restricted to the midrib and portions of the wings adjacent to the midrib.

Spores of the Crypsinoideae are of the bilateral type, devoid of a perine and having a thin granulose to spinose exine. Spore germination is of the Vittaria-type and prothallial development is of the Drynaria-type. The germ filaments are often more slender than in other Polypodiaceae. Sex organs are of the common Leptosporangiate-type. Irregularly shaped, small, male prothalli occur frequently. The antheridium is small, subglobose, with a saucer- or cup-shaped basal cell; it opens by collapse of the cap cell at maturity. The archegonial neck is slender and curved away from the apex of the prothallus, with the neck canal cell binucleate at maturity.

CONCLUSIONS

It is apparent that the prothallus of homosporous ferns provides a wide range of dependable taxonomic criteria. For an understanding of the evolutionary process in this group of plants the more significant features of prothallial morphology are the nature of spore-germination, the pattern of prothallial development, the form of the adult prothallus, the nature of prothallial trichomes, and the morphology of sex organs. In addition to these, the nature of rhizoids, possession of special modes of vegetative propagation, etc., provide useful comparative criteria in some groups. In combination these aspects of prothallial morphology serve to characterize most of the larger groups of homosporous ferns, nearly as clearly as sporophyte morphology. Also, a comparative study of gametophyte morphology in the various taxonomic groups (Fig. 80) clearly indicates the trends of evolution of the gametophyte among homosporous ferns. As could be expected of such a vast and varied group of plants as the ferns, the gametophyte has undergone evolution along different lines of specialization. Each of the comparative criteria mentioned above appears to have followed a process of evolution independently of the others.

With regard to spore germination, it is suggested (Nayar & Kaur, 1968) that the Vittaria-type of germination is the most advanced and the

Amorphous-type, resulting in the formation of a mass of cells, the most primitive. Vittaria-type of germination is characteristic of all the more advanced groups of homosporous ferns, i.e., groups which represent the distal branches of the evolutionary tree (Fig. 80). In contrast, Amorphous-type of germination is restricted to the most primitive groups like the Ophioglossidae, Marattiidae, some taxa of the Gleicheniaceae, and some of the Schizaeaceae. The Amorphous-type, in which cell divisions occur in all the three planes and thus results in the formation of a nearly globose mass of cells as in the Ophioglossidae (possibly also in *Stromatopteris*), is apparently the most primitive. Partial suppression of cell divisions by walls parallel to the equatorial plane of the germinating spore results in a dorsiventral circular mass as found in the Marattiidae. The Mecodium- and Hymenophyllum- types of germination are apparently derived from this by suppression of all cell divisions in the equatorial plane. From this, as suggested by Stokey (1940), the Trichomanes-type is possibly derived by suppression of the first two cell divisions in the Hymenophyllum-type. A further step in this reduction series is found occasionally in some of the trichomanoid ferns. Instead of developing three peripheral lenticular cells (one each at the three corners), which would result in three-directional growth of the prothallus, only two are developed, resulting in two-directional growth; one lenticular cell usually forms a germ filament, while the other develops into a rhizoid and both grow in nearly opposite directions. The Gleichenia-type of germination, in which growth is two-directional and in opposite directions along the equatorial plane of the germinating spore, is possibly derived in this way. On the other hand, the Osmunda-type of germination, in which also growth is two-directional and in opposite directions but along the polar plane of the germinating spore, is derived from the three-dimensional Amorphous-type in a different manner. If all divisions by walls parallel to the polar plane are suppressed (instead of suppression of all cell divisions by walls parallel to the equatorial plane, as occur in the Hymenophyllum-type), a plate expanded along the polar plane of the spore will result. The Osmunda-type of germination is possibly derived through such a hypothetical condition. A three-celled plate of cells in the polar plane of the spore, resembling this hypothetical polar plate, is formed in the Anemia-type. The first two-cell divisions in the Anemia-type are similar to those in the Hymenophyllum-type, except that the plane in which they occur is perpendicular to the plane in which cell divisions occur in the Hymenophyllum-type. If the first division in the Anemia-type of germination is suppressed, it will result in the Cyathea-type. Thus, in the Cyathea-type, instead of a group of three cells, only two cells are formed at germination, one producing the rhizoid and the other the germ filament (the large cell at the distal end of the spore in the Anemia-type being unrepresented). Comparative morphology indicates that the Vittaria-type is evolved from the Gleichenia-type, Anemia-type as well as the Cyathea-type, since it occurs in all groups of ferns believed to have evolved from the

Gleichenia-, *Cyathea*-, and *Anemia*- lines of evolution (viz., Polypodiaceae of *Gleichenia*-line; Aspleniaceae, Blechnaceae, Davalliaceae, Dennstaedtiaceae, Dryopteridaceae, Hypolepidaceae, Lindsaeaceae, Lomariopsidaceae, Oleandraceae, and Thelypteridaceae of the *Cyathea*-line; Adiantaceae, Cheilanthaceae, Parkeriaceae, Pteridaceae, and Vittariaceae of the *Anemia*-line of evolution). Also, in the Polypodiaceae both Gleichenia-type and Vittaria-type of germination occur, the more primitive genera (Platycerioideae) having the Gleichenia-type and the comparatively more advanced ones (Crypsinoideae, the drynarioid genera of Microsorioideae) having the Vittaria-type.

Considering the patterns of prothallial development, the one which involves the formation of a dominant apical meristematic cell early during developmental history is obviously the more primitive one. The formation of an elongated uniseriate germ filament before a meristematic cell becomes established or a plate is formed (as found in the majority of homosporous ferns) appears to be the first step in evolution. Accordingly, genera in which the germ filament is characteristically short (Osmundaceae, Gleicheniaceae, and most Cyatheaceae) are more primitive compared to those in which the filamentous stage is more pronounced. Also, those ferns in which an apical meristematic cell is developed early during the formation of a prothallial plate (Adiantum-type of development) appear to be more primitive compared to those in which formation of a meristematic cell is delayed (Drynaria-type of development). Usually, accompanying this delayed development of the meristematic cell, there is a distinct reduction in the activity of the meristematic cell. Thus, in prothalli having the Adiantum-type of development, growth and expansion of the young thallus are mainly by the activity of the meristematic cell, whereas in thalli having the Drynaria-type of development, growth of the young thallus is to a great extent by diffused meristematic activity, the meristematic cell being rather sluggish. As suggested by Nayar & Kaur (1969c), a further step in advancement is the elimination of the meristematic cell and the development of a pluricellular meristem directly from the marginal cells of nonmeristic prothallial plates, as found in several cases among the more advanced groups of ferns. The elimination of a meristematic cell as well as a pluricellular meristem, as found in the Kaulinia-type of prothallial development, appears to represent the most advanced condition.

Another line of advancement in the pattern of prothallial development appears to have been in the direction of a suppression of apical growth in young prothalli. Such a suppression of apical growth in the germ filament is found in the Aspidium-type of prothallial development, in which the germ filament ends in a terminal hair and a prothallial plate is developed by the activity of the intercalary cells. However, retardation of apical growth may manifest itself unaccompanied by hair formation also. In extreme cases the entire anterior region of the germ filament including several cells may become quiescent, and a prothallial plate is developed towards the middle of the germ filament as reported in *Stenochlaena palustris* (Stokey & Atkinson, 1952a; Nayar, Bajpai, & Raza, 1966). In some ferns a retardation or cessation of apical growth, instead of becoming manifest at the filamentous stage, may become manifest after a broad prothallial plate is developed. In such cases growth becomes restricted to one side, and a meristem is developed laterally in the plate as in the Ceratopteris-type of development. Thus, the Kaulinia-, Aspidium-, and Ceratopteris- types of prothallial development appear to be the more advanced types, while the Adiantum-type is comparatively primitive.

As regards the form of adult prothallus, the massive Tuberous-type has long been recognized as the most primitive condition among ferns. It is the least specialized and closest in its resemblance to the sporophyte. The fleshy, cylindrical, erect-growing prothallus of *Ophioglossum, Helminthostachys, Actinostachys,* etc., closely resembles the rhizome of the sporophyte in its form, and like the rhizome grows by the activity of a four-sided apical meristematic cell. As should be expected, Tuberous prothalli are restricted to the most primitive taxa of ferns. Conceivably, all the other prothallial forms are evolved from the massive tuberous type. Comparative morphology indicates that the first major step in this evolution, leading to the thalloid forms, is a superficial, chlorophyllous, creeping, dorsiventral, tuberous prothallus. A change in the form of the thallus from cylindrical to dorsiventrally flattened seems to have accompanied this change. This change of form is brought about by the formation of a dorsiventral flange on each side of the cylindrical thallus. The dorsiventral, creeping prothallus of *Botrychium,* with its median longitudinal ridge bearing sex organs and rhizoids, apparently represents an early stage in the evolution of the fern prothallus. The keynote in the process of evolution of the different prothallial forms from such tuberous dorsiventral type is apparently a process of reduction during which the photosynthetic flanges became wings one cell thick, and the median cylindrical region (midrib) of the thallus is progressively reduced till it becomes indistinguishable from the wings. Thus, in the more primitive ferns having a dorsiventral thalloid prothallus, the thallus is large, with a massive median midrib and heavy wings (several cells thick near the midrib and progressively becoming one cell thick towards the margins) as found in the Marattiidae and the Osmundaceae. Retardation of apical elongation accompanied by comparatively extensive expansion of the wings results in a cordate anterior region. Such a prothallus differs from the Tuberous-type (as found in the Ophioglossidae) in one important aspect. Its apical (meristematic) region is only one cell thick and, at least in the early stages of development, has a three-sided meristematic cell (with two lateral oblique cutting faces) instead of a four-sided one as found in the Tuberous-type. The tuberous prothallus of *Lophidium* provides a possible clue to the derivation of this condition. In *Lophidium* the meristematic anterior region of the prothallus is uniseriate, and growth in length is effected by transverse divisions of the apical cell. In such a thallus, if lateral wings were to develop and apical elongation were retarded so that wing formation was initiated in the penultimate cell, the uniseriate apical meristematic cell would be squeezed by the rapidly expanding daughter cells of the penultimate cell into a wedge-like form (having two oblique cutting faces instead of one flat basal one). During development of thalloid prothalli the rate of apical elongation progressively decreases from the younger to the older stages, and the proportionate rate of lateral expansion increases. This results in wing development being initiated in the anteriormost cell itself and leads to the replacement of the obconical apical meristematic cell by a pluricellular meristem.

The ultimate step in the evolution of the thalloid types of fern prothalli is evidently the Ribbon-shaped prothallus in which the midrib is all but lost. Remnants of the midrib persist, however, as cushions on which sex organs are borne. It appears that this form of the adult prothallus is derived differently in the Hymenophyllaceae on the one hand and the Polypodiaceae on the other. In the latter group it is obviously derived from the Cordate-thalloid through the Strap-shaped type. The midrib, which is often interrupted in the Strap-shaped type, is reduced to cushions scattered along the median plane. In the Hymenophyllaceae it seems that the prothallus has evolved directly from the Tuberous-type by total flattening of the thallus. Instead of the central region remaining cylindrical and flattened flanges developed on either side, the central region became thin and flattened, leaving marginal thickened ridge-like regions on either side, bearing sex organs. These ridges became discontinuous, forming the characteristic marginal cushions of the Hymenophyllaceae. Thus, the Ribbon-shaped prothallus of *Hymenophyllum* is equivalent to the midrib of the Cordate-thalloid prothalli, the wings being unrepresented. The Filamentous-type of adult prothallus (as found in *Schizaea* and the trichomanoid genera) apparently represents a separate line of evolution. It is probably derived by suppression of all cell divisions in the longitudinal plane in a thallus like that of *Lophidium.* Photosynthetic efficiency is achieved in this line of evolution by profuse branching of the thallus.

In the evolutionary history of the ferns, prothallial trichomes have developed in only a few of the groups, a large majority of the ferns having naked prothalli (Fig. 80). Possibly the possession of similar types of trichomes by apparently unrelated groups led to the current concept that prothallial trichomes are of little value in taxonomic and phyletic studies (Stokey, 1951, 1960; Atkinson & Stokey, 1964). However, the restricted distribution of hairy prothalli among the various phyletic groups and the possession of certain characteristic types of trichomes by some related groups (e.g., acicular hairs in the Thelypteridaceae and Grammitidaceae) apparently indicate that trichomes are of value in comparative studies. As with other features of gametophyte morphology, the tendency to develop trichomes seems to have evolved independently in the different phyletic groups of the Filicideae. Obviously the more primitive condition among ferns is to have naked prothalli; the prothalli of the relatively primitive groups of homosporous ferns (Ophioglossidae, Marattiidae, Osmundaceae) are naked. Prothallial trichomes appear in the course of evolution in the Filicideae among the main line of evolution in the Cyatheales and Gleicheniales as well as in a branch line of evolution among the Schizaeales (Anemiaceae). Apparently the more primitive types of prothallial trichomes are the gleicheniaceous and cyatheaceous ones, which develop from special, large, wedge-shaped initial cells. The more advanced types develop from superficial, small, lens-shaped initials. It seems that the former types are morphologically different from the latter; possibly they represent branches comparable to the filamentous branches of limited growth as found on the tuberous prothalli of *Stromatopteris* (Bierhorst, 1967b), while the latter are comparable to the dermal appendages of the sporophyte.

In all groups of ferns having hairy prothalli, papillate secretory unicellular hairs are the most common type. Club-shaped multicellular hairs are found mixed with them in the comparatively more advanced families like Polypodiaceae, Tectarioideae, Davalliaceae, Lomariopsidaceae, and Grammitidaceae. However, in all these groups the ultimate tendency appears to be towards reduction of hairs, as is evident in the Polypodiaceae. In this family the more primitive genera (Platycerioideae, the less advanced taxa of Microsorioideae like *Microsorium*) are profusely hairy while some of the obviously more advanced taxa (*Drynaria* and *Leptochilus* of Microsorioideae) possess nearly naked prothalli. Among the Gleicheniales the more primitive families (Matoniaceae, Cheiropleuriaceae, Dipteridaceae, all of which possess prothalli having several primitive features) possess naked prothalli. The modern Gleicheniaceae, which are comparatively more advanced in their gametophyte morphology, possess club-shaped hairs that develop from wedge-shaped, large, initial cells, whereas the Polypodiaceae (evidently the most advanced family in the Order) have profusely hairy prothalli with hairs developing from small lens-shaped initials. So also, the prothalli of the more primitive taxa of Cyatheales (Hymenophyllaceae, Cibotioideae, Dicksonioideae, Thyrsopteridoideae) are naked and in some of the branch lines of evolution (Dennsteadtiaceae-Lindsaeaceae group) the prothalli do not show any tendency to have trichomes. The Cyatheoideae and Loxsomaceae (which are evidently more advanced than the Thyrsopteridoideae, etc.) have hairy prothalli, the hairs being large, complex structures developing from large, wedge-shaped initials. Hairs developing from small, superficial, lens-shaped initials are found in the more advanced families. Even among these groups the comparatively more primitive taxa have naked prothalli. The Thelypteridaceae and related Grammitidaceae (Nayar, 1970, 1971) are unique among ferns in possessing acicular hairs.

With respect to the sex organs produced by fern prothalli, the concept of primitive and advanced types has been fairly clear for a long time. As far as the archegonia are concerned, the relatively massive type with the neck much elongated, stout, and either straight or pointed towards the growing apex of the prothallus, is obviously the more primitive. So also is the tendency towards the possession of a divided neck canal cell and more than two nuclei in the neck canal cell. An archegonial neck embedded in the prothallial tissue, as in the Ophioglossidae and Marattiidae, represents a still more primitive condition, an exposed neck being characteristic of all the more advanced groups of ferns. Evolution of the fern archegonium has been towards reduction in size (including that of the neck) and towards having the neck pointed away from the apex of the thallus. In the relatively advanced forms, the neck of the archegonium consists of three or four cells per each of the four rows of neck cells.

Comparatively, the more primitive type of antheridium is the Eusporangiate-type, with its massive sperm output and complicated wall structure. As in the case of the archegonium, the embedded nature of the antheridium is found only among the more primitive groups of homosporous ferns (Ophioglossidae, Marattiidae). An exception is the Parkeriaceae, which has characteristic Leptosporangiate-type of antheridium partially surrounded by the gametophytic tissue. This probably is a state derived during evolution, in response to the peculiar conditions under which the prothalli of this family grow, viz., on marshy ground which is repeatedly inundated. Among all the homosporous ferns the Parkeriaceae alone are adapted to an aquatic habit. Considering that antheridial dehiscence in ferns generally takes place in the presence of free water, the embedded and thus protected position of the antheridium should be an advantage to a fern like *Ceratopteris* (Parkeriaceae) the gametophytes of which are liable to repeated flooding. The advancement during evolution of the antheridium has been, as in the case of the archegonium, a process of reduction in size and complexity. Thus, from the massive Eusporangiate-type has evolved the simpler Leptosporangiate-type of antheridium, with a small sperm output and a simple wall composed of three cells. The process of this reduction is well illustrated in the Cyatheaceae, in which some of the more advanced groups (Cyatheoideae) possess an antheridium intermediate between the Eusporangiate- and Leptosporangiate- types. Other than the Eusporangiate and Leptosporangiate nature, the mode of antheridial dehiscence and the shape of the basal cell in the Leptosporangiate-type of antheridia appear to be of significance in comparative studies.

The evolutionary tendencies of the gametophyte are apparently the same in the different phyletic groups of the Filicideae (Fig. 80). In the Order Gleicheniales the more primitive family Gleicheniaceae includes genera which possess a tuberous, erect-growing, subterranean prothallus. A Cordate-thalloid form is evolved within the family. The thallus is slow-growing and massive in all the earlier groups of the Order (Gleicheniaceae, Matoniaceae, Cheiropleuriaceae, Dipteridaceae), and spore germination results in a plate of cells or a short germ filament that soon forms a plate. Prothallial development in them is of the Drynaria-type. Sex organs in all these groups are of the primitive Eusporangiate-type. The prothallus is naked in the Matoniaceae, Cheiropleuriaceae, and Dipteridaceae, but in the Gleicheniaceae some genera bear typical club-shaped multicellular hairs developing from wedge-shaped initial cells. The spores are of the tetrahedral type in the Matoniaceae and Cheiropleuriaceae; a transition to the bilateral form occurs in the Gleicheniaceae, and spores are typically of the bilateral type in the Dipteridaceae. Spore germination is of the Gleichenia-type in the Gleicheniaceae. In the more advanced Polypodiaceae, tetrahedral spore form is absent. Spore germination is of the Gleichenia-type in the comparatively less advanced members of the family (Platycerioideae, some of the Polypodioideae and Microsorioideae), but is of the more advanced Vittaria-type in the more advanced members (Pleopeltidoideae, Crypsinoideae). In all cases the germ filament is long. As in the Gleicheniaceae, prothallial development is of the Drynaria-type in the Polypodiaceae, and the adult prothallus is Cordate-thalloid though small and less massive. Comparatively large thalli with heavy midrib are found in the Platycerioideae and the less advanced genera of the Microsorioideae. A transition from Gleichenia- to Vittaria-type of germination, Drynaria- to Kaulinia-type of development, and Cordate-thalloid to Strap-shaped and ultimately Ribbon-shaped adult form is found among the various genera of the Microsorioideae and Pleopeltidoideae. Sex organs in all the Polypodiaceae are of the advanced Leptosporangiate-type. In addition to club-shaped multicellular prothallial hairs, the Polypodiaceae possess papillate unicellular secretory hairs. A tendency towards reduction and ultimate loss of hairs is evident in the Microsorioideae and Pleopeltidoideae. The Loxogrammaceae exhibit a combination of both primitive and advanced features in their gametophyte morphology. They recall the Gleicheniaceae in having tetrahedral as well as bilateral spores and the Gleichenia-type of spore germination. However, the prothallus is of the advanced type in having a Kaulinia-type of development pattern, Ribbon-shaped adult form and Leptosporangiate-type of sex organs, as found in the more advanced taxa of Polypodiaceae.

With respect to gametophyte morphology, the Schizaeales appear to include three separate lines of specialization, parallel to those recognized on the basis of sporophyte morphology (Fig. 80). The primitive Tuberous-type of prothallus, from which the other types are apparently derived, is found only in the family Schizaeaceae. Within this family prothallial evolution has been towards the development of a Filamentous adult form. Also, a transition from tetrahedral to bilateral spores occurs in the family. All the other taxa of the Order have evolved a thalloid type of prothallus, and the tetrahedral spore-form persists in all except the Vittariaceae, which possibly represents the most advanced family of the Order. In the more primitive families, Anemiaceae and Lygodiaceae, spore germination is of the primitive Anemia-type and the germ filaments are short. The adult thallus is Cordate-thalloid and has a massive midrib which exhibits a tendency in some Anemiaceae to revert to the ancestral tuberous form (cylindrical, erect-growing and devoid of wings). In the Anemiaceae and Parkeriaceae a Ceratopteris-type of prothallial development has become established, whereas in Lygodiaceae and the more primitive members of the families derived from Lygodiaceae, prothallial development is of the more primitive Adiantum-type. A transition from the Adiantum-type to a Ceratopteris-type is found in nearly all families derived from lygodiaceous ancestors (Fig. 80) while a still more advanced Kaulinia-type characterizes the most advanced family of the order, the Vittariaceae. In addition, the Vittariaceae have evolved special means of vegetative multiplication by means of gemmae. In all the three lines of evolution among the Schizaeales the more advanced Leptosporangiate-type of sex organ is evolved rather early in the evolutionary history. So also, the prothalli of the Schizaeales except of the Anemiaceae and *Notholaena* (Cheilanthaceae) have never developed any trichomes.

As evident from sporophyte morphology, the Order Cyatheales is the most varied with regard to gametophyte morphology also. The primitive tuberous-type of prothallus is not met with in the Order. As in the case of Schizaeaceae among the Schizaeales, the Hymenophyllaceae seem to represent a line of evolution separate from that followed by other taxa of the Cyatheales. The adult prothallus has evolved a specialized, Ribbon-shaped form with marginal cushions in the *Hymenophyllum*-group of species, and a Filamentous form in the *Trichomanes*-group. Spores in both are of the primitive tetrahedral type and spore germination of the Hymenophyllum-type. However, prothallial development is of the advanced Kaulinia-type in the *Hymenophyllum*-group. Also, the Hymenophyllaceae have evolved a specialized method of vegetative propagation by gemmae. At the same time sex organs of the family are of the primitive Eusporangiate-type. Thus, the gametophytes of Hymenophyllaceae possess a mixture of advanced and primitive characters, clearly indicating that evolutionary progression in the various aspects of gametophyte morphology has been independent of each other.

Among the main group of families of the Cyatheales, the Cyatheaceae, and Loxsomaceae represent the more primitive elements. The prothallus in these families is of the slow-growing, massive, Cordate-thalloid type, with a tendency in some Cyatheaceae for the thallus to revert occasionally to the cylindrical tuberous form. The spores are of the tetrahedral type. Spore germination is of the primitive Cyathea-type, and the germ filaments are short at plate formation. Prothallial development is of the Adiantum-type in the Cyatheaceae and Drynaria-type in the Loxsomaceae. Sex organs are of the Eusporangiate-type, though simplification of the antheridium leading on to the simple Leptosporangiate-type is found in the Cyatheoideae. Characteristic, large, palea-like trichomes developing from special wedge-shaped initials are found in both the Loxsomaceae and the Cyatheoideae, while the prothalli are naked in the other subfamilies of the Cyatheaceae.

On the basis of sporophyte morphology, three separate lines of evolution are recognized from the primitive cyatheaceous stock (Fig. 80). In all of them the adult prothallus is of the Cordate-thalloid type, showing a transition to the Strap-shaped form in the most advanced families of the group. Each of the three lines of advancement from the cyatheaceous stock has evolved independently as far as their gametophytes are concerned. The Dennstaedtiaceae-Lindsaeaceae line among them has evolved a thin Cordate-thalloid prothallus which is naked as in the ancestral group, Dicksonioideae. In the comparatively more primitive family Dennstaedtiaceae, the spores are tetrahedral, whereas there is a transition to bilateral spore-form in the more advanced Lindsaeaceae and Hypolepidaceae. Spore germination is of the advanced Vittaria-type in all. In contrast to this group, both the Dryopteridaceae-line and the Thelypteridaceae-Grammitidaceae-line have evolved hairy prothalli. The prothallus is naked in some taxa of the Dryopteridaceae, Blechnaceae, and Davalliaceae of the dryopteridaceous complex and some of the Aspleniaceae of the thelypteridaceous complex. In the majority, hairs are papillate unicellular and secretory. Some of the more advanced taxa of the dryopteridaceous group (Tectarioideae, Lomriopsidaceae, Davalliaceae) possess club-shaped multicellular hairs in addition. Among the thelypteridaceous group, the more advanced taxa of Thelypteridaceae and the Grammitidaceae bear characteristic acicular hairs in addition to papillate hairs, while some Aspleniaceae have multicellular club-shaped hairs as in the dryopteridaceous ferns.

In the dryopteridaceous complex of families the adult prothallus is of the Cordate-thalloid type, except in some of the Lomariopsidaceae. In the latter there is a tendency for the thallus to be elongated in some, while in some others (*Elaphoglossum, Rhipidopteris*) it is Strap-shaped. Spores are characteristically of the bilateral type with a distinct perine derived within the group. Spore germination is of the advanced Vittaria-type in all. Prothallial development is of the Adiantum-type (Onocleiodeae, Athyrioideae) ranging to Drynaria-type in the comparatively primitive genera and of the Aspidium-type in the others. A transition from Adiantum- to Aspidium-type is met with in the Dryopteridoideae, Lomariopsidaceae, Oleandraceae, Davalliaceae, and Blechnaceae. Among the thelypteridaceous complex of families the adult prothallus is Cordate-thalloid except in the Grammitidaceae, which possess Strap-shaped prothalli. The Aspleniaceae represent the more primitive element in so far as that the prothallus is naked in some and in some others shows a transition to hairy condition. As in the dryopteridaceous group, advancement in the pattern of prothallial development in the Aspleniaceae is from the Adiantum- to Aspidium-type. So also is the tendency in the family to develop club-shaped glandular hairs in addition to papillate hairs. In contrast, the spores are mostly tetrahedral in the Grammitidaceae, though a transition to bilateral form is evident in the family. But the prothalli of the Grammitidaceae are comparatively the most advanced in the group in being Strap-shaped, bearing profuse acicular hairs as well as branched club-shaped hairs, and in possessing a specialized method of vegetative propagation. With respect to spore morphology, the Thelypteridaceae are more advanced than the Grammitidaceae; except in very rare cases (Nayar & P. Chandra, 1966) the spores are bilateral in the family and possess a distinct perine in the majority. But the prothalli are Cordate-thalloid bearing papillate hairs, though in some of the more advanced genera acicular hairs are found mixed.

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