3. THE MORPHOLOGY OF FERNS

A fern plant consists of a stem, bearing leaves and roots. The leaves (or some of them) bear dehiscent *sporangia*, each sporangium containing unicellular spores, which are in most cases wind-dispersed. A spore germinates to produce a small green plant called a *prothallus*. The prothallus bears sexual organs *(archegonia* and *antheridia)*. After fertilization by an antherozoid, the female cell in an archegonium grows to form a new fern plant. The life cycle of a fern thus has two phases, asexual (the fern plant) and sexual (the prothallus). These phases are also called the *sporophyte* and the *gametophyte*. The sporophyte is much longer-lived, larger and more diversified than the gametophyte, and its characters are mainly used in taxonomy. The following statement deals with the parts of the sporophyte in turn, with discussion of the kinds of modification of each which occur, and of special terminology. Finally, a note on the gametophyte will be given, including reference to the not infrequent condition in which the sexual process is omitted.

Stem. (a) *Shape, size, and habit of growth.*—A fern stem may be long and creeping or climbing, in which case it is usually called a *rhizome*, or it may be short and compact, in which case it is often called a *stock*, *rootstock* or *caudex*. If it grows erect, as in tree-ferns, with a tuft of leaves at its apex, it is called a *trunk*.

A creeping stem or rhizome may be *dorsiventral* or *radial* in construction. In the former case the leaves (or their stalks) are borne on the upper surface (often in two alternate rows, sometimes more than two), the roots entirely or mainly on the lower surface; the internal vascular structure corresponds to this external differentiation. In a radially constructed rhizome leaves and roots are borne on all sides (though of course the leaf-stalks all grow upwards), and the vascular system shows a corresponding radial symmetry.

A short stem or rootstock, bearing crowded leaves, is usually radial in construction. Such a stem may be quite erect, but more often it is more or less decumbent; the presence of a persistently erect rootstock is sometimes an important diagnostic character. Tree-ferns, and others in which the erect rootstock grows to an appreciable height above the surface of the ground, have numerous roots which may form a close covering on the lower part of the stem, thus giving stability to the plant.

(b) *Branching.*—In a few cases this is by simple *dichotomy* (the apical growing-point dividing into two equal parts). More frequently branches arise in association with the bases of leaf-stalks, usually on the outside. The method of branching may be important taxonomically; it has been too little studied.

(c) *Hairs, Bristles and Scales.*—The young parts of a stem are in almost all cases protected either by scales or hairs; similar scales or hairs also cover the very young leaves before they uncurl. Such scales and hairs are more or less persistent on older parts of stem and leaves.

Hairs consist of a single cell or of a single row of cells, and in different ferns are of characteristic length and thickness; the thicker ones are sometimes quite rigid and bristle-like. True *bristles*, which are more than one cell thick at the base, but round in section, also occur in some cases. *Scales* are flat plates of cells, one cell thick; the details of their structure (especially characters of edges, base and apex, and the presence or absence of superficial outgrowths) are often very important taxonomically and may need microscopic examination. A *peltate* scale is one attached at some point on its surface, not on its edge. Where lateral cell-walls of a scale are thickened so as to form a distinct lattice-work pattern, the scale is called *clathrate;* the upper and lower walls may or may not be translucent.

(d) *Internal Structure.*—The most important internal structure is the vascular tissue. The vascular strands which pass into leaves and roots are connected to the vascular system of the stem; the latter is called a *stele*, or if at any cross section it consists of more than one part, the parts are called *meristeles*. The simplest kind of stele is a *protostele;* in this there is one single solid strand of xylem with phloem around it, the whole surrounded by an endodermis. In some cases the xylem of a protostele is not solid, but has a core of non-vascular tissue; such a structure is called a *medullated protostele*. In some long-creeping rhizomes (*e.g. Microlepia*) the stele is a hollow cylinder, with phloem and endodermis both inside and outside the xylem; this is called a *solenostele* or *siphonostele*. In this case there is usually a gap in the stele where the vascular supply to a leaf is attached; such a gap is called a *leaf-gap*. Rhizomes of this type are usually dorsiventral. In *Davallia*, the solenostele does not consist of a continuous hollow cylinder, but the cylinder (not circular in section) is composed of a network, most of the gaps in which are not leaf-gaps. This may be called a *dissected solenostele;* in the case of *Davallia* it is dorsiventral, the ventral meristele being broader than the rest and bearing roots. In stems of radial structure bearing many leaves close together, the stele usually forms a hollow cylinder in which there are many leaf-gaps, these gaps being like the meshes in a network. Such a stele is called a *dictyostele*. In a few ferns there are additional steles internal to the principal stele (*e.g. Matonia*, some species of *Pteris*); also in a few there is a cortical system of stem-bundles outside the principal stele (*e.g. Stenochlaena*). Besides vascular tissue, most fern-stems contain thick-walled tissues which serve to give mechanical strength; the presence (or absence) and distribution of such tissue may be important.

Roots. Roots are all adventitious. The primary root of a fern-embryo, having no power of increasing in thickness, is soon inadequate to supply the needs of the growing plant, and further roots must grow from the stem (in some cases also from leaf-bases). Little use has been made of root characters for taxonomic purposes, but there is considerable diversity of root-structure among ferns as a whole. In some species of *Hymenophyllaceae* there appear to be no roots, the rhizome being covered with hairs which function as root-hairs.

Leaves. VEGETATIVE CHARACTERS. Fern-leaves are usually called *fronds;* their stalks or petioles are called *stipes;* the blade or flat green part of a leaf is called the *lamina*. The lamina is usually divided into parts called *leaflets;* the axes on which leaflets are borne are called *rachises* (*rhachis* is the more correct spelling, but rachis is in general use in English). Fronds may be *sterile* (lacking sporangia), or *fertile* (bearing sporangia); sterile and fertile fronds may be alike in form, or dissimilar (*dimorphous*).

(a) *Stipes.*—A stipe may be *jointed* or *articulated* at its junction with the stem, or in some cases it is articulated to an outgrowth from the stem called a *phyllopodium* (*e.g. Elaphoglossum, Oleandra*); but more commonly it is not articulated. Externally a stipe usually bears hairs or scales like those of the rhizome or caudex, but often smaller; sometimes the scales are borne at the ends of warts or thorns. In some cases where the rhizome bears only scales, the stipe (and rachis) may also bear hairs. The character of the hairs, whether unicellular or multicellular (with transverse *septa*), and whether terminating in a glandular cell, is always important. In a few ferns the stipe has slime-glands, producing mucilage when the fronds are very young, and elongate *aerophores*, the latter often in association with much-reduced leaflets. In any case, there is usually a pale and more or less raised line along each side of the stipe. This line is also an aerophore; there are stomata on it, and internally the tissue is thin-walled, with air-spaces between the cells. The line is sometimes not continuous but broken, and sometimes doubled (*Cyathea*). Internally the number and arrangement of the vascular bundles in a stipe is important; often the number and arrangement change between the base and apex.

(b) *Branching of fronds.*—Fronds may be *simple* (consisting of a continuous lamina, which may be *entire* or *lobed* in various ways), or they may consist of two to many leaflets which are borne by the rachis or its branches. The commonest arrangement is for the main rachis (continuing the line of the stipe) to be almost straight, bearing leaflets (stalked or not, articulate or not) along its sides; such a frond is said to be *pinnate*, and the leaflets are called *pinnae*. Like a simple frond, a pinna may be entire or lobed; if pinnately lobed, the leaflet is *pinnatifid*, if palmately lobed, *palmatifid*. Where the rachis bears branches, these are usually arranged in a pinnate manner; if each such primary branch bears leaflets, the frond is said to be *bipinnate*, and the leaflets are called *pinnules*. If each primary branch bears secondary branches pinnately arranged, and the secondary branches bear leaflets, the frond is said to be *tripinnate*, and the leaflets are of the *third order;* fronds may also be *quadripinnate*. Pinnae or rachis-branches are usually *alternate* on the two sides of a main rachis, but in some cases they are regularly almost exactly *opposite (e.g. Gleichenia)*. The edge of a leaflet on the side towards the apex of the frond is called *acroscopic*, that towards the base of the frond is called *basiscopic*. The terms *upper* and *lower* are used for the two surfaces of the leaflets; the upper surface is that facing the stem-apex (also called the *adaxial* surface, the lower surface being *abaxial*).

There are some cases in which the stipe is not continued into a single straight rachis, but forks into two equal branches at its apex; such a *dichotomous* branching is seen in fronds of young plants of *Lygodium*. The dichotomy may be repeated, in which case a fan-shaped frond results (*Schizaea dichotoma, Dipteris lobbiana*); or only the outer branch at each dichotomy may fork again, in which case *pedate* branching results. The ultimate branching of large fronds or of their veins is also often dichotomous, and one can trace a transition from dichotomous to pinnate branching in descending a frond to its base; the pinnate condition can thus be regarded as a development from the dichotomous one. *Pseudo-dichotomy* occurs in a few cases (notably in *Gleicheniaceae* and in *Lygodium*); in these a rachis bears a pair of opposite branches and then stops growing, its dormant apex remaining between the branches.

(c) *Shape of rachises and of junctions between them and with leaflets.*—In addition to the characters of superficial hairs and scales, and of internal vascular systems, rachises of ferns provide characters of another kind which are useful taxonomically. These characters relate to the way in which the structure of a smaller rachis is adjusted to that of a larger one where the two join, and ultimately to the relationship of a lateral leaflet to the rachis which bears it. Some rachises are rather deeply grooved on the upper surface, and where a smaller rachis joins a larger one, the groove of the latter is opened to admit that of the former. In some such cases (*e.g. Dryopteris, Athyrium, Pteris*) the midrib of a leaflet is also grooved, and a rachis-groove is open to admit the midrib-groove of a lateral leaflet; the edge of the leaflet is then more or less decurrent down the side of the rachis. In other cases the thickened basiscopic edge of a leaflet is decurrent on the edge of the rachis-groove (*e.g. Lindsaea*). Other rachises are not or only slightly grooved on the upper surface and there is no opening of the groove of a main rachis to admit that of a smaller one (*e.g. Thelypteris, Ctenitis*). In such cases the base of the lamina of a leaflet is decurrent on the side of the rachis, sometimes forming a small continuous ridge or wing. Characters such as this are constant throughout a genus, or even throughout a group of genera, and are often valuable diagnostically, especially in sterile fronds. I believe also that they may provide valuable evidence for those who are seeking a natural classification of ferns.

(d) *Venation.*—Veins mark the course of the vascular bundles in a leaf; they are usually evident on the surface, as the surface tissue over a vein is different from that over the rest of the lamina. The pattern of venation is always important taxonomically. In fronds which are thick and fleshy or leathery the veins are sometimes quite invisible on the surface, or only the larger ones may be prominent; the pattern of venation can then be seen by clearing the frond (boiling it and then treating it with a bleaching agent; or boiling alone may be sufficient, due to replacement of internal air by water).

In large much-branched fronds the ultimate leaflets are usually small, with few veins in each, and these veins commonly end in lobes or teeth at the edge of the lamina. Such veins are *free;* a vein may fork once or more times, but the branches do not unite again at any point. Where leaflets are very small, the veins are often dichotomously branched, while larger leaflets usually have a *midrib* or *costa* with lateral veins which are simple or forked.

In larger leaflets the vein-pattern may be more complex, still with free veins. The sides of a leaflet may be deeply lobed (pinnatifid) with pinnate vein-groups in each lobe; the main vein of a lobe is then called a *costule (e.g. Thelypteris, Cyathea).* In a large number of ferns with large leaflets, the veins join neighbouring veins after branching, thus forming areas of lamina surrounded by veins; such areas are called *areoles,* and veins which unite with others are said to *anastomose.* The anastomosis may consist only in the formation of a single series of areoles along costae or costules (the rest of the veins ending freely) or it may form a more or less elaborate network occupying almost the whole lamina. In the latter case there are several possible patterns *(e.g. Cyclosorus, Tectaria, Goniophlebium, Acrostichum).* One useful character is the presence or absence of small veins which end freely inside the areoles.

At the ends of some veins are water-excreting pores or *hydathodes,* often evident on the upper surface of the lamina as distinctive spots (round or elongate) which in some cases may ultimately become covered with white scales due to deposits of salts left after the water originally holding them has evaporated. Such hydathodes may provide useful diagnostic characters *(e.g. Pyrrosia, Grammitis, Coniogramme).*

(e) *Surface characters of lamina.*—The lower surface of the lamina may be *glaucous* (covered with a pale blue-green waxy layer); this character often disappears if specimens are subject to much heat in drying. The lower surface in other cases may be more or less completely covered with a layer of white or yellow loose waxy powder; this is excreted from glandular hairs *(e.g. Pityrogramma).* Hairs on the lamina are always important, and often need to be examined with a microscope for the structure to be clearly evident. The nature and arrangement of stomata may in some cases be significant *(e.g. Schizaea).* The patterns of thickenings on walls of epidermal cells may be characteristic (or of the single cell-layer of filmy ferns); and in some ferns there are narrow *spicular cells* containing silica *(e.g. Vittaria).* In some ferns there are *false veins,* which are lines along which surface cells are more or less elongate and sometimes devoid of stomata, simulating the surface appearance of veins but with no underlying vascular tissue *(e.g. Angiopteris, Trichomanes sect. Crepidomanes).*

(f) *Polymorphism of fronds.*—In many ferns, the fronds of young plants have a distinctive shape different from that of fronds of mature plants; such young plants may offer useful diagnostic characters. Some high-climbing ferns of the *Lomariopsis* Group have leaves of distinctive shape on those parts of the plant which are near the ground (always in moist shady evergreen forest) on rocks or tree-trunks; such leaves are called *bathyphylls,* and the leaves of high-climbing parts of the same plants are called *acrophylls.*

FERTILE LEAVES. (a) *Sori.*—In most ferns sporangia are borne in distinct groups called *sori.* In some cases the sori spread along the veins to such an extent that they can hardly be called groups of sporangia, and this leads to the acrostichoid state (see below). Many sori are protected by *indusia,* which are thin outgrowths from the surface of a frond. The sori of other ferns are *exindusiate,* but in some of these the sori are protected by being produced in depressions or grooves, or by being covered when young by *paraphyses* (hairs of various forms, or scales, borne among the sporangia). The position and shape of sori and of their indusia (if present) are always important taxonomically. The older schemes of classification, and also that of HOOKER and BAKER *(Synopsis Filicum,* 1868) were based entirely on these characters. But species closely related in every other respect may differ in presence or absence of an indusium, or in shape of sori (especially if these lack indusia) and a natural classification must take such facts into consideration. The Orders *Ophioglossales* and *Marattiales* are quite different from *Filicales* in the form and arrangement of their sporangia (see statement on sporangia below); further remarks here refer to *Filicales*.

A sorus may be more or less circular, or elongate. If circular, it may be at the end of a free vein (at the edge of the lamina or not) or seated upon a free vein, or at the junction of veins in a network, or at the end of a free vein enclosed in an areole surrounded by other veins. In any of these cases it may be protected by an indusium, which may be pocket-shaped (attached at base and sides), or kidney-shaped, or circular and attached by the edge or the centre, or cup-shaped, or of other shapes, or it may have no indusium. If the sorus is at the end of a vein, it may be protected by the thin reflexed edge of the lamina, or by two more or less equal outgrowths from upper and lower surface *(Dicksonia)*, the two outgrowths sometimes more or less joined to form a protective funnel or cup *(Trichomanes, Dennstaedtia)*. Sori which are elongate may spread along free veins, or along veins which anastomose, or they may spread along the margin, joining the ends of veins which in a sterile leaflet would be free *(fusion-sori* or *coenosori)* or they may lie close to the costa of a leaflet *(Blechnum)*. Marginal fusion-sori are sometimes protected by an inner indusium *(Lindsaea)*, sometimes also by the reflexed margin *(Pteridium)*, but if the margin is reflexed, the inner indusium may be lacking *(Pteris)*. It is especially exindusiate sori which spread along veins away from the margin, often to a different extent in closely related species. The above survey of soral form is not exhaustive, but is intended as an indication of the possibilities and as a guide in using the keys which follow. Details of individual soral forms will be given in the taxonomic treatment of the families and genera.

(b) *Dimorphism of leaves.*—In many ferns the fertile fronds differ in shape from sterile ones. In such cases the fertile fronds often have a lamina of reduced size; this reduction may be slight or it may be so considerable that the sterile and fertile fronds are quite different in aspect. Fertile fronds also often have longer stipes than sterile, and in some cases this may be the chief difference between the two.

(c) *The Acrostichoid state.*—Where sori spread along all the veins of a fertile leaflet and the leaflet is of reduced size as compared with a sterile one of the same species, the ripe sporangia may be so close together that they entirely cover the lower surface of the fertile leaflet (they may also grow from the surface of the lamina between the veins); this is called the *acrostichoid* condition, the name being taken from the *Acrostichum*, in which only the upper leaflets are fertile in this way. Formerly all acrostichoid ferns were included in the genus *Acrostichum*, but the acrostichoid state has certainly arisen along several different evolutionary lines, and a genus based on it alone is a very unnatural one. In some acrostichoid ferns there is an additional vascular system close to the lower surface of the lamina, in addition to the normal system found in sterile fronds of the same species.

Sporangia. (a) *Ophioglossales.* —Here the sporangia are large, spherical, opening by slits, and are attached to spike-like or branched outgrowths from the base of the lamina; the fertile part of the frond is thus not fern-like in aspect.

(b) *Marattiales.*—In this Order the sporangia are also large, more or less laterally joined together in linear or circular groups on the surface of the lamina (along veins or at vein-junctions); they do not have an annulus comparable with that of members of the Order *Filicales*.

(c) *Filicales.*—In the great majority of this order the sporangia have a basically similar structural plan, in which dehiscence is caused by contraction on drying of a more or less complete ring of cells (the *annulus*) which have inner walls thickened but outer walls thin; there is also a particular place *(stomium)* where rupture occurs. The more primitive families *(Osmundaceae, Schizaeaceae, Gleicheniaceae)* have a less specialized development of the annulus, that of *Osmundaceae* being the least specialized (its annulus is not ring-shaped). In *Hymenophyllaceae, Cyatheaceae, Plagiogyria* and some other genera the annulus is complete and *oblique* in its position on the sporangium; in the great majority of genera the annulus is almost *vertical* and incomplete, being broken by the stalk, but even in these cases the structure of the sporangium is not perfectly symmetrical when divided along the plane of the annulus. In some members of the *Adiantum* Group the cells of the annulus are broad and more or less uneven. A detailed study of the development and structure of sporangia has been made in comparatively few fern-genera.

Spores. Fern spores are always produced in groups of four *(tetrads)*, each tetrad normally the result of the meiotic divisions of one spore-mother-cell. A spore may have either of two distinct shapes, *monolete* (or *bilateral*), and *trilete* (or *tetrahedral*). Monolete spores are more or less bean-shaped (like a *Phaseolus* seed), with an angle along the straight edge where the spore is in contact with the similarly angled edge of another spore of the tetrad; in each tetrad there are two such pairs. Trilete spores meet together on three faces, and at the angles between them, all four spores meeting at the centre of a tetrad. Usually all species in a genus have spores of the same shape, but there are certainly some genera in which both shapes of spores occur *(e.g. Dicranopteris)*, and I have seen evidence that even within a single species there may be spores of both kinds.

The inner layer of cells in the wall of a sporangium (called the *tapetum*) breaks down during the development of the tetrads of spores, its substance being absorbed by the spores during their development. In some cases part of the substance of the tapetum forms an external covering on each spore, known as a *perispore*. The perispore is usually more or less folded into rather irregular wing-like structures, or sometimes into more regular spines. Other genera of ferns lack a perispore, and then the wall of the spore itself may be variously sculptured into a more or less complex pattern of warts or ridges. The presence or absence of a perispore, its structure if present, or the wall-characters where there is no perispore, are always of taxonomic importance as well as the actual size of the spores.

In the case of hybrids, where normal meiosis does not occur, there are often shrivelled empty spores, and the presence of such is always significant. In the case of apogamous ferns (see note on the gametophyte below) the spores are of at least two kinds, large functional ones and smaller ones which are not functional (for a detailed statement, see MANTON, *Problems of Cytology and Evolution in the Pteridophyta*, Cambridge, 1950).

Gametophyte. In *Ophioglossales* the gametophytes are subterranean and saprophytic, and obtain their nutriment through the activity of an endophytic fungus. In all other ferns the gametophytes are green, and in the vast majority of cases they are more or less heart-shaped, with a growing-point in the sinus between the two lobes; they are thickened in a median area which bears the rhizoids, antheridia and archegonia on the lower surface. Distinctive characters are provided by shape of the whole prothallus (in some cases this is asymmetric or elongate), presence of superficial hairs of different kinds, colour and septation of rhizoids, and especially in details of structure of archegonia and antheridia. In a few cases the gametophyte is more or less filamentous *(Schizaea, Hymenophyllaceae)*, or irregularly lobed (*Vittaria* and allied genera).

In *apogamous* ferns, no sexual process occurs. The prothallus is developed from a diploid spore; it bears antheridia but no archegonia, and gives rise to a new sporophyte by vegetative budding. The diploid antherozoids of such a prothallus may fertilize haploid archegonia of a sexual prothallus of an allied species, the result being a triploid hybrid sporophyte. Such a hybrid is normally sterile, but may develop vegetative means of propagation not involving the formation of a prothallus; and some such hybrids have become apogamous. Higher polyploid plants are also not uncommon among ferns, and in such cases cytological evidence is of great taxonomic value.

Heterosporous Ferns. The two families *Salviniaceae* and *Marsileaceae* are very different from other ferns in many respects. They have spores of two kinds, large and small, in separate sporangia. The small spores produce very small gametophytes which are male, and the large spores produce larger female gametophytes. Both kinds of sporangia are formed inside closed structures called *sporocarps*, borne by the leaves. These ferns are all aquatic, and they are sometimes collectively called *Hydropterideae* or *Hydropteridales*, but the two families are not closely related, and probably had quite different evolutionary histories.