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CHAPTER I

THE LIFE-HISTORY OF A FERN

THE present volume will treat generally of the Plants included in the Class of the Filicales, or as they are commonly called, the Ferns. Any such treatise must take as its starting point a knowledge of the usual structure and successive phases of life of the plants in question. Experience shows that the cycle of life is uniform in its essentials for all normal Ferns, while its features correspond also to those seen in land-living plants at large. That life-cycle comprises two alternating phases, or "generations." The one is the relatively large leafy plant popularly recognised and designated as the "Fern-Plant": the other is a relatively small and simple green scale-like structure, called the "Prothallus." The relation of these to one another, and the constant alternation which they show, are best illustrated by a description of the successive incidents seen in the life-history of some common Fern. The familiar Male Shield Fern (*Dryopteris* (*Nephrodium*) *Filix-mas*, Rich.) will serve as a suitable example.

This Fern is known to everyone as growing in woods and hedgerows, and even in more exposed situations, such as open gills and hill-sides of higher-lying districts (Fig. 31, p. 26). It presents a robust appearance, and when fully developed it consists of a simple shoot with an oblique and massive stock, which is relatively short. This is entirely covered over by the bases of the leaves, of which the youngest form a closely packed terminal bud (Fig. 1, *A*, *D*). Those leaves which are seated further from the apex, and immediately below the terminal bud, may in summer be found to be of large size and complex structure (Fig. 2). Collectively they form a crown-like series surrounding the apex of the stem that bears them. Passing again further back from the apex of the stem, the surface is found to be closely invested by the bases of the numerous leaves of former seasons, the upper portions of which have rotted away. Clearly then the leaves are borne upon the stock in acropetal succession. While young they are densely covered by chaffy flattened scales, which take a rusty colour with age; but they mostly fall away from the mature leaf, though often persisting on its stalk (Fig. 2). If the plant be dug up, and the soil be carefully removed from it, an ample root-system will be seen, consisting of thin, wiry, and dark-coloured fibrils, which spring from the basal parts of the leaves.

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All these parts of the Fern-Plant consist of tracts of tissue differentiated to subserve distinct functions. The most notable is the Vascular Skeleton, which appears in the Male Shield Fern as a cylindrical network of strands within the massive axis (Fig. 1, *E*, *F*). It throws off branches on the one hand

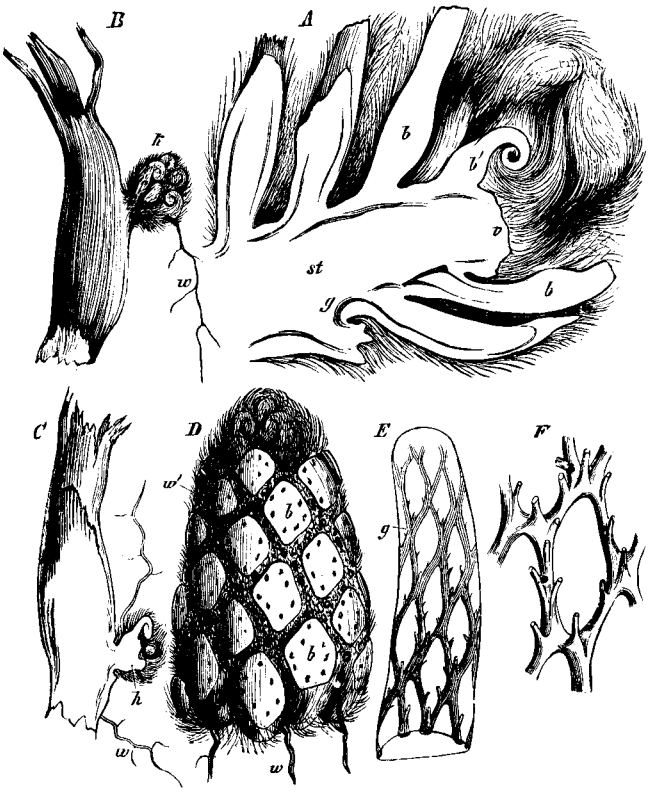

Fig. 1. *Dryopteris* (*Nephrodium*) *Filix-mas*, Rich. *A* = stock in longitudinal section: *v* = apex: *st* = stem: *b* = leaf-stalks: *b'* = one of the still folded leaves: *g* = vascular strands. *B* = leaf-stalk bearing at *k* a bud with root (*w*), and several leaves. *C* = a similar leaf-stalk cut longitudinally, bearing bud (*h*), with root (*w*). *D* = stock from which the leaves have been cut away to their bases, leaving only those of the terminal bud. The spaces between the leaves are filled with numerous roots, *w*, *w'*. *E* = stock from which the rind has been removed to show the vascular network (*g*). *F* = a single mesh of the network (foliar gap) enlarged, showing the insertion of the leaf-trace strands. (After Sachs.)

into the leaves, where they ramify and extend upwards to the extreme tips and margins. On the other hand strands of vascular tissue, springing from the leaf-bases, extend towards the tips of the roots, and laterally into their branchlets. The Vascular System is thus a connected conducting system throughout the plant. It is embedded in soft parenchymatous tissues,

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which serve various purposes in different parts. Thus in the root they may be absorbent, while on the other hand they transmit the fluids absorbed to the conducting system. In the stem they may serve the purpose of storage of reserve materials, while in the leaf the parenchyma carries on the function of photo-synthesis, together with the passing on of the supply thus acquired to the conducting system. The parts exposed to the air are covered by an

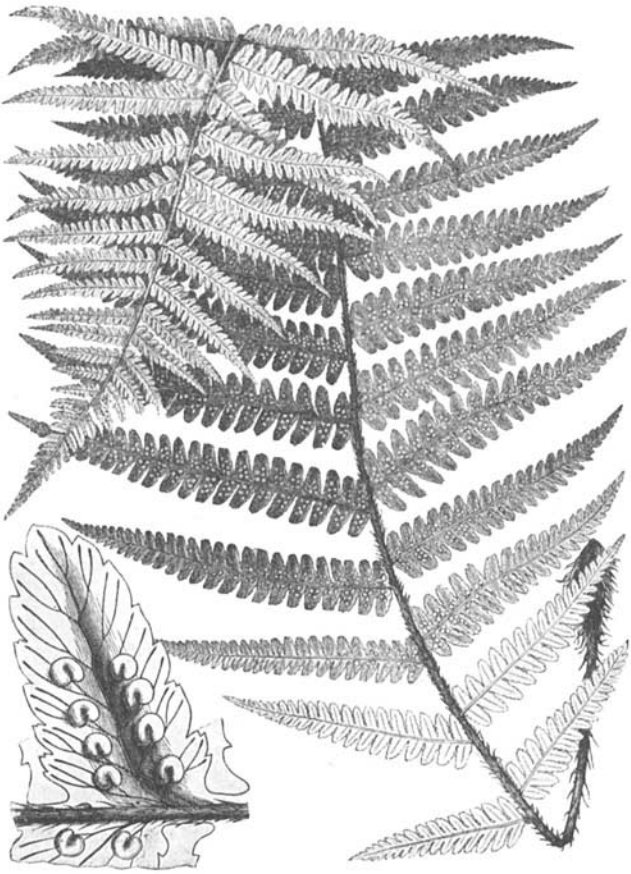

Fig. 2. *Dryopteris Filix-mas*, Rich. Fertile leaf about one-sixth natural size, the lower part with the under surface exposed. To the left a single fertile segment, bearing kidney-shaped sori, enlarged about seven times. (After Luerssen.)

epidermal layer with a cuticularised external wall, which prevents the indiscriminate loss of water by surface-evaporation. But the epidermis is perforated by numerous stomata the mobile guard-cells of which according to circumstances can control the width of the pores leading to the ventilating spaces within. Finally, there are also firm brown resistant tissues disposed sometimes near the outer surface, as in the stem and leaf-stalk: sometimes

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more deeply seated, as in the root, while in the leaf they follow the course of the vascular strands. These give to the several parts increased mechanical strength, while their thickened walls have also a special power of retaining water within their substance.

Thus constituted the Male Shield Fern is an organism which is capable of leading an independent life on exposed land-surfaces. It is in a position to nourish itself by taking up from the soil the water and salts which it requires, and to elaborate therefrom, and from the carbon-dioxide of the air, fresh supplies of organic food. Further, though it is frequently found

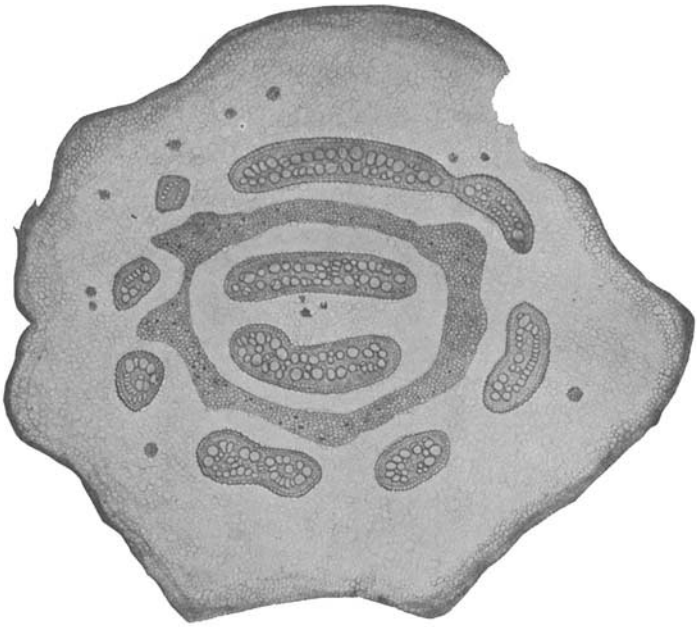

Fig. 3. Transverse section of rhizome of Bracken *Pteridium aquilinum*, showing the outer and inner series of meristeles, and the irregular bands of sclerenchyma between them. These are embedded in soft ground-parenchyma, with a hard sclerotic rind. (× 10.)

growing in situations where moisture is abundant and the air moist, still it can resist considerable drought, and is capable of living under as exacting conditions as any ordinary terrestrial plant.

For comparative purposes the vascular tissues, which are so marked a feature of land-living plants generally, are those which command the greatest attention. For the study of the tissues composing a vascular strand, or *meristele* as it is called, a rhizome with long internodes, such as the Bracken, gives the best results. In a transverse section of it taken between the leaf-insertions, an outer and an inner series of vascular strands are found, separated

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by an incomplete ring of sclerenchyma. The outer series correspond to the mesh-work of *Dryopteris* (*Nephrodium*), the inner are accessory or medullary meristeles (Fig. 3). Each one is a compact body of vascular tissue, and is circumscribed by a complete endodermal sheath, which delimits it sharply from the surrounding parenchyma. The details are shown respectively in transverse and in longitudinal section in Figs. 4 and 5. Each meristele consists of a central core of xylem, surrounded by phloem. A small part of one of them, examined either in transverse or in longitudinal section under a high power, gives the following succession of tissues (Figs. 4, 5). Passing inwards from the starchy ground-tissue, with intercellular spaces (*g*),

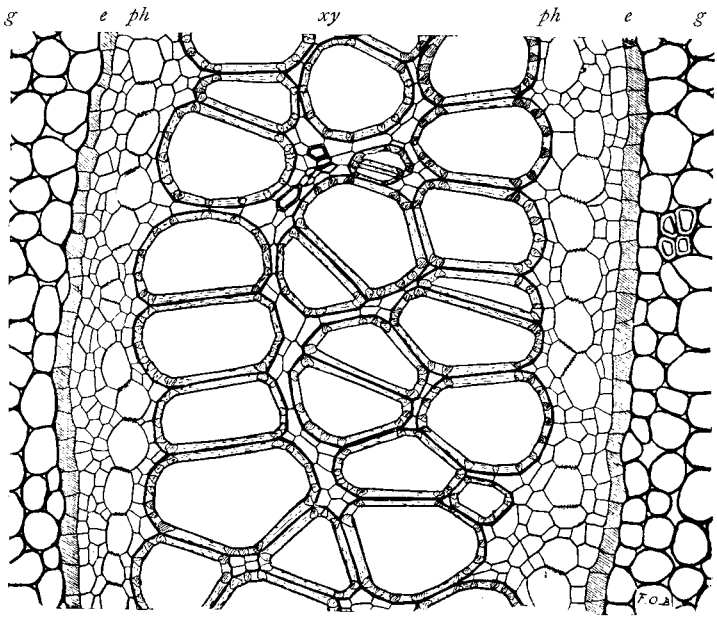

Fig. 4. Part of a transverse section of a meristele of Bracken. *g* = ground parenchyma. *e* = endodermis. *ph* = phloem with sieve-tubes. *xy* = xylem, with large scalariform tracheides. Some smaller tracheides lying centrally are the protoxylem. Note that no intercellular spaces are seen within the endodermis. (× 75.)

the layer of brownish cells of the *endodermis* (*e*) forms a continuous barrier, delimiting the strand sharply. Within it follows the *pericycle*, with its cells not very regularly disposed, but corresponding roughly to the cells of the endodermis, both having been derived by division from a single layer. Within this comes the *phloem* (*ph*), with large *sieve-tubes* as the characteristic elements. They are thin-walled, with watery contents. The lateral walls where two adjoin bear the sieve-plates, and are recognised by glistening globules that adhere to them. They are embedded in parenchyma, which extends inwards into the xylem, and may be called collectively *conjunctive*

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parenchyma. The chief features of the *xylem* (*xy*) are the *tracheides*, which are relatively large, with a very characteristic polygonal outline. They have woody walls, and no protoplasmic contents. Where two adjoin the walls are flattened, and of double thickness, showing that each has its own share of the thickening, which overarches the pit-membrane as in the pits of Conifers. But where the tracheide abuts on parenchyma-cells the pits are narrower. Internally, and usually about the foci of the elliptical meristele, smaller tracheides are found. These are the first-formed tracheides, or *protoxylem.* The meristele of a Fern is thus concentric in construction; it is strictly delimited, and has no provision for increase in size.

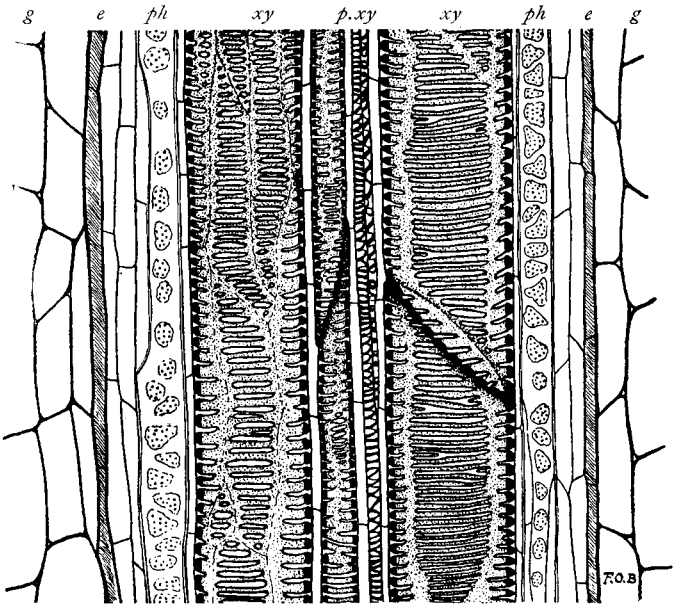

Fig. 5. Longitudinal section of meristele of Bracken. Lettering and magnification as in Fig. 4.

A transverse section (Fig. 4) gives only one aspect in which such complicated tissues can be studied. Its interpretation is aided by longitudinal sections (Fig. 5). It is then seen that the sieve-tubes, which are elongated and pointed, bear their numerous sieve-areas upon the lateral walls: and that the spindle-shaped tracheides bear also upon their lateral walls those transversely elongated pits which give them the so-called scalariform appearance. Interspersed between the tracheides and sieve-tubes are cells of the conjunctive parenchyma, and the meristele is delimited by endodermis (*e*), as seen in the transverse section.

The *tracheide* of the Fern resembles that of the Pine in being of spindle form, with its thickened lignified walls marked by bordered pits. But whereas the pits in the Pine are

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circular, those in the Fern are liable to be transversely elongated, as is natural in tracheides so wide as these are. Their features are well seen in longitudinal sections, but better if they are isolated by maceration (Fig. 6, *A*). The elongated pits lie parallel to one another, and this is specially well seen where two wide tracheides have faced one another. From the ladder-like appearance that results they have been called *scalariform tracheides*. Examined under a high power the double outline of the pits is seen, and when the pits are small and circular the similarity to those of the Pine is plain (Fig. 6, *B*). In most Ferns the pit-membranes persist, but in *Pteridium* they appear to be liable to be broken down, and the cavities of adjacent tracheids thrown together as they are seen to be in vessels. The tracheides of the protoxylem are seen in longitudinal section to be spiral or reticulate, as in other Vascular Plants (Fig. 5).

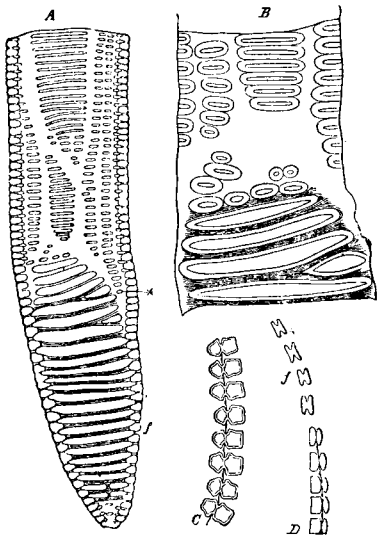

Fig. 6. Tracheides of *Pteridium*. *A* = the end and about one-third of the length of a tracheid, with part of the lateral wall in surface view, showing scalariform marking (× 100). *B* = part of *A* magnified 200. *C* = thin longitudinal section through a lateral wall where two tracheides adjoin (× 375). *D* = similar section through oblique wall at *f* (× 200). There the pit-membranes are not visible. (After De Bary.)

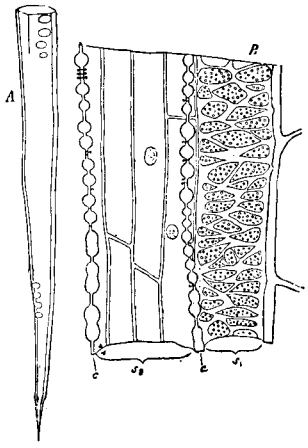

Fig. 7. Sieve-tubes of *Pteridium*. *A* = end of a tube separated by maceration (× 100). *B* = longitudinal section through phloem showing one sieve-tube with the sieve-plates (s_1) in surface view. *c*, *c* are walls shown in section, bearing sieve-pits (× 200).

The *sieve-tubes* are also spindle-shaped, and are without companion-cells. Their cellulose walls are swollen. Where two sieve-tubes adjoin, numerous thinner sieve-areas of irregular outline are borne. They are found to be perforated by very fine protoplasmic threads extending between highly refractive globules that adhere to the walls (Fig. 7). Such tracheides and sieve-tubes are characteristic of Ferns and, with differences of detail, of other Pteridophytes as well.

The anatomy of the *leaf* in Ferns resembles that of Seed-Plants down even to the collateral structure of the vascular strands. Being chiefly shade-loving plants chlorophyll is usually present in the cells of their epidermis,

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and the differentiation of the mesophyll into palisade and spongy parenchyma is not marked (Fig. 8). In these respects they resemble the leaves of Angiosperms of similar habit. In the *roots* of Ferns, as in those of Seed-Plants,

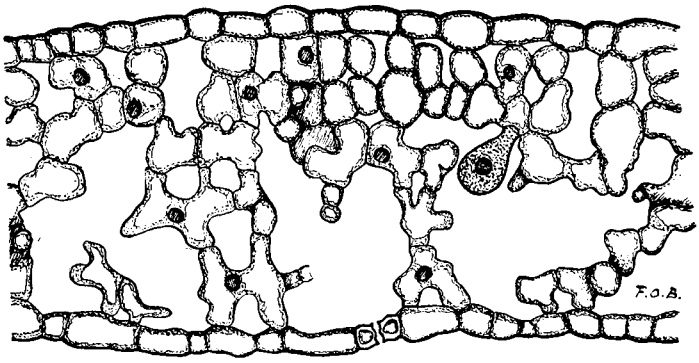

Fig. 8. Transverse section of part of pinnule of *Dryopteris* (× 150), showing epidermis, and the spongy mesophyll, with an internal glandular cell.

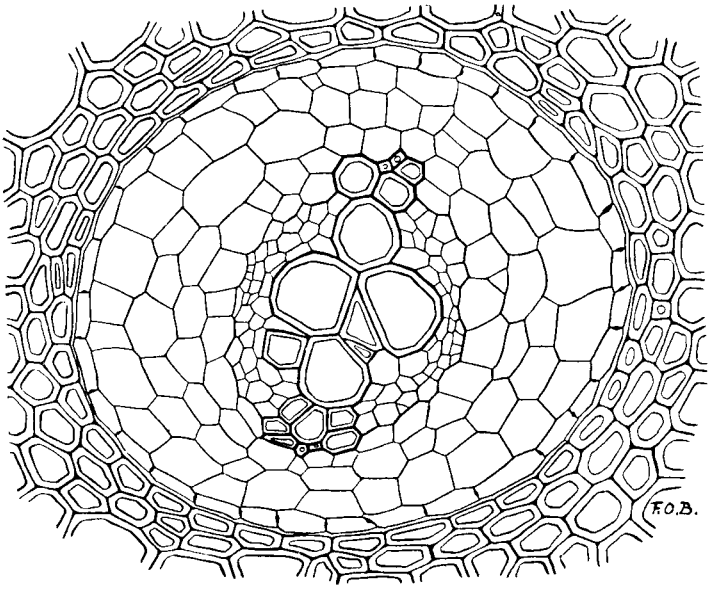

Fig. 9. Transverse section of a root of a Fern (*Pellaea*) (× 150). Outside lies the sclerotic cortex, limited internally by a definite endodermis. There are two groups of protoxylem; a very broad pericycle, of 3 or 4 layers, surrounds the vascular tissues.

there is a superficial piliferous layer, a broad cortex, and a contracted stele. But usually the inner cortex is very strongly lignified, up to the endodermis, which is thin-walled (Fig. 9). The pericycle which follows is variable, sometimes being greatly enlarged as a water-storage-tissue. The protoxylems

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are peripheral and two or sometimes more in number, the phloem-groups alternating with them. In fact the root of a Fern is constructed essentially on the plan of that in Seed-Plants. As there is no secondary thickening the roots of Ferns are all fibrous. The lateral roots arise opposite to the protoxylems, and there they originate from definite cells of the endodermis, which may often be recognised beforehand by their size and contents.

While we recognise the substantial similarity of Ferns and Seed-Plants in respect of form and structure of stem, leaf, and root, these plants differ in the construction of their *apical meristems*. In Seed-Plants these are small-celled tissues, and more or less definitely stratified. In Ferns such as *Osmunda*, *Dryopteris* or *Polypodium*, a single large cell, the *apical or initial cell*, occupies the tip of each growing part. It has a definite shape, and segments are cut off from its sides in definite succession. As the whole

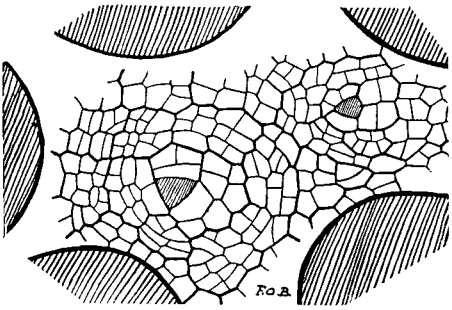

Fig. 10. Apex of stem of *Osmunda regalis*, seen from above, showing the three-sided apical cells of stem and of leaf shaded. The successive segments of the apical cell form the whole of the apical cone. (× 83.)

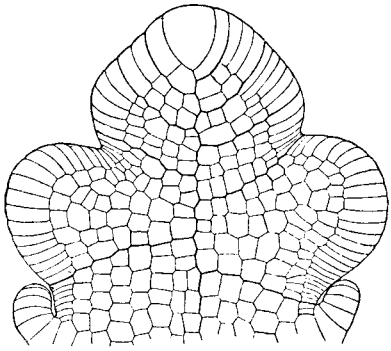

Fig. 11. Young leaf of *Ceratopteris*, in surface view, after Kny; showing two-sided apical cell; and the marginal series, continuous round the young pinnae. The latter do not correspond to the segments from the apical cell.

tissue of the stem, leaf, or root is derived from such segments, the whole of each part is referable in origin to its apical cell, which maintains its identity throughout. The form of the cell in roots, in most stems, and in some leaves (*Osmunda*) is that of a three-sided pyramid; but where the organ is flattened, as in some stems (*Pteridium*) and almost all leaves, it has two convex sides and is shaped like half of a biconvex lens. In the former case the segments are cut off in regular succession from the three sides (Fig. 10), in the latter alternately from the two sides (Fig. 11). The further subdivision of the segments to form the tissues is represented in surface-view for the case of *Osmunda* in Fig. 10: and Fig. 11 shows in the surface-view of a young leaf of *Ceratopteris* how the whole member may be built up from such segments. In roots the segmentation is complicated by the origin of the root-cap. This is provided by a segment cut off from the frontal face

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of the pyramid, after each cycle of three has been cut off from its sides (Fig. 12). Thus every fourth segment goes to form the protective cap, and renews it from within. Not only does the leaf show continued growth and apical segmentation from its two-sided apical cell, but the lateral wings or flaps originate by the activity of rows of marginal cells. There is also a definite segmentation seen in the origin of the sporangia. Thus Ferns have not stratified meristems like Seed-Plants. The tissues of all their parts originate from segmentation of superficial cells. This is a general character of the Pteridophyta, though the details of their segmentation and the number of the initial cells are open to variation.

Thus constituted the Fern-Plant carries out its Life on Land in essentially the same way as Seed-Plants. The structural differences are those of detail, the most important being the absence of secondary thickening in the

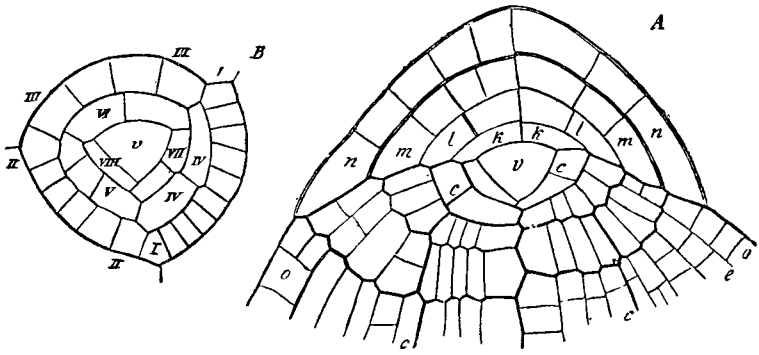

Fig. 12. (×250.) *A* = longitudinal section through apex of the root of *Pteridium*. *B* = transverse section through the apical cell of the root and neighbouring segments of *Athyrium*. (After Naegeli and Leitgeb.) *v* = apical cell. *k, l, m, n* = successive layers of root-cap. *o* = dermatogen. *c* = limit of stele. (From Sachs.)

stem. These plants have no automatic provision for increasing mechanical strength with size. In Tree Ferns this deficiency is partly made up by masses of hard brown sclerenchyma, which accompany and enclose the flattened meristeles; and their margins are usually curved outwards, thus securing increased mechanical resistance on the same principle as in corrugated columns. Their strength is further increased according to size and age by the development of masses of sclerotic, adventitious roots, matted together to form a thick investment to the original trunk, and adding to its stability by a method comparable mechanically to a cambial thickening, though quite different in origin (see Fig. 152, p. 158). But such mechanical provision for increase in size is only partially effective. There is no evidence that Ferns ever ranked among the largest of living Plants.

Many Ferns increase in number by *vegetative propagation*. This may follow simply on continued growth and branching, as in *Pteridium*, where

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