Two Malayan 'Myrmecophilous' Ferns, *Polypodium* (*Lecanopteris*) *carnosum* (Blume), and *Polypodium sinuosum*, Wall.

BY

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With Plates X, XI, and XII.
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INTRODUCTION.

IN Hooker's 'Species Filicum,'¹ published in 1864, occurs the following passage:—

'Notwithstanding the striking difference between the fronds of this remarkable plant (*Polypodium lomarioides*, Kze.) and those of *Polypodium sinuosum*, Wall., I am disposed to think, from the nature of the caudex and the venation, that these two may prove not specifically different. On mentioning to Mr. J. Smith my views regarding the unity of these two very distinct-looking Ferns, he not only was disposed to agree with me, but suggested that another Fern, viz. *Lecanopteris carnososa*, Blume, universally looked upon as a distinct genus, was equally an abnormal form of our present *Polypodium*, and

¹ Hooker ('64), p. 79.

he is perfectly correct. The caudex (perhaps in itself abnormal, but the same in all three) and the fertile segments are abnormal, inasmuch as there is a suppression of the substance of the frond between the sori; the consequence is that these segments form marginal lobes, which in a dry state are turned back on the upper side of the frond (as the fructifications of *Nephroma resupinata* among the Lichens). The venation is the same in all three; and if we can believe that *Lecanopteris carnosa* is a state of *P. sinuosum*, Wall., there will be no difficulty in referring Blume's *L. pumila* to *L. carnosa*.'

It is with the anatomy, biology, and systematic position of *Lecanopteris carnosa*, Bl., and *Polypodium sinuosum*, Wall. (two of the Ferns referred to above) that this paper proposes to deal.

The systematic position of these two Ferns will be discussed later, as well as the question of the identity of *L. carnosa*, Bl., and *L. pumila*, Bl.; but in the meantime it is interesting to note, in view of the passage quoted above, that although *Lecanopteris carnosa* and *Polypodium sinuosum* are beyond doubt specifically distinct, and differ widely in external appearance, yet an examination of their internal structure reveals the fact that, after all, their resemblances are more remarkable than their differences, and that instead of being placed in separate genera, they must be recognized as closely allied species.

That being so, *Lecanopteris carnosa*, Blume, will be in future referred to in this paper as *Polypodium (Lecanopteris) carnosum*, (Blume), or, to avoid needless repetition, as *Polypodium carnosum*.

Both of these Ferns belong to the so-called myrmecophilous plants. Their thick, fleshy rhizomes are tunnelled by a system of galleries, which are invariably inhabited by colonies of ants. They are both epiphytes of the Malay region.

Polypodium carnosum grows only on the higher branches of trees, and usually, at all events, on fairly high mountains. It forms thick encrusting masses, often several feet in length,

completely encircling the branches of its host, and is fully exposed both to the rains and the scorching sun of its tropical environment.

Blume's type specimens were collected in the Moluccas, but the plant is also known from the Philippines, Celebes, Borneo, Java, Singapore (Mr. Ridley informs me that it grows on Bukit¹ Timah, at a height of about 600 ft. above sea-level), and the following localities in Perak (one of the western states of the Malay Peninsula):—Birch's Hill; Gunong² Bubu, 5,000 ft.; Larut, 3,000–5,000 ft.; while the material used in the preparation of this paper was collected by myself³ on Gunong Inas (4–5,300 ft.), a mountain on the northern borders of Perak.

Polypodium sinuosum, on the other hand, is often found almost at sea-level. Its creeping rhizomes (which do not form such compact and massive growths as those of *Polypodium carnosum*) are frequently to be seen quite near the ground, and usually on the trunk itself or on the main branches of its host. It may thus be shaded to some extent from the rays of the sun by the foliage of the tree on which it grows⁴.

Its distribution is more extended than that of *P. carnosum*. It has been recorded from Malacca and other parts of the Malay Peninsula as far north as Mergui; Amboyna, Isle of Jobi, &c.; while eastwards it extends to the New Hebrides and the Solomon Islands. The spirit-material I have examined is from the Botanic Gardens at Singapore. I am greatly indebted to Mr. H. N. Ridley for his kindness in preserving and forwarding this material to me.

Some idea of the general habit of these remarkable Ferns may be obtained from the photographs forming Figs. 1 and 2.

¹ *Bukit* in Malay means a hill.

² *Gunong* is a Malay word for mountain, not necessarily a larger peak than *bukit*, but usually more precipitous and rugged.

³ During the Cambridge expedition of 1899–1900 to the Siamese-Malay states, under the leadership of Mr. W. W. Skeat.

⁴ Karsten ('95, p. 182), however, states that in Amboyna he has found it growing in very sunny exposed situations.

That of *P. carnosum* (Fig. 1) was taken near the summit of Gunong Inas in Perak, at a height of 5,300 ft. At that elevation the jungle is dwarfed sufficiently to allow a photograph of the Fern as it appears in nature to be taken without much difficulty.

The photograph of *P. sinuosum* (Fig. 2) was taken on Pulau¹ Redang, the largest of a small group of islands in the China Sea, a little to the N.E. of Trëngganu, one of the eastern states of the Malay Peninsula. The tree on which it grew was only a few feet above sea-level, at the edge of the jungle which covers these islands, as indeed it does almost all the available land in this region.

Although these Ferns are referred to in the works of numerous authors, yet comparatively little is known of their anatomy, their external features alone having attracted attention in most cases. So far as I am aware, the only papers dealing with their internal structure are those by Goebel² and Karsten³. These authors limit their descriptions to a few of the most striking points, and in either case very little mention is made of *Polypodium carnosum*. The descriptions are, moreover, supported by but few figures.

I. POLYPODIUM CARNOSUM (Blume).

External Morphology.

(a) *Stem.* The rhizome is thick and fleshy, glabrous but for the presence of minute multicellular hairs, which are often branched (Fig. 13), and are scattered over the surface of the young parts of the stem, especially on the flanks, but generally completely disappear from the older parts. It is furnished with a thin covering of wax, which is doubtless of importance in the reduction of transpiration, serving a purpose similar to that of the dense covering of peltate scales found in *Polypodium sinuosum* and other allied Ferns.

¹ *Pulau* is Malay for an island.

² Goebel ('88), pp. 16 et seq.; see also Goebel ('89), pp. 204 et seq.

³ Karsten, loc. cit., pp. 178 et seq.

The stem has a dorsiventral structure, being roughly semi-circular in cross-section, except near the apex, where it is more nearly circular. The lower surface, however, is often by no means flat, as it has to adapt itself to irregularities of the substratum.

The numerous dark-brown roots are confined to the lower surface, and appear to be developed irregularly.

The leaves arise in regular acropetal succession¹ on the upper surface of the rhizome, and have a distichous arrangement, the members of one longitudinal series alternating with those of the other. The petioles are articulated upon large, more or less conical processes of the rhizome, which are usually directed forwards, i. e. towards the apex of the stem (Fig. 23). These conical projections or leaf-cushions are, especially on the main stem, often flattened antero-posteriorly. They are closely set together (two consecutive leaves of one longitudinal series being rarely more than 1.7 cm. apart, and usually less), and are separated from each other by transverse furrows on the stem. The surface of the rhizome thus presents a very rough and irregular appearance, broken up as it is and bristling with these conical leaf-cushions, which persist after the fall of the leaf (Figs. 3 and 19).

The branching of the rhizome is, as in all Polypodiaceae², monopodial. Lateral branches are given off from both sides of the main stem with great regularity (Fig. 6), each branch arising opposite to one of the leaf-cushions of its own side. The branches originating in this way are closely set together, and as they themselves give rise to secondary or tertiary branches in a similar manner, whenever space and other conditions allow of this, and these branches frequently creep over the older parts of the rhizome which come in their way, the final result is a compact, tangled mass of interlacing branches, so tightly packed as to form practically one solid

¹ At least the leaf-cushions (*vide infra*) are developed regularly, though many of them, especially those on the smaller branches, have apparently never borne leaves.

² Campbell ('95), p. 321.

whole, almost every crevice of which is filled up by the growth of some branchlet or other. The mass thus formed may acquire a thickness of 10 or more cm., and as it completely encircles the branch on which it grows, the total diameter may reach, in the case of old plants, and depending of course on the thickness of the supporting branch, upwards of 30 cm., with a length of several times as much.

In the living state the younger portions of the stem are, in the specimens I have seen, of a pale greenish-yellow colour, though in Burck's figure¹ they are represented as being a very decided green. The older parts are black and apparently dead. Thus, as the plant grows, the mass may come to consist of a number of living plants, isolated by the dying-off of the older parts behind, but still connected together by these persistent, apparently dead parts². That the oldest parts of the rhizome in such a mass are really dead, even when few visible signs of decay are present, is, I think, a fact, though the stem, or parts of it, may undoubtedly continue to live for a considerable time after the blackening process has set in. This is proved by the following facts: first, that living and healthy leaves may be present on parts that have become perfectly black, which shows that the vascular bundles at least are still living; and secondly, one occasionally finds small greenish knobs of living tissue isolated amongst completely blackened parts (*a, a*, Fig. 6). These occur in the position where lateral branches normally arise, and are, in fact, incipient branches which have either developed unusually late, or have lain dormant during the further growth of the parent branch.

In both the above cases the living parts, whether leaves or incipient branches, are never very remote from the apex, but are only found on parts of the rhizome near the young growing portions.

(*β*) *Leaf*. The fronds are dimorphic, the fertile ones being

¹ Burck ('84), Plate VII.

² This condition of things is somewhat analogous to that found in a branched colony of corals.

usually confined to the main stem and the largest and most vigorous branches. Both kinds are glabrous, pinnatisect with a terminal lobe, lamina glaucous and sub-coriaceous, petiole, rachis and midribs dark brown.

Sterile fronds 2-9 cm. long (including petiole), 1.5-4.5 cm. wide, with one terminal lobe and 1-3 pairs of lateral segments. Segments shortly-oblong to oblong-ovate, obtuse, somewhat contracted at the base, margin entire or repand. Veins immersed except the midribs, which are more prominent on the upper than the lower surface. The lateral veins branch and anastomose freely, forming on each side of the midrib two or three series of areolae enclosing free veinlets with swollen terminations. The costal series of areolae is the largest (Fig. 45). Petiole short, 2.5 cm. at most, somewhat semicircular in cross-section (the flatter side facing apex of stem), usually slightly winged almost to the base.

Fertile fronds often 30 cm. or more long (including petiole), and 4 or more cm. wide, with one terminal lobe and 15-25 pairs of lateral segments, the lower sterile and similar to those of the sterile fronds, the upper fertile, narrowly oblong, obtuse, bearing 2-12 marginal lobes, each of which bears one deeply sunken sorus. The size of the segments diminishes slightly from base to apex.

The sori are circular, and commence in slight depressions on the lower surface of the marginal lobes of the leaf-segment. During development, the depressions become deeper and deeper until they assume a cup or bucket shape. Meanwhile, the soriferous lobes bend gradually upwards, until they are completely reflexed upon the upper (ventral) surface of the leaf. In order to accommodate the depth of the sorus-cups, the margin of the leaf is also bent upwards. Various stages in this process are shown diagrammatically in Fig. 42, *a, b, c, d*. As is usual in the Polypodiaceae, the sori contain sporangia in all stages of development. When mature, the sporangia are long-stalked, but in a young sorus the stalks do not elongate until the sorus-cup is almost fully formed. At this stage the mouth of the cup is oblong, but as the sporangia mature and

fill up the cup, the mouth becomes oval-orbicular in shape. The longer diameter of a mature sorus-cup is about 2.2 mm., and its depth about 2 mm. A drawing of part of a fertile segment with several sori is seen in Fig. 43, while Fig. 4 shows a number of the reflexed sori on part of an adult fertile frond.

In Presl's¹ description of *Lecanopteris* it is said that the receptacle is covered with hairs ('undique capsulis pilisque densissimis obtectum'). Hooker², in the description accompanying Bauer's figures of *Lecanopteris*, reproduces the same phrase, though no drawing of the hairs in question is given. I have found no trace of such structures in my material; a few paraphyses are present amongst the sporangia, but these are quite minute, and could not possibly be the hairs referred to. The most probable explanation is that given by Fée³, i. e. that these hairs are merely sporangia stalks. In every mature sorus numbers of these hair-like stalks may be found (Fig. 39), and it seems highly probable that these form the structures referred to.

The sporangia themselves will be described under the section on the internal structure of the leaf.

The venation of the fertile segments is similar to that of the sterile except as regards the supply to the sorus-cups. The main lateral veins run almost direct to the margin, where they enter the soriferous lobes. The latter are also supplied by one or two smaller veins, usually coming from the margin of the leaf (Fig. 46).

Petiole about 9 cm. long, slightly winged for a short distance below the lamina. In both the sterile and fertile fronds the petioles often undergo a torsion through an angle of about 90° or more.

Nearly all the leaves found, of whatever size, were mature. One or two immature fertile fronds are present, but no unfolding fronds or rudimentary leaves could be found. This may perhaps indicate that growth in this fern is very slow,

¹ Presl ('36), p. 203.

² Hooker and Bauer ('42), Tab. CX, B.

³ Fée ('50-'52), p. 259.

and that the leaves are long-lived, being formed only at comparatively long intervals. It might perhaps be expected that young leaves would be formed chiefly at certain periods of the year, but it is curious to note that the specimens of *P. carnosum* collected by myself were found in December, towards the close of one of the rainiest periods of the year, while the material of *P. sinuosum* sent me by Mr. Ridley, which appears to be equally devoid of immature leaves, was collected in March, soon after the commencement of rainy weather, which had been preceded by an unusually long spell of drought¹.

The description of the external features of *Polypodium carnosum* as given above is taken from the specimens collected on Gunong Inas; those from other mountains in Perak are precisely similar. The description given by Burck² of Javanese specimens differs only in a few unimportant details, but the specimens from other parts of the Malay Archipelago, which include Blume's types, differ somewhat more extensively. These differences will be discussed at greater length in the section devoted to systematic position.

Internal Structure.

A. Rhizome. A cross-section through an old stem reveals the presence of an extensive system of hollow spaces in the ground-tissue (Figs. 14 and 15). These are the ant-galleries. If they are followed towards the apex of the stem, they are found to be replaced in the younger parts by a fragile, large-celled, thin-walled tissue, which by breaking down gives rise to the galleries: the latter are therefore of lysigenous origin.

Externally the rhizome is coated with a thin layer of wax, while on the dorsal and lateral surfaces, in the young parts at least, are small scattered epidermal hairs, one of which is

¹ Although some periods of the year in the Malay Peninsula can usually boast a considerably greater rainfall than others, there are no well-marked wet and dry seasons, the climate being more or less hot and moist all the year round.

² Burck ('84), p. 96.

shown in Fig. 13. I have found no mention of these by previous writers.

Immediately below the epidermis is a somewhat ill-defined hypoderma, consisting of several layers of small and comparatively thick-walled cells. Internally the latter pass by degrees into the larger parenchymatous cells of the ordinary cortex. On approaching the galleries the cells of the ground-tissue again diminish in size, and form a zone of small cells, several layers deep, surrounding the galleries. The cells of this zone also form numerous more or less irregular promontories projecting for a short distance into the lumina of the galleries (Fig. 12). The walls of these small cells are considerably thinner than those of the hypoderma. In the partition-wall between two adjacent galleries the ordinary cells of the ground-tissue are usually narrow, and elongated in the direction of length of the partition-wall. They present the appearance of having been crushed.

At a comparatively early period, prior to the disintegration of the large-celled tissue, the walls of the two or three layers of small cells immediately surrounding it become impregnated with a yellowish-brown colouring matter (Figs. 9 and 12), which is probably the same as that found in the sclerenchyma of most Ferns. The same is true of the thick-walled hypoderma. Later, the brown colour gradually extends to the whole of the ordinary ground-tissue, until the latter, when seen in mass, has a deep-brown or almost black appearance. It is this wholesale impregnation of the cell-walls with colouring matter that causes all except the youngest parts of the stem to appear black and dead. According to Walter¹, the brown colouring matter itself is a substance called phlobaphene. As Poirault² and Boodle³ have found in other Ferns, the cell-walls can be decolourized by Eau de Javelle, and will then give the cellulose reaction with Schultze's solution. Poirault⁴ also states that membranes impregnated with this brown colouring matter are much more resistant

¹ Walter ('90), p. 18.

² Poirault ('93), p. 127.

³ Boodle ('01), p. 361.

⁴ Poirault, loc. cit.

than are those composed of mere cellulose, even sulphuric acid requiring considerable time to act on them. This I have also found to be the case in the tissues of *Polypodium carnosum*. But whilst increasing the resistance of tissues, the brown substance by no means renders them impervious to water, for even the living and apparently functional root-hairs of this Fern are deeply stained with it.

The cell-walls of the ground-tissue are, when mature, considerably thickened. During the primary thickening of these walls, minute spindle-shaped thin places are left, which give the walls a faintly punctate appearance. Later on, broad thickening bands are laid down, which may join or cross each other so as to form an irregular network (Fig. 30). According to Baranetzki¹, the thickening of parenchymatous cell-walls by threads or bands is very common, but is not always easily seen without the use of special staining methods. He remarks that lignification often makes it more obvious. This is also true of the brown colouring matter referred to above, as the thickening bands stand out with perfect distinctness on the brown walls of the old ground-tissue, while they are much more difficult to see before the tissue is coloured.

A striking feature of the ground-tissue is the almost entire absence of intercellular spaces, both in the young and old parenchyma: at all events, I have been able to recognize only a very few, and these extremely minute ones in the thick-walled hypoderma.

The vascular system. The structure of the steles is of the polypodiaceous type, and their arrangement resembles that found in other species of *Polypodium* with dorsio-ventral rhizomes². The modifications in the course of the bundles are connected chiefly with the arrangement of the ant-galleries.

In a transverse section of the stem, there is seen a single median ventrally-placed gallery, surrounded by a single ring of steles. These steles anastomose to form a network which has the shape of a modified cylinder.

¹ Baranetzki ('86), p. 135.

² Cf. Klein ('81), pp. 335 et seq.

Dorsally, along the median line, there runs a single vascular bundle, a little thicker than the rest, in a slightly sinuous course. On either side of this, in two alternating longitudinal rows, are the large foliar gaps. These are oblong in shape, and about 11–12 mm. long, by 5–6 mm. wide (*d.* Fig. 35).

On either side of each foliar gap, two vertical steles are given off, one from the hinder corner and the other about half-way along the gap. These branch and anastomose with each other and with the steles from the other side of the gap to form a network extending up into the leaf-cushion and arching over the gap, completely roofing it in except in front. A horizontal section through a leaf-cushion thus shows a horseshoe-shaped arrangement of bundles (with the open part pointing forwards) passing up towards the petiole (Fig. 18). Each foliar bundle given off from the central dorsal stele usually branches into two. One branch forms the anterior bundle (on the inner side) of one leaf-trace, and the other the posterior bundle of the next leaf-trace on the other side of the middle line (*a.* Fig. 35). Sometimes, however, these two bundles may arise separately from the dorsal stele. The consecutive foliar gaps of one longitudinal series are separated by a single transverse row of small meshes (*b.* Fig. 35).

Laterally the vascular cylinder is composed of small polygonal meshes, about 4–5 mm. long, and not quite so broad. Its continuity is interrupted opposite each foliar gap of the same side by a large gap corresponding to the origin of a lateral branch (*c.* Fig. 35). The meshes bounding this gap are continuous with those forming the cylinder of the branch.

Ventrally the meshes are similar to the lateral ones. At irregular intervals, either from the side of a mesh or from a point of anastomosis, a stele is given off which passes obliquely downwards and forwards to a root.

The connexion between the vascular system and the galleries will be described later.

The individual stele is of the bicollateral type, and need

not be described in great detail. It is of small size, and is elliptical in cross-section. The xylem, as in many Polypodiaceae¹, consists entirely of tracheides, and is somewhat scanty in amount. Between the phloem and the endodermis (which has the usual thickened radial walls) is the pericycle. This is composed of one or two layers of relatively large cells, which are superposed upon those of the endodermis (*vide* Fig. 33). This probably indicates that we are here dealing with a so-called 'double endodermis' and not a true pericycle².

The bundle is surrounded by a dark-brown sheath composed of a single layer of cortical cells, with very much thickened inner walls (*s.* Fig. 33). These walls are traversed by numerous large radial pits.

Origin of the galleries. The growing point of the stem is fleshy and presents a blunt, somewhat rounded appearance. There is nothing to indicate the exact position of the actual apex. Several attempts were made, by means of serial sections, both freehand and microtome, to determine whether a single apical cell is present or not, but without success.

Immediately behind the growing point a transverse section of the stem is very uniform in appearance, consisting, with the exception of the epidermis and the procambial strands, of very thin-walled parenchymatous cells, more or less equal in size. About 1 or 2 mm. from the apex, however, the cells in certain definite areas may be seen to increase in size at a greater rate than do the surrounding cells. This differentiation becomes more marked the greater the distance from the growing point, for not only do these cells themselves increase enormously in size, without undergoing much, if any, division, but the cells surrounding them begin to divide by radial³ and also to some extent by tangential walls. An early stage in the differentiation is shown in Fig. 8 and a much later one in Fig. 9. The large-celled tissue thus formed is surrounded when mature by a belt, several layers deep, of

¹ De Bary ('84), p. 344.

² Cf. Van Tieghem ('88), p. 404.

³ Radial as regards these large-celled areas.

relatively small, brown cells. The development of these smaller cells is most marked at those angles which form the meeting-point of several of the outermost large cells. The result of this is that projections (occasionally of considerable length) of the small-celled tissue are found extending between the large cells. Thus the peripheral cells of the large-celled tissue come at length to occupy pocket-like depressions in the small-celled zone. This arrangement can perhaps be rendered more intelligible by the aid of figures. The inward projections of the small cells are seen in longitudinal section in Figs. 9 and 12. Fig. 10 represents a section taken parallel to the surface of the small-celled tissue, and passing transversely through the free ends of a number of these processes. A section in the same direction, but nearer the periphery of the large-celled tissue, is seen in Fig. 11; this shows several of the pocket-like depressions in the zone of small cells, occupied by some of the outermost large cells.

During life the cells of the large-celled tissue are filled chiefly with water, their thin walls being merely lined by a film of protoplasm. The tissue thus probably functions as a water reservoir¹. In appearance it strikingly resembles the special water-storing tissue of some desert plants².

Finally the large-celled tissue breaks down, and is rapidly disintegrated, its place being taken by the ant-galleries. In my material the aqueous tissue was rarely intact at a distance of 2 cm. from the apex of the stem, and was often entirely broken down before that point. Fig. 12 is a microphotograph of a section taken through some partially broken-down aqueous tissue.

Arrangement of the galleries. The system of galleries thus formed by the breaking down of the large-celled tissue,

¹ The translucency of the tissue, the thinness of its cell-walls, and the absence of intercellular spaces, all point to its being a true aqueous tissue. Cf. Warming ('96), p. 199.

² Cf. Volken's ('87), p. 59. Figs. 2, 3 and 4 on Taf. XII show a very similar tissue in the stems of several flowering plants. The resemblance is increased in these cases by the similar ingrowths of a small-celled tissue between the large cells.

though somewhat complicated, is arranged on a perfectly definite plan, following the same course through the stem as that taken by the aqueous tissue just described. As will be seen, the system appears to bear special relation to the large conical leaf-cushions which form such a prominent feature of the exterior of the stem.

There is, as mentioned above, a single median, ventrally-placed gallery, which runs, in a slightly sinuous course, through the whole length of the stem (Figs. 16, 22, &c.). This gallery is usually about two or three times as broad as it is deep, its floor being convex and its roof concave. At regular intervals the central gallery gives off a lateral gallery to each branch of the stem, and a vertical one to each leaf-cushion. As both the leaves and the lateral branches of the main stem are arranged in two longitudinal series, it follows that (unless this regularity is interrupted, as it may be, e.g. if some of the branches do not develop) there are two series of lateral galleries and two series of dorsal ones leaving the main gallery.

One of these lateral galleries originates beneath each leaf-cushion, and passes out immediately below a foliar gap, through the large gap in the vascular cylinder where the branch cylinder (which thus encircles the lateral gallery) leaves the main one. It curves slightly as it does so, first backwards and downwards and then forwards, finally entering a lateral branch, where it behaves like the corresponding gallery of the main stem. A second gallery leaves the central one close to the point of origin of the side-gallery (*a*, Fig. 20). This travels almost vertically upwards through the large foliar gap, and ends blindly in the leaf-cushion, under the base of the petiole (Fig. 15). Before entering the leaf-cushion, however, it sends out a forward diverticulum (Fig. 23) which passes outside the vascular system altogether, by means of the gap in the horseshoe-shaped network of the leaf-trace. This diverticulum immediately branches into two. One branch (*b*, Fig. 21) passes outwards, backwards, downwards and finally upwards, ending blindly in the same leaf-

cushion as the parent gallery. The other branch runs forwards and slightly inwards, and ends blindly in the leaf-cushion next in front, on the other side of the stem.

Thus each leaf-cushion contains a transversely arranged series of three blind galleries, of which the middle and outer ones communicate with the ventral gallery at a point immediately below the cushion itself, while the third, or inner one, does so at a point below the leaf-cushion next in order behind. These three galleries are seen in Fig. 18, which shows a horizontal section through a leaf-cushion, some distance below the articulation of the leaf; while Fig. 15 shows the same in vertical section. There are, at least in the case of the larger leaf-cushions, external indications of these three diverticula in the form of slight bulgings of the cushions. These are shown on several of the leaf-cushions in Fig. 19.

The whole system then consists of a central median ventral gallery which gives off, alternately on either side, lateral galleries to the branches, and a dorsal series of chambers, each branched into three. The branches of these chambers are arranged roughly in the form of an *h*, each limb of which finally turns upwards, the two lower ending blindly in one leaf-cushion, and the upper in the leaf-cushion next in front on the opposite side of the stem. These dorsal chambers communicate with the main gallery close to the points of origin of the side-galleries. Fig. 20 represents diagrammatically a plan of the main gallery and its lateral branches, and Fig. 21 a plan of the dorsal chambers.

The arrangement of galleries in the branches is essentially the same as that of the main stem, except that in those cases where the lateral branchlets of the branches themselves are suppressed, the side galleries are of course not fully developed. Fig. 22 represents a nearly median vertical longitudinal section through the rhizome; it shows the main ventral gallery, and also cuts through the two series of forwardly directed branches of the dorsal chambers. Fig. 23 is a similar section passing through the apices of one of the two longitudinal

rows of leaf-cushions (across *cc* in Fig. 20). The slightly sinuous course of the ventral gallery is shown by its interruption at various points. Three of the vertical galleries with their forward diverticula are also shown.

The galleries communicate with the exterior by means of little passages tunnelled by the ants through the outer tissues of the stem. Fig. 5 is a photograph of a transverse section through one of these excavations. It will be noticed that the internal edges are irregular, and show signs of having been gnawed by the ants, while the long processes so characteristic of the naturally formed galleries are quite absent. The external openings of these tunnels are usually situated on the ventral surface of the rhizome, a little below the apices of small branches (*a.* Fig. 15). Shallow pits may also occasionally be found in similar positions. These pits are evidently of the nature of wounds, as the epidermis which should cover them is missing, while the adjacent tissues are usually coloured brown, and are often contracted as if evaporation of water had taken place from the wounded surface. It seems probable that the pits are really the beginnings of tunnels to connect the galleries with the exterior. If this is so, it would appear to be usual for subsequent boring operations, as well as the original ones, to be conducted from the outside. The apical regions of the stem are probably selected by the ants because the tissues there are more easily excavated than are those of the older and tougher parts.

B. Root. Adventitious roots are given off at fairly frequent intervals from the ventral meshes of the vascular cylinder of the stem. They commence just below the growing point and develop by means of a single, three-sided apical cell¹. The developing root passes obliquely forwards through the cortex, and emerges from the stem some little distance in front of its point of origin. Van Tieghem and Douliot² have pointed out that this cortical part of the 'root-stele' possesses in reality the structure of a stem-stele and not that of a root. This is the case also in *P. carnosum*, the general arrangement

¹ Cf. Bower ('89), p. 309.

² Van Tieghem and Douliot ('88), p. 533.

of the stelar tissues as well as the sclerenchymatous sheath conforming to the usual structure of a stem-stele in this Fern. As the young root emerges from the cortex, it is at first covered by a cap formed of the epidermis of the stem. This cap finally ruptures, and is left behind as a collar encircling the root close to where it emerges from the stem¹. Fig. 37 shows a layer of these collar-cells (*c*) external to the piliferous layer of the root.

The mature root has a diameter of about 1 mm. It possesses a diarch xylem plate, containing only a few tracheides. The one or two central elements of the metaxylem² remain unlignified until quite a late stage (Fig. 34). The stele is enclosed in a sclerenchymatous sheath, which, like those in the stem, is of a dark-brown colour. It is composed for the most part of two or three layers of cortical cells with very thick walls and extremely small lumina, while outside there is a layer whose inner walls only are thickened. Opposite to the two protoxylem groups, however, the sheath is very much thinner, and consists merely of the thick inner wall of one large passage-cell (sometimes there are two such cells placed side by side). This thick wall of the passage-cell is traversed radially by very large pits.

The outer cortex consists of about six or seven layers of cells, and is bounded by a piliferous layer. The whole, including the root-hairs, is stained a yellowish-brown with phlobaphene. The cell-walls of the outer cortex are thickened in a similar manner to that described for the stem parenchyma, but in the root the thickening bars are much thinner, and form a more definite and regular network (Fig. 31). In the peripheral part of the cortex the network is comparatively coarse, but on travelling radially inwards the network becomes finer, and many of the thickening rods still thinner, until in the region of the passage cells the walls are covered by a very

¹ Van Tieghem and Douliot, loc. cit., p. 533, describe similar cases in other Ferns.

² *Metaxylem* is used here in the same sense as that employed by Boodle ('00), p. 458, i. e. to include all xylem other than protoxylem.

fine, delicate reticulum with minute, irregular meshes. The appearance of these thickened cell-walls, especially those of the outer cortical cells, reminds one forcibly of the tracheidal cells in the velamen of an epiphytic orchid¹. Possibly they function in a somewhat similar way, though it must be remembered that these cortical cells are living, while the velamen tracheides are dead. At all events, the numerous and comparatively large thin places between the thickening rods would probably greatly facilitate the transport of water, which would be of service to the plant, as, being an epiphyte with large water-storing capacity, rapid absorption of water during rains would be advantageous. The cortical cells themselves also might very well store the water temporarily, until the somewhat limited vascular tissue of the root could carry off the surplus.

Apparently neither the piliferous layer nor the very persistent root-hairs ever possess this thickening network.

Lateral secondary roots are of frequent occurrence, and are developed in two ranks, emerging from the sclerenchymatous sheath at the thin places opposite to the two protoxylem groups.

C. Leaf.—Petiole. In transverse section the petiole is seen to be slightly winged, and more or less semicircular in shape with the flatter side directed towards the apex of the stem (Fig. 38). Beneath the epidermis, which has a rather thick cuticle, is the usual well-marked hypodermal tissue of thick-walled fibrous cells, with pointed ends and no intercellular spaces. The outer layers of the hypoderma are coloured brown, the inner are colourless and pass over into the larger cells of the ordinary petiole parenchyma. At two points, i. e. just behind the two wings, the fibrous hypodermal zone is interrupted by a thinner-walled spongy tissue (*a.* Fig. 38). Communication is thus established between the stomata, which only occur above the spongy tissue, and the intercellular spaces of the internal parenchyma. This tissue, as is often the case in Ferns², extends in two narrow, continuous

¹ Cf. Haberlandt ('96), p. 201, Fig. 77.

² Gwynne-Vaughan ('01), p. 83.

bands along practically the whole length of the petiole. Viewed from the exterior, these bands are lighter in colour than the rest of the petiole, owing to the absence of the dark-brown fibrous cells. Gwynne-Vaughan¹ suggests that this spongy tissue represents modified traces of a mesophyll decurrent along the sides of the petiole, and remarks upon its significance with reference to Bower's view that the leaf of the Ferns is a rachis or phyllopodium, fundamentally winged along its whole length².

Fig. 32 is a photograph of a longitudinal section through part of the apex of one of the conical leaf-cushions, showing the articulation between petiole and stem. The parenchyma of the leaf-cushion is seen to be deeply coloured with phlobaphene, while the tissues above, with the exception of the stelar sheath, are free from it. At the junction of petiole and leaf-cushion, there is a slight swelling, visible in the photograph as an outward bulging of the tissues. At this point a zone of rather small, isodiametric cells, several layers deep, stretches right across the leaf-base. Leaf-fall occurs by disarticulation along this zone of cells.

As previously mentioned, a horizontal section through a leaf-cushion shows a horseshoe-shaped arrangement of bundles, passing upwards to the leaf, and partially surrounding the central gallery of the cushion. The concavity of the horseshoe is adaxial, its free ends being formed by two bundles which are rather larger than the others. These two bundles, together with several smaller ones (often making a total of six), enter the petiole. Gradually the free ends of the horseshoe³ converge, and finally the two large bundles fuse with each other, though this does not occur in some cases until the summit of the petiole is nearly reached. The fate of the smaller bundles is not always the same. In the smaller leaves the rule is for the petiole, except at its base, to be

¹ Gwynne-Vaughan, loc. cit.

² Bower ('84), p. 606.

³ Gwynne-Vaughan, loc. cit., p. 95, points out that the vascular arrangement in the petioles of Ferns almost invariably takes the form of (in cross-section) a more or less modified horseshoe.

provided with only two steles (Fig. 38). Of these, the larger, which is adaxial in position, is, at least in some cases, formed by the fusion of the two large bundles and two of the smaller ones; the other is composed of the remaining two small bundles. In the larger leaves, however, there is not such complete fusion of the steles. The smaller ones anastomose or separate at intervals, but still retain to some extent their individuality.

Lamina. The mesophyll, as seen in a transverse section of a leaf-segment, is differentiated into two parts. The first consists of a single layer of large cells, lying immediately beneath the upper epidermis (*a*. Fig. 51). At the margin of the leaf this layer may be doubled, its cells at the same time becoming smaller. On the under side it passes into the spongy mesophyll. Viewed in optical section, by means of clearing the lamina with Eau de Javelle and staining, this layer is seen to possess no intercellular spaces. Its cells have more regular outlines than those of the ordinary mesophyll. They contain no chlorophyll when mature, and little or none even in the younger stages. This tissue may perhaps be regarded as a hypodermal water reservoir, similar to that found in the leaves of certain Orchidaceae, Velloziaceae, &c.¹ The bulk of the mesophyll, however, consists of the usual spongy tissue, composed of branched cells with irregular outlines and many, though comparatively small, intercellular spaces.

The epidermis has a fairly thick cuticle. Its cells, except the guard-cells, apparently contain no chlorophyll. Stomata are numerous on the lower surface of the leaf, but are absent on the upper. The guard-cells are on the level of the ordinary epidermal cells and are not sunken, as is so often the case in the leaves of xerophytes. Their development corresponds to that described by De Bary² for various other Ferns. Successive stages in the formation of young stomata are shown in Fig. 49, *a, b, c, d*, and a mature stoma in Fig. 50.

The general course of the veins in a leaf-segment has been

¹ Cf. Warming ('96), p. 201.

² De Bary ('84), p. 41.

described above. The midrib projects considerably on the upper surface of the segment, but very little on the lower. It contains a single rather small stele, provided with a brown sclerenchymatous sheath similar to those of the stem and petiole. Between the stele and the epidermis (both upper and lower) are thick-walled mechanical elements, completing what is thus an efficient I-shaped girder. The stelar sheath is continued for a short distance only round the main lateral veins, the smaller bundles possessing neither the thick-walled sheath nor the strengthening mechanical tissue. In optical section it can be seen that the bundles usually contain few tracheides, but their number is often increased by the interpolation of a few short curved ones at points where the veins branch or anastomose. The free vein-endings are swollen, and contain numbers of short scalariform tracheides. In the fertile segments the veins supplying a sorus run down the proximal side of the sorus-cup, and form an irregular plexus under the placenta, containing numerous short tracheides (Fig. 46). At the point where the soriferous lobe is sharply bent back upon the rest of the leaf-segment, the vascular bundles are also bent, even the individual tracheides taking part in this curvature.

The sorus-cup differs somewhat in structure from the rest of the lamina. Its mesophyll has a more uniform appearance, and possesses only small intercellular spaces. Normal stomata occur on the inside of the cup (morphologically the lower surface of the leaf), but they are not very numerous.

A mature sorus (Fig. 39) contains sporangia in all stages of development, numerous sporangium stalks, and lastly, a few short paraphyses with small, somewhat club-shaped heads. The sporangia have long stalks, composed of three rows of cells, most of which are extremely elongated (Fig. 44).

The total length of a mature sporangium and stalk is usually about 1.7 mm. The annulus is vertical and incomplete. The inner and radial walls of the three cells of the annulus immediately above the stomium remain comparatively thin (Fig. 44), though all the walls of these cells are deep

brown in colour. The spores are tetrahedrally arranged, are slightly curved with blunt, rather narrow ends, and have smooth outer walls.

II. POLYPODIUM SINUOSUM, Wallich.

External Morphology.

(a) *Stem.* The rhizome resembles that of *Polypodium carnosum* in its dorsi-ventral structure, the lower surface (which bears the roots) being flattened, except near the growing point; also in its swollen, fleshy habit, and in the distichous arrangement of its leaves, which are similarly borne on prominent swollen leaf-cushions. It is, however, smaller; my specimens rarely have a greater width than 1.4 cm., though the plant may attain a larger size than this, Christ¹ stating that they are 3 cm. broad.

The surface of the rhizome (including the leaf-cushions) is densely covered near the apex with adpressed, imbricating peltate scales, which arch over and protect the growing point. On the older parts they become somewhat more scattered, owing to the elongation of the stem. They are found, though rather more sparingly, on the lower surface² as well as the upper. These scales are nearly orbicular in shape, usually about 2 mm. in diameter, and are composed of numerous, radially arranged cells³. The centre is black and slightly raised, and is surrounded by a brown zone, while the margin of the scale is white and scarious.

The leaf-cushions are less swollen in the transverse direction than in *P. carnosum*, and are not placed so close together, two consecutive cushions of the same side being often as much as 4 or 5 cm. apart.

The branching in the two Ferns is similar, but much less frequent in *P. sinuosum*. It is, however, usual to find at

¹ Christ ('97), p. 112.

² Christ, loc. cit., only describes the scales on the upper surface.

³ See figure in Diels ('99), p. 320.

about the level of each leaf-cushion, on the opposite¹ side of the stem, a slight lateral projection (*a*, Fig. 7). These projections sometimes develop into lateral branches, but more often lie dormant. As a result of this limited branching, the rhizomes never form a compact, solid mass such as is seen in *P. carnosum*, though they may overlap each other to a considerable extent².

(β) *Leaf.* The fronds are sub-dimorphic, entire, glabrous and sub-coriaceous. The petiole and the midrib are brown.

Sterile fronds 9–12 cm. long (including petiole), and about 2 cm. wide; elliptical-oblong to oblong, obtuse, margin entire, gradually narrowed at base into the petiole, sometimes cuneate.

Fertile fronds 11–22 cm. long, 1–1.5 cm. broad; linear-oblong, obtuse, margin minute, base as in sterile fronds. Sori about 4–5 mm. long, oval or oblong, often becoming nearly circular towards apex of frond. They are rather deeply sunken (the pits producing oval projections on the upper side of the frond), and are arranged in a single longitudinal row on each side, nearer the margin than the midrib.

The venation is of the same type as that of *P. carnosum*, but the costal areolae are longer and narrower in *P. sinuosum* (Figs. 47 and 48), and in the sterile fronds the larger areolae may contain smaller ones, formed by the anastomosis of the enclosed veinlets.

Petiole 2–3.5 cm. long, approximately circular in cross-section.

Internal Structure.

The structure of *P. sinuosum* closely resembles in many respects that of *P. carnosum*, and need not be described in very great detail. Only those points in which the two Ferns differ markedly from each other will be dealt with at any length.

¹ In *P. carnosum* the branches arise at about the level of the leaf-cushions of the same side.

² Cf. Mr. Parish's remarks in Hooker ('64), p. 62.

a. Rhizome. Here and there, in a transverse section of the stem, occur pit-like depressions, the sides of which are lined by the epidermis. From the floors of the pits spring the cylindrical stalks of the peltate scales. These stalks are composed of a number of elongated cells, with very thick brown walls. The cells immediately above the stalk have comparatively large lumina, and these pass in all directions into the shallow, radially arranged cells of the scale. The radial walls of the latter cells are marked with numerous large pits¹.

There is no special thick-walled hypoderma.

The vascular cylinder in this Fern is somewhat flattened dorsi-ventrally. In a transverse section of the stem it appears as an oval ring of steles (Figs. 24, 25). A semi-diagrammatic drawing of a dissection showing the dorsal part of the vascular cylinder is seen in Fig. 36. The meshes of the network are small and elongated. It is difficult to define the actual limits of the foliar gaps, but apparently they are much elongated, with pointed ends. The supposed boundaries of one of them are indicated in Fig. 36, by the slightly thicker steles lying between the points *a* and *b*. From the edges of this gap numbers of steles are given off, which branch and anastomose to form an extensive network (similar in appearance to that of the main cylinder) arching over the foliar gap behind, but rising more abruptly in front to enter the leaf-cushion. Laterally, secondary cylinders are given off to the branches, and from the ventral meshes steles pass downwards to the roots, much in the same manner as in *P. carnosum*. In fact, the whole vascular cylinder of *P. sinuosum* much resembles that of *P. carnosum*, if we can imagine the latter stretched or pulled out in a longitudinal direction².

¹ Karsten ('95), p. 180, describes the structure of these scales in detail. He regards their function as twofold, (1) to protect the stem against excessive transpiration, (2) to collect and temporarily store water during the fall of rain, for the subsequent use of the roots. Water is quickly sucked up by the expanded part of the scale, but from the structure of the stalk Karsten thinks it unlikely that any finds its way directly into the stem.

² Boodle ('01, 2nd paper), p. 739, points out that strongly xerophytic conditions are likely to conduce to shortening of internodes and decrease of rate of growth in stems. Probably the shorter internodes (and therefore the apparently contracted

The stele is of the same type as that of *P. carnosum*. The pericycle, in this case also a false one, as it originates from the same layer as the endodermis, is here only one layer thick throughout. The sclerenchymatous sheath is similar, but the radial pit-canals are often much more branched than is the case in *P. carnosum*.

In the material at my disposal the impregnation of the cell-walls by phlobaphene is most marked in the two or three layers of small cells surrounding the galleries, the general ground-tissue never assuming the deep brown colour found in *P. carnosum*: this, however, may be due to the fact that my material did not include any very old pieces of stem. Moreover, the thickening of the cell-walls by bands is largely confined to these small cells. In *P. carnosum*, on the other hand, the small-celled zone seldom, if ever, has the thickening bands developed on its cell-walls to any extent. Probably correlated with the early thickening of the walls of these small cells in *P. sinuosum* is the fact that although the cells do divide in early stages of growth, yet this division is never carried so far as in *P. carnosum*. Thus the curious projections of the small-celled zone between the large cells of the aqueous tissue (which originates in a similar manner in both Ferns) are never found in *P. sinuosum*.

The aqueous tissue finally breaks down and forms galleries similar to those of *P. carnosum*.

The arrangement of the ant-galleries in *P. sinuosum* has been described by Goebel¹, but a few points may be added to his description, and a comparison made with the gallery-system of *P. carnosum*. As in *P. carnosum*, there is a single main ventral gallery, three or four times as wide as deep. It is seen in transverse section in Figs. 24 and 25, in median vertical longitudinal section in Fig. 28, and in horizontal longitudinal section in Fig. 27. Laterally it gives off side-galleries to

condition of the vascular cylinder) of *P. carnosum* may be correlated with its very exposed situation, which renders it liable to intense insolation. It cannot, however, be assumed, merely on general grounds of this sort, that originally the stems of the two Ferns were precisely similar in this respect.

¹ Goebel ('88), p. 16.

the branches, but in *P. sinuosum* the latter being much less numerous than in *P. carnosum*, the lateral galleries are not developed with such regularity. Sections, however, taken through those lateral projections of the stem which we have seen are to be regarded as undeveloped branches, show pocket-like diverticula of the main gallery extending into them (*d* in Figs. 24 and 27).

Each leaf-cushion contains a single vertical gallery (oblong in cross-section) which ends blindly some distance below the leaf-articulation. Just after leaving the main gallery, it sends out a single diverticulum which does not branch, but travels backwards in a straight line for a distance of about 1 cm., and ends blindly in a blunt point. There is usually an external swelling on the stem corresponding to this diverticulum (Figs. 29 and 36).

The relation of this dorsal chamber to the vascular system differs from the arrangement found in *P. carnosum*. In both Ferns the vertical gallery passes outside the vascular cylinder through a foliar gap, but while in *P. carnosum* the diverticulum given off from this gallery is directed forwards, and passes out through the gap left in the network of foliar bundles, that of *P. sinuosum* is directed backwards, and does not pass to the exterior of the vascular system at all, as the foliar bundles form a vaulted network over it.

The gallery system communicates with the exterior both by the dying-off of the older parts of the stem¹, and also, as in *P. carnosum*, by means of small lateral or ventral openings made by the ants themselves.

b. Root. The root of *P. sinuosum* is an almost exact counterpart of that of *P. carnosum*, but on a smaller scale.

The outer cortex is only about three or four cells thick, including the piliferous layer. The walls of its cells possess the same prominent network of thickening bars as do those of *P. carnosum*, while the cells of the inner cortex form a sclerenchymatous stelar-sheath of precisely the same nature.

c. Leaf. The petiole is generally almost circular in transverse

¹ Goebel, loc. cit., p. 17.

section throughout the greater part of its length, though towards its summit it is more or less winged, the leaf-lamina being often slightly decurrent. The arrangement of tissues is the same as in *P. carnosum*. There are the same brown hypodermal fibrous cells, interrupted by the two lateral lines of spongy tissue, above which are the stomata, in this case even fewer in number than in the other Fern. The steles are usually two in number, a large elliptical one, adaxial in position, and a smaller circular one.

The leaf-lamina, too, has a similar structure in both Ferns, but in *P. sinuosum* the large cells under the upper epidermis appear to contain a certain number of chloroplasts. This is, no doubt, correlated with the difference in habitat of the two plants, *P. sinuosum* usually growing in somewhat shadier situations than *P. carnosum*.

A diagrammatic drawing of a transverse section through a sorus is seen in Fig. 40. It is not so deeply sunken as the sorus of *P. carnosum*, and consequently the stalks of the sporangia are shorter; the sporangia themselves, also, are not quite so large. Paraphyses, consisting of simple filaments of four or five cells, the terminal one rounded but not swollen, are fairly numerous. That part of the leaf-lamina which constitutes the bottom of the sorus-pits is thinner than is the case elsewhere. At the edges of the sorus-pits the cells of the epidermis are considerably deeper than is usually the case (*a.* Fig. 40).

BIOLOGICAL CONSIDERATIONS.

Under this heading may be discussed the curious reflexed position of the sori in *Polypodium carnosum*, and the meaning to be attached to the galleries which occupy such extensive tracts in the tissues of the stem in both Ferns. With the latter point is connected the question of the relations existing between the ants and their hosts.

The reflexing of the sori of *P. carnosum* upon the upper surface of the leaf is a phenomenon in all probability nearly unique in Ferns, the only other cases of which I am aware

being found¹ within the limits of Blume's genus *Lecanopteris*². The meaning of the flexion is not at first sight obvious. The only explanation that suggests itself to me is that it may possibly be connected with spore distribution. As we have seen, *P. carnosum* grows on mountains, as an epiphyte on the *upper* branches of trees. Often these trees are tall³, and it is only when the jungle is dwarfed on the highest mountain tops that it approaches at all near to the ground. Now the reflexing of the sori causes most at least of the little sorus-cups to face skywards instead of towards the ground (*vide* Fig. 1). The effect that this position of the sori would have on the ejection of the spores would probably be to cause most of them to be ejected from the sorus only when a considerable wind was blowing. Thus, if the sporangia had previously dehisced, a large proportion of the spores would still remain inside the sorus-cup or even on the concave upper surface of the leaf-segment, until the force of the wind were sufficient to shake the frond and carry them away. Under these conditions, the spores would have a much better chance of reaching their destination, i. e. the topmost branches of trees, than if they fell to the ground first, as would often happen on still days, if the sori occupied the position usual in Ferns⁴.

P. sinuosum, being a low-growing epiphyte, would have much less need of an adaptation of this sort.

The reflexed sori, in their new position, would of course be more exposed to the effects of the heavy tropical rains than before. This, however, in all probability would not be a very serious drawback, as their most vulnerable part, i. e. the long thin stalks of the sporangia, would be safely hidden

¹ In a few Ferns sori may be actually borne upon the upper surface of the frond; e. g. *Deparia Moorei*, Hook., whose sori are usually marginal, frequently bears additional sori scattered over the upper surface of the leaf.

² This genus is characterized by having the sori borne on marginal lobes, which are either bent back upon the upper surface of the leaf, or twisted to one side.

³ Mr. Ridley informs me that on Bukit Timah, in Singapore, *Polypodium carnosum* never grows at less than eighty feet from the ground.

⁴ Mr. F. Darwin has suggested to me that this may be compared with the 'Censer' mechanism found in the fruits of the Poppy and other flowering plants.

away behind the walls of the deep sorus-cups¹; while above, the tightly packed sporangia, protected by their strongly thickened annuli, would probably suffer little, even in the heaviest downpour.

The question as to the function to be ascribed to the galleries in these Ferns is more complicated. Three possibilities present themselves. First, that the galleries are a special adaptation on behalf of the ants, both the plant and its guests deriving benefit from the symbiosis. The second is that they are more or less accidental, simply replacing the effete aqueous tissue of the stem, and themselves serving no special purpose; while a third possible explanation is that they may be connected with the interchange of gases in the stem, as suggested by Treub² in the case of the ant-galleries of *Myrmecodia*.

Nothing approaching the extensive and regular system of hollows traversing the stem in these Ferns appears to be known among the other Filices, though a few closely allied Malayan species³, which are also inhabited by ants, in all probability possess similar structures. At the same time, cavities in the stems of other Ferns are by no means unknown. For instance, *Ceratopteris thalictroides*, Brong., possesses hollow spaces of schizogenous origin in the cortical tissues of both stem and root. Campbell⁴ states that—

‘In *Onoclea struthiopteris* characteristic air-chambers are formed in the young medulla at an early period. At certain points the cells become longer and their contents more transparent. These cells divide less rapidly than the surrounding tissue, and large intercellular spaces are formed. The loose cells about these form masses of trichomes, either

¹ Christ ('96), p. 93, points out that many of the species of *Polypodium* found in the rainy mountainous districts of the Malay Archipelago possess these deeply sunken sori. He regards them as a protection against heavy rains, such an adaptation being especially necessary in this genus, as the indusium found in most other Ferns is absent.

² Treub ('88), p. 206.

³ Such are *Polypodium lomarioides*, Kze., *P. sarcopus*, De Vriese et Teysm., and the remaining species of Blume's genus *Lecanopteris*.

⁴ Campbell ('95), p. 323.

hairs or scales, which later dry up and leave a large empty space, which may or may not communicate with the exterior through the foliar gaps.'

A plant which may perhaps afford in some respects an interesting parallel to the case of the Ferns under consideration is *Polypodium bifrons*, Hook. The following note is appended to Hooker's description of this Fern¹:—

'Hab. Ecuador, on a tree by the river side . . . the plants were partially immersed in water, and to the root or caudex were attached hollow succulent tubers, in which the ants had taken refuge.'

Unfortunately nothing appears to be known respecting the origin of the hollows referred to.

The association of ants and Ferns is by no means limited to the cases already mentioned. Beccari² and Goebel³ quote a number of instances in which the relationship varies from cases where the ants actually inhabit cavities in the substance of the plant itself, down to those where the insects merely nest in the humus which collects around the roots and leaf-bases of so many epiphytes, both Ferns and flowering plants. In fact, one of the things which first strikes an observer in the tropics is the fact that ants are almost everywhere present. Any convenient hole or corner, whether above or below the ground, generally affords shelter to a colony of ants. It is not surprising therefore that such eminently suitable nests as are afforded by the ramifying galleries of these Ferns, and the similar ones of *Myrmecodia* and *Hydnophytum*, should be so invariably appropriated by ants⁴. The very ubiquity of the ants, however, combined with their undoubtedly high degree of intelligence, would suggest that they, like bees and other insects, may not have been without their influence on the evolution of plants⁵. Undoubtedly the mere presence of ants does sometimes protect plants from their insect enemies. Ludwig⁶ cites several instances in which

¹ Hooker ('64), p. 79.

² Beccari ('84-'86), pp. 243 et seq.

³ Goebel ('88), pp. 16 et seq.

⁴ Cf. Treub ('88), p. 207.

⁵ Cf. Lubbock ('91), p. 57.

⁶ Ludwig ('95), p. 243.

this protection is purposely utilized by man. For instance, the Chinese of Canton, who cultivate orange-trees in large groves, connect the trees together by means of long bamboo staves, so that the tree-dwelling ants may readily travel from tree to tree, and thus prevent the ravages of insect pests.

In many instances the relations between ants and plants are without doubt of a merely casual nature, to which no special biological meaning is to be attached; but these chance alliances may on the other hand, when mutual benefit results, lead on to such cases as those of various species of *Cecropia*, in which, as shown by Schimper, the adaptation would seem to be truly reciprocal¹.

As, in the numerous cases of so-called myrmecophily, different parts of plants, plants of different genera and orders, and ants of different genera are concerned, Professor Bower² suggests that the origin of the inhabited hollows and the question of the mutual advantage derived from the symbiosis should be considered independently in each case. It is, moreover, desirable to collect all available data regarding the food and habits of the ants, and the homes inhabited by the different species.

Dr. August Forel has very kindly undertaken the identification of the ants found in the two species of *Polypodium*. The ant inhabiting the material of *P. sinuosum* from Singapore proved to be *Technomyrmex albipes*, Smith, which belongs to the sub-family Dolichoderinae³. That found associated with *P. carnosum* is a new species of *Cremastogaster*, *C. Yappi*, Forel⁴. In addition to the ants, an egg-capsule of a species of cockroach⁵ was discovered in the galleries of *P. sinuosum*,

¹ Schimper ('88). Buscalioni and Huber ('00) have recently arrived at rather different conclusions from those of Schimper, i. e. that the ants have taken to live in the *Cecropias*, not in quest of food, but in order to get a nest above flood level.

² Bower ('87), p. 320.

³ Forel ('94), p. 496, states that most of the species of this group keep no plant-lice, but lick up secretions of plants, or else live on insects.

⁴ Forel ('01), p. 374.

⁵ Goebel ('89), p. 208, states that cockroaches were found by Guppy in the chambers of a species of *Hydnophytum*; but the galleries of *P. sinuosum* are small,

while a centipede (*Mecistocephalus punctifrons*, Haase) and two small specimens of some lepidopterous larva¹ were found in *P. carnosum*. Moreover, the roots of an epiphytic orchid, growing on the massive stem of this Fern, had in some cases penetrated to the interior of the galleries.

Nothing, so far as I am aware, is known of the special enemies of these two Ferns, or whether indeed they have any, and consequently it is impossible to state anything definite respecting the protection afforded them by the ants. It is true that on attempting to remove a plant of *P. carnosum* from the tree on which it grew, great numbers of its tiny inhabitants sallied forth and attacked the intruder with great pugnacity; but this proves nothing, as the case would be an exceptional one.

Unfortunately I was unable to procure any young plants of either species, and so could not investigate the origin of the first-formed gallery. From analogy with the case of *Myrmecodia*², however, it would seem probable that the presence of ants is unnecessary for its formation.

On the whole, although the possibility of the existence of a true adaptation between the ants and these Ferns cannot be denied, yet such evidence as is available seems to point to Goebel's³ view being the correct one, i. e. that the ants are merely 'Raumparasiten' or dwellers in cavities formed without reference to their future inhabitants; and this more particularly so, as no attractions in the form of food appear to be offered to the ants.

It seems to me most probable that the large-celled tissue

and it seems scarcely likely that cockroaches would live in them. This solitary egg-capsule may very well have been carried in by the ants.

¹ Dr. Sharp concludes, from the absence of colour and other markings, and the presence of only simple hairs on the bodies of these larvae, that the dark recesses of the stem of this Fern form their natural habitat. Larvae, such as *Zeuzera* or *Hipialus*, which live in dark confined places, usually have these characteristics. Meyrick ('95), p. 782, instances the case of a moth (*Myrmecozela ochraceella*, Tgst., one of the Tineidae) whose larva lives in ants' nests (*Formica rufa*), both in England and on the Continent, though he states that this appears to be unique amongst known Lepidoptera.

² Treub ('83), p. 154.

³ Goebel ('88), p. 21.

of the stem is developed in the first instance as a special water reservoir¹. The character of the tissue; its remarkable similarity to the aqueous tissue of certain other xerophytes; its position with regard to the leaf-cushions, which is such as would ensure an abundant supply of water to the young developing leaves; the fact that during life it does undoubtedly contain large quantities of water; and finally, the statement made by Goebel² that a leaf attached to part of the stem remained fresh for a number of days in a warm dry room, afford, I think, sufficient evidence of this.

At the same time, we have to explain the somewhat remarkable fact that this elaborate tissue has an extremely short life. In *P. carnosum* I have rarely found the aqueous tissue intact at a distance of 2 cm. from the growing point; though in *P. sinuosum* Goebel³ states that the living aqueous tissue is found at distances varying from 2 or 3 to 7 or more cm. from the apex of the stem. Karsten⁴, however, says that this is exceptional, the stem being usually hollow at a point 1-2 cm. behind the apex.

Now although the oldest parts of the rhizome in both Ferns are usually quite dead, the ordinary tissues of the stem have a much longer life than the aqueous tissue, so that the galleries do undoubtedly penetrate living parts of the plant. The question is whether these galleries, as such, fulfil any useful purpose, or whether they merely take the place of the aqueous tissue, when this tissue has fulfilled its function, and is now no longer required. It is possible that the latter may be the true explanation, but in view of the short life of the water tissue, it would seem to be hardly sufficient.

There remains yet the third possibility, i.e. that these cavities may act as air-shafts, a function suggested by

¹ Goebel, loc. cit., p. 16, regards it as a true aqueous tissue, but Karsten ('95), p. 182, appears to think that the function of water storage is equally well fulfilled by the other tissues of the stem. He lays stress on the absence of the tissue in other Ferns, and its early degradation in cases where it exists.

² Goebel, loc. cit., p. 18. Of course the external cortical parenchyma might have contributed some at least of this supply of water to the leaf.

³ Goebel, loc. cit., p. 18.

⁴ Karsten ('95), p. 182.

Treub¹ for the galleries of *Myrmecodia*. He supposed that aeration of the fleshy tissues of the swollen stem is affected by means of these moist chambers, without an undue loss of water. Haberlandt² adopts this view, but Goebel³ remarks that while there is much to be said for it, yet the need for this elaborate mechanism for the interchange of gases is, in the case of *Myrmecodia*, by no means proved, especially as the tuber is not green, and therefore cannot assimilate. Karsten⁴ is of the opinion that the galleries of *P. sinuosum* serve for the purpose of aeration.

Now in spite of the fact that the younger parts of the rhizomes of these Ferns contain chlorophyll⁵, there appear to be no stomata on the stem. Moreover, the system of intercellular spaces usual in massive tissues⁶ is here almost entirely absent⁷. To whatever cause this latter fact is to be ascribed⁸, it would seem possible that in a tissue which is practically devoid of the usual adaptations for gaseous inter-

¹ Treub ('88), p. 206.

² Haberlandt ('96), p. 350.

³ Goebel ('89), p. 212.

⁴ Karsten, loc. cit.

⁵ This is certainly true for *P. carnosum*, and I believe for *P. sinuosum* also.

⁶ Devaux ('91), p. 311.

⁷ The rhizomes of several other Ferns (i. e. *Polypodium conjugatum*, *P. aureum*, *P. quercifolium* and *Davallia Fijiensis*) were examined. The intercellular spaces varied considerably in size in different species, in some being very minute, but in each case they were better developed than in the two species under consideration.

⁸ External conditions, resulting in the marked xerophytism of these Ferns, may perhaps be sufficient to account for this [cf. Stahl ('83), p. 17, on the relative sizes of intercellular spaces in sun and shade leaves]. It is also conceivable that the absence of intercellular spaces may be a more or less mechanical effect, due to the formation of the aqueous tissue itself. This tissue, when alive, usually contains large quantities of water. Now even a thin-walled cell, when perfectly turgid, can exert an enormous outward pressure [cf. Pfeffer ('00), p. 139]. Such hydrostatic pressure (aided perhaps by the growth and division of the cells immediately surrounding the aqueous tissue) exerted at a time when the remaining tissues of the stem were soft and plastic, might possibly inhibit to some extent the formation of intercellular spaces. The crushed appearance of many of the ground-tissue cells, seen more especially in the partitions between adjacent galleries, as also the fact that in *P. sinuosum* the walls of the small cells surrounding the galleries have their stoutest thickening bands more or less radial in position [cf. Baranetzki ('86), p. 199, on the mechanical principle involved], would seem to point to some such force having acted radially outwards from the region occupied by the aqueous tissue.

change, and which yet assimilates, there may exist a tendency to a state of partial asphyxiation, such as that stated by Devaux¹ to exist, even at normal temperatures, in the deeply seated tissues of many woody stems. This state of affairs, if it exists, would be relieved by the early breaking down of the aqueous tissue, resulting in the formation of extensive compensating air-passages. In any case, it seems probable that, whatever its original significance, this system of galleries, which penetrates to almost all parts of the rhizome, and is in communication with the outer air, does, to some extent at least, assist in the interchange of gases in the stem. Moreover, Karsten² states that water applied to the layers of small pitted cells surrounding the galleries of *P. sinuosum* is at once sucked up by these cells. He thinks that water-vapour given off into the galleries when the stem is heated by the sun, would condense again on their walls and be reabsorbed. Further, during heavy rain, it is possible that a certain amount of water may find its way into the galleries, and probably this would be similarly absorbed by the plant. Thus the galleries, in addition to allowing gaseous interchange to take place without undue loss of water, may be perhaps, so far as water is concerned, an actual source of gain³.

Fresh observations, if possible by direct experiment on the living plants, are needed to further elucidate the true function of the galleries. The result of one such experiment is recorded by Goebel⁴. He states that a plant of *P. sinuosum* in the Buitenzorg Gardens, Java, developed side-shoots when its galleries were stopped with paraffin. The precise bearing of this on the matter in question is not quite obvious.

¹ Devaux ('99), p. 94, but cf. also ('99, 2nd paper), p. 129.

² Karsten, loc. cit., pp. 180 et seq.

³ Goebel ('89), p. 208, and Forbes ('85), p. 79, record cases in which the galleries of certain species of *Myrmecodia* and *Hydnophytum* actually contained fluid water. Probably this would rarely happen in the two *Polypodia*, as the external openings are more or less ventral in position.

⁴ Goebel ('88), p. 18.

SYSTEMATIC POSITION.

While very little doubt as to the fact of *Polypodium sinuosum* being a true *Polypodium* appears to have ever existed, the position occupied by *P. carnosum* has been a debatable one.

Reinwardt¹ originally placed it in the genus *Onychium*, but a few years later it was described as the type of a new genus, *Lecanopteris*, by Blume², who shortly afterwards in the *Flora Javae* (Filices)³ published figures of two species, *L. carnosa* and *L. pumila*. The latter species never appears to have been described. Several closely allied species, however, have since been discovered, which Baker⁴ has placed in the same genus. *Polypodium patelliferum*, Burck⁵, is probably identical with *L. carnosa*, though Beccari⁶ regarded the name as a synonym of *L. deparioides* (Cezati).

The majority of writers⁷ have maintained *Lecanopteris*, Blume, as a genus, though, as we have seen, both Hooker and Smith⁸ recognized its close affinity to *Polypodium lomarioides* and *P. sinuosum*. Christ⁹ includes *Lecanopteris* as a sub-genus, in *Polypodium*; another sub-genus, to which he gives the name *Myrmecophila*, comprises *P. sinuosum*, *P. lomarioides*, and one or two closely allied forms which are similarly inhabited by ants. Diels¹⁰ maintains *Lecanopteris* as a distinct genus, at the same time admitting to generic rank *Drynaria*, *Niphobolus*, and other groups often regarded merely as sub-genera. In 1892 Baker¹¹ wrote, 'I now think that *Lecanopteris* will have to stand as a distinct genus, in the neighbourhood of *Dicksonia*, from which it differs in having an indusium

¹ Reinwardt ('25), p. 48.

² Blume ('27), p. 120.

³ Blume ('29), tab. 94.

⁴ Baker ('92), p. 19; also ('94), p. 123, and Cezati ('76), p. 13.

⁵ Burck ('84), p. 97.

⁶ Beccari ('84-'86), p. 244.

⁷ Amongst others, Presl ('36), p. 202; Fée ('50-'52), p. 259; and Moore ('57-'63), p. 80.

⁸ Smith ('75), p. 106, retains the genus *Lecanopteris*, regarding the names *P. lomarioides* and *P. sinuosum* merely as synonyms of *Lecanopteris carnosa*.

⁹ Christ ('97), p. 116.

¹⁰ Diels ('99), p. 326.

¹¹ Baker ('92), p. 19.

formed of only a single valve, and in the curious rootstock.' The indusium, says Mr. Baker, consists of 'a cup, formed from the edge of the frond, holding a small globose sorus.' Christ¹, however, has pointed out that there is really no true indusium. Blume² and Mettenius³ also distinctly refer to the sori as being non-indusiate. What has been regarded as an indusium is in reality part of the ordinary leaf-lamina, which here, as in many other species of *Polypodium*, forms a deep pit, at the bottom of which lies the placenta (compare Figs. 39, 40 and 41). Moreover, the inner wall of the sorus-cup possesses normal stomata, though these are comparatively few in number. This again would suggest that we are simply dealing with part of the leaf-lamina. The extraordinary rhizome of this Fern being already paralleled in the genus *Polypodium* by those of *P. sinuosum* and other forms, the only reason that remains for retaining *Lecanopteris* as a distinct genus is the curious reflexed position of the sori⁴. In all other respects these plants would fall naturally into the section *Phymatodes*⁵ of the genus *Polypodium*. The wisdom of maintaining such huge, unwieldy genera as *Polypodium* may perhaps be doubted⁶, but so long as distinct groups like *Drynaria*, &c., are retained merely as sub-genera of *Polypodium*, I think that this is at most the highest rank that should be given to *Lecanopteris*.

Further, as has been seen, the internal structure of *P. carnosum* is in many respects very similar to that of *P. sinuosum*. One of the most striking of these resemblances is the possession by both species of a specialized water-storing tissue in the stem, whose mode of origin, distribution and fate, though not in all respects identical, is substantially the same in both. These similarities, coupled with the external resemblances

¹ Christ ('98), p. 73.

² Blume ('27), p. 120.

³ Mettenius ('56), p. 38.

⁴ Some other species of *Polypodium* also have their sori borne on marginal lobes, though these are not reflexed as in *Lecanopteris*, e.g. *P. (Phymatodes) sorridens*, Hook.; vide Hooker ('64), p. 60, Tab. 283 B.

⁵ As defined by Hooker in the *Species Filicum*, vol. v, p. 55.

⁶ Cf. Fée ('50-'52) in the preface to his 7th *Mémoire*.

recognized by some of the older botanists, seem to indicate that a close relationship exists between the two Ferns. It may be pointed out, moreover, that certain other species, which are also ant-inhabited epiphytes of the Malayan region, are apparently, so far as their external features are concerned, actually intermediate between our two forms; e.g. *P. lomarioides*, Kze., and *P. sarcopus*, De Vriese et Teysm., possess the peltate scales of *P. sinuosum* but have pinnate fronds, whilst the habit of *P. sarcopus* and *P. carnosum* is almost precisely similar¹.

In fact, when the structure of these additional forms is more fully known, it may perhaps be possible to place them all (including *Lecanopteris*) into a single natural group, which might either stand as a section of the genus *Polypodium*, or as a subdivision of the section *Phymatodes*. To this group the name '*Myrmecophila*,' adopted by Christ² in a rather more limited sense, might not inappropriately be applied.

Some such arrangement as the following may perhaps be found convenient:—

MYRMECOPHILA. Epiphytic Ferns whose fleshy creeping rhizomes are traversed by a regularly arranged system of galleries, which are inhabited by ants. Leaves borne on prominent, more or less conical leaf-cushions.

- a. Rhizome covered with peltate scales. Sori sunken, but not borne on marginal lobes. This sub-group (which forms the *Myrmecophila* of Christ³) would contain such forms as *P. sinuosum*, *P. lomarioides* and *P. sarcopus*.
- β. Rhizome without peltate scales. Sori sunken, and borne on marginal lobes, which are either reflexed upon the upper surface of the leaf, or twisted to one side, so that the sorus faces the apex of the frond.

This would include *P. carnosum* and the other species of Blume's genus *Lecanopteris*.

¹ Christ ('98), p. 160, and Pl. XVI, Fig. 25c.

² Christ ('97), p. 112.

³ Christ includes *P. imbricatum*, Karsten, in this group: but this differs from the other species in possessing black scale-hairs, and apparently also in the structure of the stem [Karsten ('95), p. 168].

Mention has been made of the fact that Blume figured two species of *Lecanopteris*, though he only described one. The differences between the figures of these two species seem to lie chiefly in the respective shapes of the leaf-segments. Those of *L. carnosa* are represented as comparatively wide, and tapering to the acuminate apex, those of *L. pumila* as narrower, and rounded at the apex.

Lecanopteris pumila is not represented in the Kew Herbarium, while there are seven sheets of specimens identified as *L. carnosa*. Of these four are from Perak, one from the Philippines, and two from the Malay Archipelago. The plants from these several localities differ from each other in the size and shape of the leaf-segments. Those from the Malay Islands correspond to Blume's type figure of *L. carnosa*, that from the Philippines forms a type by itself, while those from Perak bear considerable resemblance to Blume's figure of *L. pumila*. In the absence of more complete material, it is difficult to decide whether *L. pumila* can be maintained as a species or not, but in view of the great variability of the leaf-lamina in many Ferns, it would seem likely that these three forms may be nothing more than local varieties of *L. carnosa*. For the present therefore, it will be best to leave the Perak specimens (including those from Gunong Inas) under the name of *Polypodium (Lecanopteris) carnosum*; though, if *P. (Lecanopteris) pumilum* (Blume) should ultimately be found to be a distinct species, they would in all probability belong to it rather than to *P. carnosum*.

SUMMARY.

1. *Polypodium carnosum* and *P. sinuosum* are two Malayan epiphytes, whose thick fleshy rhizomes are tunnelled by a system of galleries, similar to those of *Myrmecodia* and *Hydnophytum*, and, like them, invariably inhabited by ants.

2. In both Ferns a tissue consisting of large cells with thin walls and no intercellular spaces is formed in certain definite areas near the apex of the stem. This tissue breaks down at

an early period, its place being taken by the ant-galleries, which are thus of lysigenous origin.

3. The gallery system consists in both cases of a main ventral gallery which runs longitudinally through the stem, giving off two lateral series of galleries to the branches, and two series of vertical ones leading to the swollen leaf-cushions. Soon after leaving the main gallery the vertical ones branch so as to form two longitudinal series of dorsal chambers. In *P. sinuosum* these are entirely internal to the vascular system, and each consists of two limbs, one of which (the continuation of the vertical gallery itself) ends blindly in the leaf-cushion, while the other passes backwards through the tissues of the stem. In *P. carnosum* each dorsal chamber (the greater part of which is external to the vascular system) consists of three limbs; two of these finally end blindly in one leaf-cushion, whilst the third passes forwards and ends in the leaf-cushion next in front on the opposite side of the stem. Thus each leaf-cushion in *P. carnosum* contains three blind galleries (arranged transversely), those of *P. sinuosum* being only provided with a single one.

4. Communication between the galleries and the external air is effected by means of short passages excavated by the ants themselves in the soft tissues of the younger parts of the stem.

5. The character and topographical position of the large-celled tissue seem to indicate that it was developed in the first instance as a special water-reservoir; but the fact that it is so soon disintegrated may perhaps point to some degree of change of function, i.e. that the galleries which replace it have some important function to fulfil. There is no evidence that the galleries are an adaptation on behalf of the ants, and indeed their meaning is still somewhat obscure. Perhaps they serve as organs for the aeration of the stem, which is in both cases almost devoid of intercellular spaces. It is also possible that they assist to a slight extent in the absorption of water.

6. The sori of *P. carnosum* are borne on marginal lobes,

which are reflexed when mature upon the upper surface of the frond. This is possibly an adaptation to prevent the scattering of the spores unless a considerable wind is blowing. This plant is only found on the topmost branches of trees, and so it is during a wind that the spores would have the best chance of reaching their ultimate destination.

7. Though formerly placed in different genera, both the external features and internal structure of these two Ferns indicate that they must be regarded as closely allied species.

In conclusion, I desire to express my thanks to Mr. A. C. Seward for his valuable advice and suggestions during the progress of this investigation. Also to Professor A. Forel, Dr. Sharp, and Mr. F. G. Sinclair for information concerning the ants and other animals found in the galleries of the Ferns.

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EXPLANATION OF FIGURES IN PLATES X, XI, AND XII.

Illustrating Mr. Yapp's paper on 'Myrmecophilous' Ferns.

Unless otherwise stated, the figures refer to *Polypodium carnosum* (Blume).

The arrows accompanying some of the figures point in each case towards the apex of the stem.

The microphotographs constituting Figs. 5, 12, and 32 were taken by Mr. W. Tams of Cambridge.

PLATE X.

Fig. 1. *Polypodium carnosum*, showing its natural habitat.

Fig. 2. *Polypodium sinuosum*, ditto.

Fig. 3. *P. carnosum*, part of the mass of interlacing rhizomes seen in Fig. 1.

Fig. 4. Upper part of a single fertile frond.

Fig. 5. *P. carnosum*, transverse section through a tunnel leading to the exterior, excavated by the ants.

PLATE XI.

Fig. 6. *P. carnosum*, diagram showing mode of branching of stem. *a. a.* knobs of living tissue (incipient branches).

Fig. 7. *P. sinuosum*, ditto. *a. a.* undeveloped branches.

Fig. 8. *P. carnosum*, transverse section of part of the stem near the apex, showing an early stage in the formation of the large-celled tissue. ($\times 42$.)

Fig. 9. Later stage, showing aqueous tissue fully formed. ($\times 33$.)

Fig. 10. Section through the aqueous tissue taken parallel to the small-celled zone, and cutting transversely several unusually long small-celled projections. ($\times 33$.)

Fig. 11. Ditto, taken close to periphery of aqueous tissue, showing four of the pocket-like pits occupied by one or two large aqueous cells. ($\times 33$.)

Fig. 12. Microphotograph of a section showing the large-celled tissue breaking down to form a gallery.

Fig. 13. A single branched epidermal hair. ($\times 75$.)

Fig. 14. A section through part of a mass of stems, showing the way in which the younger stems overlap the older. The galleries are seen cut in various directions. *b.* twig of host tree. ($\frac{5}{8}$ nat. size.)

Fig. 15. A transverse section through an old piece of stem, showing the galleries. The section also cuts a very short branch longitudinally, at the apex of which is an opening (*a.*) to the exterior made by the ants. ($\frac{3}{4}$ nat. size.)

Figs. 16 and 17. Two transverse sections near apex of rhizome. Aqueous tissue is still present. *v.* position of main ventral gallery. ($\frac{3}{4}$ nat. size.)

Fig. 18. Horizontal section near apex of leaf-cushion, showing the three blind galleries cut across. ($\frac{3}{4}$ nat. size.)

Fig. 19. External view of part of main stem, showing the commencement of two lateral branches. (Nat. size.)

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Fig. 20. Plan of main ventral gallery, showing lateral galleries (*l.*), and the position (*a.*) of the vertical galleries with respect to them.

Fig. 21. Plan of the dorsal chambers. *a.* position of vertical gallery; *b.* outermost branch of one of the chambers.

Fig. 22. Median vertical longitudinal section of stem. ($\frac{3}{4}$ nat. size.)

Fig. 23. Vertical longitudinal section of stem, passing through the series of leaf-cushions of one side, i. e. across line *c. c.* in Fig. 20. ($\frac{3}{4}$ nat. size.)

Fig. 24. *P. sinuosum*, transverse section of stem, passing vertically through a leaf-cushion. *d.* a diverticulum of main gallery entering an incipient branch. ($\frac{3}{4}$ nat. size.)

Fig. 25. Ditto, passing through main gallery and also a blind dorsal gallery. ($\frac{3}{4}$ nat. size.)

Fig. 26. *P. sinuosum*, plan of dorsal chambers. *a.* is position of vertical gallery, communicating below with the ventral gallery. *c.* blind dorsal gallery. ($\frac{3}{4}$ nat. size.)

Fig. 27. *P. sinuosum*. Plan of ventral gallery and its lateral branches. *d.* a pocket-like diverticulum entering an incipient branch. *ag.* partly broken down aqueous tissue. ($\frac{3}{4}$ nat. size.)

Fig. 28. *P. sinuosum*. Median vertical longitudinal section of stem. ($\frac{3}{4}$ nat. size.)

Fig. 29. *P. sinuosum*. Vertical longitudinal section passing through two leaf-cushions. *c.* a blind dorsal gallery. ($\frac{3}{4}$ nat. size.)

Fig. 30. *P. carnosum*. Some of the old ground-tissue cells of the stem, to show band-like thickenings. ($\times 105$.)

Fig. 31. *P. carnosum*. Three cortical cells from a longitudinal section of a root. ($\times 190$.)

Fig. 32. *P. carnosum*. Microphotograph of a longitudinal section through base of petiole, showing its articulation with the leaf-cushion.

PLATE XII.

Fig. 33. *P. carnosum*. Transverse section of a stem-stele. *e.* outer endodermis. *p.* false pericycle or inner endodermis. *s.* sclerenchymatous sheath. ($\times 258$.)

Fig. 34. *P. carnosum*. Part of transverse section of root. ($\times 67.5$.)

Fig. 35. *P. carnosum*. Dorsal part of vascular cylinder. *a.* one of the foliar bundles leaving the edge of the foliar gap. *b.* small meshes separating two foliar gaps. *c.* place of origin of a lateral branch cylinder. *d.* a foliar gap. ($\times$ about $1\frac{1}{2}$.)

Fig. 36. *P. sinuosum*. Semi-diagrammatic drawing of a dissection showing the dorsal part of the vascular network. *a. b.* supposed limits of a foliar gap. ($\times$ about $1\frac{1}{2}$.)

Fig. 37. *P. carnosum*. Part of a longitudinal section of a root, showing the collar (*c.*) formed by the ruptured epidermis of stem. Beneath this is seen the piliferous layer of root. ($\times 75$.)

Fig. 38. *P. carnosum*. Diagrammatic transverse section of petiole. *a.* interruption of thick-walled hypoderma by the thin-walled spongy tissue.

Fig. 39. *P. carnosum*. Diagrammatic section through a sorus-cup.

Fig. 40. *P. sinuosum*. Diagrammatic section through a sorus. *a.* enlarged cells of epidermis at edge of pit.

Fig. 41. *Polypodium nigrescens*. Diagrammatic section through a sunken sorus, to show its similarity to that of *P. carnosum*.

Fig. 42. *P. carnosum*. Diagrammatic sections showing successive stages (*a. b. c. d.*) in the reflexing of the soriferous lobes.

Fig. 43. *P. carnosum*. Part of a fertile leaf-segment, showing reflexed position of mature sori. ($\times$ about 3.)

Fig. 44. *P. carnosum*. A sporangium. ($\times$ 92.)

Fig. 45. *P. carnosum*. A sterile leaf-segment, bleached by Eau de Javelle, and stained to show venation. ($\times$ 3.)

Fig. 46. *P. carnosum*. Part of a fertile leaf-segment treated in the same way. The sorus-cup is diagrammatically represented as if no flexion had occurred. ($\times$ 8.)

Fig. 47. *P. sinuosum*. Part of a fertile frond, to show venation. *s.* sorus. ($\times$ 3.)

Fig. 48. *P. sinuosum*. Part of a sterile frond. ($\times$ 3.)

Fig. 49. *P. carnosum*. Developing stomata, taken from an upper leaf-segment of a young frond. *a. b. c. d.* successive stages. ($\times$ 197.)

Fig. 50. A mature stoma. ($\times$ 197.)

Fig. 51. *P. carnosum*. Part of a transverse section through a leaf-segment. *a.* layer of large colourless cells beneath the upper epidermis. ($\times$ 246.)

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