

XX.—The Anatomy and Affinity of *Platyzoma microphyllum*, R. Br. By John M'Lean Thompson, M.A., B.Sc., Chief Assistant in Botany and Robert Donaldson Research Scholar, Glasgow University. Communicated by Professor BOWER, F.R.S. (With Four Plates.)

(MS. received February 7, 1916. Read February 7, 1916. Issued separately November 6, 1916.)

In the year 1810 there appeared in ROBERT BROWN'S *Prodromus Floræ Novæ Hollandiæ et Insulæ Van Diemen*, p. 160, a brief description of a rare Australian Fern to which the generic name *Platyzoma* was given. The habit of stem and leaf, and in general the form and position of the sporangia, led BROWN to the conclusion that *Platyzoma* was of Gleicheniaceous affinity. It was noted that the plant was heterophyllic; for not only did it possess pinnate leaves suggestive of those of certain Gleichenioid forms, but also small, compressed, and filiform leaves devoid of pinnæ. To the form of the larger and pinnate leaves BROWN paid particular attention, noting chiefly that the leaves of *Platyzoma* were unbranched, whereas a branched condition was typical of the leaves of *Gleichenias*. This unbranched condition of the leaf seemed to BROWN a sufficiently distinctive feature to justify the foundation of a new Gleicheniaceous genus—the monotypic genus *Platyzoma*; and he named the single species *Platyzoma microphyllum*.

BROWN'S opinion was, then, that *Platyzoma* was allied to *Gleichenia*, but was, at the same time, worthy of recognition as a distinct genus. It would appear, however, that at a later date BROWN doubted the value of the character on which he had laid most emphasis in founding the genus *Platyzoma*, for in 1814* he wrote: "Among the Australian Ferns there is no genus absolutely confined to that country, except *Platyzoma*, but this, perhaps, ought not to be separated from *Gleichenia*." Still later, in 1838, while describing *Polypodium* (*Dipteris*) *Horsfieldii*,† BROWN referred to the axis of *Platyzoma*, and indicated that it differed anatomically from the axis of all *Gleichenias* he had examined.

The pinnate leaves and sporangia of *Platyzoma* were figured in 1842 by BAUER in Sir WM. HOOKER'S *Genera Filicum*, and here it was affirmed that "*Platyzoma* differs from *Gleichenia* more by its undivided leaves, than by any differences in their sporangia." In the *Synopsis Filicum*, 1874, 1883 (HOOKER and BAKER), *Platyzoma* was placed as the first genus of the *Gleicheniaceæ*, and a note was appended affirming that *Platyzoma* is "a genus which has been too

* General Remarks, Geographical and Systematic, on the Botany of Terra Australiensis: Misc. Bot. Works of Robert Brown, vol. i, p. 59, Ray Society Publications, 1866.

† *Plantæ Javanicæ Rariores*, p. 2.

nearly allied to *Gleichenia*." F. MÜLLER, however, rejected the opinion expressed in the *Synopsis Filicum*, and maintained that *Platyzoma* should be considered a species of *Gleichenia*; accordingly, he named it *Gleichenia platyzoma*. In 1878, BENTHEM endorsed the opinion of HOOKER and BAKER, and, writing in *Flora Australiensis*, vol. vii, p. 696, he held that *Platyzoma* "is a genus limited to the single species endemic in Australia. The great difference in 'fructification' as well as in habit appears to preclude its union with *Gleichenia* as proposed by F. MÜLLER." In 1897, H. CHRIST* sank *Platyzoma* in *Gleichenia*, and named it *Gleichenia microphylla*, while in 1902 DIELS† followed a similar course. And lastly, in 1906, CARL CHRISTENSEN, in his *Index Filicum*, placed *Platyzoma* in very close relationship to *Gleichenia*, but at the same time was not disposed to reduce *Platyzoma* to the rank of a species of *Gleichenia*. It will be noted, then, that the systematists, without exception, have followed BROWN's example in placing *Platyzoma* in the *Gleicheniaceæ*, and that the only point upon which opinions have differed is the rank which *Platyzoma* merits within this group.

The following characters of *Platyzoma* have been recorded by the systematists:—The axis is a short, horizontal rhizome beset with a thick covering of long, glistening, golden-brown hairs. The branching and fibrous roots spring from the lower surface, and occasionally from the sides of the stem. Regarding the heterophylly there is but a single statement, namely, that which is found in BROWN's original description of *Platyzoma*. It is remarkable that later systematists have not even referred to BROWN's remarks on this feature, for he stated clearly that *Platyzoma* possesses not only undivided pinnate leaves, but also leaves of a compressed and filiform character. The pinnate leaves range from about 6 inches to 1 foot in length. They are densely crowded upon the upper surface and sides of the rhizome; they are dark and sclerotic, and their bases are surrounded by clumps of firm hairs. They are simply-pinnate and unbranched, and both petiole and rachis are smooth and slender. The pinnæ are small and numerous, and seldom exceed 2 mm. in length. They are ovate-orbicular in outline, and their margins are so revolute that the stomata—which are restricted to the lower surface—are in a nearly closed cavity. The upper epidermis is smooth and strongly cuticularised, and much of the mesophyll is composed of water-storage tissue. The margins of the pinnæ bear numerous minute irregular hairs, and similar hairs are distributed upon the lower surfaces of the pinnæ. The venation is a short sympodium. There are but a few sporangia in any fertile pinna. They are disposed terminally upon the lateral branches of the sympodium, and are at maturity globular and almost sessile. They are hidden beneath the broad revolute margin of the pinna; they are irregular in form, and their dehiscence is variable.

BENTHEM has noted (*loc. cit.*) the localities from which *Platyzoma* has been

* *Die Farnkräuter der Erde*, p. 339.

† ENG. and PRL., i, 4, p. 355.

recorded. In N. Australia both BROWN and GULLIVER collected this plant by the Gulf of Carpentaria, while MÜLLER found it by the Fitzmaurice River and at Providence Hill. Later on, MARTIN encountered *Platyzoma* by the Glenelg River on the north-west coast. In Queensland, both BROWN and HILL have found *Platyzoma* at Facing Island, while other collectors have discovered it at York Peninsula, Rockingham Bay, and on the downs of the interior. In the *Synopsis Filicum* it is referred to as inhabiting the tropical and subtropical regions of Australia. In 1901, BOODLE* laid emphasis on the xerophytic nature of *Platyzoma*; and in 1910, H. CHRIST† figured a heterophyllic specimen, and referred to *Platyzoma* as a xerophytic plant from the desert zones of Australia.

Regarding the anatomy of *Platyzoma* very little is known. In 1893, POIRAULT‡ briefly described the rhizome, and referred to its curious type of stele. It was here noted that there is a central sclerotic pith, completely surrounded by an endodermis, outside which is a zone of parenchyma surrounded by a broad ring of parenchymatous xylem. It was further noted that at the periphery of the xylem there is a narrow zone of phloëm, which is in turn surrounded by a large-celled pericycle and an endodermis. Special reference was made to the shortening of the internodes, and the crowding of the leaf-traces in the cortex. No leaf-gaps were recorded by POIRAULT. Nevertheless, he considered this anomalous stelar state to have arisen by obliteration of the leaf-gaps from an original solenostele. We are indebted to BOODLE§ for fuller information regarding the rhizome. He discussed in greater detail the medullate stele, with its annular xylem and internal endodermis, and described the origin of a leaf-trace by the nipping out of a group of phloëm and xylem elements from the periphery of the stele, and indicated the collateral nature of the leaf-trace on its way out through the cortex of the rhizome. He regarded *Platyzoma* as "a xerophytically reduced form in which the leaf-traces have become small and crowded." He also indicated the possibility of *Platyzoma* having been derived from a solenostelic form by obliteration of the leaf-gaps and disappearance of the internal phloëm of the stele. But, on the other hand, he emphasised the possibility of *Platyzoma* having been derived from a protostelic *Gleichenia*, by the formation *de novo* of a pith and internal endodermis. On the one hand it was noted that the stele in *Gleichenia* is typically protostelic, and on the other that a widely different type of structure—a solenostelic structure—exists in one species, *Gleichenia pectinata*. *Platyzoma* might then be regarded as occupying—as far as stelar construction is concerned—a position intermediate between *Gleichenia pectinata* and all other known *Gleichenias*.

To the view that the present stelar condition of *Platyzoma* has arisen by transformation of a solenostele both JEFFREY and TANSLEY have lent their support, the

* "Anatomy of the Gleicheniaceæ," *Ann. Bot.*, xv.

† *Die Geographie der Farne*, p. 180.

‡ "Recherches sur les *Cryptogames vasculaires*," *Ann. des Sciences Nat. Bot.*, 7^e sér., tom. xviii.

§ "Anatomy of the Gleicheniaceæ," *Ann. Bot.*, xv, 1901.

latter stating definitely * that "*Platyzoma*, with its extreme xerophily and anomalous leaf-traces, may almost certainly be regarded as reduced from the solenostelic type." BOWER and others have inclined to the belief that the original condition of *Platyzoma* was protostely. But in any case, BOODLE considered that the construction of the stele of *Platyzoma* was sufficiently individualistic to justify the separation of *Platyzoma* from *Gleichenia*, as proposed by HOOKER and BAKER. It is then evident that the facts advanced regarding the stele have led neither to the removal of *Platyzoma* from the *Gleicheniaceæ* nor to a definite settlement of its position within this group.

A brief consideration of the characters which have been employed in determining *Platyzoma*'s systematic position may not be out of place at this point. The habit of stem and leaf, and in general the form and position of the sporangia, led BROWN to place *Platyzoma* in the *Gleicheniaceæ*. These same general features have likewise been the main guides of later systematists. But at the present day, when convergent evolution is being widely recognised among Ferns, it is necessary, for systematic determinations, to be provided with detailed knowledge of the anatomy of stem, leaf, and root, and of the original position and form of the sporangia. The exact position and form of the annulus and the form and output of spores per sporangium are of much importance. The nature of the dermal appendages should also be determined. In fact, it has been found that while general habit has frequently proved a true index in phyletic groupings, at other times—when taken by itself—it has led to gross error. In the case of *Platyzoma* no definite information has hitherto been advanced regarding the anatomy of leaf and root, nor has any accurate account been given of the form and development of the sporangia, the character of the annulus, and the spore form and output.

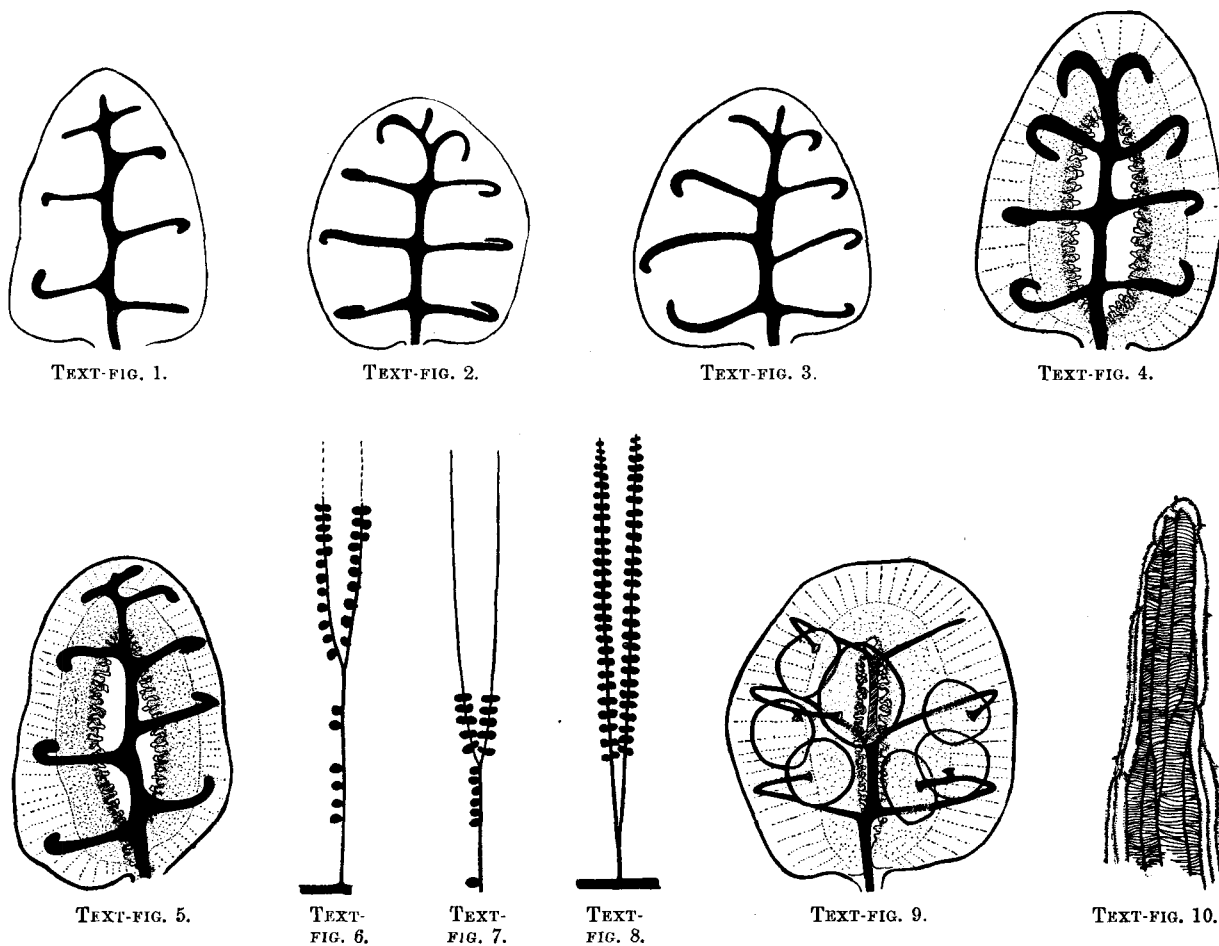
Both POIRAULT and BOODLE have contributed to our knowledge of the stele of *Platyzoma*. Nevertheless, a wider knowledge on this subject is necessary, and the facts already advanced are far from sufficient to prove or disprove the proposed *Gleicheniaceæ* affinity. Further, one would have expected that the heterophylly noted by BROWN, and shown in CHRIST's figure, was a character of too great importance to be neglected by the systematists. BOODLE has informed me that in five of the sheets of specimens of *Platyzoma* in Kew Herbarium the heterophylly is clearly shown; while in a beautiful specimen, collected in 1902 by Professor BALDWIN SPENCER at Booroolooloo, N.T., and kindly supplied to us by the authorities of the National Herbarium of New South Wales, Sydney, this heterophylly is a conspicuous feature (figs. 6 and 8).

As to the original distinction drawn by BROWN between the branched leaves of *Gleichenia* and the unbranched leaves of *Platyzoma* a few remarks are necessary. It was noted by BOWER in 1899 † that the pinnate leaf of *Platyzoma* is occasionally forked, as is seen in specimens of a "*forma furcata*" sent by the late Baron Sir F. V.

* "Lectures on the Evolution of the Filicean Vascular System," *New Phytologist*, 1908.

† "Studies in the Morphology of Spore-producing Members," *Phil. Trans. Royal Soc. London*, iv.

MÜLLER to the Kew Herbarium. Regarding this branching I am indebted to BOODLE for fuller information. Forking of the leaf is shown in two cases in which the leaf branches once. In the first (text-fig. 6) the leaf is attached to the rhizome, the branching takes place at some distance from the base, and pinnæ are distributed on the rachis below the forking. The terminal portions of this leaf had been damaged. In the second specimen (text-fig. 7) pinnæ are again developed on the rachis below the point of branching; and while it is impossible to determine the length of the



unbranched portion of the rachis—since the leaf is detached,—the branching is suggestive of a dichotomy. And further, in a specimen in the herbarium of Glasgow University a pinnate leaf was found showing perfect dichotomy (text-fig. 8). In this case the branching occurs close to the base of the leaf, and there is no pinnation below the point of forking. It is worthy of note that both simple and branched leaves are found in *Gleichenia speluncæ*, Br. (*Gl. circinata*, Sw.); while in *Gleichenia simplex*, Hk., is found a species characterised by simply-pinnate leaves. From consideration of these points it is apparent that the chief distinction drawn by BROWN between *Platyzoma* and *Gleichenia* has broken down, and the question remains

whether or not there are other characters which will justify their separation. And finally, a brief consideration of the facts above detailed regarding *Platyzoma* will suffice to show that the Gleicheniaceae affinity has not been proved, and that, even supposing *Platyzoma* be admitted to this group, its nearer relationships are in much doubt.

In this paper are set forth some additional facts gleaned from the specimen supplied to us from Sydney Herbarium. It is still impossible to speak with assurance of the affinity of *Platyzoma*, but the facts here detailed may serve as a basis for comparisons at a later date, when the development of the sporangium will be described.

The axis is a slender, horizontal rhizome measuring some $2\frac{1}{2}$ inches in length (fig. 6). It is closely invested by a dense covering of beautiful golden-brown unbranched hairs (figs. 2 and 8), which spring from all sides and cluster around the leaf-bases. The roots are inserted on the lower surface and occasionally on the sides of the rhizome. They are strong and fibrous and are frequently branched. The root hairs are remarkably long and persistent, and their walls are thick and brown. The heterophylly is well shown. The large pinnate leaves are about 11 inches long, while the small filiform leaves vary from about $2\frac{1}{2}$ inches to $\frac{1}{3}$ inch in length. The petiole of the pinnate leaves measures about 1 inch. The leaves are closely crowded upon the condensed and apparently slow-growing rhizome, and are definitely zoned, so that, if the leaves of a single year's growth be examined, they are found to divide roughly into two groups. Of these the first are composed almost exclusively of long pinnate leaves, the second of delicate filiform types. At first sight it might be concluded that the pinnate leaves definitely precede the filiform leaves in order of development. Further, the majority of the pinnate leaves spring directly from the upper surface of the rhizome, and only a few encroach slightly upon its sides. No pinnate leaves arise from the lower surface of the stem. The filiform leaves are inserted upon the sides and lower surface of the rhizome, and, curving forwards and upwards, pass out in a fairly definite group in front of the pinnate leaves. There might be a slight tendency towards a succession from pinnate to filiform leaves in a season's growth, but this is not the chief cause of the zoning. It is due primarily to a definite tendency in this rhizomatous plant to initiate the larger leaves on or towards the upper surface, and the smaller leaves upon the sides and lower surface.

The length of the pinnate leaves varies from about 10 inches to 12 inches. They are either sterile or fertile, but stature is of little value as a guide to their sterility or fertility. The filiform leaves are invariably sterile. The pinnate leaf is typically unbranched, but, as has already been noted, a dichotomous branching may occur. Only slight differences exist between the pinnæ of sterile and fertile leaves, and, further, a leaf may be partly fertile and partly sterile. The fertile pinnæ are, if anything, more robust than the sterile pinnæ, and their margins are strongly revolute (compare text-figs. 1 to 5 and 9). The vascular supply is in both cases a sympodium

which varies in detail from pinna to pinna. Irregularities in the numbers of the lateral branches of the sympodium, and the tendency to establish sympodial dichotomies, are the features worthy of note (text-figs. 1 to 5). The filiform leaves varied much in both length and form. The longest measured some $2\frac{1}{2}$ inches, while the smallest were minute and slender structures of about $\frac{1}{3}$ inch in length. The larger filiform leaves were inserted chiefly upon the sides of the rhizome; the smallest sprang, almost invariably, from the lower surface. In fig. 7 a filiform leaf, which measured about $1\frac{1}{2}$ inch, is represented as seen from its lower surface. Three distinct regions—a basal, middle, and terminal region—are recognisable. The basal region measures about $\frac{1}{3}$ inch. Its superficial tissues are dark brown and sclerotic, and on its upper surface it widens out on both sides into a distinct flange. Beneath each of these flanges is a shallow lateral groove. The flanges die out as the middle region of the leaf is approached, but the grooves persist, and, having passed to the lower surface, they deepen and run parallel until the terminal region is reached. The middle region constitutes the greater part of the leaf, and variations in its length are mainly responsible for variations in the length of the larger filiform leaves. It is a more slender and delicate region than the leaf-base. Its superficial tissues are not sclerotic, but its epidermis is strongly cuticularised. As has been indicated, it is deeply grooved on both sides of its lower surface. On its upper surface are found a pair of grooves, similar to those already noted on the lower surface. These upper-surface grooves likewise continue to the terminal portion of the leaf. The terminal region is short and bulbous. In it, both the upper and lower pairs of grooves become rapidly shallow, and finally die out just before the leaf-tip is reached.

A leaf of the smaller type taken from the lower surface of the rhizome, and which had remained almost hidden among the hairs, is represented in fig. 3. It measured about $\frac{1}{3}$ inch, and its tip was distinctly circinate. But in this case no division into basal, middle, and terminal regions could be made, and no distinct grooves were recognised. The leaf became gradually slender, and the superficial tissues passed gently from a sclerotic to a strongly cuticularised condition, as one passed forward. The great majority of the filiform leaves were of the first type, and only a very few resembled the second type described.

Four remarkable leaves formed a reduction series, illustrating a transition from the typically pinnate to a filiform condition. The first stage in this reduction is shown in fig. 5, which illustrates a leaf found among the broken petioles of discarded leaves. It measured about $1\frac{1}{2}$ inch in length, and possessed about 20 pinnæ of very variable size and irregular distribution. The lower third was entirely devoid of pinnæ, and might therefore be considered petiole. The remainder of the leaf was mainly pinnate, and was therefore undoubtedly rachis. Here, then, as in the typical pinnate leaf, the rachis bulked more largely than the petiole. The superficial tissues of both petiole and rachis were sclerotic, as in the typical pinnate leaf, and neither

basal flanges nor grooves were present. Despite the fact that the pinnæ varied greatly in size, their venation was invariably a sympodium. This leaf was inserted upon the upper surface of the rhizome, and might be regarded as a pinnate leaf which had suffered extensive reduction of its rachis.

The second step in leaf reduction is shown in fig. 9. It represents a leaf which measured roughly 1 inch in length. The numerous pinnæ were crowded upon a condensed rachis which measured little more than $\frac{1}{2}$ inch in length. The venation of the majority of the pinnæ was a simple midrib, but no vascular supply was discovered in several of the smaller terminal pinnæ. At the base of the rachis an abortive branch arose as a short and slender projection. The nature of this branching will be discussed later. In this leaf, then, is seen a further reduction of the rachis, and a simplification, and even total loss, of the venation.

A third step in this reduction process was shown by a leaf which is depicted in fig. 2. Of the $\frac{2}{3}$ inch which it measured, the greater part consisted of petiole of the smaller type of filiform leaf already described. The pinnate portion of this leaf had been damaged, but the vascular supply to each of the four persisting pinnæ was a simple unbranched vein. As will be shown later, when the anatomy of these reduced leaves is being described, the rachis of this leaf had been very short, and the number of pinnæ which had been destroyed was probably very small. There is here, in fact, a leaf in which the rachis has been reduced to a small and condensed column, bearing a few small pinnæ with the simplest possible venation.

The fourth step in leaf reduction remains to be considered. It is illustrated by a small leaf, $\frac{1}{5}$ inch long, which was found among the hairs on the side of the rhizome (fig. 12). Its tip was hooked, suggestive of an original circinate vernation, and it bore almost terminally two small pinnæ, to which the vascular supplies were simple unbranched veins. There is here the minimum of pinnation, and one step further in reduction would lead to the smaller type of filiform leaf. It is a far cry from the elaborate pinnate leaf to this smaller type of filiform leaf, but the reduction series here briefly outlined can bridge the gap between them.

It may be asked what is the position of the larger filiform leaves in this varied aggregation of leaf types. It is my purpose to show in succeeding paragraphs that the larger and smaller filiform leaves alike are reductions from, or replacements of, larger pinnate types. It is believed, indeed, that the leaves of *Platyroma* have undergone drastic morphological changes, resultant from the present rhizomatous habit and extreme xerophytic conditions. But the small filiform leaves, and the pinnate leaves showing reduction, were rare occurrences in my specimen, while, on the other hand, the larger filiform leaves were numerous. I am of the opinion that, when abundant material has been examined, it will be found that the larger filiform leaf is the typical reduction leaf of the present day, just as the *unbranched* pinnate leaf, and not the *branched* pinnate leaf, is typical of *Platyroma* in its present condition. The forked pinnate leaf, the reduced simply-

pinnate leaf, and the smaller filiform leaf, may be regarded as harkings back to steps taken earlier in an evolution of reduction, from which the unbranched pinnate leaf and the larger filiform leaf have emerged as dominant types. The anatomy of the various leaf types recorded can be considered when we have before us the main facts concerning the anatomy of the rhizome.

It will be convenient to delay the consideration of the sporangia until the end, and accordingly the examination of the chief anatomical features of *Platyzoma* will now be made.

The axis of *Platyzoma* possesses a broad cortex, developed peripherally as a strong zone of sclerenchyma, and more centrally as a mass of storage parenchyma (fig. 1). The stele is centrally placed, and from it depart a close succession of leaf-traces and roots, which pass out rapidly through the cortex and emerge in close succession upon the surface. The leaf-traces, on their way out through the cortex, are oval or almost circular in transverse section, and vary in size from large traces, originating mainly from the upper surface of the stele, to smaller traces, which arise from the sides and lower surface of the stele. The majority of the roots come off from the lower surface of the stele, but occasionally they have a lateral origin. There is a bulky central sclerenchymatous pith. Its cell walls are not, however, strongly thickened, and centrally they are of a light brown colour, and enclose mucilaginous protoplasts. The pith is surrounded by an uninterrupted endodermis, which is immediately followed by two or three layers of large-celled parenchyma. There is no inner phloëm, and the large-celled parenchyma is followed immediately to the outside by a remarkable ring of xylem. The xylem-ring varies in thickness as one passes from the upper to the lower surface of the stele. On its upper surface the ring is invariably thin, while on its lower surface it is relatively thick. The thickness of the xylem-cylinder increases gradually during the passage from the upper to the lower sides of the stele. At some points along the course of the rhizome this difference in the thickness of the upper and lower portions of the stele is only slightly marked (figs. 4 and 10), while at other points it is a very conspicuous feature (figs. 1, 13, and 63). The bulk of the sclerenchymatous pith does not, however, vary to any great extent from point to point, for increase in the thickness of the lower side of the xylem is not attained so much by encroachment centrally, as by a centrifugal thickening.

The xylem-cylinder is composed of scalariform tracheides together with chains and groups of parenchymatous cells, which follow irregular courses between the tracheides, and which fuse and branch repeatedly. No protoxylem elements can be recognised, but the xylem-cylinder can be divided roughly into two concentric cylinders according to the characters of the tracheides and the distribution of the parenchyma. The inner cylinder is composed of wide storage tracheides associated with numerous chains and masses of parenchyma. It forms, essentially,

the parenchymatous part of the xylem. The outer cylinder is composed of small and narrow tracheides which are more closely packed than are the tracheides of the inner cylinder. Parenchyma does not bulk largely in the organisation of this outer cylinder, but the chains and groups are short and narrow, and the elements composing them are few in number. This outer cylinder is alone involved in the process of supplying the traces of the leaves and roots.

It has been noted that the xylem is thin on the upper surface of the stele, while on the lower surface it is usually comparatively thick. It may be stated at once that the difference in xylem thickness, between the lower and upper sides of the stele, is not primarily due to a progressive thinning of the xylem on the upper surface as a whole. It is mainly due to an increase in the bulk of the parenchymatous storage xylem towards the lower surface of the stele (figs. 1, 4, 10, 13, 63). The outer xylem-cylinder does not vary markedly as one passes from the upper to the lower surface of the stele. It is true that it is of irregular thickness from point to point, but it is maintained consistently on all sides of the stele, whereas the inner xylem-cylinder may be locally massive towards the under surface, and at the same time reduced almost to the vanishing point on the upper side of the stele. It is therefore evident that it is the parenchymatous inner portion of the xylem-cylinder which is most liable to fluctuations, either in the direction of increase or reduction (figs. 4 and 63).

Further, the great increase in the parenchymatous xylem just noted is subject to local accentuation; for, while this type of xylem is certainly conspicuous at all points along the lower surface of the stele, it becomes very massive in those regions where the numerous and closely crowded traces are being liberated (figs. 13 and 63). On the other hand, it is usually less dominant in those portions of the stele where the leaf-traces are less numerous and crowded.

As to the absence of definite protoxylem groups a word may be said. It is generally recognised that the presence or absence of definite protoxylems depends upon the degree and rate of extension which take place in the xylem. There can be no doubt that the axis of *Platyzoma* is either slow-growing or is subject to little or no extension as maturity is approached. To this the close succession of the leaves and the condensed nature of the rhizome bear ample witness, and accordingly the absence of protoxylems need be cause for no surprise. The absence of protoxylems may then be regarded as indicative of a slow rate of growth or of but slight extension of the stele. It is an index of the peculiar physiological conditions of *Platyzoma*, but as a systematic character it is unreliable.

The phloëm follows almost immediately upon the outer surface of the xylem. It is separated from the xylem only locally by a single layer of small parenchymatous cells; it is from three to five layers broad, and is composed entirely of typical fern-sieve tubes. It is only interrupted at points where leaf- and root-traces are departing. The phloëm is followed externally by a large-celled pericycle of three to four paren-

chymatous layers, and beyond this is an outer endodermis separating the stele from the cortex.

This curious stele has been interpreted by various observers as a reduced solenostele which has lost its inner phloëm. But while the leaves are numerous, and many of them are relatively large and are provided with strong leaf-traces from the stele, no leaf-gaps involving a breaking of the continuity of the stele occur at *any* point. As will be shown directly, the outer endodermis is in *no* case even temporarily incomplete when a trace is being liberated. A break in the endodermis does certainly arise, but the cortex cannot invade the stele. Further, the xylem of the stele may be so depleted by the demands of a leaf-trace that at the point of departure of the trace the xylem-ring may be broken or traversed by a sheet or mass of parenchyma. But at *no* point along the entire length of stele examined was the inner endodermis found to be defective. It was neither broken nor did it show any tendency to break, opposite any leaf-trace or at any other point. POIRAUT has attempted to explain this stele as a reduction from a solenostele from which leaf-gaps have been obliterated. But it may be remarked that not only are leaf-gaps non-existent in the stele of *Platyzoma*, but no anatomical evidence can be advanced in support of the suggestion that they have existed at any time. There is no connection whatever, either by leaf-gaps or perforations, between the cortex and the pith, and the pith is accordingly recognised as a completely isolated mass of sclerenchyma, bounded on all sides by an unbroken endodermis. But if no evidence can be advanced in support of POIRAUT's suggestion of a solenostelic origin for the stele of *Platyzoma*, a serious objection has presented itself to JEFFREY's theory of the origin of the pith in *Pteridophytes*. JEFFREY has maintained that the pith is, *in all cases*, of cortical origin, and that it has arisen through an invasion of the stele by the cortical parenchyma at the points of departure of leaf-traces, or at other points. It seems more than difficult to explain the origin of the bulky pith of *Platyzoma* by such a theory, since neither leaf-gaps nor perforations, nor any tendency towards the formation of such gaps and perforations, have been found in the stele. And further, even supposing the inner endodermis could be shown to be locally imperfect or interrupted—so that parenchymatous connections could exist between the cortex and pith—the stele of *Platyzoma* would still be open to interpretation as of directly protostelic origin. For if the Gleicheniaceae affinity of *Platyzoma* could be definitely established, its stele might be interpreted as a transformed protostele, in which sclerenchymatous replacement of the xylem core has taken place, and an inner endodermis has arisen, *de novo*, around the pith. With one exception—namely, *Gleichenia pectinata*—the genus *Gleichenia* is protostelic. The core of the typical Gleicheniaceae protostele is a parenchymatous mass of large storage tracheides; and if the stele of *Platyzoma* has been originally protostelic, the inner parenchymatous xylem-cylinder—which has been described as the most variable part of the stele—might be considered the last remnant of a solid xylem core. LANG has shown recently that endodermis can

arise *de novo*,* and it will be shown immediately that, in the liberating of the leaf-traces of *Platyzoma*, endodermis is formed where and when required. It is then not impossible that the inner endodermis of *Platyzoma* is of relatively recent origin, and has been at no point in descent in connection with the outer endodermis, either through leaf-gaps or perforations. If this be so, the pith of *Platyzoma* cannot have been of cortical origin, and the stele cannot be interpreted as a reduced solenostele.

We come now to the origin and nature of the leaf-traces. There are both large and small leaf-traces (figs. 1, 4, and 13). The largest traces arise typically from the upper surface of the stele, but occasionally their points of origin are at a slightly lower level. The smallest traces originate from the lower surface of the stele, and between the largest and smallest types traces of intermediate size exist. These latter are inserted typically upon the sides of the stele. There is, then, a gradation in the sizes of the leaf-traces as one passes from the upper to the lower surface of the stele. Slight differences of detail occur from trace to trace, but one general method is adopted throughout in the formation of the leaf-traces. It will suffice to describe, in detail, the departure of a large leaf-trace, and to indicate briefly such points as are of interest in the smaller types.

The first indication of the formation of a leaf-trace is the marking out and projection of a peripheral, tangential band of tracheides from the outer xylem-cylinder (fig. 41). Beneath this band of tracheides a definite mound of parenchyma has formed, while above it the phloëm, pericycle, and endodermis have been raised in a gentle curve. As the band of xylem becomes more distinctly curved and projecting, the band of phloëm, displayed upon its convex side, becomes thinner. Very soon the xylem band begins to free itself from the xylem of the stele, and to pass out as the crescent-shaped xylem of a leaf-trace (fig. 42). It may sever its connections with the stelar xylem simultaneously at both sides, or it may become free on one side more rapidly than on the other. But in any case, while the phloëm which clothes the outer surface of the leaf-trace xylem has become thinner, no diminution of phloëm has taken place at the points where the leaf-trace xylem has freed itself. In fact, no sooner has an edge of the leaf-trace xylem become free, than phloëm begins to appear in the gap which separates it from the stelar xylem, and, as the gap widens, a sheet of phloëm appears in the parenchymatous mass lying beneath the leaf-trace xylem (compare figs. 42 and 43). This sheet of phloëm is an inward continuation of the stelar phloëm beneath the developing leaf-trace. It is destined to meet a similar phloëm sheet projecting inwards from the gap which separates the leaf-trace xylem from the stele at the other edge; and when these phloëm sheets have met and fused, a continuous layer of phloëm will be spread once more over the surface of the stelar xylem. Two stages in this process are represented in figs. 43 and 44. Meantime the leaf-trace xylem and its accompanying crescent of phloëm have continued their outward course, and very soon the phloëm of the leaf-trace

* *Ann. Bot.*, 1913, pp. 236-239.

becomes free from the phloëm of the stele (compare figs. 44 and 45). The endodermis and pericycle have moved outwards in order to accommodate the xylem and phloëm of the leaf-trace, and when the limit of this accommodation has been reached the leaf-trace is a crescent of solid xylem, with phloëm on its convex surface and around its margin (fig. 45).

When any gap which had arisen in the peripheral cylinder of stelar xylem has been repaired, and when the phloëm covers the stele once more as a continuous sheet, endodermal cells appear on both sides of the leaf-trace (fig. 45). These new endodermal cells spread obliquely inwards from points upon the outer endodermis, and, having passed rapidly inwards, unite to form a continuous endodermis which completely shuts off the leaf-trace from the stele (fig. 46). But further, no sooner has this endodermal formation been completed, than the curved portion of the endodermis, which has accompanied the leaf-trace on its outward course, becomes free as a crescent-shaped band, following the general outline of the leaf-trace. The endodermis of the leaf-trace is then, at this point, of an imperfect character, being maintained upon the outer side of the trace, but absent from the inner side. This condition is not, however, long maintained, for an inner band of endodermis soon appears, repairing the gap (fig. 46) and determining the contour of the leaf-trace as it passes out through the cortex. It is here a solid though narrow band of xylem, with a thin layer of phloëm upon its convex surface, and a well-developed pericycle (fig. 47). It is well to note that in this process of leaf-trace formation the inner endodermis is in no way involved, and, further, that there exists *no* point where the stele is not *entirely* enclosed in *outer* endodermis. Not only has it been established that the cortex and pith are connected at no point, but it will now become evident that no connection exists between the cortex and the pericycle at the point of final liberation of the leaf-trace into the cortex. The possibility of such a connection has been removed by the local doubling of the outer endodermis as described above. It frequently occurs, however, that when the liberation of a leaf-trace imposes a large drain on the tracheides of the outer stelar cylinder, a parenchymatous bridge appears passing athwart the xylem-ring (fig. 63). But many chains of parenchyma traverse the xylem from side to side—though their courses may be irregular and narrow,—and in no case do these bridges disturb the inner or outer endodermis. It happens occasionally that the xylem of the leaf-trace is, at the point of departure of the trace, a compact mass of tracheides which appears almost circular in section; but as the trace is followed outwards, the xylem becomes extended laterally, and when sectioned shows the typical crescent arrangement described above.

The smallest leaf-traces may now be considered. Two stages in the liberation of a small trace from the lower surface of the cylinder are represented in figs. 48 and 49. It will be evident that they reproduce, in miniature, the method of trace-departure described above for the largest leaves. As they pass outwards into the cortex the steps described for the large leaf-traces repeat themselves, and when the

traces are free within the cortex, they appear, in transverse section, as represented in fig. 51. They merely reproduce, in miniature, the characters of the largest leaf-traces.

A leaf-trace of the transitional type, and springing from the side of the stele, is represented in transverse section in fig. 50. It shows the re-formation of the layer of stelar phloëm below the departing leaf-trace, and the liberation of the leaf-trace phloëm from the stelar phloëm. I am not aware of any leaf-trace departure which is exactly comparable with the one described in these paragraphs, and for the present we may consider it an unique type.

The origin of the roots presents no points of special interest. The roots are restricted to the lower surface and lower portions of the sides of the stele. They originate, as do the leaf-traces, by a protrusion of the outer xylem-cylinder (figs. 1 and 52). When they have entered the cortex they appear in transverse section as a solid mass of xylem, with small peripheral and larger central tracheides. Around this xylem core is a narrow zone of phloëm, a well-developed pericycle, and an endodermis (fig. 53). A typical root-structure is not established until the cortex has been traversed. When free from the cortex, the root has typically a diarch stele (fig. 54). The pericycle and phloëm are well developed, and the endodermis is of large and delicate cells. A two-layered zone of sclerenchyma gives the fibrous character to the mature roots, and the outer part of the cortex consists of two or three layers of large parenchymatous cells, with which are associated numerous, long, and often persistent root-hairs. There is nothing remarkable in the roots except the persistency of the long root-hairs and the cortex. This persistency was so marked a feature that perfect sections could be obtained from old roots of the specimen which I had at my disposal.

The largest leaf-traces pass into the large pinnate leaves and the smallest traces typically supply the filiform leaves. The traces of intermediate size divide roughly into two groups. The first group includes traces of moderate size which spring from the upper portions of the sides of the stele, and, as a rule, supply pinnate leaves. The second group is composed of traces springing from the lower portions of the sides. Almost invariably they supply filiform leaves. The leaf-zoning has therefore found its explanation in the dispositions of the large and small leaf-traces upon the stele.

Passing now to the anatomy of the leaves, the outstanding features of the typical simply-pinnate leaf may be considered first. The petiole is circular or oval in section (fig. 14). The epidermis and the peripheral zone of cortex are markedly sclerotic, but the inner cortex is composed mainly of large-celled parenchyma with thin walls, and mucilaginous protoplasts. The protoplasts of the cortical sclerenchyma are also highly mucilaginous, and the general condition of the cortex is indicative of extremely xerophytic conditions. The trace is roughly oval in section, and the endodermis is slightly indented on the upper surface. There is practically no

pericycle, and the phloëm is a narrow band displayed over the lower convex surface of the xylem and around its hooked margins. The xylem is an extended narrow strap, which is composed of two types of elements. The lower, central, and more massive portion is composed mainly of large tracheides. The incurved margins of the strand are of numerous, very small, and relatively thin-walled tracheides. This marked difference in size between the elements of the central and marginal portions of the xylem is a conspicuous feature throughout the greater portion of the leaf. The incurved xylem-strap encloses a parenchymatous ground tissue, and if protoxylems are at all developed they are involved in the small-celled and arched margins of the strap. As the rachis is approached the petiole becomes somewhat flattened dorsiventrally, and this is accompanied by a lateral extension of the trace.

Within the rachis itself little or no change takes place in the epidermal and cortical tissues, but the leaf-trace has become extended laterally, and the margins of the xylem-strap have become thinner and more attenuated (fig. 15). The pinna-traces are small, and of extra-marginal origin. They are given off from the convexity of the incurved leaf-trace, their xylems being contributed by the sharply curved parts of the small-celled and incurved margins of the xylem-strap. The pinna-traces pass quickly through the cortex to the almost sessile pinnæ. The venation of the pinnæ has already been indicated. Towards its distal end the rachis becomes slender and laterally compressed. The xerophytic characters of the superficial and cortical tissues already noted are still dominant, and the leaf-trace, though now greatly reduced in bulk, retains the general features noted in the lower regions of the leaf (fig. 16). The pinna-traces are still of extra-marginal origin, but now the drain made by the pinnæ upon the sharply curved portion of the xylem-strap leads frequently to a depletion of the small tracheides; so that, when seen in section, the margins of the xylem-strap appear fragmented, and separated from the main lower and central portion of the strap. The margin of the xylem-strap is, in fact, in process of reduction. Close to the apex of the leaf the rachis has become very slender. Its cortex is greatly reduced, and the leaf-trace, though now very small, is still clearly defined (fig. 17). The infolded margins of the xylem-strap have been entirely reduced at a lower level, and the strap has become a thin, irregular, and disintegrating assemblage of tracheides, from which the last few small pinnæ cannot fail to be supplied in a marginal manner. From what has been recorded, it will be evident that in general form of leaf-trace, and in the dominantly extra-marginal origin of the pinna-traces, the pinnate leaf of *Platyzoma* falls easily into line with most Gleichenioid types.

From the section of a small pinna shown in fig. 17, it will be clear that the epidermis is well developed, and that the mesophyll of the pinna is partly lacunar. The upper epidermis is strongly cuticularised, and is devoid of stomata. The stomata are restricted to the lower surface, and lie hidden within the almost

closed cavity formed by the infolding of the membranous leaf-margins. Hairs arise from the leaf-margins and along the course of the veins, and assist still further in the protection of the stomata. The anatomy of the pinnate leaf has revealed characters expressive of extremely xerophytic life conditions.

It will be convenient to record, at this point, the anatomical features of the forked pinnate leaf which I had at my disposal (text-fig. 8). It forked near to its base, no pinnæ appeared *below* the point of forking, and the leaf-branches were of equal length. The pinnate portions of this leaf were of no special interest, for they agreed in general plan with the rachial part of the simply-pinnate leaf. The branching petiole was, however, of considerable interest, for its trace was found to undergo a perfect dichotomy. The leaf-trace—in transverse section,—as seen in the leaf base, is shown in fig. 28. There is not so marked a difference in size of element between the central and marginal portions of the xylem-strap as existed in the simply-pinnate leaf, but the general plan of construction of leaf-trace is the same in both cases. The leaf-trace of the dichotomising leaf was larger than that of the simply-pinnate leaf, and its xylem was more extended. As the petiole of the forked leaf was ascended, a small group of tracheides appeared in the parenchymatous bay enclosed in the curved xylem-strap (fig. 29). At a still higher level, the trace had become extended laterally, and the island of tracheides in the bay of parenchyma had grown considerably (fig. 30). Very soon a junction was established between the island and the middle portion of the much extended xylem-strap (fig. 31), and two promontories had developed—one to right and the other to left of the free end of the original island,—so that two parenchymatous bays were now formed on the upper or adaxial side of the leaf-trace. A split then developed in the middle region of the xylem-strap (fig. 32). It traversed the strap from its upper to its lower surface, and divided it into two similar portions. Further on, when the endodermis, pericycle, and phloëm had become nipped across along the same direction-line, there were formed two similar leaf-traces (fig. 33) which supplied the two limbs of the dichotomised leaf. It would be of interest to know what takes place in the branching of the leaf in the two specimens already referred to as belonging to Kew Herbarium. It seems probable that they too are dichotomous branchings, but their further interest lies in the facts that they are pinnate *below* the points of branching, and that they branch at points considerably removed from their bases. It is doubtful whether these bifurcations of the leaf of *Platyzoma* will bear any phyletic interpretation. The bifurcations are seen to occur at various levels, and seem to have no particular relation to the pinnæ. They are probably of the same nature as those bifurcations found in many other Fern leaves, *e.g.* *Polypodium vulgare*, *Scolopendrium*, *Nephrodium molle*, etc., and are akin also to those distal forkings which give rise in varying degree to the "*forma furcata*" varieties. The remarkable point is that the forking should occur in such a Fern as *Platyzoma*, for it is more usual in advanced Leptosporangiates. But nevertheless it is seen in *Osmunda*.

The typical filiform leaf is now to be described. At its point of insertion upon the axis it is compressed laterally and its epidermis is thickened (fig. 18). The cortex is composed of mucilaginous cells which form a bulky water-storage tissue towards the lower side. The leaf-trace is small and compressed, and has altered very little from the condition which it showed on its way through the cortex of the rhizome. A slight indication is already present of the formation of the flanges which are so conspicuous in the basal region. Fig. 19 represents a section at a slightly higher level. The trace has become slightly more bulky, and the xylem-strap has become thinner and broader. The flanges are clearly established, and the lateral grooves are apparent. In fig. 20 a typical section of the basal region is depicted. The flanges are well developed, and the cortex is lacunar. The trace has grown considerably, and, while the xylem-strap has extended, no very marked differences can be recorded between the elements of its middle and marginal portions. The passage from the basal to the middle region is characterised by the possession of two pairs of grooves—one pair on the upper surface, and the other on the lower surface. The grooves on the lower surface of this middle region are the continuations of those grooves which exist in the basal region, and which have passed to the lower surface at the junction of the basal and middle leaf-regions. The grooves on the upper surface are new grooves which have commenced at the base of the middle region. A typical section of the lower half of the middle leaf-region is shown in fig. 21. The epidermis is strongly cuticularised, but not thickened as is the epidermis of the basal region. Stomata are occasionally found in the grooves on the lower surface. The xylem of the trace is of particular interest. It has developed into a broad strap with long, thin, curved margins. The margins are composed of small tracheides, while the middle is a zone of large, thick-walled tracheides. It will be apparent that in this region the trace thus resembles the trace of the simply-pinnate leaf in the rachial portion particularly. But this condition of the xylem-strap is not always found. In a number of filiform leaves the condition represented in fig. 22 is found. It is clear that the margin of the xylem is not characterised by small tracheides, and, in fact, short storage tracheides are irregularly distributed in both the middle and marginal portions.

Passing forward in this middle region the grooves on the upper surface deepen, and the xylem of the trace undergoes remarkable modifications. As is shown in fig. 23, the middle zone of the xylem remains typically large-celled, but the margins have become extended until they have met to form a practically closed tube of xylem around a core of parenchyma. Here again there are variations, for in several leaves the condition found at this region is as shown in fig. 24. The xylem is more massive than in the former case, the parenchymatous core is almost obliterated, and there is not so marked a difference in size between the tracheides of the middle zone of xylem and those of the revolute and now fused margins.

Sections through the tips of the terminal lobes of two filiform leaves are represented.

sented in figs. 25 and 26. In the first of these the lower surface grooves had died away before the upper grooves, while in the second the upper surface grooves had been lost first. In both cases the infolded margins of the xylem-strap are being reduced, and storage tracheides are appearing in the middle xylem-zone.

The anatomy of these remarkable filiform leaves has then shown that the trace is of an elaborate type, comparable in form with the trace of the pinnate leaves; and that, while the trace is admirably constructed for the supplying of extra-marginal pinna-traces, similar to those which feed the ordinary pinnæ, no pinna-traces are initiated in the filiform leaves. It may be that the ridges of tissue which run along the margins of the filiform leaves mark the middle zone as of rachial nature. But until definite evidence is advanced, showing that those ridges represent coalesced and aborted pinnæ, no definite opinion can be formed regarding the interpretations of the three regions of the filiform leaves. That these leaves are reduction forms seems undeniable; but whether they are useless abortions or serviceable structures cannot be determined from an herbarium specimen.

The anatomy of the transitional leaf-forms remains to be considered. Regarding the small filiform leaf with the circinate tip, represented in fig. 3, it will suffice to note that for the greater part of its length its leaf-trace remained of the type shown by the basal region of the longer filiform leaves, and that, as the leaf-tip was approached, the margins of the xylem-strap were reduced and the trace died out.

The anatomy of the first of the reduction series of four leaves (fig. 5) showed no essential points of difference from an ordinary simply-pinnate leaf. It might be considered a pinnate leaf in miniature. The anatomy of the second leaf of the reduction series (fig. 9) showed two points of interest. In its basal portion it resembled the foregoing leaf, but at a point near to the rachis the petiole became distended. At this point the stele showed a peculiar condition. The xylem-strap was, as usual, divisible into the marginal and middle regions, but a parenchymatous replacement of the tracheides was taking place in the centre of the strap (fig. 27). This led, finally, to what appeared to be an equal division of the stele into two parts. Of these, the one part passed into the pinnate branch, but the other rapidly degenerated, and only an irregular group of tortuous tracheides and a few softer elements entered the aborted branch. I am of the opinion that this leaf might have developed a true dichotomy, but that it became malformed during development. No pinna-trace was found supplying the minute pinna-like protuberances which stood distally on the pinnate branch.

The terminal portion of the small leaf which provided the third step in the reduction series is worthy of remark (fig. 11). At least five pinnæ were supplied with traces. The supplies for the basal pair of pinnæ are represented in fig. 34 on their way through the cortex. In fig. 35 the trace to one of the second pair has already been liberated, while the second trace is in process of separation. It is noteworthy that the second pair of traces are here much more bulky than are the first or lower

pair. This seems to be due mainly to a thickening of the extraordinarily extended leaf-trace margins, at the points where the infolding of the margins takes place. This thickening of the margin is more pronounced in fig. 36, which shows the extra-marginal departure of the fifth pinna-trace. When this last pinna-trace had departed, the xylem became suddenly a solid mass of tracheides (fig. 37). It is probable that this marked the approach of the leaf-tip, and that few if any more pinnæ were developed on this leaf.

And lastly, in the pinnate portion of the small leaf which is represented in fig. 12—and which showed the simplest possible pinnate condition—the supply to the pinnæ is of extra-marginal origin. Three stages in the preparation of the pinna-traces of this leaf are shown in figs. 38, 39, and 40. The condition typical of the trace in the rachis of the pinnate leaf, and in the middle region of the larger filiform leaf, was found to dominate the stalk. It is depicted in fig. 38. Fig. 39 shows the lateral extension of the trace as the pinna-traces begin to form, and in fig. 40 one of the two pinna-traces is almost liberated.

The facts regarding those various leaf-types have been recorded in some detail; for not only was it necessary to recognise the transitions from pinnate to filiform leaves by external form, but a knowledge of the anatomical features could provide a valuable check on any conclusions which might be drawn. On the ground of external form, it seemed almost certain that the large filiform leaves might justifiably be regarded as reductions from pinnate leaves, and the evidence which has now been advanced—both regarding these filiform leaves themselves and also the “transitional” types—seems to lend strong support to this opinion. It is not to be supposed that the “transitional” types are considered illustrations of definite transitional *forms*, lying between the departure from the pinnate leaves and the arrival of the filiform leaves, but *in themselves* they are proofs of leaf-reductions in *Platyzoma*, and the filiform leaves may be resultants of a like reduction process.

The sporangia remain to be considered. At present I am unable to give an account of their development, but there are certain outstanding features which may be noted here. They are developed either terminally upon the main lateral branches of the sympodium, or, if more than one sporangium is developed upon a branch of the sympodium, the distal portion of the branch is forked and the sporangia are again terminal (text-fig. 9). The bundle-endings which thus supply the isolated sporangia are worthy of note. They are composed of long tracheides with spiral and reticulate markings, and a sheath of long, narrow, and delicate cells which persist to the very tip of the bundle (text-fig. 10). I am not aware of any other Leptosporangiate Fern in which the condition just described exists. It may be most nearly matched by some early Eusporangiates. The sporangia in any one pinna vary in size, but no definite arrangement of the sporangia according to size can be followed. There are large and small sporangia,

and, between these, transitional forms exist (text-fig. 9, and figs. 55-62, 67-68). The large sporangia contain small numbers of large spores, the small sporangia larger numbers of small spores (figs. 64, 65, and 66). The small sporangia are invariably short-stalked, but in form they are very variable. In some cases the capsule is globular, in others it is ovoid or almost pear-shaped, while frequently it is very lopsided (figs. 55-59, 61, and 62). The annulus is variable in position and form. It is seldom, if ever, perfectly regular, and is frequently very irregular. In a few cases it was found to be almost horizontal, passing round the capsule as an irregular and broken ring, and having no organised stomium (figs. 61 and 62). But in the majority of the sporangia examined the annulus was almost vertical, though typically irregular or broken. These sporangia possessed a definite stomium (figs. 55-58). Figs. 55-58 show a single sporangium from above (fig. 57), below (fig. 58), back (fig. 55), and front (fig. 56). From these it is apparent that the annulus begins at the stalk, passes obliquely and with irregularities upwards, and, having passed over the top of the capsule, descends to the stalk once more as an irregularly developed stomium. The annulus is, then, interrupted by the stalk. A more regular—though also more oblique—annulus is represented in back view in fig. 59, while in fig. 60 the wall of a sporangium which has been opened out is represented. It is apparent that in this case the annulus began close to the stalk, and passed almost vertically over the summit of the capsule. But here an irregularity arose. This led to a displacement of the stomium, so that it did not descend directly to meet the stalk, but, having passed to one side of it, came into close contact with the end of the annulus which had met the stalk.

The number and the size of the spores which were found in those smaller sporangia varied. The largest number of spores found in any small sporangium was 32, and such numbers as 30, 29, 28, and 26 were frequently counted. The spores are tetrahedral, and the lines of junction of the tetrads are well marked (figs. 64 and 65). The exospore is beautifully sculptured, there being numerous small areas enclosed by wavy borders, and possessed of little mounds which give an added roughness to the spore coat. The smallest type of spore found in a small sporangium is shown in fig. 65. It was taken from a sporangium containing 32 similar spores. The largest type of spore found in a small sporangium is shown in fig. 64. It was taken from a sporangium containing 29 similar spores.

One of the largest sporangia found is represented in figs. 67 and 68. It is apparent from the back view (fig. 68) that the annulus stops short at the stalk and passes irregularly over the top of the capsule. The stomium is shown in fig. 67. It is separated from the annulus, and passes downwards obliquely to the stalk. The largest number of spores found in a large sporangium was 16; 14 was an average count, and 12 was a rare number. A typical large spore is shown in fig. 66. It resembles the smaller spores in form and external markings, but differs from them remarkably in size. Two large sporangia contained both large and

small spores. In the first of these there were 14 spores of the largest type and two of the intermediate size; in the second instance there were 14 large spores and one small spore. It is impossible to decide at this point whether there is here a true heterospory, or the variation in spore size is merely the result of peculiar local nutritive conditions. I have not yet examined the contents of these remarkable spores, and accordingly can give no indication from this standpoint of the significance of the variation in spore size and output per sporangium. It is hoped to throw more light on the nature of these spores when the development of the sporangium has been studied and the spores can be germinated. But while in general form of sporangium, and obliquity and irregularity of the annulus, *Platyzoma* somewhat resembles some species of *Gleichenia*, the differences of sporangial and spore size and the small spore output are not characteristic of any known *Gleichenia*.

The chief facts obtained from the specimen of *Platyzoma* have now been considered. The habit of the plant, upon which the systematists chiefly relied, has sunk in importance before the remarkable characters of the stele, the leaf-traces, the leaves, and the sporangia. This plant has proved anomalous at almost all points, and in fact it would be difficult to indicate any known Fern with which *Platyzoma* can be reasonably compared. One is forced to the conclusion that it is not a *Gleichenia*. The development of the sporangia and the true nature of the spores may throw a fuller light upon its true affinity; and until information on these points is forthcoming, it would be foolish to separate *Platyzoma* from a relationship which may prove to be its nearest affinity. But although one cannot speak with any degree of confidence regarding the actual place of *Platyzoma* in the phyletic system, the study of its anatomy has laid bare facts regarding the stele, reduction processes in the leaf, and sporangial characters which may be of value in later discussions. The material available for the investigation was an herbarium specimen, and accordingly it was impossible to do more than collect the most important facts of mature anatomy. The present memoir is to be regarded as an instalment of the facts relating to this remarkable Fern, and the statement is not to be considered a final one. This being so, it has been thought well not to enter upon detailed comparisons, though the remarkable facts relating to *Platyzoma* provoke them. It has likewise been deemed well to abstain from any very definite statement as to the systematic position of *Platyzoma* until the sporangial conditions have been more fully examined. These matters can be better dealt with when properly preserved materials are available.

I am indebted to the Director of Sydney Botanic Garden for the specimen upon which these observations have been made; to Professor BOWER for much valuable guidance and criticism; to Mr BOODLE for information regarding the Kew specimens of *Platyzoma*, and to the Carnegie Trust for their assistance in the production of the illustrations.

SUMMARY.

The chief facts obtained from the single herbarium specimen available of *Platyzoma* have now been described. At some points the account has been less complete than would have been the case if sufficient material, properly preserved, had been at hand. Development has been necessarily omitted. But the fuller facts relating to mature structure which have been acquired may help towards establishing the position which this plant should hold in relation to other ferns. The habit of the plant is chiefly notable in relation to the heterophyllous character of its xerophytic foliage. The horizontal rhizome bears with some degree of regularity zones of smaller—probably reduced—foliage leaves with pinnæ vestigial or absent, and these alternate with zones of larger pinnate leaves which are mostly fertile. The rhizomatous condition is probably derivative from one in which the axis had an upright habit, and the heterophylly has probably followed upon the change of habit. Occasional cases of bifurcation of the leaves have been seen. It is probable that these are of the same nature as those branchings seen in the "*forma furcata*" of many Ferns. The crowded grouping of the leaves is a feature in strong antithesis to the isolation of the leaves prevalent in the *Gleichenias*, with which *Platyzoma* has habitually been grouped. The presence of hairs and absence of flattened scales accords with what is seen in *Gl. linearis* and *pectinata*, and is again a point marking *Platyzoma* off from many of the *Gleichenias*; while it is in itself a character of relatively primitive Ferns. But external habit, upon which the systematists have hitherto placed their chief reliance, has sunk in importance before the remarkable characters of the stele, the leaf-trace, and the sporangia.

The stele is little removed from the protostelic state. It consists of a continuous ring, which has never been seen to be broken by leaf-gaps or perforations. Definite protoxylem has not been recognised. But the xylem is differentiated into two zones, an outer consisting of smaller tracheides with occasional parenchymatous groups and chains, the inner of large storage-tracheides intermixed with larger groups and chains of parenchymatous cells. The inner zone appears to be primarily a storage zone. Centrally lies a bulky pith which is sclerotic and mucilaginous. It is surrounded by a continuous inner endodermis which is throughout distinct and separate from the outer endodermis. Between the inner endodermis and the xylem-ring lies a narrow zone of parenchyma, but no phloëm. Externally to the xylem-ring lies a continuous narrow zone of phloëm, a pericycle, and external endodermis.

The leaf-traces depart without any leaf-gap. They vary in size according to the dimensions of the leaves which they serve, but even those of the largest fertile leaves, though they may interrupt the xylem to its inner limit, do not disturb the inner parenchymatous zone or the inner endodermis: thus there is no leaf-gap. The leaf-trace draws off from the outer zone of xylem as a crescentic mass of tracheides, accompanied by an outer arc of phloëm. There is no definitely constituted proto-

xylem. As this simple leaf-trace separates from the stelar cylinder, the stelar phloem and xylem right and left of it close behind the outgoing leaf-trace. Meanwhile the outer endodermis is unbroken—a state which is maintained until the stelar ring has been reconstituted. Only then does the arc of outer endodermis accompanying the departing leaf-trace break its connection with the remainder of the endodermis. This it does at two points right and left. An outer separate arc of endodermis is thus liberated, and it accompanies the outgoing leaf-trace. Meantime the continuity of the outer endodermis of the stele has been maintained by the appearance of tracts of endodermis, right and left, which finally meet beneath the leaf-trace before the arc of leaf-trace endodermis has become detached. Following the leaf-trace outwards, its peripheral arc of endodermis is soon extended on the adaxial side, and completes the enclosure, in which state the trace enters the leaf.

The zonation recognised externally is seen anatomically to be apparent rather than real. For it is found that the leaf-traces directed downwards are smaller and supply the smaller vegetative leaves; those towards the upper side of the rhizome are larger and supply the larger and fertile leaves. The apparent zonation depends upon the separate grouping of the larger and smaller leaves in their forward and upward course. The smaller and larger leaf-traces originate from the stele in the same way, and differ only in the extent to which they affect the stele on their departure. This accords with the facts of abortive pinnation of the vegetative leaves—an indication that they are of reduced type. The leaf-trace remains undivided throughout, and the pinnation is always of extra-marginal type, except towards the tip of the leaf, where a reduced condition exists.

The sporangia are distributed solitarily upon the lower surface of the pinnæ, and terminally on the veins. They do not constitute definite sori. A well-developed bundle ending runs to the base of each sporangium. There is no indusium, but hairs are distributed along the veins and the revolute margins of the pinnæ. The sporangial stalk is short and consists of three rows of cells; the head is globular and lopsided. The annulus is typically oblique, but is irregular in position and in constitution. The number of cells of the annulus is variable, and their succession is apt to be irregular and interrupted. The annulus is always interrupted at the stalk. The stomium is variable in form and position, and where the annulus is almost horizontal no organised stomium is found. This indicates a transitional state. Roughly, the sporangia are differentiated into two types—the larger sporangia with few large spores (16, 14, and 12), the smaller with more numerous small spores (32–26). In actual dimensions a large spore may be many times the size of a small spore.

The facts above detailed would still allow of a Gleicheniaceous relation for *Platyzoma*. But their divergence from the *Gleichenia* characters is so pronounced that it seems quite impossible to retain a view of close affinity. The sporangial characters are specially divergent, and indicate a probable derivative position for *Platyzoma* from some Gleicheniaceous source. Meanwhile the retention of hairs and

the anatomical state show a greater conservatism. In fact, *Platyzoma* is again a type somewhat anomalous in its characters. Like *Cheiropleuria* it shows sporangial advance with a relatively primitive vegetative condition.

DESCRIPTION OF FIGURES IN THE TEXT.

Figs. 1-3. Diagrams of 3 sterile pinnæ of *Platyzoma*, seen from the upper surface. They show the chief variations in the sympodial venation.

Figs. 4, 5. Diagrams of 2 sterile pinnæ of *Platyzoma*, seen from below. They show further variations in venation. The strongly revolute margins of the pinnæ bear fringes of small teeth-like hairs.

Fig. 6. Diagram of a forked pinnate leaf of *Platyzoma* in Kew Herbarium. The leaf is attached to the rhizome, and bears pinnæ both above and below the point of branching. The terminal portions of this leaf are damaged.

Fig. 7. Diagram of a forked, and probably dichotomised, pinnate leaf of *Platyzoma* in Kew Herbarium. The leaf was detached from the rhizome. It bears pinnæ both above and below the point of branching.

Fig. 8. Diagram of a perfectly dichotomised leaf of *Platyzoma*, taken from an herbarium specimen in Glasgow University. The leaf dichotomised at a point near to its base, and no pinnæ were developed below the point of branching.

Fig. 9. Diagram of a fertile pinna of *Platyzoma*, seen from below. The margins are very revolute. The sporangia are of variable size, but are *invariably* inserted *terminally* upon the main lateral veins or upon branches of these.

Fig. 10. Bundle-ending of a vein, supplying a sporangium of *Platyzoma*. It consists of a conspicuous group of long reticulated tracheides, and a sheath of more delicate and narrow cells which persist to the tip of the bundle.

DESCRIPTION OF FIGURES IN THE PLATES.

PLATE I.

Fig. 1. Transverse section of the rhizome of *Platyzoma*. Four large leaf-traces are seen on their way out through the cortex; a fifth is being liberated from the upper surface of the stele. On the right a small leaf-trace is separating from the stele, and on the left a root-trace is departing. ($\times 12$.)

Fig. 2. A multicellular unbranched hair taken from the rhizome. ($\times 10$.)

Fig. 3. A filiform leaf with circinate tip, and measuring about $\frac{1}{3}$ inch. It was taken from the lower surface of the rhizome. ($\times 6$.)

Fig. 4. Transverse section of the stele of *Platyzoma*, showing a large leaf-trace about to be liberated on the upper surface. Small leaf-traces are being separated from the sides and lower surface. The xylem of the stele is clearly differentiated into an outer zone of small tracheides, and an inner zone of broad tracheides intermixed with many parenchymatous groups. ($\times 24$.) Towards the upper side of the stele the inner xylem-zone is greatly reduced.

Fig. 5. A reduced pinnate leaf, taken from the upper surface of the rhizome. It was about $1\frac{1}{2}$ inch long. The pinnæ are variable in size, but their venation is invariably a sympodium. ($\times 6$.)

Fig. 6. A photograph of the specimen of *Platyzoma* upon which this paper is founded. ($\times \frac{1}{2}$.)

Fig. 7. A typical filiform leaf measuring about $1\frac{1}{3}$ inch, seen from its lower surface. ($\times 6$.) It is differentiated into a broad basal region, a slender middle, and a bulbous terminal region.

Fig. 8. A photograph of part of the specimen upon which this paper is founded. The heterophylly is clearly shown, and the crowding and grouping of pinnate and filiform leaves is demonstrated. (Natural size.)

Fig. 9. A "reduction" leaf which measured about 1 inch. The venation of the majority of the pinnæ

is a simple midrib, and no vascular supply is seen in the small terminal pinnæ. At the base of the rachis is a small aborted branch devoid of pinnæ. ($\times 6$.)

Fig. 10. Transverse section of the stele of *Platyzoma*. The sclerenchymatous pith is breaking from the stelar ring along the inner endodermis. In this section the difference in thickness between the upper and lower sides of the xylem-cylinder are not so pronounced as in figs. 1, 4, 13, and 63. ($\times 36$.)

Fig. 11. An incomplete "reduction" leaf, $\frac{2}{5}$ inch long. Only a few terminally aggregated reduced pinnæ are developed. ($\times 6$.)

Fig. 12. A "reduction" leaf, $\frac{1}{8}$ inch long, taken from the side of the rhizome. Towards its hooked tip are two small pinnæ with simple unbranched veins. ($\times 6$.)

Fig. 13. Transverse section of the stele of *Platyzoma*, showing 3 large leaf-traces departing from the upper surface; a trace of intermediate size being liberated on the upper portion of the right side; and small traces departing on right and left towards the lower surface. ($\times 36$.)

PLATE II.

Fig. 14. Transverse section at the base of the petiole of a typical pinnate leaf of *Platyzoma*. ($\times 15$.)

Fig. 15. Transverse section of the *lower* part of the rachis of a typical pinnate leaf. ($\times 15$.)

Fig. 16. Transverse section of the *upper* part of the rachis of a typical pinnate leaf. ($\times 15$.)

Fig. 17. Transverse section of the *terminal* part of the rachis of a typical pinnate leaf. ($\times 15$.)

Fig. 18. Transverse section of the very base of a typical filiform leaf. ($\times 15$.)

Fig. 19. Transverse section of the same leaf at a slightly higher level in the leaf-base and showing the establishment of the lateral grooves. ($\times 15$.)

Fig. 20. Transverse section of the same leaf-base at a still higher level. The xylem of the leaf-trace has widened laterally, the water-storage tissue is established towards the lower surface, and the flanges and grooves are fully developed. ($\times 15$.)

Fig. 21. Transverse section at the base of the middle zone of a typical filiform leaf. ($\times 15$.)

Fig. 22. Transverse section at the base of the middle zone of another typical filiform leaf. ($\times 15$.) The xylem of this leaf is much more massive than in the leaf seen in section in fig. 21.

Fig. 23. Transverse section of the upper part of the middle zone of a filiform leaf. ($\times 15$.)

Fig. 24. Transverse section of a similar portion of another filiform leaf. The xylem is here much more massive than in fig. 23. ($\times 15$.)

Figs. 25, 26. Transverse sections through the bulbous terminal portions of two typical filiform leaves. ($\times 15$.)

Fig. 27. Transverse section of the petiole of the reduced leaf depicted in fig. 9, and showing the preparation for the splitting of the xylem prior to supplying the two branches of the rachis. ($\times 15$.)

Figs. 28-33. An ascending series of transverse sections of the stele in the basal portion of the dichotomised pinnate leaf represented in text-figure 8. The series illustrates the chief steps in this dichotomy. ($\times 15$.)

PLATE III.

Figs. 34-37. An ascending series of transverse sections of the rachial portion of the small leaf represented in fig. 11. The series illustrates the extra-marginal pinna-trace supply, and the massing and strengthening of the xylem towards the tip of the leaf. ($\times 15$.)

Fig. 38-40. An ascending series of transverse sections through the pinnate portion of the small leaf shown in fig. 12. It shows the preparation for and liberation of a pinna-trace. ($\times 15$.)

Figs. 41-47. A series of sections showing the origin and liberation of a *large* leaf-trace from the upper surface of the stele. In fig. 47 the trace is as seen in transverse section on its way out through the cortex. ($\times 15$.)

Figs. 48-51. A series of sections showing the origin and liberation of a *small* leaf-trace from the lower surface of the stele. In fig. 51 the trace is as seen in transverse section on its way out through the cortex. ($\times 15$.)

Fig. 52. A section of the stele of *Platyzoma*, showing the origin of a root-trace from the outer xylem-cylinder. ($\times 15$.)

Fig. 53. Transverse section of a root-trace on its way out through the cortex of the rhizome. ($\times 15$.)

Fig. 54. Transverse section of a root of *Platyzoma*. ($\times 15$.)

PLATE IV.

Figs. 55–58. A *small* sporangium of *Platyzoma* seen from behind, in front, above, and below. The irregularities in the nearly vertical annulus, and the interruption of the annulus by the stalk, are shown. ($\times 36$.)

Fig. 59. A sporangium with almost globular capsule, and an oblique—though almost regular—annulus. ($\times 36$.)

Fig. 60. The wall of a sporangium opened out so as to show the irregular and broken annulus. ($\times 36$.)

Figs. 61, 62. Two views of a rarer type of *small* sporangium of *Platyzoma*. The annulus is almost horizontal, but is irregular and broken, and no clearly defined stomium is developed. ($\times 36$.)

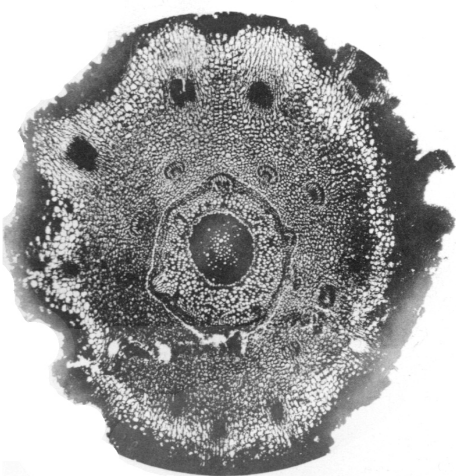
Fig. 63. Transverse section of the stele of *Platyzoma*, at a point where the xylem towards the lower surface is broad. The groups of tracheides appear *white* in the photograph, and the chains and groups of xylem parenchyma are *black*. ($\times 36$.)

Fig. 64. A spore of the *intermediate* size. ($\times 90$.)

Fig. 65. A spore of the *smallest* size. ($\times 90$.)

Fig. 66. A spore of the *largest* size. ($\times 90$.)

Figs. 67, 68. A front and a back view of one of the largest sporangia of *Platyzoma*. ($\times 36$.)



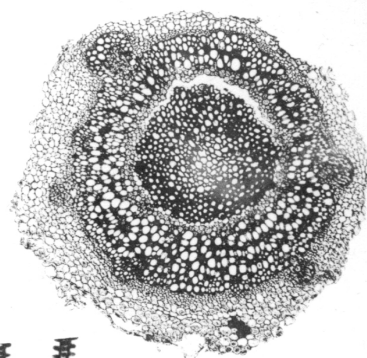
1.



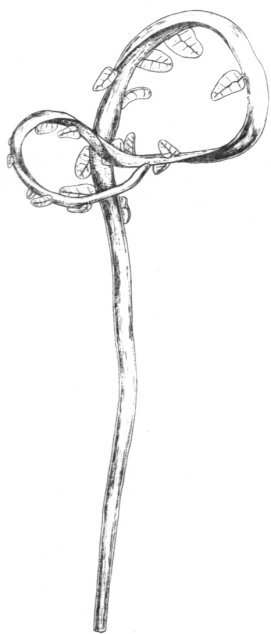
2.



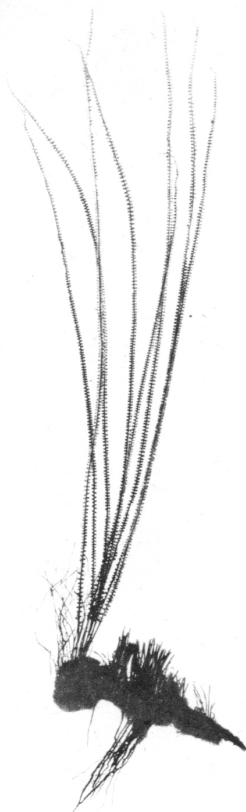
3.



4.



5.



6.



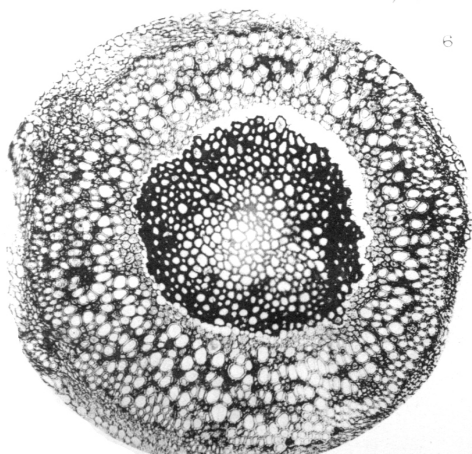
7.



8.



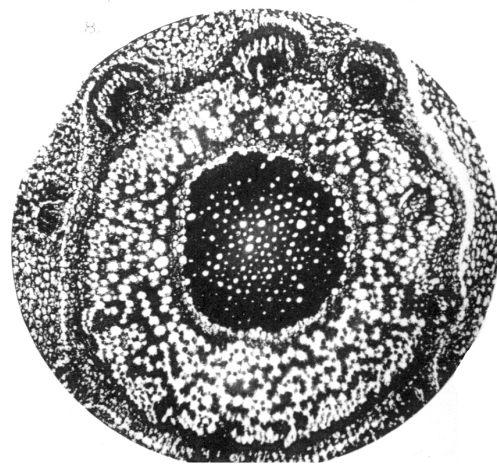
9.

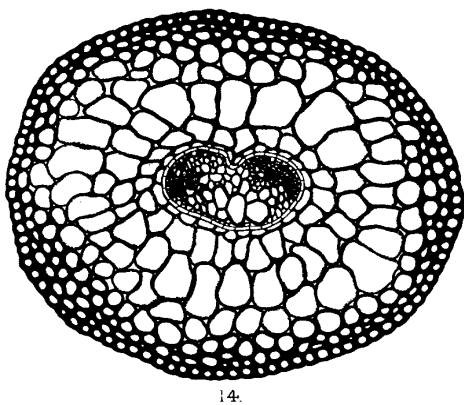


11.



12.

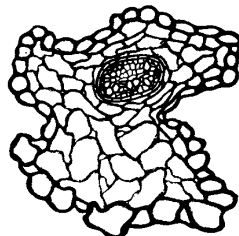




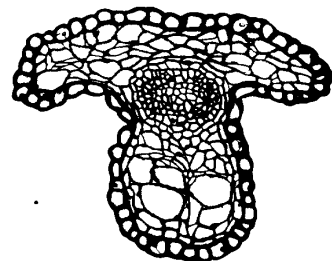
14.



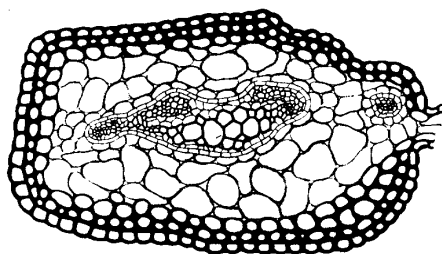
18.



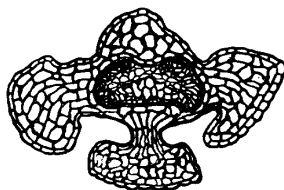
19.



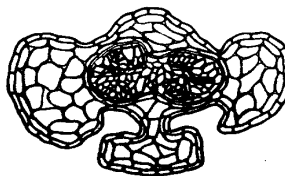
20.



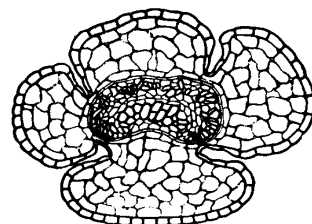
15.



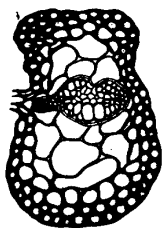
21.



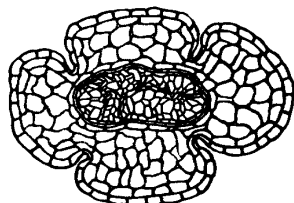
22.



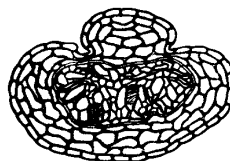
23.



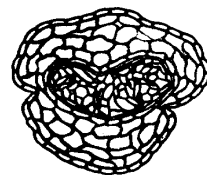
16.



24.



25.



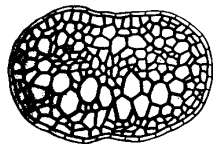
26.



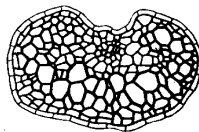
27.



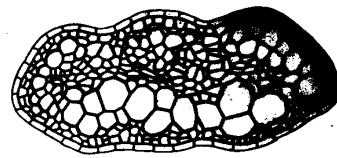
17.



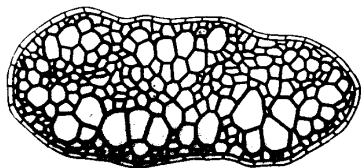
28.



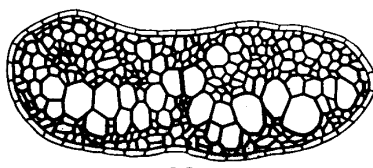
29.



30.



31.



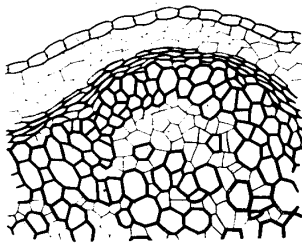
32.



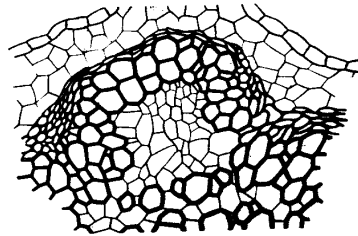
33.



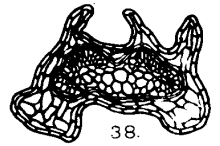
34.



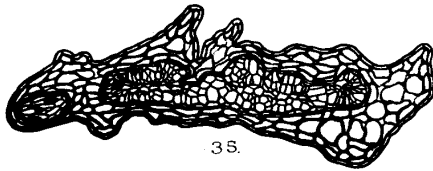
41.



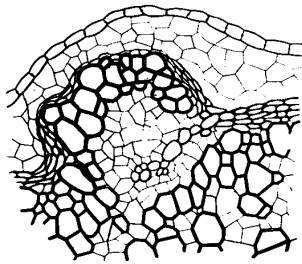
42.



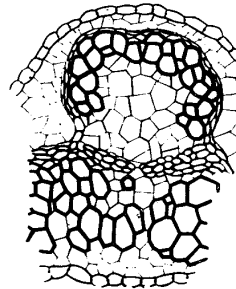
38.



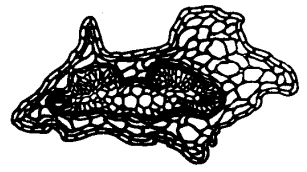
35.



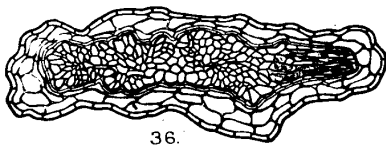
43.



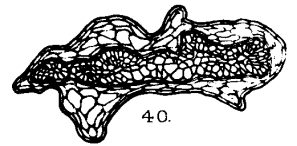
44.



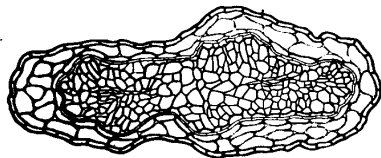
39.



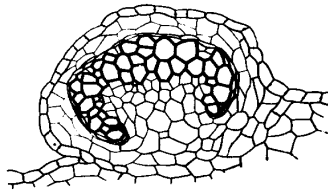
36.



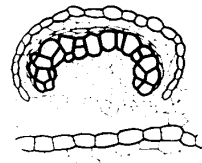
40.



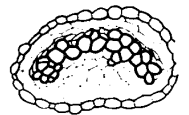
37.



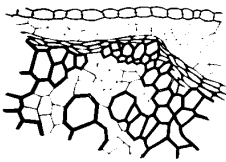
45.



46.



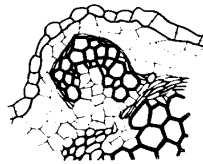
47.



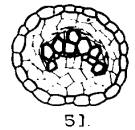
48.



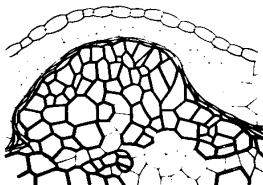
49.



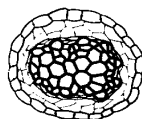
50.



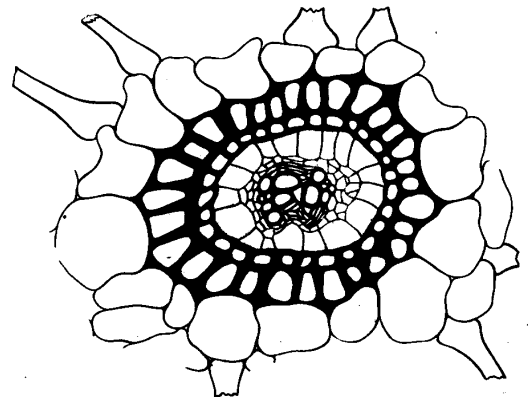
51.



52.



53.



54.

