THE DEVELOPMENT OF THE SORUS AND SPORANGIUM AND THE PROTHALLUS OF PERANEMA CYATHEOIDES, D. Don.

by

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In a paper in the Annals of Botany, vol. XXVI., 1912, it was suggested that Peranema cyatheoides, D. Don occupied a position intermediate between the Cyatheaceae and the Aspidieae group of Polypodiaceae. Various features of the mature plant, including those of the vascular system and the sporangium, suggested a relationship with the species of Nephrodium and especially with N. Filix-mas, Rich. Developmental stages of the sorus and sporangium have since been studied in material grown in the Glasgow Botanic Garden and kindly forwarded to me by Professor F. O. Bower, F.R.S. Fresh spores were sent from India through the kindness of the Director of the Calcutta Botanic Garden and young plants were reared from them by Mr. L. B. Stewart, Plant Propagator in the Royal Botanic Garden, Edinburgh. In the Edinburgh Garden there are now half-a-dozen strong and healthy plants of Peranema. I tender my thanks to the gentlemen to whose courtesy this result is due.

DEVELOPMENT OF THE SORUS.

From the earliest stages available it appears that the sorus is very soon after its appearance covered almost completely by the indusium (fig. 1). This indusium is composed, in the main, of a single series of cells, though near the highest point of its curve and near its tip there are two cell-layers. It forms a scale attached at one side along a semi-circular line to the under surface of the leaf and bent over the top of the receptacle. At one point the receptacle is, for a width of three cells, uncovered by the indusium. Below this point are one or two cells continuous with the series forming the epidermis of the leaf and with walls thickened like those of the cells of the indusium (fig.1). This suggests the presence of a small second flap./

flap. Sections through older sori confirm the suggestion, since in these a distinct small second flap or edge of a cup is present (figs. 2 and 3). In fig. 3 the further curving over of the main indusial flap is shown. This is still more accentuated in figs. 4 and 5, where the commencement of an extension of the receptacle at right angles to the leaf-surface can be distinguished. The second flap still is present as the sorus lengthens (fig. 6). When the receptacle grows out further as the narrow stalk of the sorus, the curving-over of the indusial flap is very marked. It is then curved back on one side, until the portion by which it is attached to the stalk is almost parallel to the surface of the leaf (fig. 7). The earliest indications of this recurving at the side are seen in figs. 4 and 5.

Of the second flap there remains in the older sorus only a mere knob, seen on the left side of fig. 7, at the top of the stalk. The extreme tip of the indusium is bent in, (fig. 7) and between the recurved tip and the stalk is a narrow slit, which appears on the surface of the sorus as an elongated pore. This slit marks the edge of the "cup" forming the indusium. In a transverse or oblique section of the mature sorus the two edges of the "cup" may be seen (cf. fig. 18 and Ann. of Bot. XXVI, pl. XXIX, fig. 15).

These sections through the sorus show that the indusium arises as a cup round the receptacle, that one side of the cup is strongly developed and curved over the top of the receptacle, while a small portion on the other side is suppressed in development. On this side at maturity the edges of the remainder of the indusium curve in to form a pore.

The receptacle, at first only slightly raised above the surface of the leaf (fig. 1) becomes pushed out on the side at first uncovered by the indusium (figs. 2 and 4) and may remain exposed/

exposed until sporangia appear (fig. 2). In some sori the indusium covers the receptacle entirely, even before the sporangia are fully defined (fig. 3).

As the sorus grows older, an elongation of the receptacle goes on (figs. 3, 4 and 6), the central part being continuous with the receptacle and the peripheral part continuous with the indusium. The side of the indusium in figs. 4 and 5 up almost to the "kink" represents the portion which later becomes one side of the soral stalk (the portion up to the sharp bend below the start of the indusial flap in fig. 7). The number of cells from side to side across the base of the sorus in fig. 5 is exactly the same as the number across the stalk of the mature sorus in fig. 7, while the number of cells from a to b in fig. 5 corresponds exactly with the number from a to b in fig. 7. (A counting of the number of cells in length and width of the stalk of the sorus figured in fig. 13 Ann. of Bot. XXVl, pl. XXlX gives precisely the same results. As this sorus was cut from another plant and the figure was made long before the material which forms the subject of this present paper was obtained, it is interesting to observe how closely the sori adhere to one type of construction. Comparison of Herbarium specimens collected at wide intervals of time shows how constantly the sori preserve the same size and form.) The elongated condition of the cells of the stalk in fig. 7 suggests what a comparison of figs. 4, 6 and 7 makes obvious, that, to produce the mature condition, there has been simply a lengthening of the cells at the base of the receptacle, and of the cells of the tissues which in the young sorus are continuous with the indusium. Apparently cell-divisions go on in the superficial layers of the young sorus until sporangia are initiated on the receptacle. Then a lengthening of the individual cells of receptacle and superficial layers produces the stalk of the mature sorus.

The receptacle in the youngest stages examined has in tangential section/

section the outline of an hour-glass (fig. 8). In median section it is shown curved at its tip towards the edge of the leaf (fig. 1). It widens at its apex as it grows older (fig. 3); its lower portion becomes constricted, its apex broadly dome-shaped (figs. 5 and 6). The broad dome-shape is found in the fully developed sorus (fig. 7). In even the youngest leaves which bear sporangia, the vascular tissue in the veins is defined. The young sorus is always produced below a vein and the vascular tissue of the vein runs into the base of the sorus.

In the earliest stages no tracheidal tissue is present in the upper portion of the receptacle or in the stalk (figs. 1, 2, 4 and 6), but the cells of the central series particularly in the lower part of the stalk, become very much elongated and are narrow even in a fairly young sorus (fig. 6). When the stalk reaches its full length, the cells of its central region are more or less in process of change into tracheides; tracheides are at the same time defined in the receptacle proper. In the mature sorus the tracheidal system runs as a narrow strip up through the stalk of the sorus and ends as a fan below the apex of the wide receptacle. Through the base of the stalk this tracheidal system is continuous with the series of tracheides in the vascular strand of the vein upon which the sorus is inserted (cf. Annals of Botany XXVI, fig. 13).

Sporangia appear upon the receptacle as soon as it begins to lengthen (fig. 2). The first sporangium occurs in varying positions on the surface - sometimes near the junction of the large indusial flap with the receptacle (fig. 3); sometimes near the edge of the reduced flap (fig. 2); sometimes midway between these positions (fig.4)

The first sporangium is rapidly succeeded by others, which arise close to it (fig. 4). Two sporangia of approximately the same age sometimes occupy positions near the apex of the receptacle, while others very slightly younger, appear nearer to its margins (fig. 5).

A comparison of the condition shown in fig. 5 with that in fig,7 in which the oldest sporangia occupy the summit of the receptacle,

while/

while young sporangia appear at the margins, leads us to conclude that the sequence is in the main basipetal but that the sporangia succeed one another rapidly.

In fig. 7 the youngest sporangia figured are at the apex of the receptacle, among the stalks of the oldest. This mixed condition of the mature sorus was figured in Ann. of Bot. XXVI pl. XXIX, figs. 13, 14, and 15. The suggestion made in the earlier paper (ibid. p. 254) that the sorus is of a mixed type upon a Gradate receptacle is confirmed by the details shown in figs. 5 and 7. The sequence of sporangia shown in these figs. proves that the succession of the earliest sporangia is essentially basipetal.

DEVELOPMENT OF THE SPORANGIUM.

The earliest stages of the development of the sporangium are figured in figs. 9, 10, 11 and 12. The cell which becomes a sporangium is often wedge-shaped (fig. 9). The first wall may be transverse (figs. 9 and 10) or oblique (figs.11 and 12). The oblique wall more frequently occurs, to judge by the condition of various later stages (figs. 15 and 16). Fig. 14 suggests a later condition of the type shown in fig. 9. Where the first wall is transverse the one which immediately succeeds it is oblique (figs. 13 and 14). And this second oblique wall commonly meets the first at its junction with the lateral wall (figs. 13 and 14). Where the first wall is oblique, it may meet the lateral wall at its junction with one of the walls forming the wedge-shaped base of the cell (figs. 15 and 16); it may meet the lateral wall about half-way down its length (fig. 12), or it may meet one of the basal walls (fig. 11). A wall next cuts the oblique wall at right angles (fig. 15) and that which succeeds this is parallel to the first oblique wall (fig. 16). In fig. 17 is shown the central cell of the capsule fully formed, while the cells of the stalk are definitely delimited. The later stages in the development of the sporangium and the mature sporangium itself have already been described (loc. cit., p. 254). The/

The mature sporangium is long-stalked and has an oblique annulus, the cells of which are continuous past the stalk (loc. cit. pl. XXIX, figs. 16 and 19).

We can now consider how these features of the sorus and sporangium affect the systematic position already assigned (loc. cit. pp. 264, 265) to Peranema.

The character of the vascular system and the structure of the mature sorus and sporangium led to the conclusion that Peranema occupied a position intermediate between the Cyatheaceae and the Aspidieae group of Polypodiaceae. A basal indusium of cup-type is characteristic of the Cyatheaceae (Bower, '99, p. 52). In Peranema the cup is "developed unequally on its two sides and contracted at its rim, which is turned inwards" (Davie, '12, p. 253). The early stages show that it is of the Cyathea-type, with a part of one side of the cup lagging behind the rest of the indusium (cf. above, pp. 1, 2, and 3). The stalk is apparently a late growth, due to an elongation of certain cells of the receptacle and superficial layers. The sorus with its basal cup-indusium is certainly of Cyatheaceous type. The form of the receptacle - widely dome-shaped at maturity - recalls that found among the Gradatae (Bower, Land Flora, p. 635). The first sporangia arise at the apex of the receptacle; the subsequent sporangia follow in basipetal sequence. But the mature sorus is a mixed one. This shows a step in advance of the Cyatheaceae. The sporangium develops in the manner of one of the Gradatae (loc. cit. p. 638). The wedge-shaped base and the oblique first wall correspond to similar features in the sporangia of Thyrsopteris and Alsophila (loc. cit. pp. 590, 603). The early segmentations in the sporangia in figs. 14, 15 and 16 are of the Cyatheaceous type. Those/

Those found in figs. 11 and 12 are apparently also to be found in some species of Nephrodium (Kündig, '88.). The early divisions shown in figs. 10 and 13 resemble those in the Polypodiaceous sporangium, to which the mature sporangium of Peranema, with its long stalk and almost vertical annulus bears some resemblance. Thus some sporangia figured resemble those of the Cyatheaceae, others those of the Polypodiaceae. And as a whole the sporangium of Peranema is intermediate between those characteristic of the Cyatheaceae and those found in the Polypodiaceae, although there is in it a preponderance of Cyatheaceous characters. We have then to set against a distinctly Nephrodioid vascular system, mixed sorus, and "aspidioid" spores (Davie '12, pp. 255, 264) a Cyatheaceous indusium and early sporangial segmentation, a Gradate receptacle and early sporangial sequence and spore-number (loc. cit. p. 254). We conclude that Peranema is a fern descended from a Cyatheaceous line and somewhat advanced on the main Cyatheaceous type towards a "Nephrodioid" type.

This is interesting, apart from general phyletic considerations, in the light which it throws upon the sorus of Nephrodium. If the whole of one side of the cup of the Cyatheaceous sorus were to be suppressed, and the other side much developed so as to overarch the receptacle, we should have the type of Nephrodium. In Peranema we have in the early sorus a partial suppression of the one side of the cup and a great overarching development of the remainder of the indusium. If we for the moment neglect the presence of the stalk, we have in the early Peranema sorus the intermediate stage between the type of Cyatheaceous sorus and that of Nephrodium. The extension of the sorus of Peranema beyond the level of the leaf-surface seems to permit of an increase of the receptacular area upon which the sporangia may be developed. In/

In well-developed sori the sporangia are actually produced all round the stalk (cf. fig. 18). Even in the ordinary sorus there is a tendency to extend the receptacle upwards towards the leaf-surface (the figures of the sorus are reversed from their natural position, since in nature the sorus grows vertically downwards from the under surface of the leaf), while the indusium becomes very much stretched out over this extension. The section figured in fig. 18 was cut transversely to the stalk, just above the junction-point of stalk and sorus, and it shows how the large "flap" of the indusium becomes extended on the side of the stalk from which it arose and pushed some distance along the stalk as two narrow pouches. In the sori of Nephrodium and Polystichum the receptacle is present round the stalk and, in Nephrodium, forms two pouches on one side of it - making the lobes of the "kidney". In Peranema, however, the receptacle is always above the indusium; in Nephrodium and Polystichum it comes to be below.

Apparently there arose in the sorus of Peranema a need for space in which to develop more sporangia. Instead of the receptacle being lengthened from the surface of the leaf, to which the indusium remained attached, receptacle and indusium were shot out beyond the surface, well below which the further elaboration took place. There such extensions and involutions as are figured for one sorus in fig. 18 had ample room to develop. To conclude the comparison, this parallel between the condition in the mature sorus of Peranema and that in a mature sorus of Nephrodium helps to strengthen the view that Peranema occupies an intermediate position between the Cyatheaceae and the Aspidieae group of Polypodiaceae (which includes the genus Nephrodium).

THE PROTHALLUS.

Schlumberger ('11) has described the prothalli of Diacalpe aspidioides, Bl., Woodsia obtusa, Torrey, and W. ilvensis, Br. On the prothallus of Diacalpe he found multicellular hairs, mainly on the region of the cushion. These sometimes had glandular heads, less frequently were devoid of them. Similar hairs were found on the prothalli of Woodsia obtusa, while on the prothallus of Woodsia ilvensis glandular hairs, usually on a one- or two-celled stalk, were present.

Multicellular hairs are present on the prothalli of the Cyatheaceae (Heim, '96). Thus the prothallus of Diacalpe resembles that characteristic of that family, while the Woodsia prothallus shows a movement from such an affinity towards the Polypodiaceae.

On the prothallus of Peranema glandular hairs are present, both on the margins of the wings and on the cushion. Those on the cushion are larger than those on the wings; both types are unicellular, and exactly resemble the terminal cells of the hairs figured by Schlumberger for the prothalli of Diacalpe and Woodsia. Many of the hairs on the cushion are placed upon slightly raised superficial cells (fig. 19) and resemble the example figured by Schlumberger from Woodsia ilvensis (loc. cit. fig. 1. 9). At the same time there are many which closely agree with the glandular hairs which are present on the prothalli of Nephrodium Filix-mas (Kny, '95, Taf. XCVII and C.).

From the structure of the antheridia on the prothalli described by him, Schlumberger was able to form a series linking the Cyatheaceae with the Polypodiaceae (cf. Bauke, '76). Diacalpe has a divided lid-cell in its antheridium; Woodsia obtusa has a divided lid-cell of two unequally-sized parts; Woodsia ilvensis has an undivided lid-cell. In the last species the rupture of the antheridium is brought about by the discharge of the lid-cell, just/

just as in the other two.

Heim ('96) distinguished between the more primitive families of Cyatheaceae, Hymenophyllaceae, etc., and the Polypodiaceae on the method of rupture of the antheridium. In the former the lid-cell was discharged: in the latter it was broken through (loc. cit. pp. 356, 369).

Schlumberger points out that in Woodsia ilvensis the remains of the cuticle which covers the lid-cell persist as a fringe round the neck of the antheridium after the lid-cell has been discharged. The resemblance to the ruptured antheridium of the Polypodiaceae is then so close as to destroy the value of the antheridial dehiscence-method as a differential criterion (Schlumberger '11, p. 396). In Peranema the lid-cell of the antheridium is generally undivided and is discharged at the maturity of the antheridium, which then presents exactly the appearance of the antheridium of Woodsia ilvensis, figured by Schlumberger (loc. cit. figs. 7 and 8). Only one antheridium was found with a divided lid-cell (fig. 20), though many were examined in the youngest, semi-mature and mature stages. This feature of one antheridium, taken along with the features of some of the glandular hairs, mentioned above, shows that Peranema retains a suggestion of the Cyatheaceous type in its prothallus, which on the whole approaches even more closely than that of Woodsia ilvensis to the type of the Polypodiaceae.

Among the three closely related genera within the Woodsieae-Woodsiinae group, to which Peranema undoubtedly belongs, the sequence now appears to be Woodsia - Diacalpe - Peranema. Woodsia has a Gradate sorus, and prothallial features which relate it to the Cyatheaceae; Diacalpe has a mixed sorus, with a basal indusium, and an unmistakable Cyatheoid prothallus, which give it an intermediate position; Peranema has a mixed sorus with a modified/

modified basal indusium and a Nephrodioid prothallus, which place it near to the Aspidieae. Already in the features of the sori and prothalli of Woodsia and Diacalpe we have had indications of a line pointing towards the Polypodiaceae, but clearly originating in the Cyatheaceae. The extraordinary similarity of the vascular systems of Peranema and Diacalpe and Nephrodium Filix-mas has laid the end of that line in the Aspidieae; the details in the description of the mature sporangia of Diacalpe and Peranema have confirmed the theory founded on the vascular system (Davie '12, p. 264). And now in the account of the development of the sorus and sporangium of Peranema we have evidence which strengthens this view.

Peranema is not itself a link between the Cyatheaceae and the Polypodiaceae. But features in its development, taken in conjunction with features of Woodsia and Diacalpe, suggest that the process of evolution has moved through types like the Cyatheaceae to types like those found in the Aspidieae group of Polypodiaceae. The account given above of the sorus, sporangium and prothallus of Peranema permits us with confidence to assert that the phyletic line already traced by Professor Bower from the Gleicheniaceae through the Cyatheaceae (Bower '12) has proceeded through the Woodsieae-Woodsiinae group to the Aspideae group of the Polypodiaceae. Further stages along this line probably moved from Nephrodium (of whose sorus we now possess an interpretation) through Aspidium and Polystichum to Polypodium.

SUMMARY.

1. The sorus of Peranema cyatheoides, D. Don, arises superficially on the under side of the leaf; it has a basal indusium, of cup-type, with one portion of the cup suppressed in development and the other overarching the receptacle and becoming contracted at its rim; the receptacle is of the Gradate type; the central part of the stalk of the sorus is continuous with the receptacle and the peripheral part is continuous with the indusium.

2. The early sporangia arise in basipetal sequence; the mature sorus is a mixed one.

3. The sporangium in its early segmentation sometimes follows the Cyatheaceous type, sometimes the type of the Polypodiaceae.

4. The prothallus bears glandular hairs, sometimes slightly raised above the level of the surface upon unicellular bases; the antheridium has been found in every case but one to have an undivided lid-cell.

5. On a general comparison of the features of Peranema and the closely-related genera in the Woodsieae-Woodsiinae group of Polypodiaceae, a grouping Woodsia - Diacalpe - Peranema is suggested. Woodsia comes nearest to the Cyatheaceae, Peranema to the Polypodiaceae.

6. The mature sorus of Peranema is held to be related to that of Nephrodium and a phyletic line is traced from the Cyatheaceae to the Aspidieae group of Polypodiaceae.

DESCRIPTION OF PLATES.

Figures 1, 8, 9, 10, 13, 14, 15, 16, 17 have been drawn with the aid of an Abbé camera lucida.

Figures 2, 3, 4, 5, 6, 7, 11, 12, 18, 19, 20 have been drawn with the aid of a Leitz drawing apparatus.

Fig. 1. Vertical section through a very young sorus of Peranema cyatheoides, D. Don, showing one large indusial flap almost completely covering the receptacle. No sporangia have been developed on the receptacle. At the right side there are one or two cells with thickened cell-walls, representing the laggard portion of the indusium. X 450.

Fig. 2. Vertical section through a slightly older sorus. The receptacle has become extended through the gap between the portions of the indusium. The laggard portion of the indusium is now distinct, and the whole indusium shows a cup-shape. One sporangium is initiated near the lower margin of the receptacle. X 150.

Fig. 3. Vertical section through a young sorus showing the modified cup-shape of the indusium. One portion of the indusium completely overlaps the receptacle. A sporangium is just initiated near the junction of the receptacle and the large indusial flap. X 150.

Fig. 4. Vertical section through an older sorus, showing the "kink" at the highest point of the large indusial flap. One sporangium occupies the centre of the receptacle, while a slightly younger one is initiated next to it. X 150.

Fig. 5. Vertical section through an older sorus, showing the extension of the large indusial flap over the receptacle, which is now widely dome-shaped. Two sporangia of approximately equal age occupy the summit of the receptacle; younger sporangia occur nearer its edges. X 150.

Fig. 6. Vertical section through an older sorus, showing the extension of the receptacle and the cells continuous with those of the indusium, forming the start of the "stalk" of the sorus. The cells at the base of the receptacle, in the developing stalk, are considerably elongated and narrow, but no tracheides are at this stage present in the sorus. One sporangium is seen at the summit of the receptacle. X 150.

Fig. 7. Vertical section through a semi-mature sorus, showing the "stalk" fully developed. The main indusial flap now completely covers the wide receptacle and is incurved at its tip. The small knob opposite to this incurved tip represents the remains of the laggard portion of the indusium. The "kink" shown in figures 4 and 5 has developed as the series of cells on the right of the sorus and now extends almost at right angles to the "stalk". The youngest sporangia occur among the stalks of the oldest at the summit of the receptacle; quite young sporangia appear at its margins. The sequence of sporangia is thus at first basipetal, and later mixed. X 65.

Fig. 8. Tangential section through a very young sorus, showing the receptacle and many-layered indusium. X 450.

Fig. 9. A young sporangium, showing a wedge-shaped base. The first division-wall is transverse. X 450.

Fig. 10. Another form of young sporangium, with a transverse first division-wall. X 450.

Fig. 11. A young sporangium, with wedge-shaped base and oblique first division-wall. X 660.

Fig. 12. Two young sporangia, with oblique first division-walls meeting the lateral walls of the sporangia. X 660.

Fig. 13. A young sporangium, of the type shown in fig. 10, with the second division-wall oblique and meeting the first transverse division-wall at its junction with one of the lateral walls. X450.

Fig. 14. A young sporangium of the type shown in fig. 9, with an oblique division-wall sueceeding the first transverse division-wall. X 450.

Fig. 15. A young sporangium, of the type shown in fig. 12, with an oblique second division-wall meeting the first division-wall. X 450.

Fig. 16. An older sporangium, of the type shown in fig. 15, with the covering cell of the capsule defined and an oblique third division-wall meeting the second wall and parallel to the first. X 450.

Fig. 17. A sporangium with the stalk and the central cell defined. X 450

Fig. 18. Transverse section across a mature sorus just above the junction of the stalk and the sporangium-bearing portion. The lips of the large indusial flap are shown on the upper side of the figure. On the lower side, in the right-hand corner, is one of the pocket-extensions of the indusium, covering several sporangia. In the left-hand corner is the upper part of a similar pocket, which extends further down the stalk than the right-hand pocket. X 35.

Fig. 19. Unicellular glandular hair from the cushion of the prothallus. It is situated upon a single superficial cell, the wall of which is raised slightly above the general level of the surface of the prothallus. X 660.

Fig. 20. Vertical section through an antheridium, showing a divided lid-cell, and containing several coiled spermatozoids. X 660.

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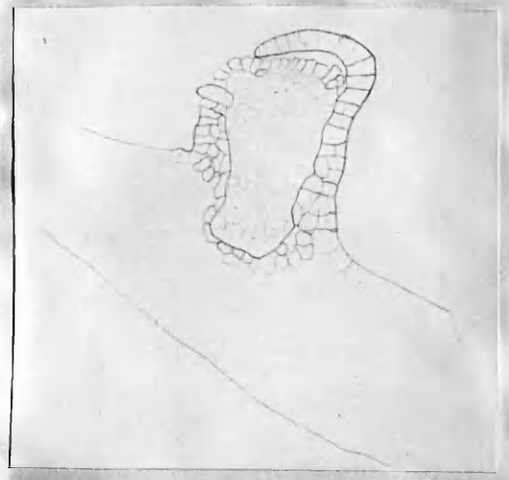

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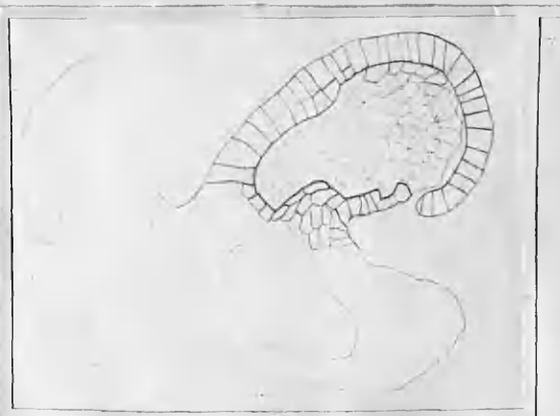

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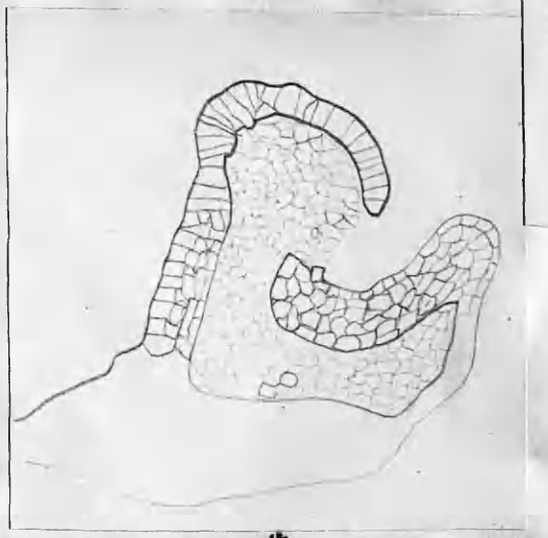

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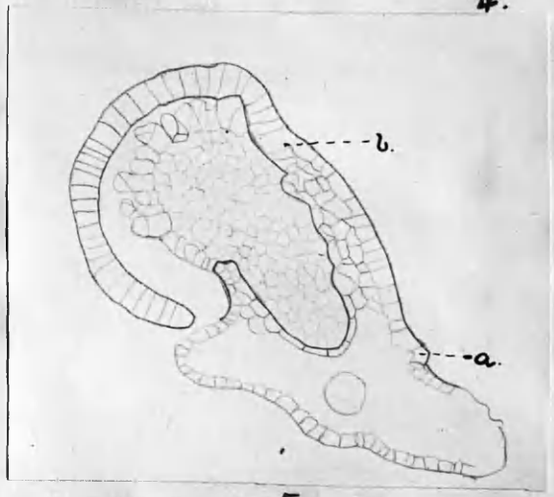

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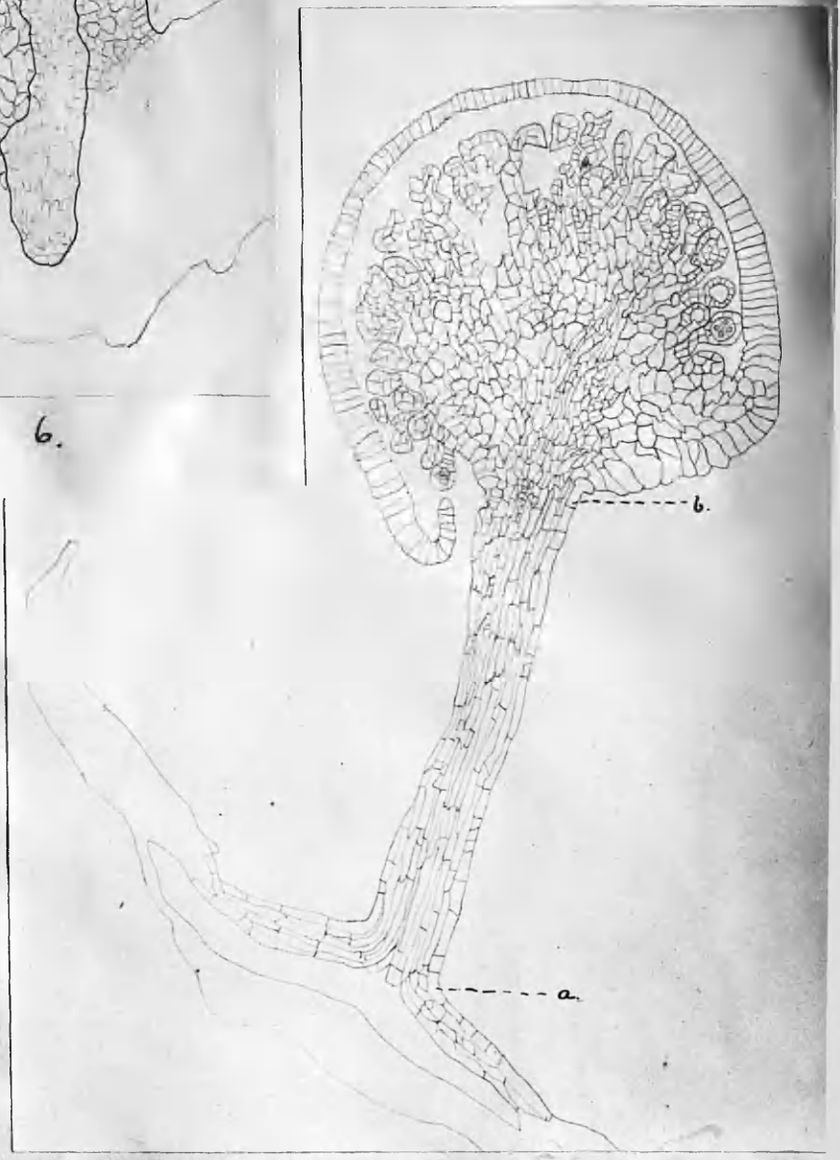

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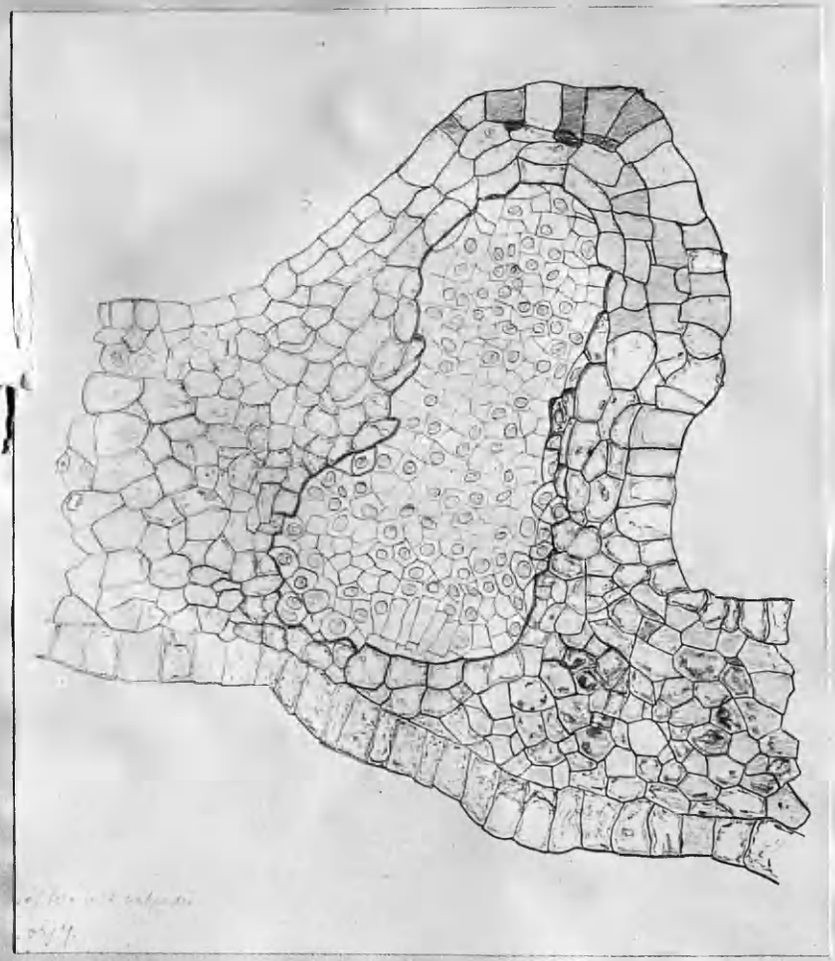

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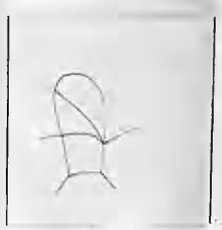

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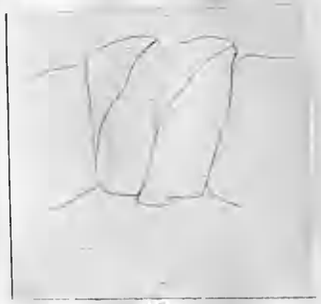

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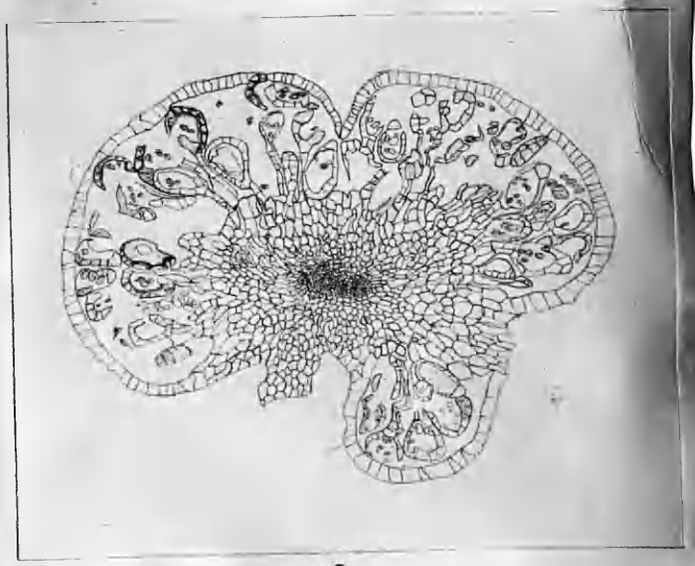

18.

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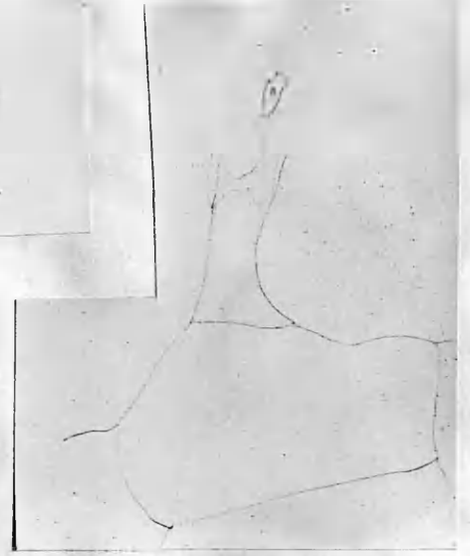
17.



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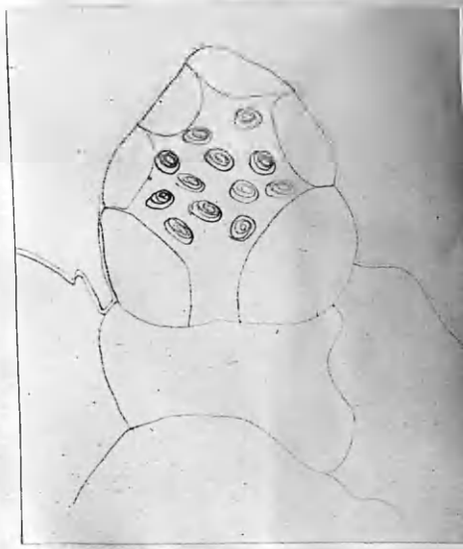

20.