The Structure and Development of the Prothallus of Equisetum debile, Roxb.

BY

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With forty-five Figures in the Text.

INTRODUCTION.

ALL the species of *Equisetum* whose prothalli had been investigated before 1905 are confined to Europe (Goebel, p. 195). The writer is not aware if any extra-European species have been investigated since then. As the prothalli of *Equisetum debile* whose range is given by Baker ('Fern Allies', p. 5) as 'Tropical Asia from the Himalayas and Ceylon eastward through the Malay Isles to Fiji', were found growing in large numbers along the banks of the river Ravi in Lahore, and as they differed in general characters from the prothalli hitherto described, it was thought that a study of the development might bring out some interesting points. The result of this study carried on in the winter of 1912–13 is given in the following pages.

Aitchison and Stewart describe *Equisetum debile* as the only species of *Equisetum* occurring in the Punjab, and certainly this is the only species met with in or near Lahore. It may be mentioned that Baker remarks that this species is doubtfully distinct from *Equisetum ramosissimum*, Desf., which is cosmopolitan in the warm temperate and tropical zones, but nothing is known as regards the prothallus of this latter species.

MATERIAL.

The plant grows in and near Lahore in great abundance along the banks of the river in sandy soil or in the shady and swampy soil of the wood along the river. In the former place it remains tufted and small, being only a foot or two high, but in the wood it may reach a height of 10 to 15 feet, being supported by the neighbouring trees, and attain a thickness of half a centimetre. For general characters Baker's 'Fern Allies' may be consulted. The small spikes are formed at the ends of ordinary branches

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and are ripe in September to October. The spores were often found in bluish-green masses filling the space between the last normal leaf-sheath and the stem below the spike.

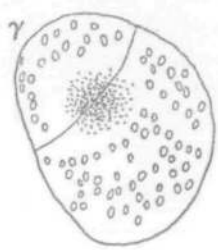
For very early stages the spores were grown in the laboratory in soil brought from the river bank where the prothalli were ordinarily found growing. The soil, which is a mixture of sand and clay, was sterilized by heat before the spores were sown. For the study of the mature prothallus, material was always collected from the river-side.

Germination of the Spore.

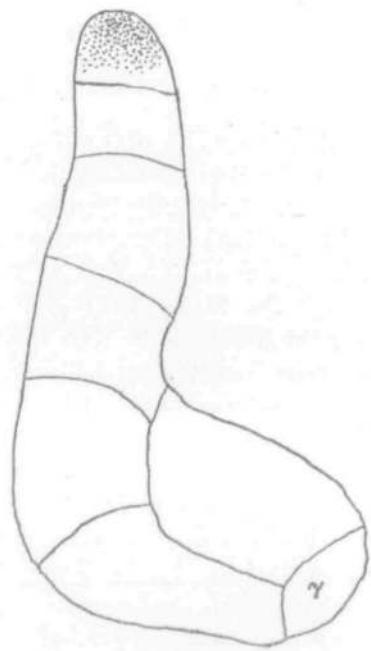
The spores germinate readily. The first wall is curved, and it divides the spore into a small cell containing a few chloroplasts and a larger cell



Text-fig. 2.

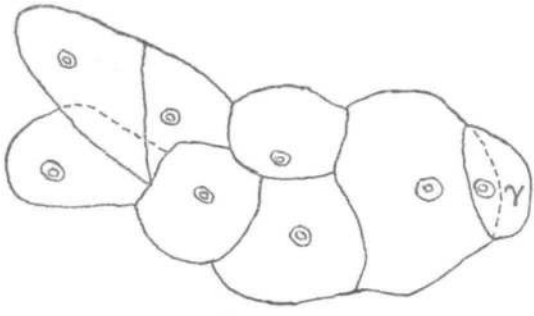


Text-fig. 1.

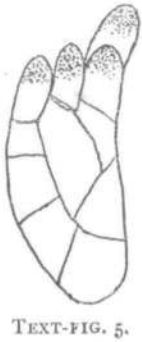


Text-fig. 3.

which contains most of the chloroplasts. Later on the chloroplasts disappear from the small cell (Figs. 1 and 2). The next divisions are very variable. The small cell may grow out soon into a rhizoid, or may remain as it is for a much longer time, or it may not grow out at all. The larger cell may grow in length and become divided by transverse walls only, so that it forms a longer or shorter filament (Figs. 2 and 10). In other cases a longitudinal wall may be first formed in the larger cell, and either one or both of the cells thus formed may grow forward or laterally and divide by transverse walls (Fig. 3). In yet other cases the walls in the larger cell may



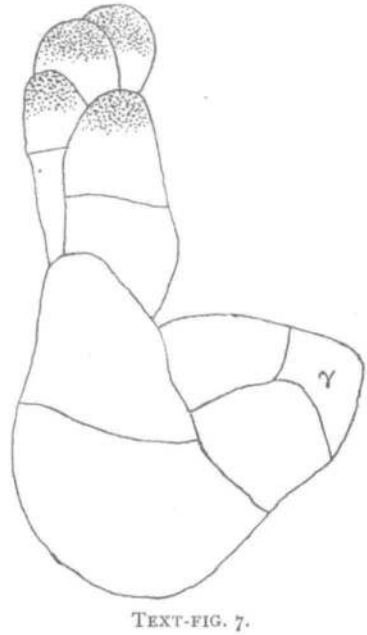
TEXT-FIG. 4.



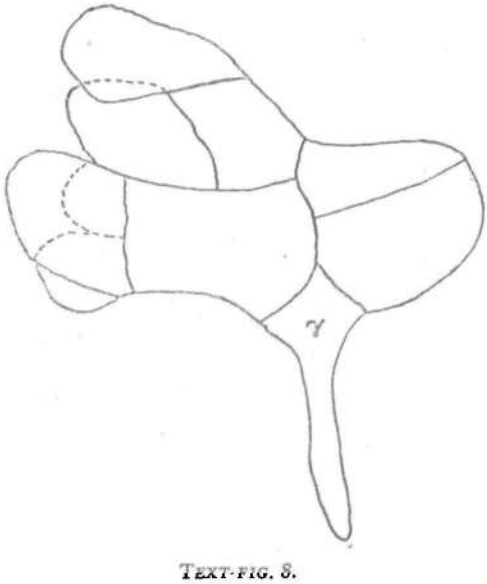
TEXT-FIG. 5.



TEXT-FIG. 6.



TEXT-FIG. 7.

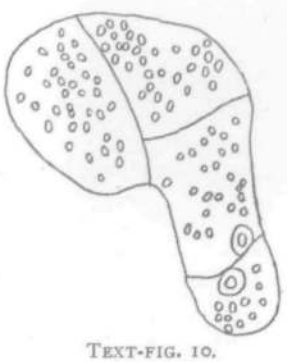


TEXT-FIG. 8.



TEXT-FIG. 9.

be so formed that a cell-mass results (Figs. 5, 7, 9). After the formation of these cell-walls, cells from the surface may project upwards by increase in length (Figs. 5, 6) and ultimately by further divisions develop into the characteristic lobes; or only a single cell projects outwards from the cell-



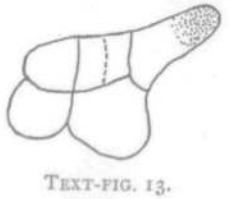
TEXT-FIG. 10.



TEXT-FIG. 11.



TEXT-FIG. 12.



TEXT-FIG. 13.



TEXT-FIG. 14.



TEXT-FIG. 15.

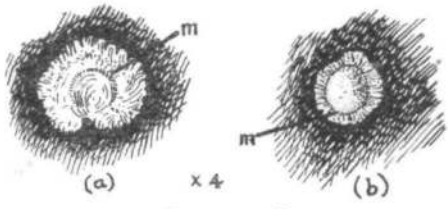
mass, and this in its turn gives rise to several cells which project upwards and form the characteristic lobes (Fig. 7). Thus when a cell-mass is first formed after the germination of the spore the prothallus body may be formed directly or indirectly through the formation of a 'primary tubercle'. In the meantime rhizoids grow out from the lower surface which fix the erect prothallus to the soil (Figs. 14, 15).

MATURE PROTHALLUS.

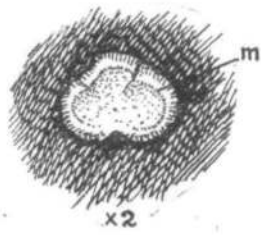
As described above, the lobes arise from single cells which have increased in length and project above the general level, and are naturally

quite small and simple at first. As these cells grow they become divided by transverse and vertical walls, and more cells from the side of these rudimentary lobes begin to grow vigorously and project outwards. Thus the lobes become branched, and although united at their bases to the main body of the prothallus (as yet only the cell-mass more or less changed by this time) and to each other, they are quite free above (Figs. 14, 15). Soon the cells at the base of all the lobes begin to divide so that they contribute to the tissue of the cell-mass below and form new lobes above. Thus the structure of the mature prothallus is established.

Numerous prothalli were found growing wild on the river bank, less than one millimetre in diameter, looking like green or red pin-heads. Even at this stage they have the same essential structure as the large prothalli of a diameter of 3 centimetres. They are minute hemispherical cushions consisting of compact parenchymatous tissue in their lower half, and of perfectly



TEXT-FIG. 16.



TEXT-FIG. 17.

erect lobes, with narrow spaces between them, in their upper half. A very good idea of their structure can be obtained by saying that they resemble miniature cauliflowers without the surrounding leaves. The prothallus is firmly fixed to the soil by numerous rhizoids. The rhizoids are so numerous and so firmly attached to the mud that it is very difficult to wash it away, and usually most of the rhizoids are removed during the operation. The rhizoids are smooth long hyaline unicellular structures and do not present any peculiarity.

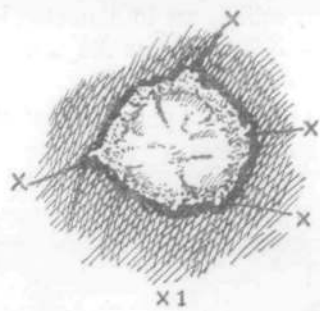
At a stage when the diameter of the hemispherical prothallus is about $\frac{1}{8}$ to $\frac{1}{4}$ of an inch (3 to 6 millimetres) it is usually of a circular outline with an entire margin (Fig. 16 *b*). Often, however, the outline is cordate or reniform with a notch on the *posterior* end, probably due to the manner of cell-division in the early stages. When a cell-mass has given rise to the prothallus directly, the outline naturally would be circular, as the meristem is developed uniformly on all sides. If the prothallus is formed after the formation of filaments or a 'primary tubercle', the meristem arises late on the *posterior* end and has a reniform or cordate outline (Figs. 16 *a*, 17). There is, however, no trace of the 'primary tubercle' in the older stages.

The lower part of the prothallus, as stated above, consists of parenchymatous cells without any air spaces between them. The cells are usually all similar, but sometimes some cells are elongated in the radial direction, and all are thin walled. All the cells in this part are full of starch grains, the chloroplasts which were present in the whole body in the early stages having been transformed into leucoplasts. This transition is gradual and the upper layers of the compact part are green like the lobes.

The meristem is situated all along the margin (Figs. 16, 17) on the under surface, and it produces the parenchymatous cells of the compact



TEXT-FIG. 18.



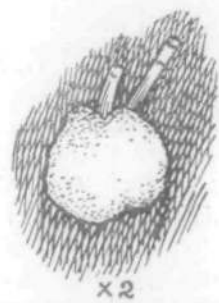
TEXT-FIG. 19.



TEXT-FIG. 20.



TEXT-FIG. 21.



TEXT-FIG. 22.

portion and the lobes of the upper spongy portion. The ventral position of the meristem explains the fact that the under surface of the prothallus is almost always concave. The upper spongy portion consists, as stated above, of lobes. Each lobe arises from the single projecting cell of the meristem, which divides at first by transverse walls and then by other walls in various directions. Later, some cells from the side of the lobe grow out and behave like the cells of the meristem, and the lobe thus becomes branched. The lobe at its base is several cells thick, but higher up it becomes thinner and the ultimate part is only a single layer of cells in thickness. The terminal cells in all cases are very turgid and either spherical or more or less deeply lobed and form a tuft (Figs. 23–27).

On account of the ventral position of the meristem the young lobes are directed obliquely forwards and upwards, but are soon carried upwards and become perfectly erect.

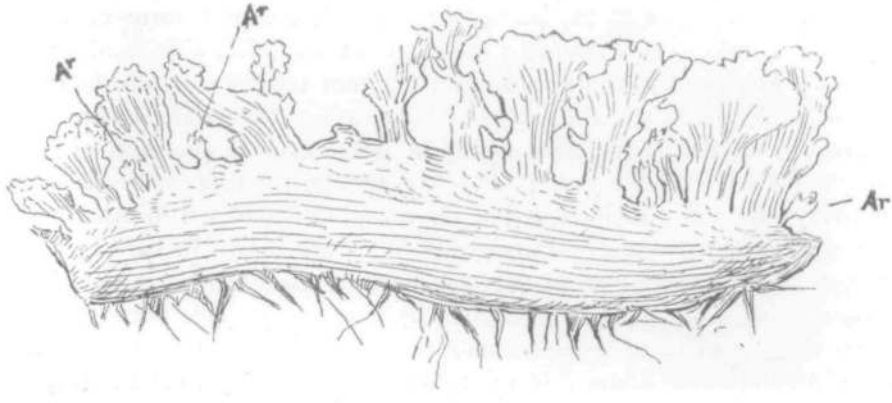
The upper surface of a comparatively small prothallus has the form shown in Fig. 22; it is quite smooth and slopes down gradually towards the margin, but in large prothalli furrows and ridges appear on the surface (Fig. 18) partly owing to the unequal height of the lobes and partly to the inequalities of the soil. These furrows are, however, quite superficial.

The margin of the prothallus is quite entire in small prothalli (Figs. 16 *a* and 16 *b*), but as the prothallus increases in size the whole body of the prothallus becomes lobed. This is chiefly due to mechanical reasons, as the prothallus in its advance comes into contact with foreign bodies which interfere with the growth. Moss plants were often found in the fissures between these lobes of the prothallus; also a compact form of *Riccia crystallina*, which is extremely common on the river-side, and similar bodies. The prothallus may have an inherent tendency to divide, but it cannot be definitely stated as regards this species. According to Campbell dichotomy of the archegonial meristem does occur in prothalli of other species ('Mosses and Ferns,' p. 453). Although the first cleft was found in many cases in the median line in many heart-shaped prothalli, this was not always the case. Two such fissures are shown in Fig. 17. The margin of the prothallus on the two sides of the fissure are in intimate contact with each other, so that there is hardly any space between them. The existence of these fissures cannot be detected from an examination of the prothallus from above; in most cases it is necessary to wash away the mud from the ventral surface to demonstrate their presence.

Looked at from above the prothallus appears merely to be spongy, and one would not suspect the existence of separate lobes inside, so closely together are they situated. This compactness, however, varies to some extent with external conditions. The colour of the prothallus also varies similarly. If the prothallus grows in an exposed place directly exposed to intense light, it is invariably compact and red in colour. (If one part of the prothallus is exposed to direct sunlight and the other shaded—e. g. if the prothallus happens to be growing in a pit obliquely—the two colours may be seen in the same prothallus.) There is absolutely no trace of the lobes from the surface. The red colour is due to the presence of a pigment in the numerous chloroplasts of the upper cells of the lobes in addition to chlorophyll. The red colour easily comes out if the prothallus is placed in absolute alcohol, while chlorophyll remains in the chloroplasts for a much longer time. The pigment is probably a decomposition-product of chlorophyll. If the prothallus grows in a shaded place under some tree or in some small pit, or if it is kept in the laboratory, it is always of a bright green colour and less compact. If a compact prothallus of a red

colour is brought to the laboratory and kept inside the room in very dim light with plenty of water, the new parts formed are yellowish green in colour and much more open than the older parts. The lobes also are longer, less broad, and more branched (Figs. 19, 23, 24, 26). This condition may be compared to etiolation in Flowering plants.

A well-grown prothallus that has been growing for some months may be as much as 3 centimetres in diameter; usually it is only 2 to 3 millimetres in height, including the lobes. The smaller prothalli also are of about the same height, so that the height does not vary so much as the diameter. Usually a little less than one-half of the height is formed by the lower compact part of the prothallus, and it consists of 6 to 12 layers of cells. The rest of the height is formed by the projecting lobes (Fig. 23).



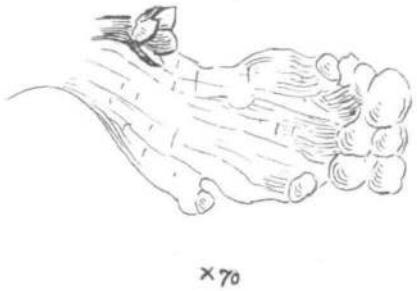
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TEXT-FIG. 23.

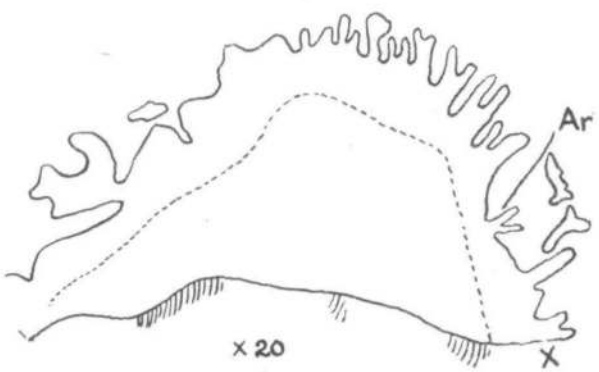
In some cases, however, the lobes were found to be very small and the lower part of the usual thickness or much thicker (Fig. 25). In Fig. 25 the thickest part of the lower half below the lobes consisted of about twenty layers of cells. In very large prothalli the central part may die, and if the prothallus is lobed the lobes may become more or less separated and continue to grow independently for some time. It reminds one of the similar process in the Liverworts.

Lastly, it may be mentioned that the prothallus is very often attacked by a fungus, often found in the upper cells of the lobes, though the cells at their base also may be sometimes affected. The fungus does not appear to do much harm: on the contrary, the prothalli seem to be flourishing vigorously. The contents of the affected cells are transformed into small and large brown globules, stained black with osmic acid. When stained with fuchsin-iodine green mixture, they take the green colour in preference to the fuchsin. The fungus multiplies by minute oval conidia formed in chains on erect

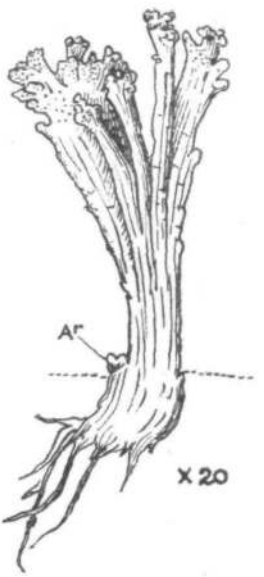
conidiophores which have come out of the cells. It is probably a case of parasitism, and as the prothallus is so large it is not very injuriously affected. Occasionally prothalli were found showing the destruction of a



TEXT-FIG. 24.



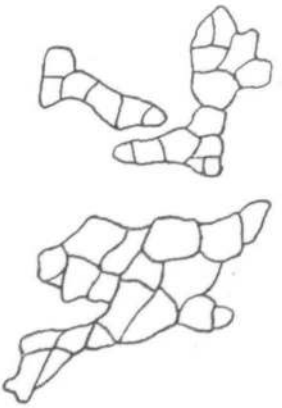
TEXT-FIG. 25.



TEXT-FIG. 26.

large patch of the terminal cells of the lobes, while the rest of the prothallus was growing normally. Infection of prothalli of other species by Fungi also occurs (Tubeuf).

The small spaces between the lobes serve to attract water by capillarity. If a prothallus is watered plentifully the water can be seen rising in various parts of the prothallus, and the whole may become quite wet, if the amount of water was sufficiently large, by absorption of water from below.



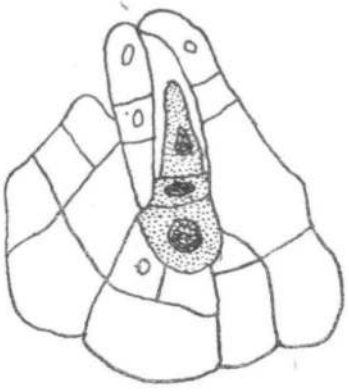
TEXT-FIG. 27.

Sexual Organs.

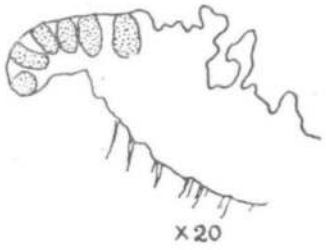
Archegonia. The prothallus invariably forms archegonia first, the antheridia being formed only on older female prothalli. Out of several hundred prothalli of all ages which were examined not one was a pure male, but most were female and others bore antheridia in addition to archegonia. The antheridia, moreover, are formed very late in the year.

Archegonia were found on prothalli less than 1 millimetre in diameter. They are formed as usual at the base of the lobes, but all the lobes may not bear them. They are formed in very large numbers and may be 200 or more in vigorous prothalli. The early stages are difficult to follow satisfactorily, as the development is very rapid and the cells in young archegonia do not differ from the ordinary cells of the prothallus. In the mature archegonium the neck projects freely and consists of four rows of cells, each row in the free part consisting of two or three cells. The terminal cells are very long, and on maturity become brownish and bend strongly outward after separating from each other. The most interesting feature in the archegonium, however, is that there is a single neck-canal cell, and not two cells as is the case in other species of *Equisetum.* The ventral canal-cell is small with only a little cytoplasm round the nucleus. The egg at this stage is concave or flat above. Later the canal-cells become disorganized, and if the archegonium is not fertilized the egg also shares their fate and becomes brown, but if fertilized the egg becomes enlarged and rounded. No embryo was found on any prothallus before the end of December. Thus all the archegonia produced before that time were never fertilized and the prothalli continued to increase in size. The fact that all these archegonia were barren is explained when it is mentioned that no antheridia were found before December. Figs. 28–30 show the structure of the archegonium.

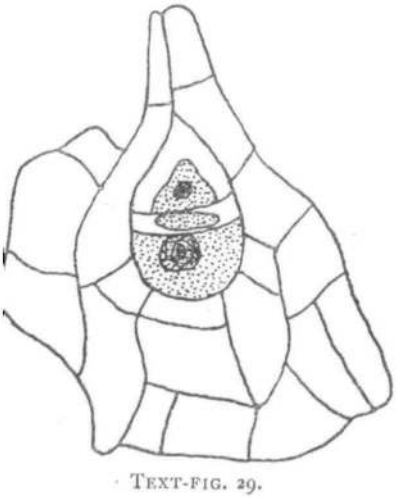
Antheridia. The antheridia are usually formed on prothalli which have been growing for months and are therefore large. Occasionally, however, they occur on small prothalli which have produced comparatively few archegonia, but in no case antheridia alone were found. They are produced at the margin by the meristem and are always embedded. They are not formed along the whole of the margin continuously (Figs. 20, 21). On account of the greater lateral development as compared with radial growth when antheridia are being formed the margins generally become folded. As a rule the formation of lobes is stopped, but this is not invariably the case. Fig. 33 shows an antheridium at the base of a lobe. Even when no large lobes are formed between the antheridia, they are represented by short filaments as shown in Fig. 32. The position, general arrangement of antheridia, and the presence of 'paraphyses' are points which strikingly recall the figures of the same objects in the prothallus of *Lycopodium clavatum* as given by Lang and Bruchmann. The paraphyses contain chloroplasts.



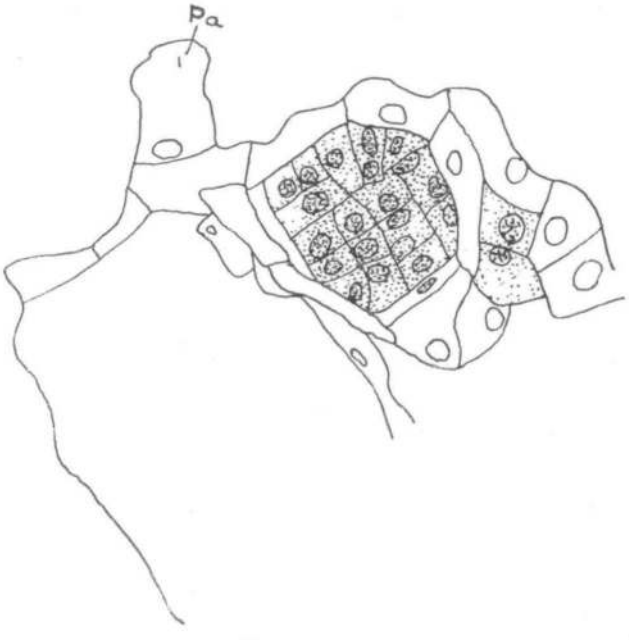
TEXT-FIG. 28.



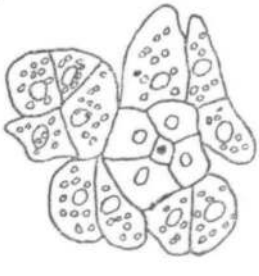
TEXT-FIG. 31.



TEXT-FIG. 29.



TEXT-FIG. 32.



TEXT-FIG. 30.



TEXT-FIG. 33.

It is very easy to distinguish the prothalli bearing antheridia. The folded margins, their red colour (deeper when the whole prothallus is red), their smoother surface, all indicate their presence.

It is known that in other species of *Equisetum* it is possible to convert female prothalli into male by starving them, and as a rule the smaller and poorly nourished prothalli are male. What are the conditions which induce the formation of the antheridia when the prothalli of *E. debile* have been forming archegonia for some time was not determined experimentally. Other considerations, however, make it probable that temperature and age are the determining factors. In the first place only a few *small* prothalli were found even in December bearing antheridia, although small prothalli are very common at that time. In the latter part of December many small prothalli were seen with one or two plants growing out of them. As regards temperature, it will be seen from the following table that the temperature gradually falls from September onwards, and the lowest mean as well as the lowest mean minimum temperature is reached in December and January. I have to thank the officials of the Lahore Meteorological Observatory for the following figures:

TEMPERATURE IN SHADE (FAHRENHEIT) AT LAHORE FOR 1912–13.

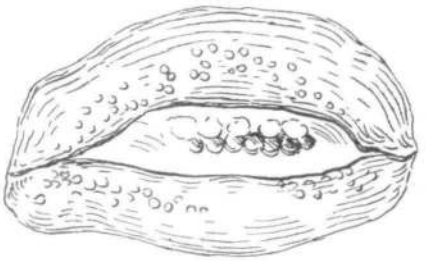
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
			Diurnal range.				
Mean maximum . .	100·2	96·3	80·7	71·9	73·1	70·4	78·0
Mean minimum . .	71·0	60·5	49·2	42·7	42·4	48·7	52·0
Mean	85·6	78·4	64·9	57·3	57·8	59·6	65·0
Average monthly .	29·2	35·8	31·6	29·3	30·7	21·8	25·9
Absolute maximum	103·3	103·4	89·6	77·6	78·4	76·3	94·6
Absolute minimum .	62·5	55·1	38·6	37·2	36·1	39·7	45·2

DEVELOPMENT OF THE ANTHERIDIUM.

It is easy to follow the development, as antheridia in various stages of development are often found in the same vertical radial section (Figs. 31, 32). Each antheridium is developed from a single superficial cell which divides by a periclinal wall; the upper cell contains a large number of chloroplasts in which the red pigment mentioned above is associated with the chlorophyll. These chloroplasts here as in other cells of the prothallus are often concentrically arranged round the nucleus. The lower cell gives rise to the spermatogenous cells. It first divides by a periclinal wall, and later on periclinal and anticlinal walls are formed with considerable regularity. The spermatogenous cells have the same structure as described by Sharp, but plastids are not generally met with. One or more nucleoli are present in the nucleus as in all the cells of the prothallus. The outer cell divides once or twice, rarely oftener, by anticlinal walls and forms a roof of 2–4, or rarely more, cells (Figs. 34, 35). Dehiscence takes place by the separation of these cells (Fig. 34), which also bend outwards. The mature antheridia are

separated from each other by at least two layers of cells, one layer forming the lateral wall of each. In the ripe state, however, the cells of these layers become compressed, and sometimes it is not possible to distinguish them. In the young state they may be separated by a single layer of cells (Fig. 32).

The chromatin in the spermatogenous cells in the early stages of antheridial development is deeply stained with gentian violet in preference to safranin when treated with the triple stain, as is stated by Chamberlain.



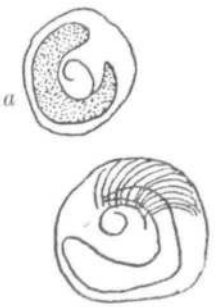
× 300

TEXT-FIG. 34.



×300

TEXT-FIG. 35.



TEXT-FIG. 36.



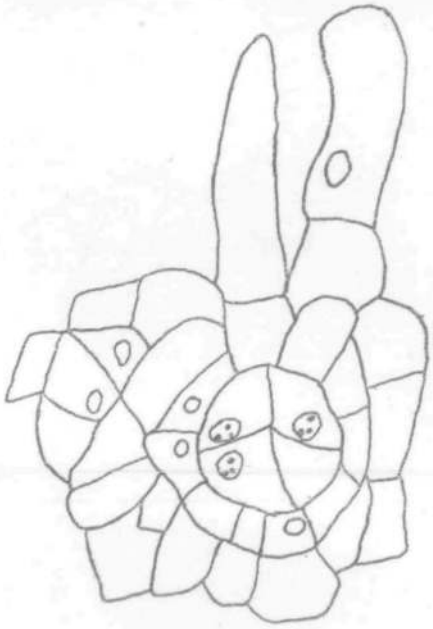
TEXT-FIG. 37.

Later on the chromatin is stained more deeply with safranin. The blepharoplast was seen in sections when the nucleus had assumed the parietal position and had begun to curve (Fig. 36). About this stage the spermatozoid mother-cells, which are already separate from each other, begin to develop a mucilaginous degeneration of their wall, and in sections or teased-out cells mucilage processes are seen spreading out in all directions from the wall, giving the cell a stellate appearance.

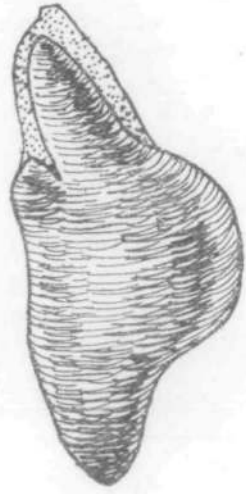
The mature spermatozoid (Fig. 37) is spirally coiled and flattened throughout the greater part of its body. The anterior end is rounded and bears numerous cilia. Quite a large part of the body is formed by chromatin and the blepharoplast. The length of the spermatozoid exclusive of cilia is about 20 μ. It is practically the same as the length of a spermatozoid of *E. arvense*, as given by Sharp, i. e. 19·7 μ.

EMBRYO.

The first wall in the fertilized egg is at right angles to the long axis of the archegonium. The second wall is at right angles to this and produces the quadrants. The octant stage is shown in Fig. 38, where the embryo is cut transversely and obliquely and shows four cells. The hypobasal half produced by the first wall gives rise to the foot and the root, and the epibasal half to the stem and leaf. The foot can be easily recognized by the larger size of its cells. It is at first quite small, but in about a week



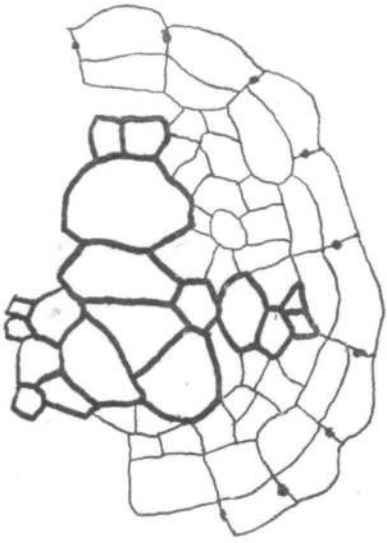
TEXT-FIG. 38.



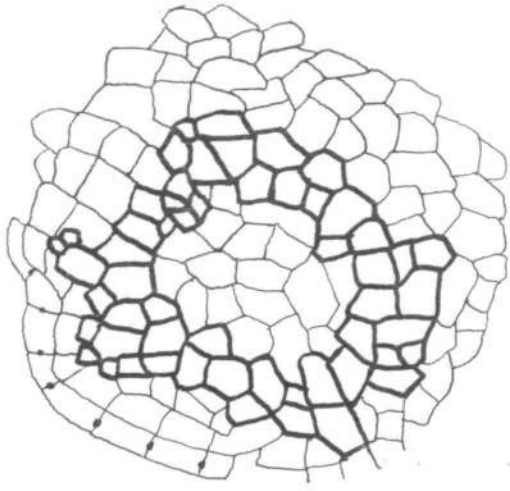
TEXT-FIG. 39.

becomes large (Fig. 39). The young embryo is surrounded by the tissue of the prothallus and the neck also has closed above in the meantime. The first leaves are usually three in number, but two or four are sometimes present as is the case in other species (Campbell). The number of bundles in the stem below the first leaf-whorl corresponds to the number of leaves. The first shoot shows no cavity in the centre, but all the later branches are hollow. The first lateral branch is given off very early and always below the first leaf-whorl. It is given off on the side away from the foot and comes out by passing under the prothallus. The structure of the hypocotyl at this point is still that of the root. Figs. 40–43 show the gradual transition from root to stem structure. The figures were drawn from a series of sections of the same plant. After the branch-stele has left the main stele

a gap appears in the latter (Fig. 41) and parenchyma passes into the middle of the stele. The two protoxylem groups bend towards each other and later turn completely inwards. The course of the third protoxylem group



TEXT-FIG. 40.



TEXT-FIG. 42.



TEXT-FIG. 41.



TEXT-FIG. 43.

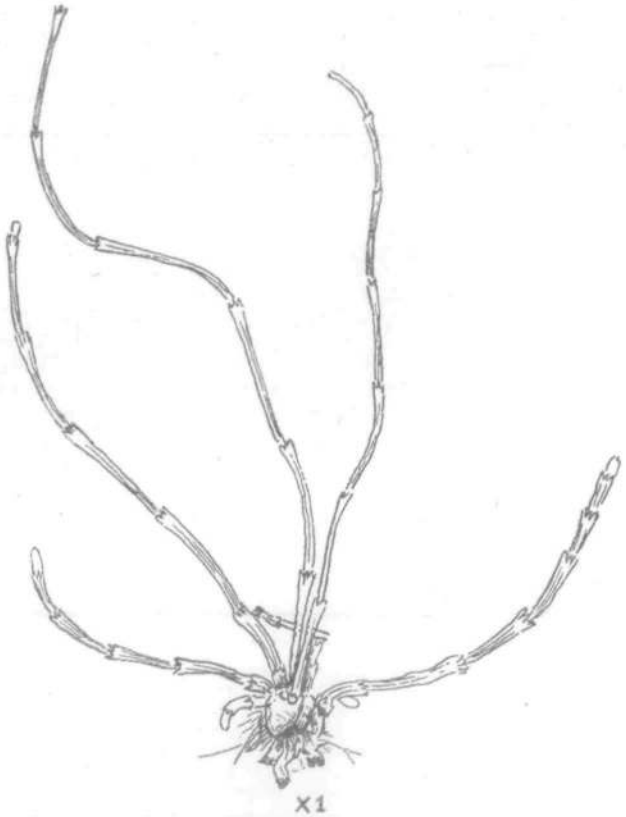
is not clear. A little higher the stele assumes the form of a hollow cylinder (Fig. 42), and still higher the bundles of the stem become separate from each other (Fig. 43). These changes are similar to those described by Jeffrey (as reported by Campbell) for *Equisetum hiemale*.

A small prothallus may bear a single plant, but eight or ten plants on a prothallus are not unusual. Fig. 44 shows a prothallus bearing fifteen plants. The prothallus was brought into the laboratory without any plants on it, and all of them were produced on that part of the prothallus which was formed while in the laboratory. The proximity of several male plants



×1

TEXT-FIG. 44.



×1

TEXT-FIG. 45.

facilitated fertilization. It may also be mentioned that it is rare to find a prothallus with antheridia and a young plant growing out of it. Self-fertilization, therefore, does not take place, as the archegonia which were produced on the bisexual prothallus would be shrivelled before the antheridia are ripe and no new archegonia can be produced, it appears, along with the antheridia. In the very few cases where a plant was found growing out of an antheridium-bearing prothallus the archegonium may have been fertilized from another prothallus. Fig. 45 shows a single plant coming out of a small prothallus. The plant here has already produced branches of the second and third order.

Concluding Remarks.

The prothallus of *Equisetum debile* is remarkable in the following features:

1. The great diversity in the methods of the formation of the walls in the early stages. Particularly interesting is the occasional occurrence of a 'primary tubercle', comparable to that of *Lycopodium cernuum* (Lotsy—after Treub—figures on p. 415 of volume ii) (Figs. 3, 7).

2. The lobes are always erect and very close together in prothalli found in nature. Even when the amount of light is very small, as inside a room in a dark corner, the lobes are still erect. It has been remarked (Campbell, p. 446) that the 'more or less upright position assumed by the prothallus of *Equisetum* is due to the amount of light'. This does not hold good for the species under consideration.

3. The radial symmetry of the prothallus from the earliest stages (Figs. 5, 6, 16 *b*, 18, &c.). Jeffrey has already compared the prothallus of *Equisetum* to that of *Lycopodium cernuum* (Campbell, p. 446); but Goebel has remarked that there is this fundamental difference that the prothallus of *Equisetum* is not radial but dorsiventral ('Organography,' Part II, p. 195) This objection, however, is not applicable to the prothallus of *Equisetum debile*. Even in the older prothalli the radial symmetry is very well seen, as in Fig. 44, where the plants are formed by the prothallus all along the circular margin. The chief difference which strikes the writer is that in the prothallus under discussion the lower compact portion is very small compared with the same portion in the prothallus of *L. cernuum*. When we consider the great diversity of form in the prothalli of various species of *Lycopodium* (Lang, Bruchmann) the difference does not seem to be very great. At the same time we must remember that the prothallus of *Lycopodium cernuum* is mycorrhizal and the great development of the compact portion is connected with the action of the external agent.

4. The large size of the mature prothallus. The latter is much larger than the largest specimens figured by Buchtien and Goebel.

5. The changes which the prothallus exhibits in the structure and colour of the upper half in relation to light, being very compact and red in bright light (direct sunlight) and spongy and green in shade.

6. The absence of purely male prothalli.

7. The protogynous condition of the prothallus, helping in cross fertilization. All female prothalli, however, do not produce antheridia.

8. In position, general structure, and possession of 'paraphyses' the antheridia resemble those of *Lycopodium* (cf. Figs. 20, 21, 31–33 of this paper, with Figs. 3 and 9 of Lang's paper, and Figs. 14 and 28 of Bruchmann's paper).

9. The archegonium has a single neck-canal cell, which is another point of resemblance with the prothallus of *Lycopodium cernuum*. It must be pointed out in this connexion that although the prothallus of *L. cernuum* is generally accepted to be of a primitive type (Lang), still it has only a single neck-canal cell. This suggests that the larger number of the neck-canal cells in other species of *Lycopodium* is a secondary feature.

The features pointed out above indicate in most cases a clear affinity with the prothallus of *Lycopodium cernuum*, and when we remember the great difference exhibited by the sporophyte generations of *Equisetum* and *Lycopodium* in their external characters and internal anatomy, the resemblance in the prothalli is at least striking.

My cordial thanks are due to Professor A. C. Seward, Cambridge, who kindly corrected the first proofs. I have seen the final proofs myself, and am alone responsible for everything contained in this paper.

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EXPLANATION OF FIGURES IN THE TEXT.

Fig. 1. First wall in the spore. × 300.

Figs. 2–13. Early stages in the development of the prothallus. Figs. 2, 3, 4, 7, 8, 9, 10 × 300. Fig. 13 × 125. Figs. 6, 11, 12 × 70. Figs. 3, 7, and 13 show the 'primary tubercle'. *r* in all cases indicates the rhizoid cell.

Figs. 14, 15. Prothalli, three weeks old. × 70.

Fig. 16 (*a* and *b*). Two older prothalli from the ventral side. Rhizoids removed. The posterior notch is seen in *a*; none in *b*. *m* = meristem. × 4. From a shady place.

Fig. 17. A prothallus rather older than Fig. 16. Ventral view. × 2. The fissures showing the division of the prothallus are seen. *m* = meristem.

Fig. 18. A well-grown prothallus growing on the soil. Nat. size. From a shady place.

Fig. 19. Another compact prothallus kept inside a room and watered plentifully for about one month. The lobes formed during that time are long and loose. Nat. size. Four young plants are seen at places marked ×.

Fig. 20. A female prothallus which has begun to form antheridia. × 2.

Fig. 21. Another and larger female prothallus with antheridia on the margins. × 2.

Fig. 22. A female prothallus with a plant growing out of it near the margin. The first lateral branch of the main shoot was already two inches in length. The main shoot was still longer. × 2. From a shady place.

Fig. 23. A vertical section through a well-grown prothallus, showing arrangement and general outline of lobes. *Ar* = archegonia. × 20.

Fig. 24. One of the lobes. × about 70.

Fig. 25. Vertical section through the marginal part of a prothallus, showing large compact portion and small lobe. Roughly, the part above the line is green, that below it is full of starch, but contains no chloroplasts. × 20. *Ar* = archegonia; *x* = meristem.

Fig. 26. A lobe from the margin of Fig. 19. *Ar* = archegonium. The line shows the upper level of the compact part of the prothallus. × 20.

Fig. 27. Horizontal sections of a few lobes at various heights.

Figs. 28, 29. Mature archegonia in longitudinal section. × 300.

Fig. 30. Transverse section of the neck of an archegonium.

Fig. 31. A part of the prothallus in vertical section, showing antheridia. × 20.

Fig. 32. Three antheridia in various stages of development. Vertical section. *Pa* = paraphysis. × 300. The spermatogenous cells in this and the two following figures are shaded.

Fig. 33. A ripe antheridium at the base of a lobe, in vertical section. × 70.

Fig. 34. An open antheridium seen from above. × 300.

Fig. 35. A ripe but still closed antheridium seen from above. × 300.

Fig. 36. Sperm mother-cells showing curved nucleus and blepharoplast. × 1250. *a*, from a complete teased-out cell fixed by osmic acid.

Fig. 37. Sperm fixed over osmic acid fumes, while swimming. × 1250. The part derived from the chromatin and the blepharoplast is shaded.

Fig. 38. Embryo in longitudinal section. × 300.

Fig. 39. Complete embryo about a week old. × 40.

Figs. 40–43. Transverse section of a young plant from the root upwards through the hypocotyl to the shoot.

Fig. 40. Transverse section of root.

Fig. 41. Formation of a gap and pith.

Fig. 42. Closed ring of the stele with pith in the centre.

Fig. 43. Stem structure with separate vascular bundles. The typical endarch structure has not yet been established.

Fig. 44. A large prothallus with fifteen plants growing out of it. Nat. size.

Fig. 45. A small prothallus with a single, much-branched plant attached to it. The roots have been cut short. Nat. size.