AN ALGA-LIKE FERN-PROTHALLIUM.—The Fern-prothallium, which forms the subject of this note, is so remarkable in character, and presents features of such general biological interest, that I have thought it desirable to offer a preliminary account.

The prothallium belongs to *Schizaea bifida*, a Fern confined to New Zealand and certain parts of Australia [1].

The prothallium is quite unlike the ordinary types of Fern-prothallia, and is strongly suggestive of an Alga. A good specimen has the form of a soft-looking round green cushion, from a quarter of an inch to half in diameter. Erect green filaments can be seen projecting above the general surface even with the naked eye.

Closer examination shows that it is composed of branched filaments. Each filament is a single row of cells, the cells being rather large, about ·25 mm. in length and a third or fourth of this in thickness, but may be longer where less illuminated towards the centre of the prothallium.

Some of the filaments lie on the surface of the ground, and from these erect filaments are given off which usually branch abundantly, and may rise to the height of 3 and 4 mm.

The development of the branches can be readily followed. Each filament has an apical cell, from which segments are cut off behind; these segments do not divide again, though any one may bud out laterally at its upper end to form a branch which repeats the features of the parent filament. Each segment commonly gives rise to but one branch, but at the centre of the prothallium branching may be more crowded. Not all the segments give rise to branches; the last branch formed may be several cells behind the apex of the parent filament. A few filaments spread through the underlying soil, and these are colourless, but otherwise of similar character, except that they bear at intervals distended, bladder-like cells, which carry short, brown root-hairs, usually two to each of the distended cells.

Filamentous prothallia are already known in *Trichomanes*, and, as is well known, small more or less filamentous prothallia occur in many Ferns when spores are sown too quickly. But these starved filamentous prothallia bear male organs only.

The prothallia of *Trichomanes* are incompletely filamentous, for although the antheridia are borne by the filaments, the archegonia

[1] The filamentous prothallium of another species of the genus is already known; see Elizabeth G. Britton and Alexandrina Taylor, Life History of *Schizaea pusilla*. Bull. Torrey Bot. Club, New York, vol. xxviii, 1901.

occur only on archegoniophores, which are masses of meristematic cells. The prothallia of *Schizaea*, however, are *completely filamentous throughout*, not only the antheridia but also the archegonia being produced on filaments.

Both kinds of sexual organs may be produced on the same prothallium, but are carried on separate branches. The archegonia are produced near the base of an erect filament, and occupy the position of lateral branches at the upper end of a cell. The cell grows out, forming a protuberance which is directed obliquely upwards. This is then cut off as an archegonium mother-cell. A second and a third mother-cell may be produced by the same cell. Often enough these are the only archegonia produced by the upright filament, but I have seen a second group of archegonia produced by the segment above. The filament which thus produces the mother-cells of the archegonia continues to grow upwards, and may be abundantly branched; the cells are not distinguishable from those of the ordinary sterile branches.

The mother-cell cut off in the way described gives rise to the whole of the archegonium. This, when mature, is flask-shaped, the neck is rather thick and of moderate length; it is composed of usually 3 tiers of cells, 4 in each tier. The cells of the terminal tier are longer than the others and diverge widely when the archegonium opens. The neck curves out below into the rather wider venter, which is narrowed a little to the base of attachment of the archegonium.

It will be seen that the archegonium is remarkable amongst Ferns in having a free venter, and in this respect it resembles the archegonia of typical Bryophytes. The neck, however, is short and not of considerable length as in Bryophytes.

Antheridia are produced in considerable numbers; they occur more or less regularly on both sides of an erect filament, which may itself terminate in an antheridium. Rather short cells, which obviously correspond to branches, grow out and curve upwards. Uusually one, but sometimes two such cells are formed from each cell of the filament from the base upwards. At the end of the lateral cell a segment is cut off as the antheridium mother-cell. The development of the antheridium follows the simple type already known in *Anemia*, and the wall which cuts off the cap-cell is nearly transverse, but it is, perhaps, somewhat more primitive. The mature antheridia are ovoid in form, the cap end being the narrower. The spermatozoids are of the usual type in Ferns.

After the first antheridium is formed the basal cell, from which the first antheridium mother-cell was cut off, may swell out laterally, and a second segment is then cut off and develops into an antheridium. Similarly a third antheridium may be formed from the basal segment.

It need hardly be said that the main, though not the sole, biological interest which attaches to the present remarkable prothallium, centres round the question whether its structure is primitive or not. Two different interpretations may be placed on such a filamentous prothallium :—

(1) It may be regarded as directly representing an algoid ancestor in the phylogeny of *Schizaea* and of Ferns generally;

(2) Or the filamentous structure may be considered to be a secondary adaptive character of no phylogenetic import.

Goebel[1] has discussed the question with reference to the filamentous prothallium of *Trichomanes*, and has pointed out that it is not clear why, amongst the Hymenophyllaceae, the species of *Trichomanes* should in general possess a filamentous prothallium, whilst those of *Hymenophyllum* are flattened cellular expansions, for they live under similar conditions. It is difficult to see, therefore, how the filamentous condition can be adaptive. The filmy character of the leaves of the Hymenophyllaceae may be an adaptive character, due to their moist environment. Species of other genera of Ferns, living under similar conditions, show corresponding adaptive modification of their leaves. But so far as is known their prothallia are never like those of *Trichomanes*, but resemble the prothallia of forms to which they are respectively related.

If we now compare *Trichomanes* with *Schizaea bifida* we find that the latter lives under conditions which are quite distinct from those necessary for *Trichomanes*. We can hardly suppose that it is moisture which has called forth the filamentous character, for Fern-prothallia generally can only grow where moisture prevails. Four other species of Fern were found growing with the present prothallia, and all have prothallia of the type common in the Polypodiaceae.

The prothallia of *Schizaea bifida* were found growing, some on damp sandy soil, others on clay soil. The ground was in places bare, but often partly covered with a growth of small Mosses and Hepaticae, and no doubt the filaments are sometimes an advantage to the prothallium in enabling it to rise up to the light between its

[1] Organographie der Pflanzen, p. 421.

neighbours. But such a growth of Mosses and Hepaticae is of such general occurrence that, if the filamentous condition be an adaptation for this special end, one can only speculate why it has not arisen in a host of other Fern-prothallia to which it would be equally useful.

Again, in *Trichomanes*, although the prothallium is generally filamentous, yet small cellular bodies or even flat expansions, which remind us of other Fern-prothallia, are formed to carry the archegonia. Goebel explains this as due to the need of a better supply of nutriment for the archegonium. On the other hand the existence of such cellular bodies might be quoted as evidence of reduction from the more usual form of prothallium. But if the retention of cellular masses for the nutrition of the archegonia was needful in the case of *Trichomanes*, why, we may ask, is a similar feature absent from the prothallium of *Schizaea*? It is difficult to imagine that the absence of the meristematic archegoniophore is an adaptive feature.

It would seem, therefore, that Goebel's explanation is the correct one, and that the condition of things in *Schizaea* is a primitive condition, even more so than that existing in *Trichomanes*.

The whole vegetative structure of the prothallium of *Schizaea* is eminently suggestive of one of the filamentous Algae. That the Ferns as well as other higher plants have descended from an aquatic ancestor is of course rendered probable by the character of the ciliate spermatozoids. But a specially interesting feature in *Schizaea* is the mode of development of both kinds of sexual organs as morphological equivalents of the ordinary branches of a filamentous prothallium, a mode which explains the character of these organs. Are we not therefore justified in regarding *Schizaea* as a primitive form?

The question, however, is not one which can be decided by the evidence derived from a single form, but must rest on a broad basis of comparison of the development in the different families of Ferns. Nevertheless the probability of the filamentous prothallium being primitive is increased by its occurrence in the separate families of Hymenophyllaceae and Schizaeaceae. When we add to this the frequency of a filamentous stage at the beginning of the development of so many different types of Ferns, and the tendency to form filamentous prothallia when nutrition is inadequate, we have accumulated a weighty body of evidence in favour of the hypothesis.

It may be observed that the characters of the Schizaeaceae show

that the family is a relatively primitive one[1]. Bower places it in his group 'Simplices,' which on comparative grounds he regards 'as being relatively primitive and less specialized types of Ferns.' The records of Palaeontology show that the group is an ancient one. *Senftenbergia* from the Carboniferous and *Klukia* from the Jurassic are referred by Potonié[2] to the family, whilst the living genus *Lygodium* dates from the Cretaceous. Apparently the family has undergone but slow modification. Hence, without committing ourselves to the view that gametophyte and sporophyte undergo modification at the same rate, have we not some warrant in looking for primitive characters in the prothallium?

In speaking of the prothallium of *Schizaea* I have preferred to compare it with an Alga rather than with the protonema of Moss, for it has appeared to me more suggestive of the former. But, in any case, the protonema of the Bryophyta is itself, in many respects, comparable with an Alga. The prothallium of *Schizaea* may be compared with the protonema of the Bryophyta, and we have, moreover, an additional point of resemblance to the Bryophyta in the free archegonial venter. But it is to be noted that the archegonium of *Schizaea* is carried upon a filament, whereas this does not appear to be the case in any known Bryophyte. The male plant of *Buxbaumia* makes the nearest approach to *Schizaea* in having the antheridia directly borne on the protonema. But the stalked antheridium is protected by a leaf-like lobe (which is without chlorophyll), so that the filamentous character is not completely retained. In the female plant of *Buxbaumia* the protonema produces a more considerable gametophore, consisting of a small stem with a few simple leaves, which are also without chlorophyll. The archegonium is at the apex of the stem. Goebel (l. c. p. 350) is inclined to consider *Buxbaumia* as a relatively primitive form which has remained at a stage that other Mosses have passed through. He suggests that such a form may have arisen from a filamentous Alga in which the branches that developed the sexual organs have become more complex. If this view be correct and *Buxbaumia* is not a form reduced in accordance with a supposed saprophytic habit (which Goebel regards as still unproved), we have an interesting form for comparison with *Trichomanes*. Even if *Buxbaumia* be reduced, the gametophores of the

[1] Bower, Philosophical Transactions, 1900, B. Vol. 192, p. 123.

[2] Die natürlichen Pflanzenfamilien, Th. I., Abt. 4, p. 371.

Phascaceae are but little further developed than those of *Buxbaumia*. But what I wish to point out here is that the prothallium of *Schizaea* is at just the same stage of evolution as the hypothetical Alga postulated by Goebel as the ancestor of the Mosses.

Many other points call for consideration, but their discussion would go beyond the scope of such a preliminary account as the present, and must be deferred. I hope, however, to shortly offer a further account of the present prothallium as well as those of other species of *Schizaea*.

It will be seen that, whatever interpretation we place upon it, the prothallium of *Schizaea* is a highly interesting form. But does not the weight of evidence justify its recognition as a relatively primitive type, which probably represents the character of the common Alga-like ancestor of both Ferns and Bryophytes more nearly than any plant hitherto described?

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ON AN UNEXPLAINED POINT IN THE ANATOMY OF HELMINTHOSTACHYS ZEYLANICA.—It has not been, I believe, hitherto recorded that in *Helminthostachys zeylanica* there are a number of small passages or canals running through the cortex from the neighbourhood of the stele to the external surface of the rhizome. These canals bear a definite relation to the leaf-insertion: one being situated in front of each leaf, opening out on to the surface immediately above the insertion of the 'stipule' of the leaf to which it belongs, not in the median line of the rhizome but well down towards the under side. The passage may, in fact, be regarded as a backward prolongation into the cortex of the space that lies between the 'stipule' and the stem as a narrow canal running right up to the stele.

The presence of these canals exercises a considerable influence upon the stele, and occasions certain modifications in structure which, I think, may best be explained by describing the manner of the departure of the leaf-trace, which the woodcut is intended to illustrate. The figure *A* is a diagrammatic longitudinal section of the stele in the neighbourhood of the leaf-gap, while *B* and *C* represent transverse sections taken at the levels *aa* and *bb* respectively. The xylem is represented by dark shading, the phloem by light, the parenchymatous tissue being left unshaded; the dotted line indicates