

## A Criticism, and a Reply to Criticisms.

BY

F. O. BOWER, D.Sc., F.R.S.

*Regius Professor of Botany in the University of Glasgow.*

IN a recent number of the *Annals of Botany*<sup>1</sup> Professor Goebel has given an epitome<sup>2</sup> of his interesting observations on the sexual generation of *Buxbaumia*, recognizing in it the simplest known type of a moss, and pointing out that it 'very nearly comes up to the hypothetical ideal of the simplest primitive moss' which he had suggested elsewhere<sup>3</sup>. I do not wish to contest the conclusion thus worded. Certain of the points brought forward should, however, suggest caution before accepting the above quotation as more than a plain statement of fact. When Professor Goebel proceeds (p. 357) to conclude 'that *Buxbaumia* is an ancient type of moss which still retains a number of primitive characters,' he enters ground which is more open for debate: it will be necessary, before accepting this conclusion, to decide whether the characters upon which it is based are really relatively primitive or the result of reduction.

There seems good reason to think that reduction has had its influence upon *Buxbaumia*: Professor Goebel himself draws attention to the absence of chlorophyll from the solitary pro-

<sup>1</sup> Vol. vi, No. 24, p. 355.

<sup>2</sup> For his more complete statement and figures, see *Flora*, 1892, p. 92, &c.

<sup>3</sup> *Morphologische und biologische Studien*, *Annales du Jard. Bot. de Buitenzorg*, I. vii, p. 111.

[*Annals of Botany*, Vol. VII. No. XXVII. September, 1893.]

tective leaf of the male plant, and to its brown colour; the leaves of the female plant are also destitute of chlorophyll, and Haberlandt<sup>1</sup> has stated that 'assimilating foliage-leaves are entirely absent in the Buxbaumiae,' while he has further drawn attention to the apparent saprophytic habit of the rhizoids, their colourless thin membranes, and their frequent, mycelium-like anastomoses, as they traverse the humus in which they grow. Professor Goebel, in discussing these characters, points out truly that there is as yet no proof that *Buxbaumia* is actually saprophytic; but it would appear that, for the purposes of his argument, the burden of proof of this point will lie with him. Before conclusions can safely be drawn whether or not *Buxbaumia* is, as he suggests, 'an ancient type of moss which still retains a number of primitive characters,' it will be necessary to be more precisely informed on the point of its nutrition: if *Buxbaumia* really derives part of its nourishment as a saprophyte from the humus, there will be strong probability that the simplicity of its structure would be due to the reduction which usually follows such a habit. If, as Goebel suggests<sup>2</sup>, the rotten tree-trunk acts only as a sponge, to hold water, and if the moss would grow equally well on a porous, inorganic substratum, such an observation would remove a serious objection to its being regarded as a primitive type: at present we are not informed on this point, and must, therefore, withhold a definite opinion. A further fact, mentioned and figured by Schimper<sup>3</sup>, and noted also by Professor Goebel, appears to me to be very suggestive: he describes<sup>4</sup> how, though the young leaves of the female plant show no special peculiarities, the peripheral cells of the older leaves grow out into filaments with brown walls; some of these do not develop further, others grow into true protonema, while others, again, penetrating the soil, and elongating as rhizoids, 'convey nourishment to the plant.' The question is, *What* nourishment do they bring to this female plant, which,

<sup>1</sup> Pringsh., Jahrb. XVII, Heft. 3, p. 480, &c.

<sup>3</sup> Bryol. Europ. vol. iv, suppl.

<sup>2</sup> Flora, 1892, p. 101.

<sup>4</sup> Flora, 1892, p. 102.

though incapable of assimilation by its leaves, is still able to support the growing embryo of a relatively large sporogonium? It is possible, as Professor Goebel suggests, that the required organic supply is entirely derived from the assimilative activity of the protonema; but in presence of such a peculiar physiological condition as that above noted, I think that more exact proof of the mode of nourishment of *Buxbaumia* will be necessary before the facts relating to it can be accepted for purposes of morphological argument. I find it difficult to believe that we really see a primitive condition in a plant in which the leaves are incapable of assimilation themselves, though the plant receives its support indirectly through them, from outgrowths of a filamentous character, formed, comparatively late, from their margins. Whether the organic supply be exclusively derived from the assimilative activity of the green filaments or in part derived saprophytically from the substratum, the *indirectness* of the mode of supply, and the late appearance of the parts which supply it, are facts not easily reconciled with the suggested primitive character of the organism.

Nor does the comparison with *Diphyscium* appear to me to strengthen the case: the relations of these genera are not very close, though the similarity of their sporogonia is greater than that of their gametophytes. It is true the seta of *Diphyscium* is short (but I do not see that this is a fact of material weight), while that of *Buxbaumia*, the supposed more primitive form, is long. In *Diphyscium* the relatively large green leaves of the female plant have not the marginal protonema as in *Buxbaumia*: on this ground, as well as from the green colour of the leaves—that is, on grounds of *directness* of nourishment—*Diphyscium* would appear to me to be the more primitive form.

The relatively large bulk of the rhizoids to the bulk of the plants in both *B. aphylla* and *D. foliosum* is certainly striking; also the exceedingly fine, hypha-like ramifications into which they run, and their very complicated anastomoses, so as to form a plexus extending far into the substratum. I have also noted a frequent, though not constant, association of

fungal hyphae with the rhizoids of both genera: these are applied closely to the surface of their walls, even in specimens of *Diphyscium* brought freshly from the country. Such a juxtaposition may be merely accidental, though common: or the fungus may be simply parasitic, though I saw no perforation: or there may be a symbiotic relation between the organisms. I think such matters as these will have to be taken more fully into consideration before it can be admitted that *Buxbaumia* is really independent of external organic supply. It is not sufficient that Professor Goebel shall conclude, however justly, that 'we have as yet no proof of the saprophytism of *Buxbaumia*' (l.c. p. 101); before his view can be established, he must show that, notwithstanding the many suspicious points about its mode of life, *Buxbaumia* is really independent of saprophytic nourishment.

I would even go further, and remark that, if *Buxbaumia* were proved to be quite independent of an organic substratum as regards its nutrition, that would not at all prove its primitive character; for a saprophytic habit is only one of the factors which conduce to morphological reduction.

The line which Professor Goebel would draw between a plant which has stood still at an early stage of development (p. 102) and such as have undergone reduction is one of the most blurred lines in all morphology. I confess that, though some of the facts adduced by him appear to support his conclusion, still, in view of the facts above noted, it seems to me at present more probable that *Buxbaumia* is a reduced rather than a really primitive type of moss; and it would appear that the reduction has affected the vegetative organs of the moss-plant more than other parts.

Professor Goebel has also compared the simple gametophyte of *Buxbaumia* with that of *Trichomanes*: the similarity is certainly obvious enough, but the question will be whether we see in it anything more than an example of parallel development—that is, of comparatively recent adaptation—of one genus or of both, to somewhat similar circumstances. There is a close similarity of the conditions to which the

gametophytes of these two genera are exposed: they both grow in a humid atmosphere, while moist humus, commonly in the form of effete and decaying superficial tissues of tree-trunks, suits them both: neither the Hymenophyllaceae nor the Buxbaumiæ can be considered entirely free from the charge of saprophytic nourishment (see Haberlandt, loc. cit. p. 482). I have elsewhere discussed this question of the similarity of the moss-protonema and the prothallus of *Trichomanes* at some length<sup>1</sup>: the main point is that the similarity depends on the *vegetative organs*, such as the filamentous protonema-like growth, and the small archegoniophore. But, though there is certainly some similarity of their antheridia, the archegonium of *Trichomanes* or of *Hymenophyllum* is a true fern-archegonium, as regards its segmentation and mature structure; and in point of its single neck-cell it is even less like a moss-archegonium than are those of certain other Vascular Cryptogams. The archegonium of *Buxbaumia* appears, however, to be a true moss-archegonium<sup>2</sup>. To me the dissimilarity of the archegonia of *Trichomanes* and of *Buxbaumia*, as regards form and segmentation, appears a more weighty fact than the similarity in vegetative conformation of the gametophyte, since the archegonium in ferns and mosses is relatively constant in its characters, while their vegetative conformation is not constant. When to this is added the suspicion of saprophytism, as well as the entire dissimilarity of the sporophyte in *Buxbaumia* and *Trichomanes*, the case against Professor Goebel's comparison appears to me to be a very strong one. In the light of the new facts contributed by Professor Goebel relating to *Buxbaumia*, I see no reason to alter the opinion set forth in my papers above quoted—viz. that such similarity of the gametophyte as is found in the mosses and Hymenophyllaceae, as regards their vegetative development, is probably the result of relatively recent adaptation, of one or

<sup>1</sup> Annals of Botany, vol. v. p. 109, &c.

<sup>2</sup> See Goebel's Figs. 12, 17, Pl. VIII, Flora, 1892; also Bruch, Bryologia Europaea, iv. Pl. I, Fig. 12.

of both, to similar external circumstances, rather than dependent upon primitive characters which they have had in common throughout their evolution.

I have elsewhere remarked<sup>1</sup> that the method of comparison of vegetative characters of the gametophyte, which Professor Goebel has adopted in treating plants so divergent in character as the mosses and ferns, is at variance with the methods commonly in use in the classification of phanerogamic plants. In these the conformation of the vegetative organs is usually treated as a secondary consideration, while the characters of the reproductive organs are given the precedence. Professor Goebel, however, appears to place the vegetative organs in the foreground of his argument, and attaches importance to their external form and structure, notwithstanding the entire dissimilarity of the sporophyte in the plants compared, and even the important difference of their archegonia. How cautious it is necessary to be in trusting to the vegetative conformation of the gametophyte in archegoniate plants is illustrated in the genus *Lycopodium*: here, without any marked difference of type of the sporophyte, the sexual plant varies within very wide limits of form, though the sexual organs remain essentially constant. The difference between the prothalli of *L. annotinum*, of *L. cernuum* and of *L. Phlegmaria* has been sufficiently demonstrated and remarked upon by M. Treub<sup>2</sup>, while he specially points out the similarity of their sexual organs as regards structure and development. Such considerations make me doubt the wisdom of so far departing from the methods in general use among the higher plants as to press comparisons, based on similarity of vegetative conformation, in plants which show marked dissimilarity in other parts of such importance as the archegonia and the whole sporophyte generation. The fact that the organisms in question are lower in the scale does not appear to me a sufficient justification of this method.

<sup>1</sup> Annals of Botany, vol. v. p. 120.

<sup>2</sup> Ann. Jard. Bot. d. Buitenzorg, v. p. 83, &c.

In the same article<sup>1</sup> Professor Goebel offers certain criticisms upon my preliminary statement of results from the study of spore-producing members of the Vascular Cryptogams<sup>2</sup>. I would here remark that this was only a preliminary statement, and that readers are not yet in possession of the full facts or figures. In the meanwhile I shall endeavour to meet the most salient point of Professor Goebel's criticism.

While studying the evidence of sterilization of potential sporogenous tissue, I recognize fully the *correlation* which so often appears between spore-production and vegetative development. Upon this subject Professor Goebel has contributed very largely to our knowledge. The essential point on which we differ is the interpretation to be put upon this correlation. When Professor Goebel says (p. 359) that 'it can be experimentally proved that the sporophylls of Leptosporangiate Ferns are modified leaves'—that is, modified foliage-leaves—he makes an assumption in which I am unable to follow him. That there is a correlation between vegetative growth and spore-production he has satisfactorily demonstrated by experiment<sup>3</sup>; but I submit that his experiments do not touch the question of priority of origin of the sporophyll, or of the foliage-leaf, in point of view of descent. He appears to me to have assumed that the type of leaf which is prior in the ontogeny was also the first to appear in the phylogeny. Now this assumption was made by Goethe, though it was expressed in different terms, as was natural for a pre-evolutionary writer; by use it has become so familiar that those botanists of the present day who entertain some form of belief in evolution hardly recognize that, if they hold this opinion, it will be their duty to substantiate it. It seems hardly to have occurred to morphologists, even yet, that Goethe's views on progressive (*fortschreitende*) metamorphosis are incompatible with a belief in the descent of plants which show consistent antithetic alternation—that is, in which spore-production was throughout evolution a constantly recurring event.

<sup>1</sup> Annals of Botany vi. p. 358.

<sup>2</sup> Proc. Roy. Soc. vol. I. p. 265.

<sup>3</sup> Ber. d. deutschen Bot. Ges. 1887.

In my view, *the progression from foliage-leaf to sporophyll, as seen in the development of the individual, cannot be assumed to illustrate the progression as regards descent.* The following considerations will explain this statement, which is made on the understanding that plants now living upon the earth illustrate, however imperfectly, the course which evolution probably took. From a comparison of these we learn that spore-production was the first office of the sporophyte, and that the spore-stage has recurred constantly in the life-cycle during descent. As the spore-production increased (the increase in numbers of spores being a manifest advantage) the powers of the gametophyte were insufficient to supply the necessary nutrition and external protection. The need for further supply appears to have led to the intercalation of a vegetative phase of the sporophyte, between fertilization and spore-production. In the Bryophyta the external protection and nutrition of the spores were supplied, but with only a minor degree of efficiency, by vegetative development of sterilized tissues of the lower and peripheral parts of the sporogonium; there is, however, no further elaboration of form beyond the occasional presence of chlorophyll, containing expansions of the apophysis. But in vascular plants the foliar development appeared: as to the details of the way in which it first arose we are still without definite information; much less do we know for certain whether the first leaves which appeared were sporophylls or foliage-leaves. When Professor Goebel writes, 'It can be experimentally proved that the sporophylls of the Leptosporangiate Ferns are modified leaves,' bringing this as an argument against me, he appears to me to assume, on ground of their priority in the ontogeny, that the foliage-leaves were of prior existence from the point of view of descent. I assert, on the other hand, that this is not proved, and that a good case could be made out for priority of the sporophyll; in which event the conclusion would need to be inverted—*the foliage-leaf would be looked upon as a sterilized sporophyll.* This would be perfectly consistent with the *correlation* demonstrated by Professor Goebel's



experiments, as also with the intercalation of a vegetative phase between the zygote and the production of spores.

But, for my own part, I should be diffident in making any general statement on the point of priority of the sporophyll or of the foliage-leaf from the point of view of descent, as applicable for all Vascular Plants; and it is not my present purpose to discuss this question at large. I desire now only to make it clear that there is an unproved assumption involved in the passage quoted from Professor Goebel's paper (p. 359), an assumption which, in the absence of proof to support it, appears to me to materially impair the validity of his argument.

If, however, it be contemplated as possible that, in certain cases, the foliage-leaf may be, in point of view of descent, a sterilized sporophyll, this would greatly alter the face of the discussion. I have already intimated<sup>1</sup> that in the Lycopods there is reason to believe that a sterilization of sporophylls has taken place, and that the result is to be seen in the foliage-leaves, which in most species differ from them in little beyond the absence (partial or complete) of the sporangium. To me, whether we take such simple cases as the Lycopods or the more complex case of the Filicineae, the sporangium is not a gift showered by a bountiful providence upon pre-existent foliage-leaves: the sporangium, like other parts, must be looked upon from the point of view of descent: its production in the individual or in the race may be deferred, owing to the intercalation of a vegetative phase, as above explained; while, in certain cases at least, we probably see in the foliage-leaves the result of sterilization of sporophylls. If this be so, much may then be said in favour of the view that the appearance of sporangia upon the later-formed leaves of the individual is a reversion to a more ancient type rather than a metamorphosis of a progressive order.

The acceptance of such views as those thus briefly sketched would materially alter the face of the discussion. While recognizing the *fact* of correlation as demonstrated by Goebel, and illustrated more or less clearly in so many spore-bearing

<sup>1</sup> Roy. Soc. Proc. vol. I. p. 270.

organisms, I hold that that fact, when stripped of any unproved assumption, is in accordance with such theoretical considerations as were put forward in the paper which Professor Goebel has criticized.

I would furthermore ask those who are disposed to disagree with me to bear in mind the opinions already expressed by me elsewhere<sup>1</sup> as to the probable relations of the Eusporangiate and Leptosporangiate Ferns. Though it is commonly held that the latter are the more primitive type, I have been led by careful consideration of the evidence to conclude that the preponderance of evidence is in favour of the view that the Eusporangiates are the more ancient forms: this question, however is still an open one, but the opinions stated in the paper quoted will necessarily affect the questions now under discussion.

Professor Goebel further remarks<sup>2</sup> that 'in *Ophioglossum palmatum* the sporophylls are still clearly recognizable as leaf-segments.' This view has also been entertained by one of my English critics, both using it as an argument against the theory that the 'fertile frond' of the Ophioglossaceae is an elaborated and partitioned sporangium, homologous with the smaller and non-partitioned sporangium of the Lycopods. I have carefully examined the numerous specimens in the herbarium at Kew, and write from previous knowledge of those in the British Museum: pending more detailed observations on alcohol-material, I find, from external examination, the following difficulties in the way of accepting the apparently simple view above quoted:—

(1) The arrangement of the 'fertile spikes,' when marginal, is indefinite, being neither regularly alternate, nor in pairs: this is, however, the usual arrangement for pinnae, including those of *Botrychium*.

(2) Many of the 'fertile spikes' are inserted *irregularly upon the adaxial surface of the frond*, not upon its margins.

(3) The 'fertile spikes' branch in very irregular fashion, there being apparently no common rule, though this is usually the case for pinnae.

<sup>1</sup> Annals of Botany, vol. v. p. 109, &c.

<sup>2</sup> Annals, loc. cit. p. 360.

By the term 'leaf-segment' or 'pinna' I understand a marginal lobe of a leaf, and pinnae are habitually arranged along the marginal lines, alternately or in pairs, and show a common rule of development. Occasional coalescence of *pairs* of such outgrowths across the adaxial face of the leaf are known. But in this case, if the 'fertile spikes' are pinnae or leaf-segments, comparable to those of *Aneimia* or of *Osmunda*, or the vegetative lobes of *Botrychium*, there must have been a frequent and irregular migration of *individual* pinnae from the margins to the surface of the frond: to such an irregular migration of individual pinnae I know no parallel. Quite apart from comparative considerations as brought forward elsewhere, this difficulty, together with the irregularity of distribution of the fertile spikes on the leaf, the frequency and irregularity of their branching, and the indefinite form of the terminal lobe, dispose me against this apparently simple explanation of the frond of *Ophioglossum palmatum*. I shall hope to have the opportunity of examining alcohol-material before stating that view of the nature of the frond in this species which I have entertained all through this work, but not yet stated, because want of alcohol-material had made a detailed examination hitherto impossible.

I wish also to reserve my answer to Professor Goebel's objections with regard to *Botrychium*<sup>1</sup>. I have long been aware of the frequent presence of sporangia on the usually sterile frond of *Botrychium*, and have had museum specimens showing it in my possession for many years: the fact of their presence is certainly a difficulty, which I shall hope to meet in the course of a general discussion of the subject.

The opinion appears to be held by some that the sporangium cannot undergo such elaboration of form and structure as I suggest. It is true that such elaboration has not hitherto been demonstrated, but those who are actively engaged in morphological inquiry will be disposed to believe all things possible, though all may not be convenient. The fact that demonstration has not yet been given does not preclude its

<sup>1</sup> loc. cit. p. 359.

possibility, and certainly does not justify the statement that it cannot occur.

The suggestions which I have offered in my studies on spore-bearing members involve the thesis that there are potentialities of elaboration of such parts as we style sporangia, analogous to the potentialities of axis, leaf, root or hair. Every one of these parts is susceptible of variations in size, form, and structure, in different plants, while all may be branched: in certain species, genera, or even families, the branching of any of these parts may, it is true, be in abeyance; but speaking of these parts generally, the potentiality of branching is one of their characters. What good reason is there for assuming that sporangia have not this potentiality, and thus differ from all other parts of the sporophyte?

In point of structure great fluctuations are seen in axes and leaves, or their parts: vascular tissues, habitually present, may be entirely absent in certain cases, while the morphological character of the part is not considered to be thereby affected. Conversely, emergences, which are commonly without vascular supply, are in some cases traversed by vascular bundles; but they are not by reason of this elevated to a higher morphological category. Accordingly, the presence or absence of vascular bundles in a given part need not affect our view of its sporangial character: it is to be noted that though vascular tissue is usually absent from sporangia, it is present in the ovules of Phanerogams, which are generally admitted to be sporangia.

With regard to branching also a similar line of argument may be used, and it may be pointed out as against the fact that branching of sporangia is not generally recognized, that branched sporangia do occur in *Salvinia natans*: while the megasporangia of this species are attached by separate stalks, the microsporangia, otherwise similar as regards position, are borne on repeatedly branched pedicels. I have not yet worked out the details of development of this interesting case, but a good representation of an advanced stage is given in Rabenhorst's *Kryptogamen Flora*, vol. iii. p. 603.

Thus, if we apply consistently to sporangia the same morphological methods as to axes or leaves, we shall be prepared to recognize in them the possible presence of vascular tissue, and the potentiality of branching; and in my opinion we should not be justified in excluding a part from the category of sporangia because it shows evidence of branching, or of vascular tissue, or even of both together.

A further factor necessary for my views is the partitioning of the sporangium: on this point it is hardly necessary to remind readers that partial sterilization of a potential archesporium has been recognized in the Bryophyta, in *Isoetes*, and in the ovules of various Phanerogams. In particular, Professor Goebel has shown that the trabeculae of *Isoetes* are produced from sterilized archesporial tissue, and he allows that they serve a useful purpose: but he remarks<sup>1</sup> that he would attach only a biological, that is, an adaptive significance to the fact that they are the result of partial sterilization of the sporogenous tissue, and that it is a question how far sterilization may proceed in sporangia and sporophylls. I agree with him that this is a question open for discussion; but it appears to me that if sterilized portions of a potential sporogenous tissue are admitted to serve a useful purpose, and if such occur in forms which we believe to be relatively low in the scale of plants, there is a reasonable probability that such sterilization will have played a part in the evolution of other forms, and it will be our duty to see whether traces of similar sterilization occur among other early types. Synangia are a marked feature in certain Vascular Cryptogams: they have commonly been looked upon as the result of coalescence of sporangia originally distinct; but I submit that it is a possible view that they may have been derived by a partial sterilization and formation of partitions in originally simple sporangia<sup>2</sup>. It is on grounds of detail of development and comparison of plants akin to one another that this question can best be solved: it would be leading us beyond the limits of such an article as this to enter now upon

<sup>1</sup> loc. cit. p. 358.

<sup>2</sup> See *Annals of Botany*, v. p. 131.

a detailed comparison: reference only will be made to communications relating to the Lycopodinae and Psilotaceae which have been laid before the Royal Society<sup>1</sup>. In these I have brought forward developmental and comparative evidence supporting the view that the synangium of the Psilotaceae is the result of septation of a Lycopodinous type of sporangium, while *Isoetes* and *Lepidodendron* provide some interesting intermediate features. If this view be correct, we should there see examples not only of partial sterilization, but of formation of complete septa from the sterile tissue: that is of partitioning of the sporangium. This is the third factor above alluded to. If this factor occur simultaneously with the other two (viz. branching and formation of vascular tissue, of which examples have been above quoted, and of which incipient steps may be seen in the Psilotaceae), then the result might very well be such elaboration as I have suggested that we see illustrated in the 'fertile frond' of the Ophioglossaceae.

The rather extensive area of facts included in the papers above cited will have to be considered by those who are in doubt as to my conclusions, and still more by those who appear disposed to take an attitude of negation. My conclusions as to the part played by spore-bearing members in the evolution of the sporophyte may be wrong, and are probably susceptible of amendment: my present object has been to show that they are not to be disproved off-hand. I have no wish to avoid criticism, but I would venture to point out to my critics that they are not yet in full possession of the facts, or of the reasoning to be based upon them. Till a full statement is published, criticism must be more or less premature; it may be accepted as 'preliminary criticism,' in the same way as the statements criticized were 'preliminary statements.'

<sup>1</sup> Roy. Soc. Proceedings, vol. l. p. 265; vol. liii. p. 19. Also abstract of the detailed memoir, part i. read June 15, 1893. The conclusion of my paper on *Lepidostrobus Brownii* (see above, p. 351, &c. of this volume of the Annals) should also be consulted.