

3. Whereas direct excitation of the anterior roots in the dog produces, as a resultant movement, extension of the lower limb, the resultant movement produced from the kinæsthetic centres of excitation of the posterior roots is always flexion. In the monkey there is not this apparent antagonism, because stimulation of the anterior roots in that animal brings out a differentiation of flexion and extension, although excitation of the posterior root gives flexion alone.

“Preliminary Statement on the Development of Sporangia upon Fern Prothalli.” By WILLIAM H. LANG, M.B., B.Sc., Lecturer in Botany, Queen Margaret College, and Robert Donaldson Scholar, Glasgow University. Communicated by D. H. SCOTT, M.A., Ph.D., F.R.S., Honorary Keeper of the Jodrell Laboratory, Royal Gardens, Kew. Received September 14, 1896.

The observations recorded in this paper were made in the course of an investigation into the relation existing between variability in the fern plant and apogamy in the prothallus. This research was undertaken at the suggestion of Professor Bower, F.R.S., and has hitherto been conducted in the Jodrell Laboratory, Royal Gardens, Kew. To Dr. Bower and Dr. Scott I am indebted for valuable assistance and advice.

In two of the species investigated, *Scolopendrium vulgare*, L., and *Lastræa dilatata*, Presl., sporangia were borne upon the prothallus. In the former they were sometimes associated with apogamous development of the sporophyte, the details of which differ, however, from previously recorded cases of apogamy. As a considerable period must elapse before an amount of material sufficient for the complete study of details of development can be obtained, it appeared advisable to describe the results obtained from the material at present available. Cultures are about to be commenced in the Glasgow Botanic Gardens for the further study of these abnormal prothalli.

The prothalli of the two species investigated will first be described, and the theoretical bearing of the results briefly considered.

Lastræa dilatata, Presl., var. *cristata gracilis*, Roberts.

The spores from which the cultures of this fern were made were obtained from a plant in the collection of Mr. C. T. Druery, F.L.S., who kindly supplied me with material. This variety was found wild in Carnarvon in 1870. Spores were sown in the first week of November, 1895, upon a carefully sterilised soil, consisting of

a mixture of vegetable mould and sand. The pot was kept constantly covered with a glass plate, and the necessity of watering was avoided by standing the pot in a large saucer kept full of water. A close crop of well-formed prothalli, on which antheridia and archegonia were present, completely covered the surface of the soil. In April, 1896, a number of the prothalli bore normal embryos in an early stage of development. Three months later numerous young plants were present, which were found on examination to be normally produced.

The prothalli which had not been fertilised had lost the heart-shaped outline and elongated considerably; some of them reached a length of 2 cm., and were 5 mm. in breadth. The archegonia were very numerous, and were situated upon a distinct cushion, which was continued in the larger prothalli as a well-marked midrib. They were arranged in transverse rows; their necks had opened in a normal manner, and the canal showed the usual brown discoloration. Antheridia were present on some of the prothalli.

In some of these prothalli the midrib was continued into a cylindrical process of variable thickness. This arose in some examples as a direct continuation of the apex, but more frequently was attached to the under surface, just behind the apex of the prothallus; in one instance it was found in a corresponding position on the upper surface. The actual apex usually loses its meristematic appearance; it grows out as a narrow triangular lobe, which consists of colourless cells, and contains tracheides. This lobe closely resembles the "middle lobe"* found in the apogamous prothalli of certain ferns, and probably corresponds to it. In a few instances this middle lobe is formed, but no cylindrical process arises; in such cases secondary prothalli are produced from the anterior margin of the thin lateral wings, and the whole closely resembles an aborting prothallus of *Aspidium filix-mas* or *Pteris cretica*. When the prothalli are seen from above, the anterior edge can be traced across the base of the cylindrical process. As will be described below, the first sporangia formed on the prothallus are usually situated on this margin, especially on the "middle lobe." The process is of the same deep green colour as the midrib. Sexual organs, often in considerable numbers, are borne upon it. They are usually well formed; the archegonia open in the usual manner, and the spermatozoids are capable of active movement when liberated. On other examples variously malformed sexual organs occur. The abnormal archegonia are seated upon small elevations composed of cells which contain chlorophyll; sometimes the neck is open, but other examples have the

* Farlow, 'Quart. Journ. Microscop. Sc.,' 1874, p. 268. De Bary, 'Bot. Zeit.,' 1878, p. 463.

neck closed and branched. The central cell of the abnormal antheridia is arrested at a more or less early stage of development, while the cells of the wall and the base take on active growth.

The sporangia are either isolated or associated together in groups, which bear a striking resemblance to sori. They are borne upon the process or close behind it upon the true middle lobe, and are rarely found upon prothalli which have not produced a cylindrical process. When this is the case, they are always isolated and situated on the edge of a thin continuation of the prothallus arising from the apical depression.

Single sporangia occur frequently on the edge of the prothallus, which, as described above, crosses the base of the process. In a number of examples a single sporangium occupied a median position, and, from earlier stages observed, it is probable that it is to be traced back to the original growing point of the prothallus. In other cases several sporangia were formed in this region. Isolated sporangia are also found on the process, but more frequently groups are met with. They occupy the upper or lateral faces of the process, and whenever sporangia in early stages of development are found, they are situated on its apex. It is probable that the groups of older sporangia had become displaced from this position by the further growth of the process. The groups were at a considerable distance from each other.

The relative positions of sporangia and sexual organs is a point of some interest, and was readily determined. Archegonia were present close to the sporangia, and at the same level on the process. When the process, after producing sporangia, had continued its growth, archegonia and antheridia were present on the portion beyond the sporangia, as well as on the older part, and, in cases in which more than one group of sporangia had developed, the intervening region bore sexual organs. Rhizoids are also produced abundantly from the shaded side of the process, and, so far as external appearance is concerned, there is no reason to doubt the prothallial nature of the region on which the sporangia are situated. The tissue underlying the sporangia, however, presents peculiarities in structure which may modify this conclusion to some extent. Beneath the single sporangia developed on the edge of the prothallus a few tracheides, which agree in every respect with those present in apogamous prothalli, were always to be found. Similar elements were always present in the tissue beneath the groups situated on the process. It is possible that here, as in the case of the sporangia upon the prothallus edge, the first tracheides are developed before the young sporangium can be recognised. All that can be stated with certainty is that they are already present beneath very young sporangia. The tracheides may become connected together into a

band, resembling a rudimentary vascular bundle, and suggesting a comparison with the vascular supply of a sorus.

The development of the sporangium could not be followed in detail in the material obtained as yet, but a sufficient number of stages have been found to make it clear that there is no difference of importance from the well known course of development of the same member on the sporophyte. In the youngest stage seen the apex of the sporangium was occupied by a tetrahedral cell, the cells destined to form the lateral portions of the wall having already been cut off from a large, dome-shaped terminal cell, the limits of which were clearly recognisable. This was borne upon a stalk cell. A tetrahedral archesporium is formed, from which tapetal cells are cut off. The tapetum subsequently becomes two-layered, and the central cell develops into a group of sporogenous cells. From these, in the most mature sporangia found, a number of dark brown spores had developed, while the tapetum was represented by numerous granules between the spores. The number of spores appeared to be the same as was contained in a sporangium developed on the sporophyte. The sporangium wall was perfectly developed; the cells of the annulus showed the characteristic thickening of their walls, which were of a dark brown colour, and a well formed stomium was present. When tested with dehydrating agents, the mechanism of the annulus was found to be perfect. The stalk consisted of four rows of cells.

No sporangia have been found in which the spores were ripe, but in view of the advanced stage of development in those observed, there is every probability that some may be obtained. It will be interesting to ascertain if the spores are capable of germination, and if the prothalli produced show any peculiarities. The spores seen already possessed a thick wall on which indications of sculpturing were apparent, and a single nucleus was present in each.

When the unnatural conditions under which they developed are borne in mind, it is not surprising that many imperfect sporangia were found. Such sporangia were in fact the more numerous. Sometimes the arrest of development had taken place before the tapetum had originated from the archesporium, but more commonly the double layer of tapetal cells was present surrounding a sporogenous cell which had become highly refractive, the nucleus being indistinguishable. The annulus could be made out, but its cells were thin walled and colourless, and the whole sporangium was pale and more flattened than one of the same age in which sporogenous tissue had formed.

No evidence has yet been obtained of the production of sporophytes, showing vegetative organs upon the cylindrical process, but one example was seen in which a group of sporangia, situated on the apex of the process, was surrounded by ramenta.

Scolopendrium vulgare, L., var. *ramulosissimum*, Woll.—The cultures of this fern were made in the manner already described for *Lastrea dilatata*. The spores were obtained from a plant grown in the open air in the Royal Gardens, Kew.

The prothalli were at first heart-shaped, and on many of them normally produced embryos developed. No further changes ensued in those on which young plants were present, and they soon became colourless and died. In those which had remained unfertilised, however, the apex continued directly into a cylindrical process,* which was of considerable thickness, and in some cases attained a length of 5 mm. The lateral portions of the prothallus showed no further growth, and became in time brown or colourless appendages to the base of the cylindrical process. On the process were numerous archegonia, and its prothallial nature was still further shown by the presence, in some instances, of thin lobes of tissue, which generally bore antheridia. Sections through the process in this stage show that the archegonia are normally formed, and reach almost to the apex, and that tracheides are absent from the tissue. The archegonia are capable of fertilisation, for in some instances normally produced embryos were found.

After the process has in this manner attained a greater or less length, its tip becomes yellowish, contrasting with the deep green colour of the region behind. Near the apex ramenta develop, which soon completely clothe the tip of the process and render it white and conspicuous. Archegonia are present to just below the ramenta. Longitudinal sections at this stage show that one or two small elevations corresponding to the rudiments of the apex of the stem, and the first leaf of the sporophyte have been formed. Beneath the broad tip a flat mass of small meristematic cells extends; the meristematic tissue is continuous with that of the stem and leaf apices, but, on passing away from these, is separated by several layers of large, non-meristematic cells from the surface. In a slightly older stage the stem apex has become conical, and a number of leaves have formed which are circinnately curved, and form a bud clothed with ramenta. In the meristematic mass numerous tracheides have been developed. One large group is central in position, and extends to the limit between prothallial and sporophytic tissue, while others are found beneath the bases of the leaves, and are in continuity with their procambial strands. The apex of the stem is occupied by an initial cell, the relation of which to the initial cell or cells of the apex of the process has not yet been traced. The young sporophyte appears to be a direct continuation of the process. It is possible that some of

* Prothalli of *Scolopendrium*, which from the brief description given of them appear to have borne similar processes, are mentioned by E. J. Lowe, in the 'Gard. Chron.,' November 10, 1895. They were not investigated further.

the cases of apogamy recorded by Stange* were of this nature, but in *Doodia caudata*, R. Br., which is the only one of his species yet investigated in detail,† the elevations, from which sporophytes developed, were situated on the under surface of the prothallus. This case appears to be intermediate in character between *Scolopendrium* and the species investigated by De Bary.‡

Several prothalli were found bearing sporangia; these were grouped together in large numbers, usually upon the upper surface of the cylindrical process, but sometimes both above and below. Archegonia were situated close to the groups of sporangia. In the region of the prothallus, underlying the group, a strand of tracheides was found; in one instance this was connected with a spherical mass of tracheides developed to all appearance within the venter of an archegonium whose neck had not opened. The tissue upon which the sporangia are inserted is thin walled, and its cells have granular contents; it contrasts sharply with the cells of the prothallus which have a large vacuole and walls which stain much more deeply with hæmatoxylin.

As in the case of *Lastrea dilatata*, the stages seen render it probable that the sporangia follow the usual course of development. Two layers of tapetal cells are formed which surround a considerable mass of sporogenous tissue. Many of the sporangia fail to attain full development; they remain colourless, and in time wither. A few have been found, however, with a well developed annulus of a dark colour; these contained spores which have not, however, been examined in detail.

In one case two rammenta overarching a group of sporangia were seen. At first sight it seemed possible that they might correspond to an indusium, but, when taken in connexion with another example in which a cylindrical process, which bore sporangia laterally, terminated in an apogamously produced bud, another explanation appears more probable; this will be referred to again below.

It is worthy of note that another variety of this species has been found to produce young plants, the first fronds of which bore numerous prothalli while still in connexion with the stem.§ The prothalli on which these plants appeared had been subjected to repeated subdivision, a process which in other species|| has been found to induce apogamous development of the sporophyte. Unfortunately nothing is known of the manner in which these peculiar plants of *Scolopendrium* were produced, but it is possible that they arose apogamously. The case of *Scolopendrium* would then be com-

* 'Ber. der Gesellsch. f. Bot.,' Hamburg, 1885, p. 43.

† Heim, 'Flora,' 1896, p. 329.

‡ *Loc. cit.*

§ In a paper by Mr. E. J. Lowe, read at the Linnean Society, February 20, 1896.

|| Stange, *loc. cit.*

parable to that of *Trichomanes alatum*,* in which apogamy and apospory co-exist. Prothalli have been found to arise directly from the older fronds of another variety of *Scolopendrium*.†

An attempt will now be made to bring the peculiar modification of the life-history cycle of these ferns into relation with previously recorded cases of apogamy, and to estimate its theoretical bearing. A full consideration of these points must be deferred until more extended observations have been made.

There seems no reason to doubt the prothallial nature of the cylindrical process: its origin, the character of its cells, the presence of functional sexual organs, the development of rhizoids, and the direct transition to an ordinary flat prothallus apex sometimes met with, are sufficient grounds for this conclusion. The distinction between its origin as a direct continuation of the prothallus, and the cases in which it arises behind the apex which has lost its meristematic character, is not an essential one. Both forms occur in *Lastræa dilatata*; in the latter case the process may be compared with the numerous elevations which appear on the under side of old prothalli of *Doodia caudata*,‡ and are capable of apogamous development. The formation of such processes by prothalli which have attained a considerable size without having been fertilised, appears to be of not infrequent occurrence, and is usually associated with apogamy. It is recorded in *Todea pellucida*, Carm., *T. rivularis*, Sieb.,§ and *Athyrium filix-fœmina*, Bernh.,|| and the writer has found in *Aspidium frondosum*, Lowe, as many as six apogamous buds, formed from the tips of cylindrical processes, which arose from the anterior margin of a prothallus.

The term cylindrical process¶ has been used to avoid confusion with the middle lobe developed in aborting prothalli of *Pteris cretica* and *Aspidium filix-mas*. This, as De Bary has shown, may be regarded as corresponding to some extent with the first leaf of an apogamous sporophyte.** A structure comparable with this middle lobe has been found in prothalli of *Lastræa dilatata*, which had also produced a cylindrical process; usually one or more sporangia were borne upon it.

Tracheides were always present in the tissue beneath sporangia,

* Bower, 'Annals of Botany,' vol. 1, p. 300.

† Druery, 'Linn. Soc. Journ.,' vol. 30, p. 281.

‡ Heim, *loc. cit.*, p. 340, fig. 12.

§ Stange, *loc. cit.*

|| Druery, 'Gard. Chron.,' November 10, 1895.

¶ It is impossible to determine whether the structure to which Wigand ('Bot. Zeit.,' 1849, p. 106) applied this name, and which he inclined to consider as a rudimentary axis, was of the same nature or was a true middle lobe, but the latter appears the more probable conclusion.

** *Loc. cit.*, p. 464.

and the question arises whether their occurrence is to be regarded as of morphological significance. They have been found in the prothalli of a number of species of ferns, and, in every case investigated, were associated with apogamy. In the case of *Pteris cretica* the differentiation of the tracheides in the prothallus precedes the origin of the bud.* This is the case also with the single sporangia formed on the edge of the prothallus, and probably holds good for the groups of sporangia borne on the process. But tracheides may occur in the prothallus at a distance from the place of origin of buds or sporangia. Putting aside the case of the middle lobe, the prothallial nature of which is open to doubt, a large bundle of tracheides was found in the substance of a fleshy prothallus of a variety of *Scolopendrium vulgare*, which bore numerous archegonia on the surfaces immediately above and below the tracheides. Elongated cells, which resemble sclerenchyma fibres, occur in the midrib of certain frondose liverworts.† A still more instructive example is afforded by the presence of tracheides in the massive endosperm of certain cycads.‡ This latter case shows clearly that such elements may be formed in the gametophyte to meet a physiological need. It seems inadvisable, therefore, to lay stress on the presence of tracheides as a means of distinguishing between the two generations, and the more so since their occurrence in a portion of the prothallus which is about to bear a bud or sporangia can be recognised as a physiological advantage. Such means of procuring a sufficient water supply may be a necessary preliminary to the development of a young sporophyte or a group of sporangia.

Lastly, it remains to consider the view to be taken of the presence of the characteristic reproductive organs of the asexual generation upon the gametophyte, and to consider its bearing upon the nature of alternation of generations in the archegoniatae. Since the discovery that in certain cases the one generation could arise directly from the other without the intervention of the proper reproductive organs, such cases have been used in support of the view that the alternation in the Archegoniatae was homologous.§ On the other hand, it has been maintained, both on grounds of the exceptional nature of these cases of apospory and apogamy, and of comparative phylogeny, that the distinction between the two generations was a much deeper one; that the alternation was not homologous, but antithetic.|| So far no case has been recorded in which the proper reproductive organs of the one generation were situated upon the

* Farlow, *loc. cit.*, p. 269.

† Goebel, 'Outlines,' p. 145.

‡ I am indebted to Professor Bower for this unpublished fact.

§ Pringsheim, 'Jahrb. f. Bot.,' bd. 9, p. 43.

|| Bower, 'Annals of Botany,' vol. 4, p. 347.

other without the intervention of the vegetative organs. At first sight such appears to be the case in the prothalli of the two species described; sporangia were present in close proximity to the sexual organs, the vegetative organs of the sporophyte being, at most, represented by a mass of cells underlying the group of sporangia, and even this distinction may not be recognisable beneath the single sporangia on the edge of the prothallus.

Several reasons may be adduced, however, against regarding these phenomena as evidence that the alternation of generations found in the ferns is not antithetic. In the first place, it is to be noted that the two forms in which sporangia have been observed upon the gametophyte are highly variable species, and that the varieties studied were well-marked crested forms. Further, the conditions under which the prothalli existed were in several respects unnatural. Among them the fact that fertilisation was prevented by not watering the cultures from above, and that a prolonged growth of the unfertilised prothalli was thereby induced, is of special interest, for it appears that apogamy is liable to occur under such conditions in ferns which, as a rule, reproduce sexually. While these considerations do not of themselves preclude deductions being made from these peculiar forms of reproduction, they necessitate especial caution in their use in the discussion of broad morphological questions.

Further, a number of reasons exist for considering the production of sporangia on the prothallus as a special case of apogamy. In *Scolopendrium vulgare* a sporophyte may develop from the tip of the cylindrical process. This may happen after a group of sporangia has been developed. In one case two ramenta were present, one on each side of a group of sporangia; they were in every respect similar to the ramenta which develop on the tip of the process when it is being transformed into the apex of a bud. Whenever a group of very young sporangia was seen it was situated upon the apex of the lobe, and the sporangia were in a more advanced stage of development the farther the group to which they belonged was removed from the apex. This has been most clearly seen in the case of *Lastræa dilatata* in which no buds with vegetative organs have as yet been seen, although in one case ramenta were associated with the sporangia, but it also holds for *Scolopendrium*. The explanation of these facts, which appears most probable, is that each group of sporangia had occupied the apex of the process when very young, and had become farther removed from this position as the process continued to increase in length. It is uncertain whether this growth is by direct continuation of the original growing point of the process, or whether the development of a group of sporangia at the apex necessitates the formation of a new growing point; possibly both forms occur. If the latter be the case a process on which several

groups of sporangia are present must be looked upon as a sympodium. Some probability is lent to this view by the fact that the first appearance of the process in *Lastrea* is usually as a sympodial continuation of the axis of a prothallus whose true apex has developed one or more sporangia.

Since the group of sporangia and the tissue of peculiar character on which they are seated are developed in the place of an apogamously produced vegetative bud, they may be looked upon as constituting a very reduced sporophyte. The drain upon the resources of the prothallus entailed by the production of this reduced bud, which is incapable of further growth, is much less than when a vegetative bud is formed. This explains why a number of such sporangial groups can be produced and supported by a single prothallus. The occurrence of a number of vegetative buds on a single prothallus is the exception, but may happen, as the case of *Aspidium frondosum*, before mentioned, shows.

It is probable that it is in the constitution of the nuclei that a means of distinction between cells of the oophyte and the sporophyte must be looked for in these cases in which the two generations are in intimate connection with each other.*

The complete life history of the fern is in these cases still further shortened than in the ordinary cases of apogamy; not merely the formation of a zygote by the fusion of antherozoid and ovum, but the formation of an embryo, in which any differentiation of the vegetative organs can be detected, is omitted, and the sporophyte is reduced to a mass of tissue which may be compared to a placenta bearing sporangia. The occurrence of single sporangia upon the edge of the prothallus may, in the light of the series of stages described, be considered as a still further case of reduction of an apogamous sporophyte. While this does not altogether prevent the explanation of the presence of sporangia upon the prothallus from the point of view of the supporters of the homologous nature of the two generations, it brings the present case into line with other exceptions to the normal life-history cycle, whose bearing on the nature of alternation has been discussed by Bower.† The present case, although more striking in its appearance, seems, so far as it has been investigated, to afford no sufficient reason for dissenting from the conclusion at which he arrived.

It is of interest to note the additional evidence, were such needed, which these observations afford of the generalization made by Goebel,‡ that the sporangium is to be regarded as an organ *sui generis*.

* Bower, 'Trans. Bot. Soc. Edinb.,' vol. 20.

† 'Annals of Botany,' vol. 4, 1890, p. 347.

‡ 'Bot. Zeit.,' 1881, p. 707.

From the staff of the Royal Gardens, Kew, I received ready assistance in many practical matters in the conduct of the cultures; my thanks are especially due to the curators, Mr. Watson and Mr. Nicholson.

November 19, 1896.

Sir JOSEPH LISTER, Bart., President, in the Chair.

Dr. Francis Elgar was admitted into the Society.

A List of the Presents received was laid on the table, and thanks ordered for them.

In pursuance of the Statutes, notice of the ensuing Anniversary Meeting was given from the Chair.

Mr. Shelford Bidwell, Professor Bonney, and Mr. Horace Brown were by ballot elected Auditors of the Treasurer's accounts on the part of the Society.

The Secretary read the Titles of the Papers received since the last meeting, which, under the new Standing Orders, had been published (see 'Proceedings,' No. 362).

The following Papers were read:—

- I. "The Reproduction and Metamorphosis of the Common Eel (*Anguilla vulgaris*). By G. B. GRASSI, Professor in Rome. Communicated by Professor E. RAY LANKESTER, F.R.S.
- II. "Total Eclipse of the Sun, 1896.—The Novaya Zemlya Observations." By Sir GEORGE BADEN-POWELL, K.C.M.G., M.P. Communicated by J. NORMAN LOCKYER, C.B., F.R.S.
- III. "Preliminary Report on the Results obtained with the Prismatic Camera during the Eclipse of 1896." By J. NORMAN LOCKYER, C.B., F.R.S.

"The Reproduction and Metamorphosis of the Common Eel (*Anguilla vulgaris*). By G. B. GRASSI, Professor in Rome. Communicated by Professor E. RAY LANKESTER, F.R.S. Received October 19, 1896. Read November 19, 1896.

Four years of continual researches made by me in collaboration with my pupil, Dr. Calandruccio, have been crowned at last by a success beyond my expectations, that is to say, have enabled me to