NOTES.

ON APOGAMY AND THE DEVELOPMENT OF SPORANGIA UPON FERN-PROTHALLI. By WILLIAM H. LANG, M.B., B.Sc.¹—The two most important deviations from the normal life-history of Ferns, apogamy and apospory, are of interest in themselves, but acquire a more general importance from the possibility that their study may throw light on the nature of alternation of generations in archegoniate plants. They have been considered from this point of view by Pringsheim, and by those who, following him, regard the two generations as homologous with one another in the sense that the sporophyte arose by the gradual modification of individuals originally resembling the sexual plant. Celakovsky and Bower, on the other hand, maintain the view that the sporophyte, as an interpolated stage in the life-history arising by elaboration of the zygote, is not the homologue of the gametophyte, and is only represented in a few Thallophytes. In the light of the theory of antithetic alternation no weight is attached to apogamy and apospory for phylogenetic purposes.

In the paper of which this is an abstract, the results obtained by cultivating the prothalli of a number of species of Ferns under conditions slightly different from the natural ones are described, and their bearing on the problem of the nature of alternation considered. The behaviour of *Scolopendrium vulgare*, Sm., and *Nephrodium dilatatum*, Desv., in which sporangia were borne upon the prothallus, has already been described in a preliminary statement². It is therefore sufficient to express the results of prolonged cultivation of these and the remaining species in a tabular form.

¹ Abstract of a paper read before the Royal Society, March 3, 1898.

² Roy. Soc. Proc., Vol. lx, p. 250.

TABLE of the Results of cultivating Prothalli for a period of Two Years and a-half.

[Note.—In every species normal embryos were produced when conditions permitted fertilization.]

Names.	Results.
<i>Scolopendrium vulgare</i> , Sm., var. <i>ramulosissimum</i> .	Gametophytic budding. Development of archegonial projections. Development of cylindrical process usually from the apical region of the prothallus. Apogamy. { Tracheides in cylindrical process. Leaves, roots, and ramenta on process. Sporangia on the process. Vegetative buds from tip of cylindrical process, or in place of an archegonial projection.
var. <i>marginale</i> .	Similar to var. <i>ramulosissimum</i> , but no sporangia, isolated ramenta, or leaves found.
<i>Nephrodium dilatatum</i> , Desv., var. <i>cristatum gracile</i> .	Gametophytic budding. Development of archegonial projections. Development of cylindrical process, usually from the under-surface just behind the apex, which formed a 'middle lobe.' Apogamy. { Tracheides in middle lobe and cylindrical process. Sporangia, sometimes associated with ramenta, on middle lobe and process. No vegetative buds.
<i>Nephrodium Oreopteris</i> , Desv., var. <i>coronans</i> .	Gametophytic budding. Development of archegonial projections. Development of cylindrical process from apex of prothallus. Apogamy. { Tracheides in cylindrical process. Ramenta on cylindrical process. Vegetative buds (rare).
<i>Aspidium aculeatum</i> , Sw., var. <i>multifidum</i> .	Gametophytic budding. Development of archegonial projections. Apogamy. { Tracheides in prothallus. Vegetative buds (rare).

Names.	Results.
<i>Aspidium angulare</i> , Willd., var. <i>foliosum multifidum</i> .	Gametophytic budding. Development of archegonial projections. Apogamy. { Ramenta on prothallus. Vegetative buds (frequent).
var. <i>acutifolium multifidum</i> .	Gametophytic budding. Development of archegonial projections. No apogamy seen.
<i>Athyrium niponicum</i> , Mett., nor- mal form.	Gametophytic budding. Development of archegonial projections. Apogamy. { Tracheides in prothalloid growths from archegonial projections.
var <i>cristatum</i> .	Similar to the normal form, but in addition a few apogamously-produced vegetative buds.
<i>Athyrium Filix-foemina</i> , Bernh. var. <i>percristatum</i> . var. <i>cruciatum cristatum</i> . var. <i>coronatum</i> .	Gametophytic budding. Development of archegonial projections. Development of cylindrical process from apex or from under-surface of the prothallus. Apogamy. { Tracheides in process. Continuation of process as a leaf. Vegetative buds.
<i>Polypodium vulgare</i> , L., var. <i>grandiceps</i> .	Gametophytic budding. Apogamy. { Isolated leaf-like growths. Vegetative buds (numerous).
<i>Aspidium frondosum</i> , Lowe (from the Pits, Royal Gardens, Kew).	Apogamy. Vegetative buds produced on short cylindrical processes before the culture had been watered. After the culture was watered, normal em- bryos.

In addition to the species mentioned in the Table above, cultures were made of crested and uncrested forms of *Nephrodium Filix-mas*, Rich., representing the three sub-species, which are sometimes distinguished in this country. Some of these (both crested and normal) behaved in a similar manner to the species referred to in the Table, though only one instance of apogamy induced by long cultivation has as yet been found. Others (crested and normal forms) produced a single bud on the under-side of the prothallus which did not bear archegonia.

Connecting this latter type of apogamy, which agrees with the description of De Bary and Kny, with the more normal prothalli, was one variety, the archegonia of which developed into typical arche-

gonial projections. In the place of the projection nearest to the apex a vegetative bud arose.

It is possible to draw some general conclusions from this series of cultures. It is a striking fact that in every one of the species, prothalli, which under normal conditions would have produced normal embryos, became, after a longer or shorter period, apogamous. Further, there was a general similarity in the changes of form and structure of the prothallus, which preceded this result. This form of apogamy, occurring after prolonged cultivation of normal prothalli under special conditions, may be distinguished as *induced apogamy*, in contradistinction to *direct apogamy*, by which is meant the immediate production of vegetative buds by prothalli, which are usually incapable of being fertilized. Both forms occur in *Nephrodium Filix-mas*.

The causes which appeared to induce apogamy in these prothalli were the prevention of contact with fluid water which rendered fertilization impossible, and the exposure to direct sunlight. Possibly the temperature also had some effect. The case of *Nephrodium Filix-mas* shows that the variable condition of the sporophyte, as indicated by cresting, &c., though possibly predisposing to the changes which lead to apogamy, does not stand in any necessary connexion with the phenomenon.

That different degrees of apogamy are distinguishable was also shown by these cultures. The cylindrical process, arising from the apex of the prothallus, or from its under-surface, is to be regarded simply as a modification in form and structure of the gametophyte dependent on the altered conditions, and possibly a direct adaptation to these. The next stage is seen in cylindrical processes, which, while bearing sexual organs, also produce isolated members of a sporophyte (roots, ramenta, sporangia). It is to be borne in mind, however, that tissue differing from the rest of the process always occurred beneath the last-named structures. The final stage is the production of a vegetative bud capable of further growth as a typical sporophyte. In this a series leading from the bud arising by transformation of the tip of a cylindrical process, to buds produced on or in the place of archegonial projections, and from this to buds situated on the under-surface of the prothallus itself, can be recognized.

The readiness with which the intermediate form between gameto-

phyte and sporophyte and the early stages of vegetative buds re-assume the prothalloid form is worthy of note, as bearing on some cases of apospory.

These departures from the normal development of the prothallus are not regarded as reversions in the ordinary sense, but as indications of the capability of direct response to altered conditions possessed by the gametophyte. Their possible importance in relation to the theory of homologous alternation appears to the writer to be of this nature. If that theory be true, the sporophyte and gametophyte are modifications of a similar form. The gametophyte, especially the simple free living prothallus of the Ferns, has departed less widely from that form. Such an organism as a fern-prothallus would therefore appear to be suitable for experimental work, in the hope that its behaviour under altered conditions would afford hints as to the sort of changes which, in the original algal form, led to the evolution of the sporophyte. The altered conditions in this series of experiments are of a similar kind to those which are assumed by Professor Bower to have occurred on the spread of algal forms to the land, and to have conduced to antithetic alternation.

The results may now be used in picturing the manner in which alternation of generations might have come about by the modification of originally similar individuals into gametophyte and sporophyte. It is assumed for this purpose that the sporophyte of the Vascular Cryptogams did not arise by the elaboration of a structure resembling a bryophytic sporogonium. It is recognized that the theory of antithetic alternation, as elaborated by Professor Bower, affords a consistent and satisfactory explanation, if the assumptions necessitated by the theory are granted. The present theory, which is put forward merely as a provisional hypothesis, is founded on another class of facts.

With the spread of algal organisms to the land, where in the absence of any vegetation affording shade some at least would be exposed to more intense illumination, the flattened form would probably be assumed. Prolonged drought and the influence of direct sunlight, inducing directly a change of form into a cylindrical body, might be accompanied by the substitution of a reproductive organ forming dry reproductive cells (spores) for those adapted to an aquatic existence. The acquisition of more highly developed absorbent organs (primitive roots) would further the existence and

growth of this modified gametophyte. This spore-producing stage would at first follow the sexual stage in any individual exposed to dry conditions. It is possible to imagine, however, how the association of the asexual with the sexual individual might come about. Absence of fluid water would prevent the liberation of motile spores from the zygote. The latter would be obliged to germinate *in situ*, and the fact that it did so under dry conditions would tend to the shortening of the sexual stage, and the speedy assumption of the sporophytic form and mode of reproduction. From the spore, which would always separate from the parent, a sexual individual would arise, since germination could only take place in a damp spot. As soon as, with the increase in size and complexity of the spore-bearing plant, a vegetation capable of affording shade came into existence, the conditions suitable for the persistence of the more primitive, alga-like, sexual stage in the life-history would be present. The latter has, of course, also been modified in various ways.

In the concluding portion of this paper, the theories of antithetic and homologous alternation are compared by considering the explanations they afford of the facts. The general conclusion reached is that, while both afford a *possible* explanation of the facts of alternation in archegoniate plants, any evidence which would render one or the other untenable is wanting. The reasons on which either is considered more probable depend on the views held as to the lines of descent which have been followed, and the degree to which the different groups of archegoniate plants have had a common origin, or represent actual steps in the process of evolution of the sporophyte. Under these circumstances the question must be regarded as an open one until the available lines of evidence have been more fully investigated.

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THE LIGULE IN LEPIDOSTROBUS.—The presence of a ligule on the vegetative leaves of *Lepidodendron* is now a well-ascertained fact, and it can be readily seen in several of the slides preserved in the Williamson Collection at the Natural History Museum. The best description and figures of the ligule in the

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