On Apospory in *Anthoceros laevis*.

BY

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With Plate XXVII.
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THE fact that under certain conditions the vegetative cells of the asexual generation could produce the sexual generation, and that the origin of the latter was not necessarily connected with the spore, was discovered in the Mosses. Pringsheim¹ first described it for three species (*Hypnum cupressiforme*, *H. serpens*, and *Bryum caespitosum*), while the independent work of Stahl² was done on *Ceratodon purpureus*. From Pringsheim's account and figures it appears that the seta of the ripe capsule was cut into short pieces, which were laid on damp sand; in Stahl's experiments the sporogonia were either simply pulled away from the moss-plant or cut off above their point of attachment to the latter. In both series of experiments, whether the sporogonia were more or less cut up or were uninjured, protonemal filaments ultimately arose from certain of their cells. Brizi³ has since shown that in *Funaria hygrometrica* this may take place from capsules still attached to the moss-plant. Without referring in detail

¹ Monatsb. d. k. Akad. Wiss., Berlin, 1876. Jahrb. wiss. Bot., Bd. xi, 1877.

² Bot. Zeit., 1876, p. 689.

³ Ann. d. R. Inst. Bot. Rom., vol. v., p. 54, 1893.

to the corresponding phenomenon since discovered in Leptosporangiate Ferns, it may be pointed out that in these plants also the sexual generation may arise from an uninjured sporophyte, or its development may require to be induced by laying pieces of a leaf on damp soil.

Although discovered in Mosses and subsequently found in a number of Ferns, apospory is not, so far as I know, hitherto recorded for any Liverwort. While working in the laboratory of the Peradeniya Botanic Gardens it occurred to me that similar treatment of the sporogonia of *Anthoceros laevis*, L., which grows abundantly in the gardens, might induce apospory. Accordingly a number of young, unopened sporogonia were taken, and the portion projecting from the calyptra cut up into lengths of about 5 mm. The pieces were laid on damp sand and covered with a bell-glass. By the end of a month they were more or less decayed, and of a yellowish-green tint. From the cut ends and sometimes from the surface, however, small outgrowths of a deep green colour could be seen to have arisen (Pl. XXVII, Fig. 1). The culture underwent but little change during the next fortnight, when it had to be stopped owing to my leaving Peradeniya for some months. None of the new growths had assumed the flattened form of the thallus, but their resemblance to the latter in its early stages and the origin of rhizoids from them (Fig. 2) sufficiently demonstrated that it was a case of apospory. Further, both in the position in which the new growths appear and in the method by which their development was induced, this case of apospory in a Liverwort corresponds closely with those recorded for the Mosses.

Before describing the pieces of sporogonium from this culture, some points in the normal structure of the corresponding region must be briefly referred to. As in most species of *Anthoceros*, the epidermis consists of long narrow cells; within this the wall of the sporogonium consists of about five layers of oblong parenchymatous cells, about four times as long as broad; the spores with the intervening trabeculae surround the columella, which is composed of

long narrow cells. In the epidermal cells are small starch-grains; in the other cells of the wall a considerable amount of starch may be present within the single large chloroplast, while the cells of the columella and trabeculae contain little or no starch. The young spores contain abundant starch. Thus the cells of the five inner layers of the wall are the least specialized of the sterile cells of the sporogonium and contain the greatest amount of reserve material, while the presence of a healthy chloroplast in them enables this supply to be increased.

After cultivation on damp sand the pieces of sporogonium became more or less disintegrated, and many of the cells composing them were evidently dead or dying. Others, however, were still healthy. Such cells occur throughout the wall, most commonly in the layers close to the epidermis, and they stand out prominently when stained with iodine owing to their chloroplasts containing starch. Many of these living cells had not divided, and only differed from the corresponding cells in the uninjured sporogonium in having rounded themselves off somewhat from their neighbours. In others, however, cell-divisions had taken place. These divisions may commence in cells which are still covered by the epidermis (Figs. 4, 5), but the new growths develop more rapidly when they are on a free surface of the piece of sporogonium. Thus those growths which arise from the cut surfaces at the ends (Fig. 1) develop first and, as the figure shows, may attain a considerable size while the epidermis is still intact. As the disintegration proceeds, however, the epidermis gets broken and in places stripped off, and then growths arising from the cells beneath, such as that shown in Fig. 3, are enabled to continue their development.

In almost every case each new growth appeared to owe its origin to a single cell of the sporogonium (cf. Figs. 3-6). The divisions, which take place in the cell, are subject to considerable variation, but the first is usually transverse and often separates a lower cell, in which few or no further divisions occur, from an upper, which gives rise to the new

growth (Fig. 3). In other cases this contrast is wanting. The general sequence of the early divisions in the cells giving rise to the new growths, and the differences between individual cases, are closely parallel to the early stages of germination of the spore of *Anthoceros*. The oldest buds obtained also resemble a stage in the germination of the spore, as will be seen by comparing Fig. 2 with such a figure as that on p. 138 of Campbell's 'Mosses and Ferns,' and that they are gametophytic is further indicated by the origin of rhizoids from them. As mentioned above the culture had to be stopped at this stage and therefore the comparison cannot at present be carried further.

There remains for consideration the evidence that these new growths, which have been seen to be gametophytic, are truly aposporous. Three possible sources of the buds had to be considered; they might have arisen from spores present in the sporogonium or accidentally introduced into the culture, or from the undivided spore-mother-cells in the spore-sac, or finally from the sterile tissue of the sporogonium. Even from external examination of the pieces of sporogonium, removed from the culture when fresh, the third of these alternatives seemed the probable one, for, when the growths arose from the cut end, they sprang from close beneath the surface, while, if from the side of the piece, the whole growth corresponded in position and size to one of the cells of the wall and was attached closely to the neighbouring cells. No trace of a ruptured spore-membrane was ever visible. The actual proof, however, could only be obtained by the study of sections; these showed that the growths might start beneath the unbroken epidermis from cells of the wall surrounded on all sides by their neighbours. Most commonly they arise from subepidermal cells, but they may start in any of the layers of the wall down to that which bounds the sporogenous layer (Figs. 4, 5). The same holds for growths originating from the cut ends (Fig. 6).

The positive evidence is thus sufficient to establish the fact of apospory in this Liverwort, and even did cells of the sporo-

genous tissue or the young spores undergo development, it would merely increase the difficulty of demonstration in the case of any particular growth. In the majority of the pieces of young sporogonia experimented with, the young spores simply disintegrated without any attempt at further development. In one case, however, growth had taken place within the spore-sac leading to the presence of young plants consisting of a few cells; from this single example it was impossible to decide with certainty whether these were referable to young spores or to spore-mother-cells.

The small number of specimens obtained from this culture did not afford material for the study of the cytological changes, which may occur in the cells destined to give rise to a gametophyte. The frequency with which the new growths start from single sterile cells of the sporogonium might make this and similar cases of apospory suitable for such observations. Even in the absence of observations on the behaviour of the nucleus, certain considerations on the point of view, from which the phenomenon of apospory is best regarded, are suggested by this case, and may be briefly referred to without entering on any general discussion of apospory.

In the normal life-history of such a plant as *Anthoceros* the fact that the fertilized ovum gives rise to the sporophyte and the spore to the gametophyte must be regarded from two points of view. In the origin of both generations the start is made from a single cell (zygote, spore) and these cells in the two cases have had very different histories. The zygote has arisen by the fusion of two cells, while the formation of the spore is preceded by the reduction of chromosomes in the spore-mother-cell. But it is not sufficient in considering the remarkable fact—that these two sorts of reproductive cells in the same species give rise to distinct and very different stages in the life-history—to note their different origin. The conditions under which they undergo their further development are also very different in the two cases. The spore, separated from the parent plant, falls on the ground, and under suitable conditions of moisture, warmth, and illumination develops

into the thallus, the material for the growth of which is provided by its chlorophyll-containing cells. The zygote enclosed in the venter of the archegonium is at first wholly dependent on the gametophyte, and the sporogonium developed from it never becomes free from the latter.

Similarly, with regard to the explanation of such a deviation from the ordinary life-cycle as apospory, both the character of the cells, from which the development proceeds, and the nature of the conditions, to which they are exposed during development, require consideration. As regards the former point, it has been shown above that certain cells or groups of cells of the sporogonial wall remain alive while others die and disintegrate. The living cells thus become to some degree isolated in position and, as may fairly be assumed, physiologically also. The cells of the cut ends, which were seen to commence growth earlier, are partially isolated by the section through the sporogonium. These cells of the wall have also been seen to be the least specialized in the sporogonium, and they are capable of the continued manufacture of organic material. Whatever the changes involved in the reconstitution of these cells may be, all these facts point to there being a general physiological distinction between them and the other tissues of the sporogonium. In *Anthoceros*, as in the cases of apospory among Ferns, the sporogenous tissue itself, if it is distinguishable, does not take part in the origin of the new growths. The only apparent exception to this, as a general rule, is in the case of the mosses, in which Pringsheim points out that the zone of the seta, from which protonemal filaments arise, corresponds to that zone in the capsule between columella and wall in which the archesporium lies. But the whole of the seta is sterile tissue and there is no evidence that archesporial cells themselves give rise to new growths. On the other hand, Stahl's observation, that apospory could be induced in the cells of the capsule-wall, shows clearly that there is no necessary connexion in the Mosses, between the archesporial region and apospory. In Mosses, as in *Anthoceros*, the growth starts from little-specialized

parenchymatous cells, which have fairly thin walls and contain chlorophyll, and probably these characters are of much greater importance than the position of the cells in relation to the archesporium.

The conditions, to which these cells were exposed, must in the second place be considered. They were essentially similar to those under which the spores develop into the thallus (moisture, sufficient temperature, light), while like the spores these cells were more or less isolated from their neighbours. Under these circumstances they developed into the gametophyte. The most important factor in the environment of the young sporophyte, its position in and nourishment by the gametophyte, is entirely absent, and it is hardly too much to say that it would be surprising if under these circumstances the cells of a decaying sporophyte of a Liverwort or Moss produced sporogonia. The cases of apospory in Bryophytes appear to indicate the important influence of the environment in determining the origin of a gametophyte from an isolated cell of the sporogonium. All the sporogonia which have been experimented with were normal, and were obtained from wild plants; there is here no question of a predisposition towards apospory such as complicates the problem in the case of some Ferns. The experimental conditions to which the cells have been submitted have brought into view certain of their properties which are not called into play in the normal life-history.

The observations made on this case of apospory only serve to suggest the use of a thorough study of the conditions, to which the tissues experimented with are exposed, both as regards the inorganic environment and the alterations in their relations to neighbouring tissues. A knowledge of the facts regarding the influence of the change of environment, as well as those relating to the possible reconstitution of those cells of the sporophyte, which develop into the other generation, is the necessary preliminary to any estimate of the evidence afforded by apospory as to the nature of alternation of generations. Until further knowledge is obtained on these points it appears

equally unsafe to assume that this deviation from the normal life-history is a reversion, or to dismiss it as a mere sport with no phylogenetic bearing.

In conclusion I have to express my indebtedness to the Director of the Royal Botanic Gardens at Peradeniya for the use of a table in the Laboratory where the culture was made and the observations commenced.

EXPLANATION OF FIGURES IN PLATE XXVII.

Illustrating Dr. Lang's paper on Apospory in *Anthoceros*.

Fig. 1. End of a piece of sporogonium after six weeks' cultivation, showing the aposporously-produced growths arising from the cut surface. $\times 80$.

Fig. 2. Surface-view of a growth like those in Fig. 1, which has produced a rhizoid. $\times 375$.

Fig. 3. Surface-view of a growth referable to a single cell of the sporogonial wall, exposed by the separation of the epidermis. $\times 375$.

Fig. 4. Longitudinal section showing the rounding off and division of a number of cells of the partially disintegrated wall. $\times 200$.

Fig. 5. Similar section to Fig. 4. The wall is hardly disintegrated; the two new growths are covered by epidermis. $\times 200$.

Fig. 6. Section through the end of a piece of sporogonium, showing the origin of two growths from different layers of the wall. $\times 200$.

Fig. 7. Section through one of the most advanced growths like that in Fig. 2. $\times 200$.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 7.

Fig. 6.

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