XVI.—*On the Phenomena of Variegation and Cell-Multiplication in a Species of Enteromorpha.* By P. GEDDES, F.R.S.E., Demonstrator of Vegetable Histology in the University of Edinburgh. (Plate XIII.)

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In the autumn of 1877 I found on stones in a sea-water aquarium in Professor HUXLEY's laboratory at South Kensington, the curious little Alga which forms the subject of the present paper. I have ever since kept specimens growing, carried them with me to various places in Britain and on the Continent, and subjected them to frequent examination at all seasons of the year. Dr BORNET has kindly identified it for me as a species of *Enteromorpha*.

Viewed with a lens, the fronds are of a beautiful green, often more or less mottled with white. Examination of such specimens with a somewhat higher power (say 1 inch) shows among the ordinary green cells others which are smaller and colourless, occurring singly or in patches of very variable size. Oftener than these variegations of the frond itself, one notices buds, or even large branches, which are completely colourless. And the extreme case—of large fronds, and indeed whole tufts, almost without any green cells, is not wanting. How are these phenomena to be accounted for?

The first hypothesis which suggests itself is that here we have an etiolation of green cells,—a mere blanching of particular cells or fronds, due to the interception of the light by the felt-work of *Oscillatoria*, *Confervæ*, &c., by which the specimens were always more or less thickly surrounded. But it will be seen from an inspection of the plate that the colourless cells are oftenest apical; and when a fragment of the very thickest part of this vegetable felt is detached and viewed under the simple microscope, colourless shoots are to be seen projecting clear above the tangled mass of other Algæ, while the portion of the frond thus shaded may be of the deepest green. Moreover, specimens kept growing for months in a window, exposed to direct sunlight for several hours daily, never lost their variegated aspect. A crucial experiment enabled me finally to exclude the hypothesis of a mere etiolation of normally green cells by deficiency of light. A flint covered with an abundant crop of the Alga under examination was broken into three pieces, of which one was exposed to sunshine for six or seven hours a day, another kept in the diffuse light of my workroom, and another placed in darkness. After the lapse of three or four weeks no change was appreciable. On the stone exposed to

direct sunlight there seemed to be as many colourless cells as ever, though it is well known that a few hours in such conditions suffice to develop chlorophyll in blanched vegetable cells. Nor did those kept in darkness show any distinct increase in the proportion of white cells to green. In fact, when the three pieces of flint were again placed together in the same aquarium, an attempt to identify them again by examination of the Algæ they bore, failed completely.

I do not deny, however, the importance of the action of light, for I have found white buds more abundantly in winter than in summer; but it is evident that such an experiment as the foregoing, twice repeated, excludes the hypothesis of etiolation. Moreover, the long period over which my observations have extended, the many changes of climate and of circumstances to which the plants have been exposed, and above all, the fact that the white shoots were more abundant the more active and more vigorous the growth, are all arguments in favour of the normality of this mode of vegetation. I should, however, consider it premature to assign any specific or generic name before examining more specimens from other sources; and it may not improbably turn out that these phenomena of variegation may occur as a kind of *sport* in many species of Algæ.

The colourless buds, then, demand a closer examination. At one side of the frond or filament, and generally midway between two green cells, is often to be seen a slight prominence of cellulose enclosing a tiny droplet of colourless non-nucleated hyaline protoplasm (figs. 1*a*, 11). A farther stage is represented in fig. 12, where there are two similar but larger masses, and a farther still in fig. 13, where there are three; in short, all stages are to be found up to a comparatively long row of colourless nucleated cells, such as that represented in fig. 14 or 23. The existence of a series of perfect gradations between a single minute non-nucleated droplet of clear protoplasm, and a distinct row of nucleated and granular cells, shows that the colourless shoot arises in a way totally distinct from that by which the ordinary green cells are developed.

Such transparent cells multiply by transverse division, and have also the power of developing chlorophyll. While the majority of the colourless shoots are sharply marked off by their colour and general appearance from the green part of the frond (figs. 13, 14), others are to be found in which there is a gentle gradation from white cells to green (figs. 1*b*, 15, 24, 28), the development of chlorophyll beginning at the base of the shoot, and proceeding upwards.

Cases in which the colourless cells are irregularly interpolated among the green, as has been already said, are not uncommon. Sometimes one finds the cells of a green filament separated by the development of one or several colourless cells (figs. 16, 19, 26); sometimes these may multiply greatly, so as to push the original green portions of the frond far apart from each other, and so

produce such extraordinary forms as those represented in figs. 18 and 19, where green shoots are seen as if arising from a colourless frond.

The co-existence of two distinct kinds of cell being admitted, it is desirable next to ascertain the process by which these arise. With the green cells there is no difficulty; their multiplication by transverse division is obvious; but it is by no means easy, without the examination of a vast number of specimens, to satisfy oneself as to the mode of origin of the colourless cells, or rather of that droplet of hyaline protoplasm (fig. 11) from which the colourless cell originates.

The cellulose of an Alga is, as has been known from the time of KÜTZING and RABENHORST, no mere structureless investment, but possesses a *capsular* structure, quite similar to that which is so easily seen in *Glæocapsa*, or to that which has been demonstrated in the matrix of hyaline cartilage. This structure is shown in figs. 2 and 3, particularly well in the latter. Its origin is obvious; a cell throws out a coat or shell of cellulose, and then divides into two new cells; each develops its own investment of cellulose, and these lie end to end within the first. The extremities of these new cells being biconvex, they are thus not in complete apposition, but an angular interspace is left, which extends ring-fashion round the filament. Any irregularity of form or growth in the cell produces a corresponding irregularity in the disposition of the cellulose, and thus too in the form of the intercellular space, perhaps suppressing it on one side and enlarging it at the other.

It is not to be expected that these laminæ of cellulose should be of precisely equal thickness and strength throughout, nor of equal permeability to fluids. Where a weak place in the cellulose wall happens to come opposite the intercellular space, a certain amount of water might easily enter the latter from the cell; this water might soften and swell the circumjacent cellulose, and thus protuberances of the cellulose, and of the cellulose alone, such as those represented at figs. 5, 6, 7, 9, and 10, would easily arise. These phenomena are most probably to be considered as pathological.

But if instead of a mere exosmose of water through the wall, we suppose the growing protoplasm itself to force a passage through the least resisting point in the innermost capsule of cellulose into the intercellular space, we have at once a reasonable explanation of the origin of the tiny drops of colourless protoplasm already described (fig. 11). Their position, almost invariably evenly intercalated between two given cells (fig. 7*a*), or at one side of the plane separating them (fig. 11); and their forms, biconcave and lenticular in the first case, hemispherical in the second, are strong proofs of their origin in this way.

The cells at the bottom of the white shoots in figs. 2, 22, 23, 26, &c., are obviously each in an intercapsular space, and their protoplasm (which has in

some cases developed a nucleus, in others none) sometimes even half surrounds the innermost cellulose capsule of the adjacent green cell, and looks almost as if it were going to enclose it altogether. Such buds as these we have been imagining, arising as they would from the colourless ectoplasm of the green cell, would necessarily be themselves colourless. And instances are not wanting in vegetable and even in animal histology of the independent development of a nucleus and nucleolus within a cell.

It is possible to verify this hypothesis of the origin of the white cells by direct observation. Generally the colourless cells seem totally distinct and separate from the coloured (figs. 1, 2, 4*a*, &c.), but occasionally one can see with the utmost clearness (figs. 4*b*, 19, 27) the process of formation of the colourless cells by the intrusion of the colourless ectoplasm of the green cell into an intercellular space. In fig. 20 are to be seen pseudopodium-like processes of colourless protoplasm pressing into soft swellings of the cellulose. At figures 19 and 27, the intercellular space is being filled up by a flow of such protoplasm from the green cell; while in fig. 4*b* the formation of a lateral bud is going on.

In this Alga, then, we have simultaneously in progress two distinct modes of cell-formation; first, the ordinary process of vegetative growth by transverse fission; secondly, a process of gemmation tolerably similar to that which takes place in *Torula*. The cells produced by this second process are often to be seen dividing transversely (fig. 31), and it is not impossible that they may also give rise to new colourless cells by the same process as that by which they themselves were produced (figs. 19, 28).

The Alga in question is also of some interest from the physiological point of view. It would be interesting to ascertain how plants so nearly destitute of chlorophyll as that represented in the last figure, which possesses only two cells capable of decomposing carbonic acid, can possibly live and grow.

EXPLANATION OF THE PLATE.

(*Figures mostly drawn with Hartnack, Oc. 3, Obj. 7 or 9.*)

- Fig. 1. Young growing fronds, showing (*a*) colourless buds of various sizes; (*b*) an originally colourless shoot of which the cells have almost all developed chlorophyll.
- Fig. 2. A frond bearing a terminal colourless shoot, and showing indistinctly the capsular arrangement of the cellulose.
- Fig. 3. Young frond treated with weak potash solution, showing very distinctly the capsular arrangement of the cellulose.
- Fig. 4. Frond showing (*a*) young colourless cell devoid of nucleus; (*b*) another budding off from green cell.
- Figs. 5, 6, 7, 8, 9, 10. Fronds showing outgrowths and thickenings of the cellulose alone.

- Figs. 11, 12, 13, 14. Showing colourless shoots of various sizes.
- Fig. 15. Colourless shoot acquiring chlorophyll.
- Fig. 16. Frond in which colourless cells are irregularly developed among green cells.
- Figs. 17, 18. Fronds in which such irregularly interposed colourless cells have greatly multiplied, so as to push the original green parts of the frond far asunder, and to produce the appearance of green shoots arising from a white frond.
- Fig. 19. Gemmation of colourless cells from green very clearly shown.
- Fig. 20. Shoot in which green cells are sending out colourless processes, probably incipient buds.
- Figs. 21, 22, 23. Apical colourless shoots of various sizes.
- Fig. 24. Shoot similar to fig. 23, developing chlorophyll.
- Fig. 25. Tip of frond of which the two terminal green cells have been carried up by the development of a colourless shoot below them.
- Fig. 26. Frond with apical white shoot.
- Fig. 27. Mode of origin of colourless from coloured cells very clearly shown (see figs. 4 and 19).
- Fig. 28. Colourless shoot developing chlorophyll, bearing already a lateral colourless bud.
- Fig. 29. Similar lateral colourless bud farther advanced.
- Fig. 30. Showing probable mode of formation of such lateral colourless buds by displacement of a cell.
- Fig. 31. Tip of colourless shoot showing its cells in process of division.
- Fig. 32. Frond entirely destitute of chlorophyll save two basal cells.