

# APICAL MERISTEMS AND GROWTH CONTROL IN *HIMANTHALIA ELONGATA* (S. F. GRAY)

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## SUMMARY

The young plant shows considerable internal differentiation before an apical meristem is organized. Once formed, the apical cell segments slowly. It is triangular in transverse section and segments cut off from its three sides are actively meristematic and soon build up an extensive meristem which enlarges and functions throughout the vegetative phase of the plant's development. Experiments have shown that the apical cell is the main seat of growth control and if it is destroyed another apical cell cannot be regenerated to take over this role. Division of the apical cell followed by division of the whole meristem into two, marks the end of vegetative growth and the onset of reproduction. Successive divisions of the meristem follow and each new meristem becomes the tip of a fertile branch or receptacle. Eventually meristematic activity at the apices declines and this decline is associated with the termination of conceptacle initiation. As the entire vegetative meristem is used up in reproductive growth, there is no meristem left to continue vegetative growth after gamete discharge. Hence reproduction terminates the life span of *Himantalia*.

## INTRODUCTION

The growth form of *Himantalia* differs from that of any other member of the Fucales. The young plants are first recognizable on the shore as small vesicles, pale greenish-brown in colour. These vesicles flatten out and after 1-2 years growth they form the small leathery disc-shaped structure which is commonly referred to as the 'button' stage. From these 'buttons' the long thongs arise, and in some habitats they may reach a length of 7 ft or more. The 'button' is generally interpreted as equivalent to the vegetative thallus of the other Fucales, while the thongs correspond to the fertile receptacles (Gibb, 1937; Naylor, 1951).

*Himantalia* grows at, or near low water level, so that in some habitats the plants are uncovered at low spring tides, whereas in other localities they may never be exposed. Gametes are shed over a long period, e.g. Gibb (1937) records for the Isle of Man that they are released from late July, on through the winter until January. On the coast of Northumberland I have found likewise; that plants shed their gametes from late July, on through the winter and into the following year if storms have not swept all the old plants away. Eggs which have been shed in late July may have grown into fully developed buttons by the following summer, whereas eggs germinating in December will have formed only small plants which will continue to grow vegetatively until the following year. Receptacles or thongs grow out from the vegetative buttons during the autumn and continue to elongate throughout the following winter and spring. Finally, gamete production starts approximately a whole year after the receptacles are initiated. Following gamete production the plant disintegrates from the tip of the receptacles downwards to the attaching disc of the button.

The anatomical structure of the mature plants has been described by Naylor (1951). Rostafinski (1876) had earlier described the form of the apical cell in the mature button. The present work deals with the mode of origin of the apical meristem and the subsequent role which it plays during the development of the plant.

#### OBSERVATIONS

##### *Origin and development of the vegetative meristem*

When the large oospheres are shed, each one is surrounded by a thick mucilaginous envelope. As Gibb (1937) observed, the protoplast streams out through a pore in this mucilage and rounds off to form a spherical egg some 250–300  $\mu\text{m}$  in diameter. A small nucleus, 10  $\mu\text{m}$  in diameter, occupies a central position and it is surrounded by a halo of large pigmented granules. The escape of the egg from its mucilaginous envelope is essential for fertilization. I have verified Gibb's observation that if oogonia have been kept out of water for some time, e.g. during periods of exposure at low tide or during transfer from the shore to the laboratory, the oospheres which are shed on to the surface of the receptacles are unable to escape from their mucilaginous envelope and so do not get fertilized. Several workers e.g. Thuret and Bornet (1887), Oltmanns (1889) and Naylor (1951) were not very successful in their attempts to germinate the eggs. These workers give no description of the methods which they used but it may be that they tried to germinate oospheres which had already been discharged from the receptacles between the time of collecting and transferring the material to the laboratory, so that they had been too long out of water to be able to escape from their mucilage envelopes.

As *Himantalia* grows well down on the shore, so that the plants are only uncovered at low spring tides, or not uncovered at all, it seems likely that gamete discharge which takes place when the plants are picked out of the sea may be abnormal, and that the gametes are normally discharged underwater. Consequently experiments on germination were set up, in which segments of mature receptacles of both sexes were placed in culture dishes containing sterile seawater. A gradual discharge of eggs and sperms proceeded. After 2–3 days the pieces of receptacles were removed. A high percentage of germination was achieved from eggs and sperms which were discharged under water in this way. They were kept in a culture room at 10° C and were given a 12 hour day/night at a light intensity of approximately 2700 lux. Sterile seawater was used as the culture medium and it was changed every 3 days. The cultures were maintained for 7 months when they had progressed to a stage at which similar ones could be picked out on the seashore. Successive stages of development were then obtained from natural populations growing in various localities on the coast of Northumberland.

As the eggs are so large and filled with dense pigments and granules, stages in their development following fertilization were best observed in sectioned material. Oospores were fixed in Langlet's solution at intervals of 6 hours during the first 4 days, and thereafter once a week. They were sectioned at 8  $\mu\text{m}$  and stained either in gentian violet for the first nuclear divisions or in alcian blue and yellow (Parker, 1966) for the cell walls.

Following fertilization, a thick membrane forms around the oospore. Nuclear divisions may not occur for a few days, but when the oospore nucleus does divide the first three divisions follow rapidly on each other and take place in the centre of the oospore. The eight daughter nuclei then migrate out towards the periphery of the cytoplasm. The large granules which up to now had been aggregated in a halo around the egg nucleus

disperse throughout the cytoplasm and then cluster around each daughter nucleus. The eight nuclei divide once or twice more so that a syncytial stage of sixteen or thirty-two nuclei is formed with the nuclei dispersed throughout the cytoplasm. Nuclear divisions up to cell wall formation are synchronous. The first cell walls occur simultaneously throughout the young plant and divide it into cells approximately equal in size. It took 5–7 days for the oospores to reach this cellular state and they were still contained within the fertilization membrane.

The outermost cells then continue to divide anticlinally while the central cells remain unchanged. As a result an outer layer of small brick-shaped cells with their narrow ends outermost comes to surround the entire young plant, and this layer already shows the characteristics of the future meristoderm. Its cells are heavily pigmented compared with the larger cells of the interior. The outermost cells in contact with the substrate start to grow out as attaching rhizoids (Fig. 1). They have first to rupture the fertilization membrane. This occurs at several points, where a single rhizoid first pushes through and other rhizoids then bend around to push through the same split, suggesting that considerable physical force may have been exerted to cause the first break. The fertilization membrane is quite distinct from the cell walls which form beneath it; it stains yellow with alcian dyes, suggesting, according to Parker (1966), that it contains a non-sulphated polysaccharide (probably alginic acid) while the cell walls beneath it are blue, indicating the presence of a sulphated polysaccharide.

While the rhizoids are developing from the peripheral cells next to the substrate, cell division is very pronounced in the outer meristoderm layer at the opposite pole of the embryo, i.e. in the region which will become the future apex of the plant as it changes from its spherical form to an elongating cylinder. As a result of periclinal divisions in the meristoderm cutting off minute cells to the interior, an apical plate of small meristematic cells is gradually built up (Fig. 2). Filaments of cells arise from the periphery of this plate of cells. They are equivalent to what are called secondary hyphae in the older plant. In the young plants they can be seen to grow down through the centre and out between the rhizoids, where they help to expand the future attaching disc. The cells of these first-formed hyphae are very long and the entire distance between the apex and the base of the plant is traversed by only two or three cells. Increased divisions and growth of the peripheral layer of cells causes the larger cells of the interior to be drawn apart. They form the medulla, and the spaces in between them are filled with a fluid. The cells immediately beneath the meristoderm correspond with the cortex of the button stage. Meanwhile the whole embryo plant has enlarged and burst out of the fertilization membrane.

By the time that the young plants had been in culture for 2 to 3 months they had the form of a cylindrical vesicle between 1 and 2 mm long. Cell division was still most rapid at the opposite poles; at the base it was associated with rhizoid production while at the tip the meristoderm was extremely small celled and rapidly dividing. Then, in the centre of this apical mass of dividing meristoderm, one cell—the future apical cell—becomes conspicuous on account of its failure to divide. As the surrounding cells were so actively dividing in both the anticlinal and periclinal planes this means that the isolated cell which ceases to divide becomes sunken below the level of the other meristoderm cells. Often it appeared drawn out into a slight papilla protruding into the cleft which ultimately became the apical groove of the vegetative button. Meanwhile the potential apical cell enlarges till it may be two or three times the width of neighbouring meristoderm cells, although in actual size it is not more than 10–12  $\mu\text{m}$  wide. During the next

few weeks this cell divides, cutting off three segments which completely surround it. After this first segmentation the apical cell has the form of an equilateral triangle in transverse section with the corners sharply pointed (Plate 2, No. 5). The first segments derived from the apical cell are as big as the apical cell itself and this accounts for the

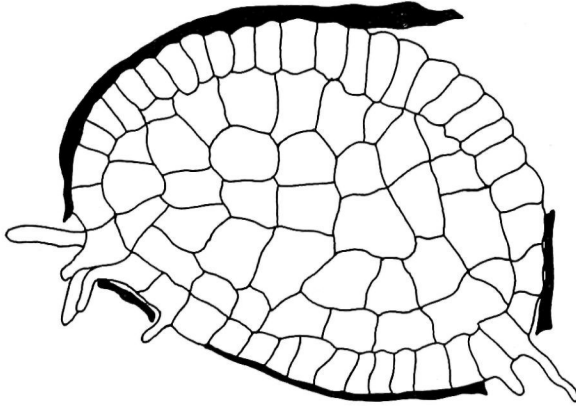


Fig. 1. Section through a young plant showing differentiation of the outer meristoderm. A number of rhizoids have already burst out through the thick fertilization membrane.

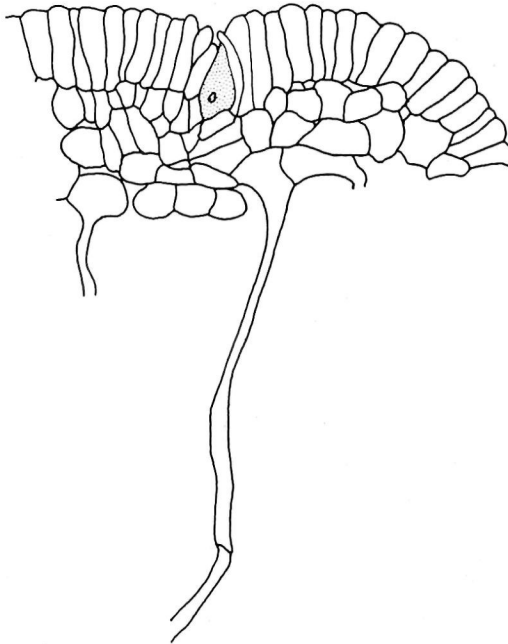


Fig. 2. The apical cell as it first appears in longitudinal section. It is already sunken below the other cells of the meristoderm. Beneath it is a plate of small actively dividing cells with secondary hyphae originating.

appearance sometimes of two or three apical initials which can be seen in longitudinal sections taken at a similar stage of development.

Once the apical cell has differentiated, it continues to function throughout the vegetative life of the plant, i.e. for a period of more than a year. A very gradual increase in

size occurs so that in a fully developed button it may be 50  $\mu\text{m}$  along its sides, i.e. with the sides of the triangles as seen in transverse sections at least four times as long as when it first became apparent in the young plant. Throughout the period of vegetative growth the apical cell maintains the form of an equilateral triangle with the corners sharply pointed when seen in transverse section. It is bluntly pyramidal with the blunt end outermost and the base frequently dipping inwards (Plate 1, No. 1). The shape as seen in longitudinal section will depend upon the plane through which it is cut; if the section is parallel with one of the sides then the apical cell appears much wider than if the section passes down one corner of the cell. It is the latter plane of sectioning which gives the biconvex cell described by Naylor (1951). In the fully developed button this apical cell lies at the base of a deep groove which is filled with mucilage.

The appearance of the apex of a vegetative button both in transverse and longitudinal sections suggests that there is a regular segmentation from the three sides of the apical cell. The segments continue from the sides part-way along the base of the cell. In spite of fixation of material at different times of the day, after periods of emergence and submergence, and after alternating light and dark periods in the laboratory I have not succeeded in obtaining an apical cell undergoing nuclear division. As growth of the plant is very slow, divisions of the apical cell are probably infrequent. But once segments have been cut off from the sides of the apical cell, these segments are actively meristematic. All phases of nuclear divisions can be found scattered among them at any stage of fixation and they divide both in the transverse and longitudinal planes. It is the rapid growth and division of these segments, originally derived from the apical cell, which build up an extensive meristem. The apical cell remains in the centre of this meristem and, as the actual size of the apical cell increases, so does the width of the entire meristem. This meristem functions throughout the phase of vegetative growth.

#### *The reproductive meristem*

When vegetative growth has reached its climax, division of the apical cell precedes the division of the meristem into two. As in each plant this division of the apical cell occurs but once, the chance of finding in transverse section the apical cell dividing into two identical halves is somewhat remote. Plate 2, No. 4 shows an early stage following the division of the apical cell. There appears to have been a longitudinal division of the cell from one corner to half way along one side. Segmentation then follows rapidly in both daughter cells along the plane of the common wall. This soon builds up an extensive zone of cells which pushes the daughter apical cells further and further apart. On their outermost sides each daughter cell has still half of the original apical meristem in contact with it, while the tissue built up between the two daughter apical cells remains meristematic and forms an extensive meristem on their neighbouring faces. But the meristematic activity of the outermost layers of the original meristem decline and the two daughter meristems which result are each considerably narrower in radius than was the original.

These two daughter apical cells are still confined at the base of the original apical groove. If the tissue between them expanded laterally than it would rupture the apical groove and expose them to the external environment. Instead the 'inbetween tissue' is forced upwards until gradually it expands to the top of the apical groove and so divides it into two (Plate 2, No. 3). The expansion of the 'inbetween tissue' causes the stretching of the apical groove so that it may change its form from a circular hollow to a longitudinal slit. This first division of the apical meristem is generally followed by a second

dichotomy resulting in four daughter meristems being formed. These four meristems may remain sunken at the base of two apical grooves for some time before the receptacles elongate, for the apical meristem of the vegetative button may divide during the early spring and the receptacles do not elongate until late summer or early autumn. After the receptacles begin to elongate dichotomy of each apex continues at intervals during the winter until eight to ten divisions may be completed.

The apex of each young receptacle has an apical groove, at the base of which is an apical cell surrounded on its sides by a meristematic zone. The apical cell appears essentially similar in size and shape to that in the vegetative meristem. But with each division the radius of the meristem decreases and after about five divisions it may consist of only three or four layers of cells on each side of the apical cell. The segments cut off from the apical cell of a receptacle are larger than the apical cell which is left and the form of them suggests that they are cut off simultaneously. When the apical cell has just segmented the resulting apical cell looks very narrow but it expands again prior to its next segmentation. Throughout these divisions the side remains of constant length; only the diameter of the cell changes; for segmenting walls run from corner to corner of the original cell. Within the apical groove anticlinal divisions predominate in the outer layer of meristoderm just as they do in the vegetative meristem. But at the tip of the receptacle, just outside the apical groove, periclinal divisions are as numerous. The cells which are cut off internally continue to be meristematic and to divide mainly in the transverse plane. This results in longitudinal files of cells being built up around the apical meristem (Plate 2, No. 3). When these cells subsequently enlarge and elongate they contribute to the rapid longitudinal growth which takes place in the young receptacles during the summer.

The apical groove of the receptacle differs markedly from the vegetative apex in that it is filled with hairs. Naylor (1951) observed these hairs lining the apical groove of young receptacles but she called them mucilage-producing hairs without realizing their significance. The hairs arise from the outermost segments close to the apical cell. Not every segment produces a hair, but those cells which do, cease to cut off cells periclinally to the interior, as does the normal meristoderm. Instead the cell grows out into a papilla which enlarges and this is cut off as a cell to the outside, projecting into the apical groove. Further growth and division occur until a filament of five to six cells is formed. Close to the apical cell a hair grows out from practically every other cell, but the intervening cells between the hairs divide many times both anticlinally and periclinally. The former divisions result in the spacing apart of the hairs at fairly wide intervals by the time they have reached the top of the apical groove. Here the hairs fall off or disintegrate, leaving the basal cell, which now enlarges. As it has not divided periclinally to cut off cells internally, as have the intervening meristoderm cells, it now remains sunken well below the general level of the meristoderm. It does in fact represent the initial cell of a conceptacle. Behind the apex these initial cells occur at frequent intervals all around the receptacle. They are formed during the winter and spring and give rise very gradually to the conceptacles which produce their gametes the following summer.

The apical cell functions throughout the spring until all the conceptacles have been initiated. Then the identity of an apical cell is lost, the apical groove flattens out and the apex consists of small parenchymatous cells which have lost their meristematic activity. In exposed habitats these apices are frequently damaged. After gamete discharge a gradual decay of the plant occurs from the apex to the base, until the entire plant is either gradually eroded or swept away by storm waves.

*Growth control by the apical cell*

As the apical cell is sunken at the base of the apical groove it is not possible to damage it without at the same time injuring some of the adjacent cells. By piercing the apical groove with a fine needle, subsequent fixation and sectioning revealed that the apical cell could be ruptured but at the same time a few of its adjacent meristematic cells were also injured. Hence in the following experiments where it is stated that the apical cell is destroyed it is most likely that in addition a few other cells were injured at the same time.

During the early summer young plants with the button about 3–4 mm in diameter were collected from the rocks at St Mary's Island, Northumberland, and brought into the laboratory for culture experiments. They were cleaned free of rock particles, animal and plant epiphytes, and washed thoroughly in sterile seawater. The apical groove is clearly visible in these young plants and a sterile needle was inserted into the apex of each one so as to destroy the apical cell. The plants were then kept in sterile seawater at 10° C and given 12 hour night/day period. At intervals, small discs were cut from the centre of some plants and fixed and sectioned, so that the effects following destruction of the apical cell could be followed.

Within a few days of damage to the apical cell some of its adjacent meristematic cells start to produce filaments which grow up and out to the top of the button through the apical groove. The number of these filaments increases so that within a few months a tuft of tangled branching filaments protrudes through what was originally the apical groove (Plate 1, No. 2). They are visible externally as a tuft of hairs, lighter in colour than the tissues of the button.

Simultaneously, the divisions of the outer meristoderm become erratic. Previously this had formed a regular compact layer of cells on the outside of the button, dividing anticlinally and periclinally in orderly sequence. Now, starting from the injured apical cell, and progressing up the apical groove and out to the periphery of the disc, growth of the meristoderm becomes disorganized. There is an increase in periclinal divisions, but the cells which are cut off to the interior do not differentiate into cortex and medulla as would normally occur. Instead they enlarge, and the outermost ones project beyond the even boundary of the former meristoderm (Plate 2, No. 6). After many months growth they appeared like apical cells of filaments growing out from the tissue into the medium in a somewhat chaotic manner.

In none of the injured plants was a new apical cell ever organized. At the end of a year these plants had a blown up, balloon-like appearance which contrasted with the normal flat or concave upper surface of vegetative plants. Occasional 'blown up' versions of buttons are found in wild populations and some of these represent plants in which the apex has been damaged. The plants in which apical cells had been destroyed were not able in laboratory culture to produce receptacles and so pass from a vegetative to a reproductive phase of growth. Presumably in a wild population they would disintegrate and get washed away.

In order to determine whether or not a new apical cell could be regenerated, segments of tissue *c.* 5 × 2 mm were cut from the upper surface of young vegetative buttons and kept in culture under similar conditions to those described previously for whole plants. Segments were sectioned at intervals and their growth studied. Very soon after being detached, cells from the cortex and medulla started to produce filaments which grew out into the medium from the wounded surfaces. As these filaments lengthened the terminal cells became very large and swollen. The filaments branched profusely and

were heavily pigmented and after some months they formed a considerable tissue made of interweaving filaments. Even after a year in culture none of these segments was ever observed to have formed an apical meristem from amongst the mass of cells produced. Once isolated, a segment of tissue has not the ability to regenerate a new apical cell. The tissues in culture continued to grow but, without the formation of a new apical cell and associated meristem, they were not able to regenerate a new vegetative button.

In the fertile thongs initiation of conceptacles seems to be controlled by the apical cell and its associated meristem. Apical cells were destroyed in a number of tips of receptacles which were kept in culture. These tips of receptacles did not elongate but they continued to enlarge laterally and the conceptacles which had been initiated before the injury of the apical cell continued to develop. But from the injured apex tufts of irregular filaments grew out much as they did from the damaged vegetative apices but no more new conceptacles were initiated.

### *Grafting experiments*

The question always arises as to what triggers off the change from a vegetative to a reproductive meristem. A disc containing the vegetative meristem was cut from the top of a small vegetative button and grafted on to the apex of a young receptacle. They were sewn together with fine nylon thread. In all, thirty such grafts were made and they were maintained in culture in the laboratory under the same conditions as before. They were sectioned at intervals to see whether or not the tissues had united at the point of grafting.

Externally, even after a year in culture both apices which had been grafted together seemed to be growing independently. The receptacle had elongated several inches, while the vegetative disc had increased slightly in size but was still vegetative. Internally there had been complete union of the tissues at the point of grafting. This was mainly due to the activity of the vegetative meristem, which had produced filaments growing up among the tissues of the elongating receptacle. The latter played little part in the union of the two for only an occasional filament could be found growing from the receptacle into the vegetative apex. Although internally there was complete union of the tissues, one apex did not influence the pattern of development of the other. Even if the receptacle apex contained substances associated with reproduction they were not translocated to the vegetative apex to convert it into a reproductive one.

### DISCUSSION

The mode of germination of the oospores which results in a syncytial stage is quite unlike that observed in other British genera of the Fucales. In these other genera, cell division follows immediately upon the first division of the oospore nucleus, cutting off the primary rhizoid at the base. According to Torrey (1967) the oospores of *Fucus* show 'asymmetry which leads directly to two unlike cells at the first division and thereafter the progeny of these cells have quite different fates'. What actually happens in *Fucus* is that the basal cell of the first division gives rise to a rhizoid while the uppermost cell undergoes repeated division. The lowermost segments so formed do in fact grow out into attaching rhizoids (Moss, 1950), i.e. the fate of some progeny derived from the uppermost cell of the first division is similar to that of the lower cell. There is, in fact, not the sharp division into rhizoid and thallus at the first division which Torrey suggests. After cell walls are laid down in the multinuclear embryo of *Himanthalia* any cell in the lower



half which is in contact with the substrate seems capable of growing out into an attaching rhizoid. These rhizoids are added to later by the secondary hyphae which are produced from internal cells close to the apex and which grow out through the base and so help to build up an attaching organ.

There is considerable internal differentiation of the plants of *Himanthalia* before any apical meristem is organized. The young plant, 1–2 mm long, is bounded by a small celled meristoderm, inside which are one or two layers of cortical cells, while the medulla cells and secondary hyphae are dispersed throughout the fluid-filled centre. Cell division is very pronounced at the upper end of the plant, where it results in an extremely small-celled meristoderm beneath which is a small plate of meristematic cells. From among several hundred of the extremely small meristoderm cells one in the centre becomes the future apical cell. What determines which one it shall be? Morphologically, it only becomes distinguishable from its neighbours when it ceases to divide and then enlarges. As a result of active divisions in the neighbouring cells this potential apical cell becomes sunken below the general level of the meristoderm, so initiating the future depression of an apical groove.

The apical cell is triangular in transverse section and, although the cell increases in size, the same shape is maintained throughout the entire life of the plant. Segmentation of the apical cell is infrequent but when it does divide, the segments which are formed remain meristematic and divide very rapidly. It is the result of the meristematic activity of these segments which builds up the apical meristem of *Himanthalia*. Once an apical cell is organized it persists as the only apical cell in the centre of the apical meristem throughout the entire vegetative phase of growth. Surgical experiments damaging the apical cell have shown that it is the centre of growth control. If it is damaged then the whole growth of the apical meristem and of the other tissues such as the meristoderm become disorganized. *Himanthalia* lacks the ability to regenerate a new apical cell, if the one and only apical cell is damaged.

After 1–2 years growth the role of the apical cell in the vegetative apex changes and it gives rise to a number of reproductive apices. This change follows on a build up of mannitol, alginic acid and proteins in the vegetative plant (Moss, 1952). It is detectable morphologically by the division of the apical cell into two exactly similar halves; a division quite distinct from its normal segmentation in orderly sequence along its three sides. The two daughter cells then segment along their common wall and the segments so formed divide very rapidly so pushing the daughter apical cells further apart. Meristematic activity continues on the neighbouring sides of the daughter cells until each one has built up a new side of meristem to partly balance that which it has inherited from the parent vegetative meristem. There is generally another division of each apical cell followed by division and renewed growth of the apical meristem so that four meristems are formed; each of which is a potential apical meristem of a fertile receptacle.

During development of the vegetative button the meristem on all sides of the apical cell is concerned mainly with lateral growth leading to expansion of the circular top of the button. As soon as the receptacles start to develop, growth is mainly lengthwise instead of lateral. Accompanying this change in the direction of main growth there is a decrease in the width of the apical meristem with each of its successive divisions. Occasionally the apical cell appears to cut off a basal segment but there is no building up of an extensive promeristem at the base of the apical cell as there is beneath the apical cell of *Fucus* (Moss, 1967). When the receptacles are elongating during the winter and spring the apical cell appears to segment more frequently than it does in the vegetative button.

Also the segments cut off are much larger; in fact they are often wider than the apical cell itself. The segments appear to form simultaneously on all three sides so that immediately following segmentation the apical cell appears very small. It enlarges again before the next lateral walls are laid down. The narrowness of the apical cell immediately following segmentation led Naylor (1951) to suggest that the apical cell of a receptacle was much smaller than that of the vegetative button.

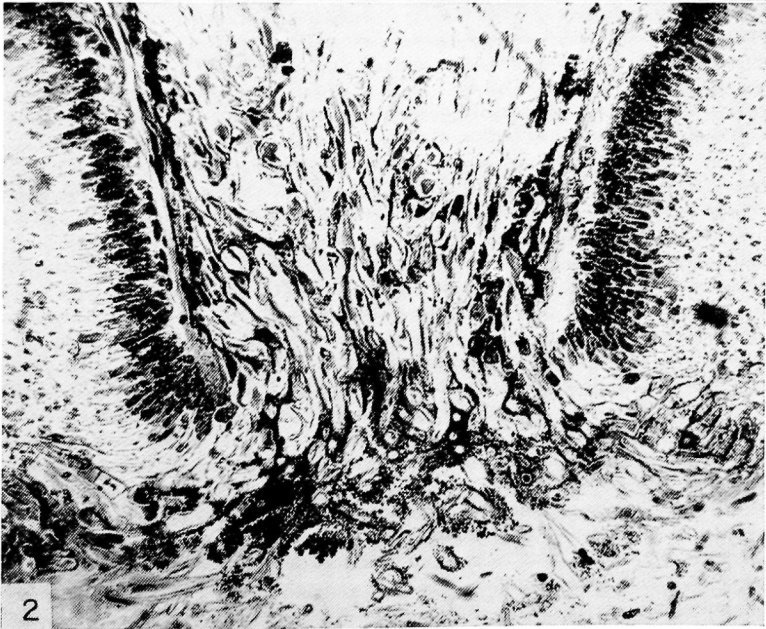
The lengthening of the young receptacle is mainly due to surface growth and stretching of the internal cells. At the top of the receptacle, just outside the apical groove, not only is the meristoderm actively dividing but the cell layers beneath it are dividing principally in the transverse plane, so building up longitudinal columns of cells similar to those already described in the vegetative apices of *Fucus* (Moss, 1967). These longitudinal columns of cells eventually elongate and form the medulla of the receptacle.

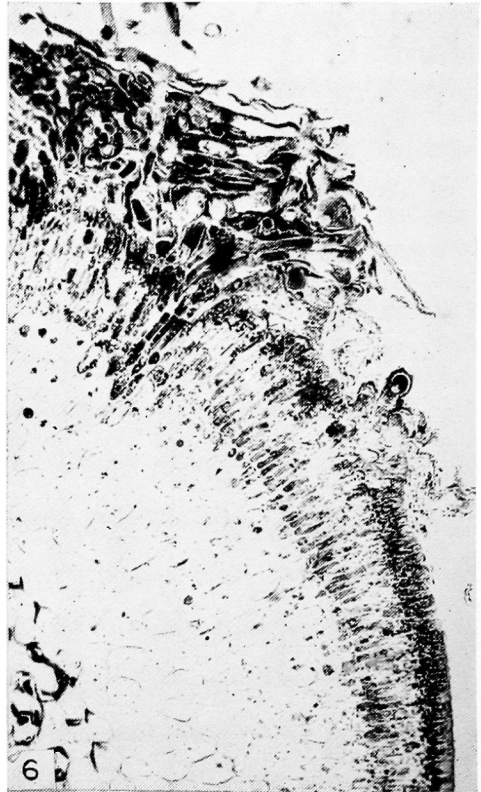
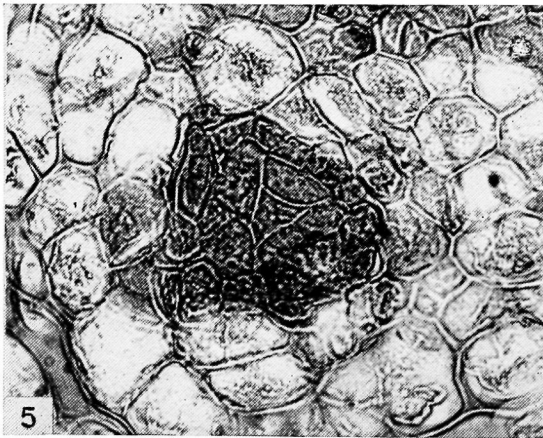
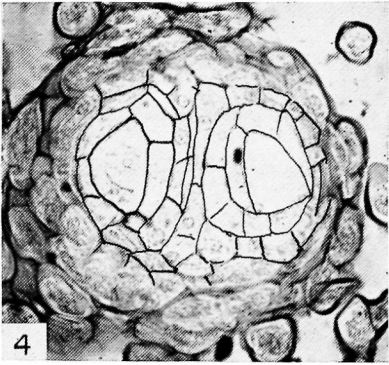
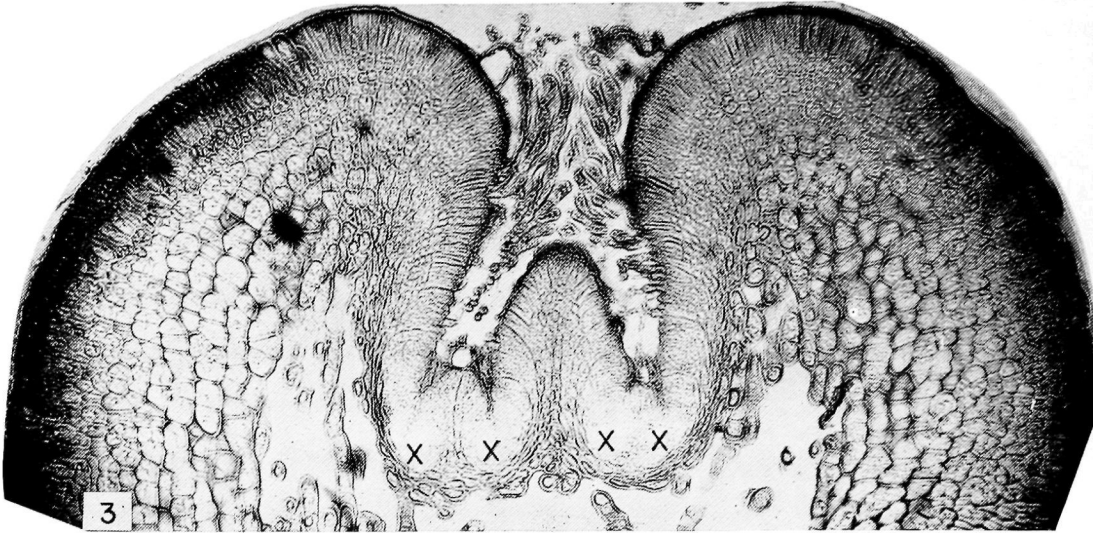
According to Neinburg (1931) the apical cell of *Fucus* is derived from the basal cell of one of the group of hairs which develop from the cells lining the apical groove of the young plant. In *Himanthalia* no hairs are associated with the origin of the apical cell of the vegetative meristem. However the apex of a receptacle is lined with hairs and the basal cell of these may become a conceptacle initial. Apical hairs in the apex of a receptacle are rare in the Fucales and appear to have been reported only in *Bifurcaria laevigata* (Laing, 1941). The description of the apical hairs and the origin of the conceptacles from them agrees exactly with what I have observed in *Himanthalia*.

In the mature plants of *Fucus* there is an annual cycle in vegetative growth followed by reproductive growth. After gamete extrusion the reproductive branch in which the identity of an apical cell and a meristem have already been lost, disintegrates. But growth of the thallus is continued from the vegetative meristems which can divide and give rise to more vegetative or reproductive meristems. In *Himanthalia* only one vegetative meristem is ever produced. The single apical cell of this divides many times; each new daughter cell becoming the apical cell of a reproductive apex. Each of these has determinate growth. By the time that the gametes are shed the identity of the apical meristem has been lost and the receptacle subsequently disintegrates. There is no meristem left on the plant to continue vegetative growth, and once an apical cell is lost the plant is unable to regenerate a new one. It is the only British member of the Fucales which becomes fertile but once, with reproduction terminating its life span for its one and only vegetative meristem is entirely used up in reproductive development.

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BETTY MOSS—MERISTEMATIC GROWTH IN HIMANTHALIA

EXPLANATION OF PLATES

PLATE 1

No. 1. Longitudinal section through the base of the apical groove of a young vegetative plant showing the apical cell and the regularly segmenting cells building up a meristem around it. The apical groove is filled with mucilage. *c.*  $\times 400$ .

No. 2. Longitudinal section through the apical groove of a vegetative plant 2 months old after the apical cell had been destroyed. Cells of the meristem have grown out into tangled filaments. *c.*  $\times 200$ .

PLATE 2

No. 3. Longitudinal section showing the form of a reproductive apex in process of branching. *x* Marks the position of four apical cells. The apical groove is lined with hairs. *c.*  $\times 100$ .

No. 4. Early stages in the dichotomy of a receptacle apex seen in transverse section. *c.*  $\times 200$ .

No. 5. The apical cell as first seen in transverse section of a young plant. *c.*  $\times 400$ .

No. 6. Following injury to the apical cell, the irregular outgrowth of meristoderm cells into filaments progresses from the apical groove (to the left of the photograph) across the top of the button (to the right of the photograph). *c.*  $\times 200$ .

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