

that there are pits between the apical and adjacent cells of Dictyota which allow continuity between the cells. The size of the sieve pores is specific, although the pores may be slightly different in different regions of size plant, as well as in different aged plants (Schmitz, 1981). An increase in pore size, decrease in the amount of callose deposition and the loss of organelles, is believed to be associated with an advance in evolution (Lee, 1980). For example, Macrocystis is suggested to be the most advanced genus due to its large pores (2.4-6.0 μ m), lack of callose and enucleated state (Sideman & Scheirer, 1977). The midrib cells of D. longifolia appear to have pores in the longitudinal walls (Pl. 12, F & G). The pores of brown algae are reported to either be arranged in pitfields or to be scattered. Without doing a more detailed study the arrangement of the pores of D. longifolia cannot be determined however, they appear to be scattered.

Most of the work performed on translocation and the related tissue types, has been performed on members of the Laminariales (Sideman & Scheirer, 1977) although there has been some work performed on members of the Dictyotales. Katsaros and Galatis (1988) reported similar observations to those discussed above for D. longifolia, in Dictyopteris membranacea. They observed an epidermis, cortex and medulla. The latter is reported to be composed of long (300 μ m), slender cells having thickened longitudinal walls with plasmodesmata. The cells are similar, in many ways, to the sieve elements reported in other brown algae, especially members of the Laminariales. These cells are most abundant in older parts of the frond where a midrib has developed. The diameter of the pores in these cells of D. membranacea are reported to be 0.06-0.10 μ m (Katsaros & Galatis, 1988). The elongated cells, unlike those in other brown algae, retain their organelles, although there is some

sign of degeneration. There is also no callose deposition and the cells are not trumpet shaped. It is however, believed that these cells are used in transport and that they are an simple stage in the evolution towards sieve-like elements (Katsaros & Galatis, 1988). Unfortunately, a detailed study of the elongated cells in D. longifolia was not undertaken however, it is presumed that the cells in this species are similar to those reported in D. membranacea (Katsaros & Galatis, 1988). Although no translocation studies have been performed on members of Dictyopteris, it is believed that, due to the size that the plants attain (60cm or more) and the presence of longitudinal midrib cells with pits, translocation does occur.

4.9.4 Structure of the Epidermal Cells

The epidermis or outer layer of cells in D. longifolia is composed of a single layer of cells completely covering both sides of the lamina. The cells appear to be similar in the wing and the midrib as well as in longitudinal section (Pl. 12, H-M). They are rectangular and are smaller than the cells of the rest of the lamina (about $\frac{1}{2}$ the size; approximately 18 μ m wide and 30 μ m long). Katsaros and Galatis (1988) report that the epidermal and meristodermal cells of D. membranacea are similar to each other and smaller than the cortical and medullary cells. The epidermal cells have a high concentration of chloroplasts and, due to this and the position of the cells on the outside of the lamina, photosynthesize a great deal. The photosynthates are transported from the epidermis to other areas of the plant (Buggeln, 1983). In the basal regions of the lamina, the epidermis develops into the meristoderm and gives rise to the rhizoids. A single cell appears to protrude to the exterior and divide (Pl. 13, A). The cell at the base then divides repeatedly. The epidermal cells appear to divide

longitudinally and perpendicular to the surface (Pl. 13, L), whilst the cells of the meristoderm divide parallel to the surface (Pl. 13, B-G). The exterior of the meristoderm is covered in a layer of material, the composition of which was not determined (Pl. 13, H). This extends over the cells in the initial stages of rhizoid production and may provide protection to the vulnerable meristoderm cells or aid in adhesion of the rhizoids. Davies et al. (1973) report that the cells of the meristoderm which give rise to the haptera in Laminaria, are highly secretory and release mucilage for protection and adhesion. The composition of the material covering this region in D. longifolia was not identified, however, comprehensive staining with a variety of stains may indicate the nature of the material. Katsaros and Galatis (1988) report that there are thin cross walls in the cells of the meristoderm near the base of D. membranacea, which are similar to those observed in D. longifolia (Pl. 13, G, K-L).

In many regions there is a layer between the dividing meristoderm cells and the rhizoids. The layer appears to be composed of small cells or large granules (Pl. 13, J-L). It is believed however, that these structures may be a layer of meristodermal cells in a different plane, as they strongly resemble a row of meristodermal cells in median, transverse plane in sections of Dictyota dichotoma (Katsaros & Galatis, 1985). Buggeln (1983) reports that the meristoderm cells of members of the Laminariales and Fucales contain large numbers of physodes and that these release polyphenols into the water (possibly involved in herbivore and epiphyte deterrence). The darkened appearance of the meristodermal and rhizoidal cells at the base of the lamina suggest that these cells contain a large number of physodes (Pl. 10, H; Pl. 13, B) which probably have a similar function.

4.9.5 Surface Appearance of Epidermal Cells

The surface appearance of the epidermal cells are markedly different in the different regions of the thallus. Even in young laminae, which lack a well developed midrib, there are differences in the surface appearance of the epidermal cells (Pl. 14, A-C). The midrib epidermal cells are narrow and elongated in surface appearance (Pl. 14, F-H) and are easily distinguished from the more irregular shape of the wing epidermal cells (Pl. 14, I-L). An important distinguishing feature of the midrib cells is the fact that they divide longitudinally while the wing epidermal cells seem to divide in all directions. An interesting feature of the wing epidermal cells is that there appear to be different densities and arrangements of cell contents in different regions of the lamina, eg in some areas the contents are adpressed against the walls, whilst in others they are scattered or concentrated around the nucleus (Pl. 14, J-L). This could possibly be due to the different ages of the regions or due to their involvement in different activities, eg growing, thickening, formation of dichotomies.

4.9.6 Holdfast

The strength of attachment to the substratum is a function of the degree of stress that the organism is placed under, and is an adaptation to the wave swept environment in intertidal organisms (Chapman & Chapman, 1973). The structure of the holdfast is thus adapted to maintaining the plant in position under varying conditions. The holdfast of *D. longifolia* may develop to a few centimetres in diameter (Section 4.7.1.1). It is composed of a mat of entangled rhizoids which give rise to numerous laminae (Pl. 15, B; Section 4.7.2.6). There is a central core of cells which appear to be similar to

those of the midrib (Pl. 15, C; Fig. 51, F; Fig. 52, H). Rhizoids similar to those of the holdfast were also observed nearer the apex of the laminae on the midrib (Pl. 15, D). These rhizoids became longer in the regions nearer the base of the lamina (Pl. 15, G). The rhizoids produced by the superficial meristoderm are branched and multicellular with, in most cases, a pointed tip (Pl. 15, K & N). Occasionally tips were observed which had a spherical shaped terminal end (Pl. 15, O & P). These are believed to be rhizoids which had become properly attached to the substratum, prior to removal for microscopy. There were also the "jig-saw tips" observed in spores (see Section 4.12.2). The latter type of rhizoid is believed to be caused by changes in the nutrient status. The rhizoids grow into the cracks and crevices of the substratum and, in many species, are reported to adhere due to the presence of mucilage (Tovey & Moss, 1978). The structure of a rhizoidal holdfast such as that of D. longifolia, is such that the firmest attachment to the substratum is achieved.

4.9.7 Surface hairs

Tufts of hairs were observed in sunken pits on both surfaces of laminae from the field and from sections of material grown in culture (Pl. 16, A-D). The presence of surface hairs appears to be a common feature in members of the genus Dictyopteris. They have been reported in D. crassinervia (Zanardini) Schmidt (Allender & Kraft, 1983), D. muelleri, D. australis (Sonder) Askenasy and D. nigricans (Womersley, 1987; Clayton, pers. comm.). Hairs with a basal meristem have also been reported in Dictyota dichotoma (Fritsch, 1945). Old and deformed tufts were also occasionally observed (Pl. 16, E & F). The blunt tipped hairs (Pl. 16, J & O; Fig. 53) in D. longifolia appeared to push through the epidermis layer and were multicellular with various cell contents visible (Pl. 16,

G-I; Fig. 53). The interesting dark brown structures visible in many of the hairs (Pl. 16, L-N) and which caused an indentation of the cell wall of the hairs, are thought to either be pale chloroplasts, physodes, endoparasites (due to their effect on the wall) or symbionts which influence the deposition of the wall. Virus-like infections have been reported in members of the brown algae (Clitheroe & Evans, 1974); however, the inclusions observed in this species would have to be studied in much greater detail before any conclusion could be made. Physodes and pale chloroplasts are reported to occur commonly in the hairs of members of the Dictyotales (Clayton, pers. comm). "True hairs" are reported to be colorless with only the remnants of plastids remaining in them (Fletcher, 1987). Oates and Cole (1987) however, report that no algal hairs have chloroplasts. The hairs observed in *D. longifolia* are trichothallic, i.e. they divide from the base (the basal cells are small and densely packed with cell contents whilst those further away are larger and less densely packed; Pl. 16, P; Fig. 53). Tufts of hairs which appear to be very similar to those observed in this study, are reported in *Hydroclathrus* (Oates & Cole, 1987). The hairs reported in the latter example are also found in pits with very short, metabolically active cells at the base and elongated cells near the tip. It is believed that the hairs found on algal thalli may enhance nutrient uptake by increasing the surface area (Norton *et al.*, 1981, 1982; Fletcher, 1987). The same authors report that some species have hairs on the small, juvenile stages which grow in the lower water velocity layers near the substratum. Small plants also have reduced area for nutrient absorption and thus require a mechanism of increasing the surface area, such as the production of hairs. These plants lose the hairs when reaching adulthood. There are also suggestions that surface hairs aid in desiccation resistance and secretion (Whitton,

1988). The same author reports that hairs may form under high light and changing nutrient conditions and could thus be adapted to maximize sudden bursts of nutrients. Fletcher (1987) also reports that hair production in brown algae is a response to the nutrient status of the medium. Some algae are reported to only produce hairs in the field (Whitton, 1988). It has also been reported that the production of hairs of Fucus species increases in summer when there is an increase in phosphate uptake (Hurd & Dring, 1990). Hairs were most common in older cultures of D. longifolia, in which the water had not been recently changed and which were thus experiencing nutrient depletion. They were also common on individuals living in very small pools in the field. They were however, also observed on plants growing in the highly wave swept areas that experience constant water (and thus nutrient) turn over. In the field, the hairs were present throughout the year but were most abundant near the end of the year. No hairs were visible in July whilst all the sites had plants with hairs in September, and H and H+ lacked them in October. This seasonality could be caused by a change in temperature, change in nutrient status or possibly by an increase in light intensity.

4.9.8 Other Structural Observations and Associations of D. longifolia.

Various other structures were observed growing from or associated with, the laminal surface of D. longifolia. A superficial investigation of these structures was performed.

4.9.8.1 Hair-like Structures

Regularly distributed clumps of hair-like structures, which were shorter than the other hairs (Section 4.9.7) and interspersed with finer hairs, were observed on both surfaces of D. longifolia. These structure were observed

on material collected at various times of the year and were observed to grow from depressions on the laminal surface of plants from all the sites (Pl. 17, A-D). They are thought to be epiphytic algae of some type. Without a more intensive ultrastructural study, these structures could not be identified.

4.9.8.2 Wound-Like Cavities

The deep wounds, which were observed to extend through a few layers of tissue, are thought to have been caused by fungal infections. This conclusion was based on the "hazy", fine grained areas (Pl. 17, E-G) which were observed in the cavities, and which are usually associated with fungus. The cultured material in which these cavities were observed, was treated with an antibiotic but not a fungicide. The regular appearance of similar structures indicates that it is unlikely that the wounds are due to physical damage during handling.

4.9.8.3 Algal Epiphytes

There were a number of epiphytic algae associated with D. longifolia (most were red algal species) and which did not appear to affect the thallus structure or inhibit growth (Pl. 17 H-M). The newly produced sections of laminae were relatively clear of epiphytic growth. There were relatively few epiphytes on D. longifolia, when comparing this species to members of the red or green algae with a similar laminal structure. This observation could be due to the release of phenols from the laminae of D. longifolia, which is reported to have an inhibitory effect on bacterial growth and herbivory (Hay *et al.*, 1988), and may thus also inhibit epiphytic growth. There are reports that Dictyotalean algae, especially towards the end of the growth period, exhibit heavy epiphytism (King & Farrant, 1987) and it is thought that this may

cause an increase in lamina breakdown in Sargassum polyphyllum (Dewreede, 1976; in Santelices, 1977). The composition of the epiphytic community on members of a monospecific population, is reported to be affected by the degree of wave exposure and the type and amount of sediment that is trapped (Gibbons, 1988). It would be interesting to determine whether wave exposure has any effect on the epiphyte populations on D. longifolia.

4.9.8.4 Sloughing Epidermis

The sloughing epidermis which was occasionally observed to occur on sections of D. longifolia lamina in culture (Pl. 17, N-P), is believed to be a mechanism to rid the plant of epiphytes. There are reports of other members of the Phaeophyceae undergoing epidermal sloughing, eg Ascophyllum nodosum which is relatively epiphyte-free (Filion-Myklebust & Norton, 1981; Fries, 1991). Kitching (1987) reports that some epiphytes overcome this removal technique by lodging in the cryptostomata of Himanthalia elongata. The process was never observed in the field or on large sections in culture, and thus there is a possibility that the sloughing observed in D. longifolia may have been initiated by damage caused during preparation of small sections.

4.9.8.5 Herbivores

Not many animals were observed to feed on D. longifolia, which is believed to be unpalatable due to the presence of phenols and other secondary metabolite, fish-deterrents such as those described for other members of the Dictyotales (Gerwick, 1981; in Littler *et al.*, 1983). However, fish bites and small herbivore damage was occasionally observed on the laminae of D. longifolia (Pl. 17, S; Fig. 54, D). The polychaete Pseudonereis variegata was frequently observed living on the plant.

This animal did not appear to eat the laminae, but caused severe deformation by rolling the basal laminae wings inwards to build its nest (Pl. 17, Q-R). Hay *et al.* (1988) report that Dictyopteris delicatula, which does produce a chemical known as Dictyoptene for defence, is preferred by immobile herbivores such as polychaetes. Fish are reported to avoid feeding on this species and this reduces the possible predation of the immobile herbivores. The same authors report that another species of Dictyopteris is eaten by fish but not by small herbivores, indicating that there may be some difference in the defence mechanisms in different species (Hay *et al.*, 1988). Van Alstyne (1988) reports that after Fucus laminae were damaged, the phenolic production increased in the wounded area and the nearby laminae. The damaged plants were avoided by herbivorous snails a few days after damage. This leads to spatial and temporal changes in herbivore preference. There is also reported to be a seasonal change in herbivore concentration due to environmental factors such as wave intensity and temperature. Seasonal variation in the production of phenolics in Fucus (Zavodnik, 1981) possibly leading to seasonal increases in palatability and thus increased grazing, has also been reported. There are reports of wave exposure greatly affecting herbivore abundance and thus plant condition, eg the abundance of the sea urchin, Diadema is reported to increase with an increase in wave exposure (Foster, 1987; McQuaid *et al.*, 1985). Different types of herbivores predominate in different areas, eg snails are found predominantly in low wave exposure areas as they are removed from the laminae in the more wave-swept environments (Dring, 1982; Petraitis, 1987). Littler *et al.* (1983) report that rubbery or tough, leathery species are most resistant to grazers due to the presence of strengthening tissue. The production of such strengthening tissue and antiherbivore metabolites is at the expense of productivity and results in a lower growth

rate, decreased digestibility, lower nutritive value and decreased competitiveness, as energy goes into manufacturing other tissue or substances instead of photosynthetic tissue (Gerwick, 1981; in Littler *et al.*, 1983). *D. longifolia* is reported to be abraded only slightly when compared to other intertidal species from the same region. This is probably due to the presence of strengthening tissue in the thallus (Savage, in prep.). It is also reported to rank low in the preference trials for the herbivorous snail, *Littorina* (Savage, in prep.). Suren (1989) reports that herbivores prefer dead tissue to living matter because the antiherbivore substances in the former have either leaked out or degraded. Phenolics released into the water may decrease the epiphyte and bacterial contamination around the plant, as well as acting in wound-healing (van Alstyne, 1988). Hannach and Santelices (1985) report that there is some difference in preference of herbivores for the gametophyte and sporophyte stage of isomorphic species. This is believed to be due to differences in the chemical or structural composition of the stages. Periwinkles are reported to graze on young sporelings of *Fucus* but benefit the older plants by removing the epiphytes instead of grazing on the thallus (Lubchenco, 1983). An increase in consumption of seaweed thallus does however, lead to a greater release of nitrates into the water from faecal waste, and a subsequent increase in the productivity of the surrounding plants (Sterner, 1986). Herbivory, even by very small herbivores, may weaken the plant to such a degree that laminae or entire plants may be lost during periods of high wave exposure. Antiherbivore metabolites and strengthening tissue such as that in *Dictyota* may be an advantage (despite a decrease in production) due to the increased survival chance in wave exposed areas.

4.10 REGENERATION

In areas of high wave exposure, where plants are frequently damaged, there has to be some method for healing and replacement of plant tissue. Regeneration or replacement of removed laminae keeps the plant perennial (Paula & Eston, 1987) despite seasonality of herbivores and high wave exposure. The most common situation in brown macroalgae appears to be a perennial holdfast organ and annually regenerating laminae, which is known as "pseudoperennial growth" (Palmisano & Sheng, 1977; Norton et al., 1981; de Paula & de Oliveira, 1982; Dawes & Tomasko, 1988). Examples of this type of growth are the holdfasts of Phaeostrophion irregulare which are reported to be more resistant to extreme conditions than the laminae (Mathieson, 1982a). Regeneration is not only important in recovery from damage, but the speed and degree of regeneration is a vital consideration in the commercial harvesting of seaweeds, eg there is reported to be greater regeneration of harvested Ascophyllum nodosum from sheltered areas than from wave exposed areas. There are numerous studies involving aspects of regeneration in commercial species, eg Nereocystis luetkeana (Roland, 1985), Laminaria longicruris and L. digitata (Smith, 1985). Regeneration potential is also important for the eradication of alien invaders, eg Sargassum muticum (Paula & Eston, 1987). Regeneration from small sections of the plant, that are removed from the parent plant and become reattached, is an important form of vegetative propagation (asexual reproduction) in a number of algae (Fritsch, 1945). An example of the latter type of propagation was reported for Rhodochorton where segments of lamina egested in the faecal pellets of herbivores were shown to be able to regenerate new individuals (Breeman & Hoeksema, 1987). New sporophytes of Laminaria have been grown from a single cell (Saga et al., 1978). Vegetative reproduction from various plant

sections does occur in brown algae and is believed to be important in highly wave exposed areas where sexual reproduction may not succeed, due to the lack of meeting of gametes (Fletcher, 1987). It is believed that this form of reproduction is potentially important in D. longifolia, as this study shows that laminal sections of different sizes have the potential to regenerate new laminae which have basal rhizoids. If a detached section of lamina was buried, entangled in rhizoids or reattached in some other way, it is believed that a new thallus and rhizoidal system would develop and become permanently attached to the substratum.

Regeneration is obviously an important part of the survival strategy of macroalgae such as Fucus (Fulcher & McCully, 1969) and D. longifolia. Regenerated material was frequently observed on D. longifolia in the field and occurred in plants of all ages, in most wave action areas. Degradation of the laminal wing material was caused by abrasion, natural senescence, herbivory, lytic enzymes or fungal attack (Pl. 18, A & B). In this study however, regeneration was most frequently observed in the high wave action areas (H+ and H). This is believed to be due to the greater degree of abrasion and wave induced damage caused to these plants, and not a variable ability to regenerate. This conclusion was drawn because at certain times of the year (near the end of the study) the plants in the high wave exposure sites (H and H+) had degenerated considerably and were exhibiting extensive regeneration from both laminal remains and the holdfast. At the same time, the plants in the calmer pools (L1, L2 and L+) showed little degeneration or regeneration. However, Keser et al. (1981) report an increase in regeneration of Ascophyllum nodosum in sheltered, as opposed to wave exposed sites. Abrasion and degeneration of D. longifolia was particularly noticeable in the middle of the year when the plants were fully grown and

had not, as yet, begun to produce new laminae. Laminae were abraded until, in some cases, only the midrib remained (Pl. 18, C-F; Fig. 54; A-C). Another species of Dictyopteris, D. undulata has also been observed to be reduced to the midrib, and to regenerate from the midrib remains (Benson, 1986). Fagerberg and Dawes (1976) report that there was no time when all members of the Sargassum filipendula population studied, had died back to the holdfasts. However, there was an increase in senescent tissue in the upper parts of the laminae and a decrease in wound response during the reproductive periods (Fagerberg & Dawes, 1976). A similar report of a correlation between sexual reproduction and subsequent die-back of the laminae has been reported for S. polyceratum (de Ruyter van Steveninck & Breeman, 1987). It is possible that the seasonal die-back of laminae observed in D. longifolia was not only due to an increase in abrasion and herbivory, but may also have been due to degeneration following seasonal reproduction (Norton et al., 1981). Regeneration was observed to occur throughout the year although there was an increase in the regenerated growth towards the end of the year when general growth increased. However, in culture, only that material that was collected in April was observed to regenerate abundantly. In D. undulata, the maximum amount of vegetative propagation is reported to occur in autumn (Benson, 1986). It has been reported that there was an increase in regeneration when new laminae began to grow from the holdfast in S. filipendula (Fagerberg & Dawes, 1976). The holdfasts of D. longifolia are perennial and the regeneration of new laminae may occur from a holdfast which lacks the remains of the old laminae (Pl. 18, L), from a holdfast which still has some remaining laminae from the previous season (Pl. 18, K) or from the remains of the old, abraded laminae (Pl. 18, G-J). Changes of growth, degeneration and regeneration could also be caused by changes in water temperature (unlikely on the

Natal coast due to the relatively small seasonal changes), or seasonal changes in the chemical composition of the water (Black & Dewar, 1949). There may be seasonal changes in the chemical composition of the water in the study area, due to seasonal changes in the predominant currents and also due to changes in the composition (related to agricultural practices up the rivers) of the run-off.

4.10.1 Regeneration from Small Sections of Lamina

Regeneration of thalli was observed to occur from a variety of wound patterns in the field, and it was thus decided to wound lamina sections in a number of different ways, in attempt to determine differences in regeneration potential. The regeneration of new laminae resulting from the different wound patterns is summarised in Figure 67.

A) It appears from the experiments performed on the small sections of laminae, that very narrow strips (4mm) of lamina are not suitable to support regeneration (Pl. 19, A; Fig. 8, A; Fig. 67, A). This is probably due to excessive damage to the sections caused during preparation. It may also be due to the small photosynthetic area available to support growth.

B) The wing material does not seem to be vital in the regeneration process, as the sections which lacked the wing margins and most of the wing tissue, but included the midrib and a small section of the surrounding lamina, did show some degree of regeneration (Pl. 19, B & C; Fig. 8, B; Fig. 67, B). There was however, no propagation of complete laminae as only rhizoid-like outgrowths with some lateral cell division were observed (Pl. 19, D-F). It appears that the midrib is necessary for regeneration.

C) The most successful regenerating sections were those which had both the wing margin and the midrib, and were at least 1cm in length (Pl. 21, A; Fig. 8, C; Fig. 67, C). These sections produced complete laminae which, in many cases, developed to an advanced stage with rhizoids, an apical pit and a prominent midrib (Pl. 19, G-K). A similar report of regeneration from wounded surfaces was reported for Fucus vesiculosus in which adventitious branches were produced on the cut edge of the section, and developed into laminae with a midrib and wing tissue (Moss, 1961; Fulcher & McCully, 1969). The fact that the laminae in D. longifolia did not develop any further than a few millimetres in length is believed to be due to the limited space and nutrient supply in the small plastic wells in which the sections were cultured for this study (Section 2.6.3). Enriched seawater was not used in this study as the sections became covered in epiphytes (Pl. 19, B). Similar reports of a lack of regeneration due to epiphytic growth in enriched media, have been reported in other brown algal regeneration studies (Fagerberg & Dawes, 1976; Mooney & van Staden, 1985). In the majority of cases, the new laminae developed from the cut edge of the section in the midrib region, although many of the laminae developed from the wing close to the midrib (there were also the occasional lamina which developed some distance from the midrib). Moss (1961) reports that Fucus vesiculosus regenerates new lamina from the wing and the midrib, although those developing from the wing grew at a far slower rate. Burrows (1955; in Moss, 1961), Oltmanns (1889; in Moss, 1961) and Fulcher and McCully (1969) all report, however, that regeneration occurs only from the midrib in Fucales. Initially it was presumed that the regeneration process was governed completely by some type of polarity controlled by the apical cells and midrib however, the presence of protrusions which developed away from the midrib suggest that, in some parts of D. longifolia, this control may be weakened or

overridden by some other factor. A possible reason may be the distance that the particular section was away from the apical region of the laminae. It has been reported that the effect of apical dominance in Sargassum muticum decreases with an increase in distance from the apex (Chamberlain et al., 1979). Moss (1961) also reports that the degree of regeneration increases away from the apex in Fucus vesiculosus, suggesting some form of inhibitory control from the meristem of the apex. Tsukidate (1984) reports differing degrees of regenerative ability from different areas of Sargassum. Any further study on the regeneration of D. longifolia should investigate the effects of polarity on regeneration, at different distances from the apical cells. Some of the sections in the study developed laminae on both cut edges while others only developed them on one edge, and none produced rhizoids. Possibly this is also related to the distance from the apical region and the control the apex has over the growth. Moss (1961) reports regeneration from both cut edges of sections (1mm wide) of Fucus vesiculosus, whilst small sections (0.5mm wide) only produce proliferations from one side. Thus the size of sections also appears to affect regeneration patterns. Fulcher & McCully (1969) report regeneration from only one side of sections close to the apex and regeneration from both sides of sections taken closer to the basal region of the parent plant. Mooney and van Staden (1985) report that only holdfast sections, and no lamina sections, regenerated laminae in Sargassum heterophyllum. This seems to suggest apical inhibition of the lamina sections. The type of tissue that is regenerated, ie rhizoidal or blade tissue, may also be determined by the position of the wound in relation to the apex or base (Lobban et al., 1985). An attempt to determine the effect of distance from the apex on regeneration in D. longifolia, was made by taking progressive sections down the laminae and placing them into culture. Unfortunately,

these sections displayed poor regenerative potential, possibly due to the time of the year at which this part of the study was carried out. There appears to be some growth regulating substance which plays a role in regeneration, eg direction of regrowth. However, the actual substance has not as yet been identified (Lobban *et al.*, 1985). A similar study was performed on a members of the red alga, Petroglossum nicaeense (Duby) Schotter, in which different sections of the lamina were put into culture and the regeneration patterns observed (Perrone & Felicini, 1972). A laminal section with the apical tip removed with a straight cut exhibited regeneration from both the cut and uncut side edges. A section across the whole lamina but lacking both the tip and the base, displayed regeneration from both the cut and uncut side edges. These authors also performed some studies using sections damaged in ways which cannot be compared to those in this study.

D) The apical tips that were removed with a v-shaped cut were also placed into culture (Pl. 20, A-H; Fig. 8, D; Fig. 67, D). These sections exhibited interesting results in that in some cases the tips continued to elongate in the same manner that they would if they were still attached to the adult plant (Pl. 20, A-C). The apical tips exhibited a gradual increase in length over time, as would be expected from normal elongation (Pl. 20, A-C; Fig. 55). These sections also developed surface hairs similar to those produced by other sections. Similar results were observed in the removed apical sections of Sargassum muticum (Fletcher & Fletcher, 1975) and Moss (1961) reported elongation of removed apical tips from Fucus vesiculosus without any regeneration. In other cases, the removed apical sections of D. longifolia exhibited some elongation of the apical regions and/or regeneration of laminae from the cut edge in a direction opposite to the original direction of growth (Pl. 20, D-

H). In some of the tips which regenerated but did not elongate, it appeared as if the tip was damaged (Pl. 20, D-F). In some damaged apical regions, regeneration of new laminae occurred from the apical tip as well as the cut edge (Pl. 20, F). Dichotomising laminal tips showed both elongation of the tip and regeneration from the cut edge (Pl. 20, G & H; Fig. 8, D; Fig. 67, D). The fact that laminae developed from the cut edge of the sections (ie in the opposite direction to original growth) so close to the apical meristem suggests that any control the laminal tip has over regeneration may be exercised very close to the tip. Another possible factor which may influence the type of regeneration or elongation exhibited by the removed apical section, is the age or maturity of the apical cells, ie there may be a different level of control exerted by an apical tip of a mature lamina compared to that of a juvenile lamina. In the study of Petroglossum nicaeense (Perrone & Scincini, 1972), the apical tips that were removed for studies described in the previous section, were also cultured and continued to grow from the tip as well as regenerate from the cut and uncut side edges.

4.10.2 Regeneration from Large Sections or Whole Laminae

Regeneration from large sections or whole laminae of D. longifolia occurred prolifically in culture. In these sections, the regenerated laminae developed to a much more advanced and larger stage, presumably due to the fact that these sections were kept in larger volumes of water (250 ml flasks and small tanks) than in the plastic wells that the smaller sections were kept in. There was thus a better supply of nutrients and more space for growth of these sections. Another possible reason for the increased development from these sections is that the parent section was larger and could thus better support the growth of new laminae (ie more area for

photosynthesis), and damage during preparation was not as extensive. Whole laminae were used in the study when they were of a manageable size and if not, similar size sections were cut and put into culture (approximately 5cm long). Once again, it must be remembered that the maturity of the lamina was not taken into account when different age sections were used. The maturity of the lamina may play a role in the regeneration response and this needs to be studied further. There is a report that there is an increase in regeneration potential of laminae segments from young laminae that have not dichotomised yet, than from mature thalli of Fucus vesiculosus (Lobban & Wynne, 1981).

E) In the sections having the midrib severed by a horizontal cut (Pl. 21, B & F; Fig. 8, E; Fig. 67, E), no regeneration occurred from the cut surfaces. This would seem to indicate that the intact tip has some sort of control over regeneration of new laminae from cut surfaces nearer the base of the lamina. However, it also suggests that the remainder of the lamina can absorb sufficient nutrients from the water for apical growth to continue without laminar transport, or that the midrib is not the only path for longitudinal movement. In the study of Petroglossum nicaeense (Perrone & Felicini, 1972), regeneration was observed to occur from cuts in the side of the lamina. However, this was not observed in D. longifolia and it must be remembered that, although the study of P. nicaeense is similar to that in this thesis, the two algae are completely different in structure.

F) Large laminal sections composed of a dichotomy having the apical tips cut off (Pl. 21, C & D), exhibited regeneration of new laminae from the apical region. The dichotomy of the midrib and wing tissue, to give rise to two new laminae, is thought to be under the control of the apical meristematic cells. Possibly the fact that

there are two apical regions acting on a single basal region (ie the single, original lamina gives rise to two branches with two apical meristematic regions) might have resulted in the regeneration from the cut edge in the apical region, and led to the lack of regeneration from the basal end of the section (Pl. 21, C & D; Fig. 8, F; Fig. 67, F).

G) Sections having the apical tip removed with a v-shaped cut exhibited regeneration along the entire cut edge, not only on or close to the midrib (Pl. 20, I-K; Pl. 21, E; Fig. 8, G; Fig. 67, G). It is possible that very close to the apical tip, the apical influence is not restricted to the midrib as it appears to be in regions further away from the apical region. Daly and Mathieson (1977) report that the subapical cells of Zonaria and other members of the Dictyotales can regenerate new laminae if the apical region has been removed by sand abrasion. Figure 56 is a silhouette of a specimen collected in the field. The tips have obviously been damaged but the midrib has remained intact and appears to have given rise to new terminal regions (not a new lamina). This was not however, observed in any of the similarly (experimentally) damaged laminae.

H) Entire plants which were kept in culture and injured to observe regeneration, exhibited extensive regeneration from the cut surfaces. The newly regenerated laminae developed to a larger size than those in the other experiments. The greater success of the regenerated thalli could either be due to the greater volume of water and thus a better nutrient supply, or due to the fact that energy necessary for growth could be provided better when the entire plant was photosynthesising. Similar to reports for Fucus vesiculosus, the tips of the newly regenerated laminae could continuously be removed (Moss, 1961) and regeneration of new laminae was initiated.

4.10.3 Process of Regeneration from Injured Laminae

The process of regeneration in D. longifolia is similar whether the regeneration is occurring from a cut surface of a section or from the surface of a lamina. Initially all the cells rounded up and the cytoplasm became concentrated. This is a similar process to the initial stages of regeneration described for Fucus vesiculosus (Moss, 1961). Only the wounded cells appear to lose their contents in Fucus (Fulcher & McCully, 1969), which is similar in D. longifolia in which the injured cells may remain as walls only (Pl. 24, A-C; Fig. 58, B & C). This is followed by a different system in F. vesiculosus in that filaments grow over the wound to form a new epidermis. A single cell protrudes from this surface and then regeneration continues as was observed in D. longifolia (Moss, 1961; Fulcher & McCully, 1969). From the sections of D. longifolia (Pl. 22, A & B; Pl. 23, A-D; Pl. 24, A-D; Fig. 58, B) it can be seen that there is the dominance of a single cell over the surrounding cells and only the single cell protrudes to the exterior, although the surrounding cells may experience some degree of cytoplasmic concentration. Lobban *et al.* (1985) report that there is a concentration of polysaccharides in the wounded cells of F. vesiculosus, presumably to aid in wound healing and to stop further leaking. Fagerberg and Dawes (1977) also report an increase of vesicles thought to be involved in wound repair. There may be various stages of regenerating laminae in a single area as was observed in F. vesiculosus (Fulcher & McCully, 1969). The protruding cell of D. longifolia enlarges and divides into a multicellular bulbous structure (Pl. 22, C-J; Pl. 23, E-S; Pl. 24, E-L; Fig. 58, E & G). From Plate 24 (E & G) which shows the dividing cell, it appears that there is a single cuticle which surrounds all the dividing cells. This is the immature lamina and it rapidly

develops a midrib and apical pit (Pl. 22, G-J; Pl. 23, J-M, O). The longitudinal, apical cells can also be distinguished after a number of days. A prominent midrib becomes apparent (Pl. 22, I & J) and rhizoids are produced from the base of the lamina at the point of attachment to the parent plant (Pl. 23, M, N, P-S; Pl. 24, L; Fig. 58, L). A similar process has been reported in Sargassum filipendula where a stipe medullary cell produces a tubular, bud-like protrusion which develops into a flattened, dichotomously branched blade (Fagerberg & Dawes, 1976). McLachlan & Chen (1972) report that no rhizoids were produced from the base of laminae regenerating from a wound in Fucus. Apical sections of Dictyota dichotoma also do not produce rhizoids however, sections closer to the base produce increasingly well-developed rhizoid systems (Russell, 1970). Near the base of the lamina, the rhizoids are produced from the lamina surface. It is believed that there is a downward inhibition of rhizoids initiated by the apex, allowing rhizoid growth near the base of the lamina only, at a distance from the apex (Russell, 1970). Regenerated thalli of D. longifolia were frequently observed to produce basal rhizoids. It is not known whether the regenerated laminae detach and are able to develop into a complete plant. In the field, regenerated laminae of a few centimetres in length were observed attached to the parent plant. Possibly these laminae continue development into complete, independent plants if they are detached, and otherwise they remain attached. It is believed that these laminae could readily develop into new individuals if they became detached from the parent plant and attached to the substratum in another area. Asexual reproduction through vegetative propagation is thus considered an important survival strategy in D. longifolia. Thalli which remain attached to the parent caused the parent plant to develop a stunted, bushy appearance. The rhizoids of the regenerated thalli may

act in nutrient uptake as well as to anchor the plant if it becomes detached. Some laminae with basal rhizoids were removed and put into culture but most did not survive. This is probably due to the low nutrient availability and the high degree of handling that they experienced. The lack of survival may also be caused by the fact that the thalli were not large enough to support themselves, or possibly regenerated thalli are not able to survive as independent individuals. Some removed laminae, however, regenerated new lamina-like structures from the surface. The fine, anatomical detail of the regeneration process was not studied but it would be interesting to compare this to the detail of regeneration in Fucus vesiculosus (Moss, 1961; Fulcher & McCully, 1969, 1971) which appears to undergo a similar process.

4.10.4 Regeneration from the Uncut Surfaces of Laminae.

Regeneration from the surface of the laminae was observed occasionally in the field, on regenerated laminae which had been removed from the parent plant and put into culture separately, on sporelings and on apical sections with damaged apical tips (Pl. 25, A-C). In the field, injured areas and small holes were visible near the base of the newly regenerated laminae, although the laminae were not observed to grow directly from damaged areas. It is believed that the surface regeneration observed in culture may have, in some of the cases, occurred from areas of injury which were not observed and may have been microscopic. Dictyopteris australis and D. crassinervia are both reported to develop new laminae from the surface of the midrib (Allender & Kraft, 1983). In culture, development of new laminae occurred from the surface of laminae which had regenerated from an injured parent lamina (ie regeneration on regeneration), as well as from sporeling laminae. In both cases the material was maintained in culture for a number of weeks and had been

subjected to a large amount of handling. The material could easily have become injured or weakened although no macroscopic injury was observed. The regeneration from the laminal surface that was observed in the field, occurred mainly from the base of the lamina in the midrib region, however, in culture laminae were produced from the wings as well as the midrib. In almost all cases of surface lamina production, the apical tips were intact, which seems to indicate that regeneration can occur from laminal surfaces under normal conditions. Although it is believed that regeneration from the surface of the lamina may occur from injuries, photographs (Pl. 25, F-H) of the initial stages of regeneration in D. longifolia (ie the initial protrusion of a single cell) show no signs of injury. Surface regeneration is however, rare in the field and is thus either the result of a hidden injury, or dependent on certain infrequently experienced growth conditions.

The process of surface regeneration is similar to that observed to occur from a cut surface. There is an initial protrusion of a single surface cell (Pl. 25, E-H), with subsequent enlargement and division of the cell into a multicellular lamina (Pl. 25, I-L). The laminae appeared to develop normally with the longitudinal division of elongated apical cells (Pl. 25, J). Rhizoidal structures were also observed to develop from the surface (Pl. 25, M-P). The development of further laminal outgrowths on the surface of the regenerated laminae were also observed.

4.10.5 Regeneration from the Holdfast

The holdfast of D. longifolia is believed to be perennial although it was observed that individuals in the field lost all or some of their laminae during the winter months (due to herbivory and abrasion; Pl. 26, A). The

holdfast of D. longifolia in the field was observed to give rise to new laminae after the old laminae had been removed. This observation was supported when pieces of holdfast kept in culture were induced to regenerate new laminae (Pl. 26, B-F; Fig. 8, H; Fig. 67, H). Perennial holdfasts and seasonal laminae are common in members of the Phaeophyceae and is an important mechanism which allows badly damaged populations to recover (McLachlan & Chen, 1972; Chapman & Chapman, 1973; Palmisano & Sheng, 1977; de Paula & de Oliveira, 1982; Scagel et al., 1982). The base of the old laminae, ie the bases of the midrib or the "stipes", were removed from the sections of D. longifolia holdfast prior to them being placed into culture. The new laminae that developed were therefore not regenerated from the remains of the old laminae, but rather from the holdfast clump itself (Pl. 26, G). As the holdfast is composed of a tangled mat of rhizoids, new laminae must develop from the rhizoids of the holdfast. Mooney and van Staden (1985) report that sections of Sargassum heterophyllum holdfast which include small portions of the main axis, produced regenerated laminae in culture. However, the latter sections of the lamina (from all regions) were not induced to regenerate, suggesting some apical inhibition. In sections of young holdfasts of S. heterophyllum, small projections developed from the remains of the axis. One of the projections developed and the rest did not, which suggests that one exerted dominance over the rest. The ability to regenerate from the holdfast and basal segments is reported to occur prolifically in S. muticum, an invading species in some regions of the world. This observation is important for future eradication programs of the species, ie the holdfast has to be removed as well as the laminae (Fletcher & Fletcher, 1975). It appears from the literature that complete holdfasts have not been observed to grow from sections of laminae, although individual rhizoids have been observed to develop (Moss,

1961). A clumped arrangement of plant distribution was observed for D. longifolia. This could either have been formed by regeneration of laminae from the rhizoids and holdfasts, or entanglement of spores and zygotes in the rhizoids. It was particularly noticeable in the high wave exposed sites (H+ and H). De Paula and de Oliveira (1982) report that the density of clumps of Sargassum cymosum increases with an increase in wave exposure. Clumping is believed to play an important role in desiccation resistance (see Section 4.8.4). Gaillard (1977) reports that another member of the genus, D. membranacea has a clumped distribution due to the production of new plantlets from the rhizoids. Clumping of holdfasts has been recorded for other species of brown algae, eg Xiphophora gladiata (Labill.) Mont. ex Kjell. however, the reasons for this arrangement are not known (Rice, 1987).

An interesting feature of regeneration from the holdfast and from rhizoid sections, is that the sections were placed into natural seawater without any nutrient additives and, as no laminae were present, little photosynthesis could occur (the rhizoids may be slightly pigmented). The holdfasts and rhizoids still underwent growth and regeneration which suggests that the holdfasts store nutrients for growth or are able to absorb sufficient nutrients from filtered seawater. There is a report that when the canopy of the kelp Macrocystis is removed, there is a decrease in holdfast growth indicating that the laminae are necessary for the growth of the holdfast (McCleneghan & Houk, 1985).

4.10.6 Regeneration from Rhizoid Sections.

It has been reported in the literature that members of the Dictyotales are capable of regenerating new thalli from sections of the holdfast rhizoids. For example, new

thalli were reported to be produced from the rhizoids at the periphery of the holdfasts of Dictyopteris undulata (Benson, 1986). Attempts to initiate the development of new laminae from short, unbranched sections of the rhizoids of D. longifolia failed, but there was regeneration of new laminae from longer, branched sections (Pl. 27, A; Fig. 8, I; Fig. 67, I). Tokida et al. (1953) reported that rhizoid-cultured sections from Dictyopteris divaricata were observed to regenerate thalli in natural seawater, as well as from old rhizoids in the field. Similar observations were made for Sargassum vulgare (Paula & Eston, 1987), D. delicatula (Tokida et al., 1953) and D. membranacea (Harvey, 1846; in Tokida et al., 1953). The regeneration of new laminae from rhizoids (of newly germinated sporelings) in the latter species, was also studied by Gaillard (1977). This author described this process as the formation of a cross wall in the rhizoid, followed by the production of an erect frond. During the production of new thalli from the rhizoid of a sporeling, a single spore may produce more than one plant (Gaillard, 1977). The abundance and structure of the regenerated plants are reported to be similar to those developing from other sources, eg spore, or zygotes (Tokida et al., 1953). Regeneration from a section of rhizoid in D. longifolia was similar to that from the lamina, in that a single cell in the rhizoid became swollen and dense with organelles (Pl. 27, B; Fig. 59, B). The cell enlarged and underwent division to form a multicellular structure (Pl. 27, C-P; Fig. 59, C-K). The laminae reached fairly advanced stages of development with elongated apical cells in a pit at the apex of the lamina (Pl. 27, K-N; Fig. 59, L) and rhizoids at the base. In some cases surface hairs were produced by the laminae (Pl. 27, L; Fig. 59, L). If surface hairs are involved in nutrient uptake, it would follow that in nutrient poor conditions such as those of the culture, small laminae would need maximum photosynthesis to

survive. In these cases, an increased nutrient supply would be necessary. The laminae developed no further and survived for a few weeks before dying. It is presumed that the mortality is due to nutrient depletion and the small water volume in the culture conditions. It is believed that the laminae would have developed into complete plants if they had been in natural conditions with a continuous nutrient supply provided by the water movement and unlimited space for growth. McLachlan and Chen (1972) report a similar process in rhizoids of Fucus, in which a single cell undergoes an increase in cell contents, swells, divides parallel to the axis and then perpendicularly, before dividing rapidly in all directions to form a lamina. These researchers report that there is frequently more than one regenerated plant from a single axis and, similar to what was observed in D. longifolia, more rhizoids are produced from the laminal base. In both Fucus (McLachlan & Chen, 1972) and D. longifolia the production of a lamina does not appear to be a wound response, but rather a spontaneous occurrence. A very similar process was observed in sections of rhizoid (3mm long) taken from Pelvetia plantlets (Saga, 1978). This author kept the sections in PES and they developed further than the sections of D. longifolia in the present study. This may indicate that the lack of advanced development of the laminae in this study could have been due to depletion of nutrients. An interesting feature of the regeneration from rhizoids is that, prior to regeneration of a lamina, there was no source of photosynthates (except stored photosynthates) available to the rhizoids. McLachlan and Chen (1972) report that there is an increase in cell contents (possibly including plastids) in the rhizoidal cell which enlarges and develops into the lamina. This may indicate that photosynthesis occurred in the cell to provide energy for division.

4.11 SEXUAL REPRODUCTION

Sexual reproduction was not originally part of the study design but, when observed on material collected in the field and on sections in culture, it was recorded. Despite reports (Denny, 1988) that sexual reproduction is often unsuccessful, especially in areas of high wave exposure (due to the removal of gametes by the water movement), this form of reproduction was observed in D. longifolia from areas of wave high exposure. The study that was performed is purely a diagrammatic and photographic representation of the structures and stages of sexual reproduction that were observed. A more detailed study would have to be performed on D. longifolia before features of sexual reproduction could be included in a taxonomic description. There are reports that the sporophyte stage of members of the Dictyotales is dominant, or that the gametophyte stage is rare or altogether lacking (Tokida et al., 1953; King & Farrant, 1987). However, Phillips (1988) reports that the gametophyte and sporophyte stages of South Australian Dictyotalean species are found together, but that there are seasonal fluctuations in gametophyte phase, eg the greatest reproduction occurs in autumn in Dictyopteris undulata (Benson, 1986). The theory that there may be varying ratios of gametophyte and sporophyte plants in a population, is possibly supported by the report that gamete production in Laminaria and other brown algae is temperature dependant (Kain, 1964). It has also been reported that algal life histories may be affected by environmental conditions other than temperature (Norton et al., 1981). For example, Cousens (1982) reports that Ascophyllum nodosum reaches sexual maturity faster in areas sheltered from wave exposure. There are also reports of gamete production being sensitive to fluctuations in the chemical composition of the seawater, eg changes in iron availability (Lobban & Wynne, 1981;

Motomura & Sakai, 1984). Hannach and Santelices (1985) report different stages (ie sporophytes and gametophytes) of the red alga Iridaea having different environmental tolerances. There may also be spatial separation of gametophytes and sporophytes, and gametophytes may be mistakenly identified as sporophytes (Phillips, 1988). Although it was not determined which of the D. longifolia individuals observed in the field were sporophytic and which were gametophytic, spore and gamete producing material were collected together. Hannach and Santelices (1985) suggest that the presence of isomorphic forms in different seasons may indicate that there is not true isomorphism, and that there are differences in each generation's genetic make-up that adapts that generation to reproduce in different seasons. The different phases thus respond differently to environmental conditions and change in relative abundance to each other. Although the Dictyotales are reported to be morphologically indistinguishable or isomorphic (Lobban & Wynne, 1981), there is a possibility that the different phases react differently to the environmental conditions and this may result in the variation in apex shape that was observed at different times of the year in D. longifolia (Section 4.1.1).

There is reported to be a periodicity of gamete release in Dictyotalean algae. For example, Dictyopteris muelleri is reported to release gametes every seven days (Phillips, 1988), Dictyota dichotoma, and D. giemensis (Phillips et al., 1990b) have a periodicity which is somehow related to the tidal cycle of the area (Hoyt, 1927; Chapman & Chapman, 1973) and Zonaria angustata (Phillips et al., 1990a) is also reported to experience gamete release periodicity. It would be particularly interesting to determine whether there is any periodicity in the gamete production of D. longifolia in areas of high wave exposure. Spontaneous release of gametes from

all members of the population would increase the chance of fertilisation, even in high wave exposure areas.

4.11.1 Antheridia

The antheridial sori of D. longifolia are light coloured, irregular patches or "blisters" (Pl. 28, A-C) similar to those described for Dictyota diemensis (Phillips et al., 1990b; Fig. 60, A & B). The antheridia were commonly observed in the field in the summer months. They are visible on both surfaces of the lamina. Most of the sori that were studied were in the early stages of development (Pl. 28, D & E). Unfortunately not all the stages of development were observed. This is thought to be due to the fact that the study was not performed over the entire year. Early stages were observed to involve a pit lined by dividing cells which developed into sori (Pl. 28, F & G). The latter became swollen above the surface of the lamina, and developed sperm cells in longitudinally arranged antheridia (Pl. 28, H & I; Fig. 60, C). In none of the laminae studied, had sperm cells been released although mature antheridia were observed.

Although the sperm release and attractant mechanisms for D. longifolia were not studied, Phillips et al. (1990b; 1990a) report that the eggs of species of Dictyota diemensis and Zonaria angustata produce sperm attracting substances known as dictyotene and multifidene, respectively. Other brown algae are also reported to produce sex attractants. It would be interesting to determine if D. longifolia has any sperm attracting substance, and if so, how well it succeeds under conditions of high wave exposure. It would also have been interesting to observe if D. longifolia has the characteristic Dictyotalean sperm which has only a single flagellum (Morris, 1967), however released sperm were not observed.

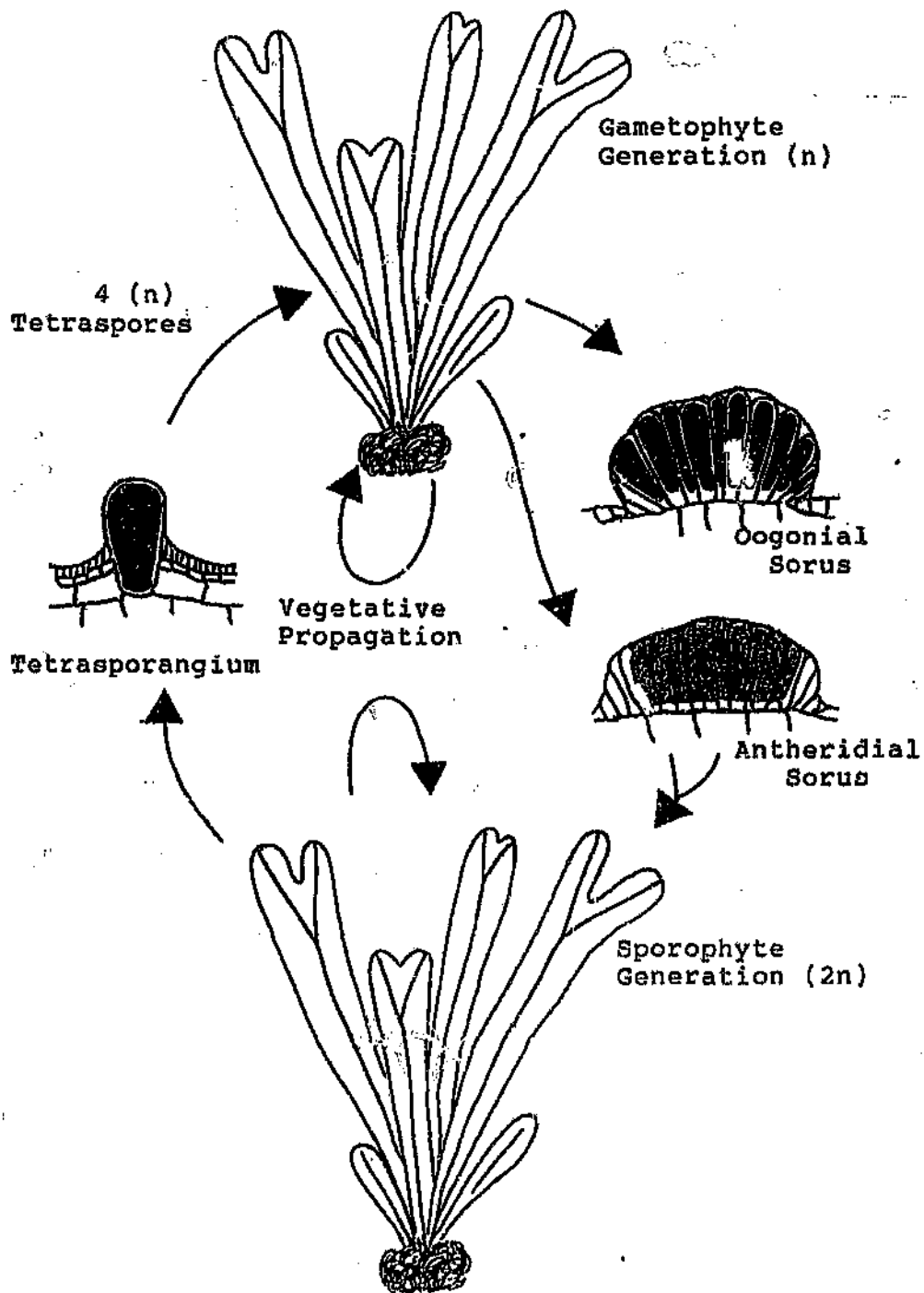


Figure 68: Diagram showing the suggested life history for *Dictyopteris longifolia*.

4.11.2 Oogonia

Structures observed and identified as oogonia in D. longifolia appeared to be similar to those described for Dictyota diemensis (Phillips et al., 1990b; Fig. 60, D & E). The oogonia were not observed as frequently as the antheridia and thus the study is much less detailed. The structures appeared to only occur on the dorsal surface (Pl. 28, J & K) of the laminae and only the early stages of development were observed. The early stages consisted of a raised area with longitudinal division of the cells (Pl. 28, L; Fig. 60, F). It is reported that the oogonia of the Dictyotales resemble the tetrasporangia and may frequently be mistaken for the latter structures (Phillips, 1988).

4.12 TETRASPOROGENESIS

Although tetrasporogenesis and the germination and development of the spores was not included in the original study design, it was frequently observed in the field and on lamina sections (width of the lamina and 1cm long; Section 2.5.6) in culture. It was thus decided to observe the process of spore formation, germination and development into sporelings as reproduction without the meeting of gametes (tetrasporogenesis and vegetative propagation) is obviously an important survival strategy for D. longifolia, particularly in the higher exposure areas (where the chances of successful meeting of gametes is reduced). Seymour et al. (1989) suggest that sporogenesis in Macrocvstis pyrifera occurs in the seasonal storm period when the wave activity is at its greatest, thus taking advantage of effective dispersal and a high nutrient supply. The greatest degree of tetrasporogenesis in D. longifolia appears to be in the middle of the year (Chihara, 1963; herbarium specimens;

per. obs.), and the material in culture produced spores in June. Tetrasporogonesis may also be one of the causes of the clumped growth habit of the plant. Clumping may however, be due to gametes becoming entangled in the holdfast, or due to regeneration from rhizoid sections.

Unlike the motile asexual spores of other brown algae, the non-motile tetraspores of the Dictyotales rely on water movement to disperse them (Fletcher, 1987). It would follow that spores would be transported over a much larger area in highly wave swept areas. This appears to be supported by the fact that the populations in the highest wave action sites (H and H+) were not only had the highest density and number of plants of the sites studied, but were also spread over a much wider area than in the other sites which were localised to a single pool or part there of. There are numerous reports involving the dominance of the sporophyte generation in Dictyotales, eg Glossophora kunthii (Malbrán & Hoffmann, 1990), however Phillips (1988) reports that there is some difficulty in distinguishing the phases of Dictyotalan algae unless the plants are in the advanced stages of reproductive cell formation, and this may lead to incorrect counts of the different generations. There may also be temporal and spatial differentiation of the phases, although King and Farrant (1987) report sporophytes of Dictyopteris acrostichoides throughout the year. This was also observed in D. longifolia where mapped individuals were present for most of the year (ie all of the study period; Section 3.6). The seasonality of tetraspore production in D. longifolia was not studied in depth, however, there are reports that Macrocystis integrifolia has recruitment from sporogenesis throughout the year (Druehl & Wheeler, 1986) and Malbrán & Hoffmann (1990) report two peaks of tetraspore production per year in Glossophora kunthii.

Chemical changes, eg salinity are reported to affect the production of sporophytes in Phaeostrophion irregulare (Mathieson, 1982b), and daylength is reported to affect sorus formation in Laminaria saccharina (Lüning, 1988). There have been a number of studies on factors effecting tetrasporogenesis in members of the genus Dictyopteris (in particular D. divaricata), eg the effect of cytochalasin B on germination (Ohmori & Ueki, 1980), the effect of wavelength of light on tetraspore formation (Ohmori & Suemura, 1978) and the effect of colchicine on rhizoid formation (Ohmori & Hashida, 1982).

4.12.1 Development of tetraspores

Characteristically, members of the Dictyotales produce four to eight, non-motile tetraspores in a superficial sporangium (Fritsch, 1945; Chapman & Chapman, 1973; Fletcher, 1987). The majority of Dictyopteris species are characterised by having sporangial sori, however, one species D. muelleri does not have sori (Clayton pers. comm.). The tetrasporangia in D. longifolia are produced on both sides of the lamina in bands next to the midrib (Pl. 29, A-E; Pl. 30, A & B), as reported for D. acrostichoides (Phillips, 1988). Ohmori and Hashida (1985) showed that the tetrasporophyte and tetraspore mother cell of D. divaricata are diploid, whilst the germlings from the tetraspore are haploid. Development of tetraspores in D. longifolia differs from that described for D. divaricata (Ishii et al., 1959; Fig. 69, A). The latter is reported to have the stalk cell divided into two to four cells, or one cell (Inoh, 1936; Fig. 69, C) and to lack an elevated cuticle. Another Dictyotalean alga, Dictyota dichotoma, has two or three stalk cells and no cuticle (Ishii et al., 1959). Dictyopteris australis and D. muelleri are reported to have a single stalk cell and D. acrostichoides to have one or two stalk cells (Phillips, 1988). D. longifolia, however, has a

single stalk cell (Pl. 31, D-H; Fig. 62, G; Fig. 69, D) and the spore mother cell elevates the cuticle (Pl. 31, C; Fig. 62, C; Fig. 69, D). This process is similar to that described for Padina japonica and P. crassa (Ishii et al., 1959; Fig. 69, B) and Dictyopteris divaricata (Inch, 1936; Fig. 69, C) in that there is one stalk cell, but P. japonica and P. crassa have elevated cuticles which D. divaricata lacks. The early stages of tetrasporogenesis of D. longifolia involves the development of the tetraspore mother cell towards the inner, cortical layers of the lamina (Pl. 31, A; Fig. 62, A), prior to the protrusion of the tetraspores to the exterior (Pl. 29, F; Pl. 30, C & D; Pl. 31, B; Fig. 61, F). This was not described in any of the other Dictyotalean species compared above. The spore mother cell of D. longifolia then divides meiotically (still within the sporangial wall) to give rise to four tetraspores (Pl. 29, G-J; Pl. 30, E-H; Fig. 61, H-J). In D. longifolia the spores were arranged in a tripartite or tetrahedral arrangement, similar to D. divaricata, P. japonica and P. crassa, whilst Dictyota dichotoma has a cruciate arrangement (Ishii et al., 1959). The spores are released and leave an empty casing (Pl. 31, L-O). The released spores settle and begin germination. The spores of Sargassum muticum are reported settle in crevices (where they are protected from water movement, grazing and desiccation) or on other plants in rough water. This may be the reason for the clumped habit that was observed in populations of S. muticum (Norton & Fetter, 1981) and which was also observed to occur in populations of D. longifolia.

The lack of separation of released spores (Pl. 29, K & L; Pl. 31, K; Fig. 61, K & L), or lack of release of spores

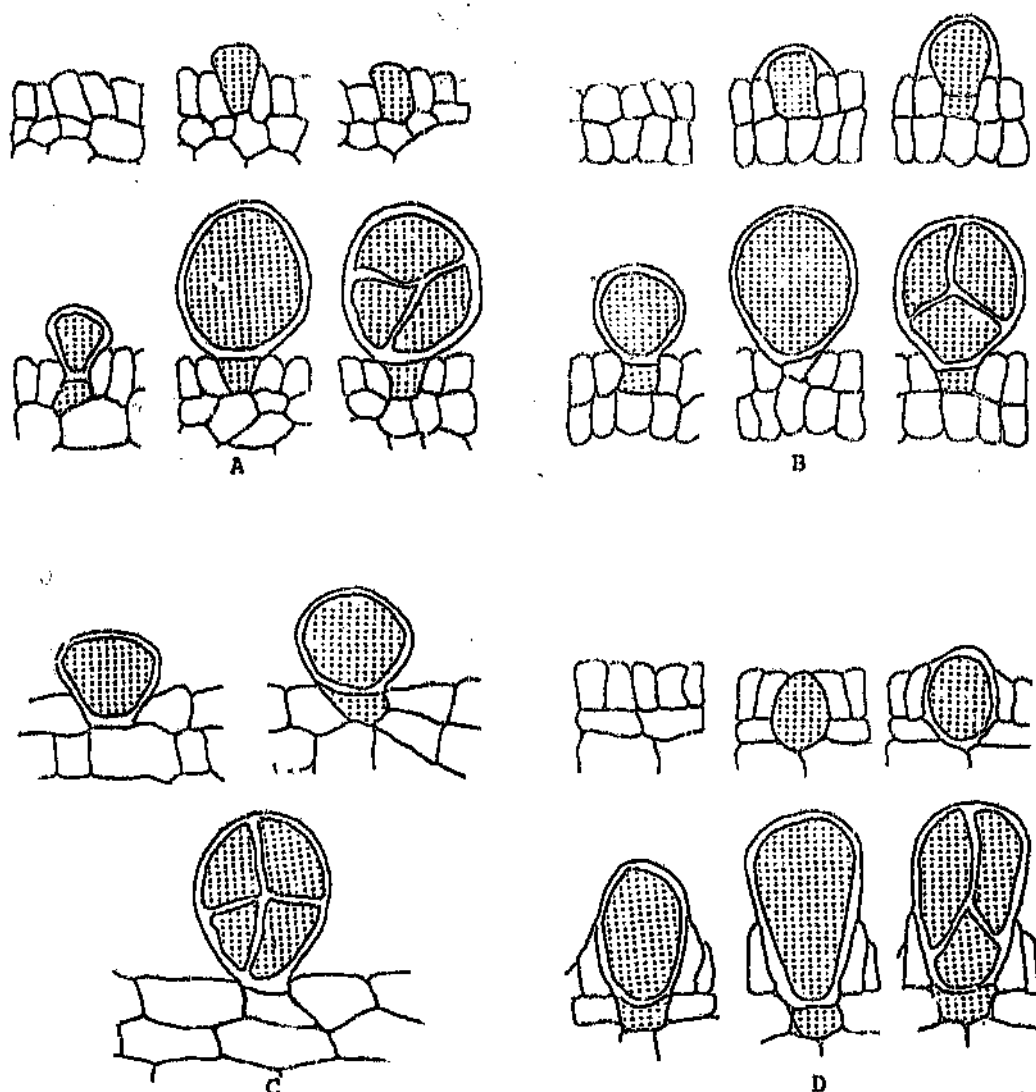


Figure 69: Diagram to show comparisons between spore formation of Dictyopteris divaricata (redrawn from Ishii et al., 1959 (A) and Inoh, 1936 (C)), Padina japonica (redrawn from Ishii et al., 1959 (B)) and D. longifolia (this study (D)).

from the sporangium altogether, prior to germination (Pl. 30, L-S; Pl. 31, I & J) was not observed to occur in the field where plants were exposed to water motion. All the aggregated spores of D. longifolia however, appeared to be equally viable in culture and germinated in the same

The spores of Padina japonica have been reported to be liberated from the sporangium and germinate together. However, in this case the germination patterns of the aggregated spores were reported to differ from those of single spores (Nishibayashi & Inoh, 1959). Norton et al. (1981) report that tetraspores in Dictyota may germinate whilst still in the sporangium and that this may lead to a change in the adult morphology by causing proliferations from the surface of the parent lamina. The reason for this aggregation (other than due to lack of separation by water movement in culture) is not known, although it has been reported that some spores produce mucilage so as to aggregate to increase the mass, and thus the sinking rate (Neushul, 1972).

4.12.2 Morphogenesis

The tetraspores of D. divaricata were described as first producing a "multicellular, oval body" that developed a protruding cell, which later became the meristematic, apical cell of the juvenile gametophyte plant (Nishibayashi & Inoh, 1959). Inoh (1936) described the division and elongation of the rhizoid, prior to the appearance of protrusion from which the thallus developed. A tetraspore may produce more than one of these protruding cells and Dictyopteris is reported to have more than one apical initial. Although D. longifolia was not observed to produce more than one protrusion, the process of protrusion from the spore (Pl. 32, D-K; Fig. 63, D-F), the initial elongation of the rhizoid (Pl. 32, G-N; Fig. 63, G-N) followed by the development of the thallus (Pl. 33, D & E), was similar in this species to that described by other authors. It appears, from developing sporelings labelled with calcofluor (Pl. 32, A-C), that new wall material is included in the protruding side of the spore cell. As in reports for other species, the cells of the thallus of D. longifolia

were observed to be much darker than those of the rhizoids (Inoh, 1936). The primary rhizoids of Fucus vesiculosus are surrounded by a mucilaginous layer which is believed to be associated with the adherence of the rhizoid to the substratum (Moss, 1961). Such a mucilaginous layer was not observed in D. longifolia, however, the rhizoid tips were observed to adhere to the substratum very early in the germination process. In Padina dubia Hauck (Ampili et al., 1987), the spores are reported to secrete an extracellular substance 1-2 hours after release, and to adhere 3-4 hours after release. The adhesive substance may contain fucoidan and polyphenols for adhesion and protection (these substances are believed to have antibacterial properties). Ampili et al. (1987) used a range of stains to obtain their conclusions about the secreted substance. Extracellular material was not noted in D. longifolia.

The development of rhizoids is sensitive to light conditions, as was shown by Ohmori and Ueki (1979) who demonstrated that the rhizoids of Dictyopteris divaricata grew away from continuous unilateral light. The growth of the sporelings of D. longifolia ceased once the thalli had developed and an apical pit, midrib and basal rhizoids were present (Pl. 33, H-K; Fig. 64, J & K). This is thought to be due to the depletion of nutrients in the culture, as well as the lack of space. Moss (1950) reports a similar lack of development in Fucus vesiculosus sporelings kept in natural seawater, and attributes this to a lack of nutrients. It has also been reported that there is a change in germination pattern with a decrease in nutrients in Fucus (McLachlan, 1977). The sporelings may also become overgrown with epiphytes and bacteria due to the lack of natural conditions, eg herbivores and abrasion (Edelstein & Womersley, 1975). Continual submersion, which does not occur in all natural conditions (eg spores released in H and H+ would

experience emersion at some time), may also affect the growth of the spores.

Initial morphogenesis of D. longifolia tetraspores was similar at all temperatures investigated. However, at the stage when a second rhizoid emerged or the thallus began development, there was considerable variation. In some cases, the second rhizoid appeared before any thallus development had occurred (in this case there appears to be more than one cell in the thallus section (Pl. 33, B, C; Fig. 64, B), whilst in other cases the thallus was fairly well developed before the second rhizoid appeared (Pl. 33, A). The peculiar growth pattern shown in Pl. 34 (A, J & K) is similar to the peculiarities observed in Dictyopteris divaricata, in which the thallus underwent division before producing rhizoids (Ohmori & Hashida, 1984). There are thus similarities between the patterns of germination described for D. longifolia and those described by Ohmori and Hashida (1984). The latter researchers report two patterns of germination in D. divaricata. First, there is the production of a primary rhizoid, followed by the division of the thallus cells. The second pattern involves the division of the thallus, followed by the production of one or more rhizoids. The significance of the different germination patterns in D. longifolia is unknown however, both patterns occurred at both 20° and 25°C.

A number of peculiarities were observed in the development of the sporelings of D. longifolia. The "jigsaw puzzle" terminal rhizoid form, has been reported for the developing tetraspore rhizoids in Dictyota dichotoma (Nishibayashi & Inoh, 1959; Gaillard *et al.*, 1986; Fig. 70, A & B). These structures consisted of lobed proliferations of the terminal cell of the rhizoid, lacking any cross-walls (Pl. 34, B-F & H & I; Fig. 70, C). Ohmori and Hashida (1983) report similar

ramifications of the rhizoid tip in tetraspores of D. divaricata kept in culture in artificial seawater containing 0.06g/l calcium chloride. This indicates that the strange terminal rhizoids observed in this study may have developed due to nutrient depletion. The rhizoid ramifications reported for D. dichotoma and those in this study were observed to be able to adhere to the substratum (Gaillard et al., 1986). Normal rhizoids undergo division of the cells at the base, ie at the meristoderm. The terminal cells do not appear to divide but continue to elongate, however, the "jigsaw" proliferations undergo growth and ramification at the rhizoid tips. Other than these peculiarities, the morphogenesis was similar to that described by Nishibayashi and Inoh (1959) and Inoh (1936), with the primary rhizoid emerging and developing (prior to the development of the thallus) from a protrusion of the original spore. It has also been reported that the zygotes of Sargassum muticum only stick to the substratum once the first rhizoid has grown and seems to be dependant on a polysaccharide which is produced by the rhizoid (Norton, 1983). Other brown algae, however, have a sticky coat around the spore or zygote. Preference is given for rough substrata where the zygote can anchor, and is protected (Norton, 1983).

It is possible that D. longifolia tetraspores that attached to the bottom of glass dishes did so with some form of adhesion compound on the rhizoids. Taking similarities of spore production, germination and juvenile gametophyte development into consideration, there seems to be a degree of consistency in the Order Dictyotales.

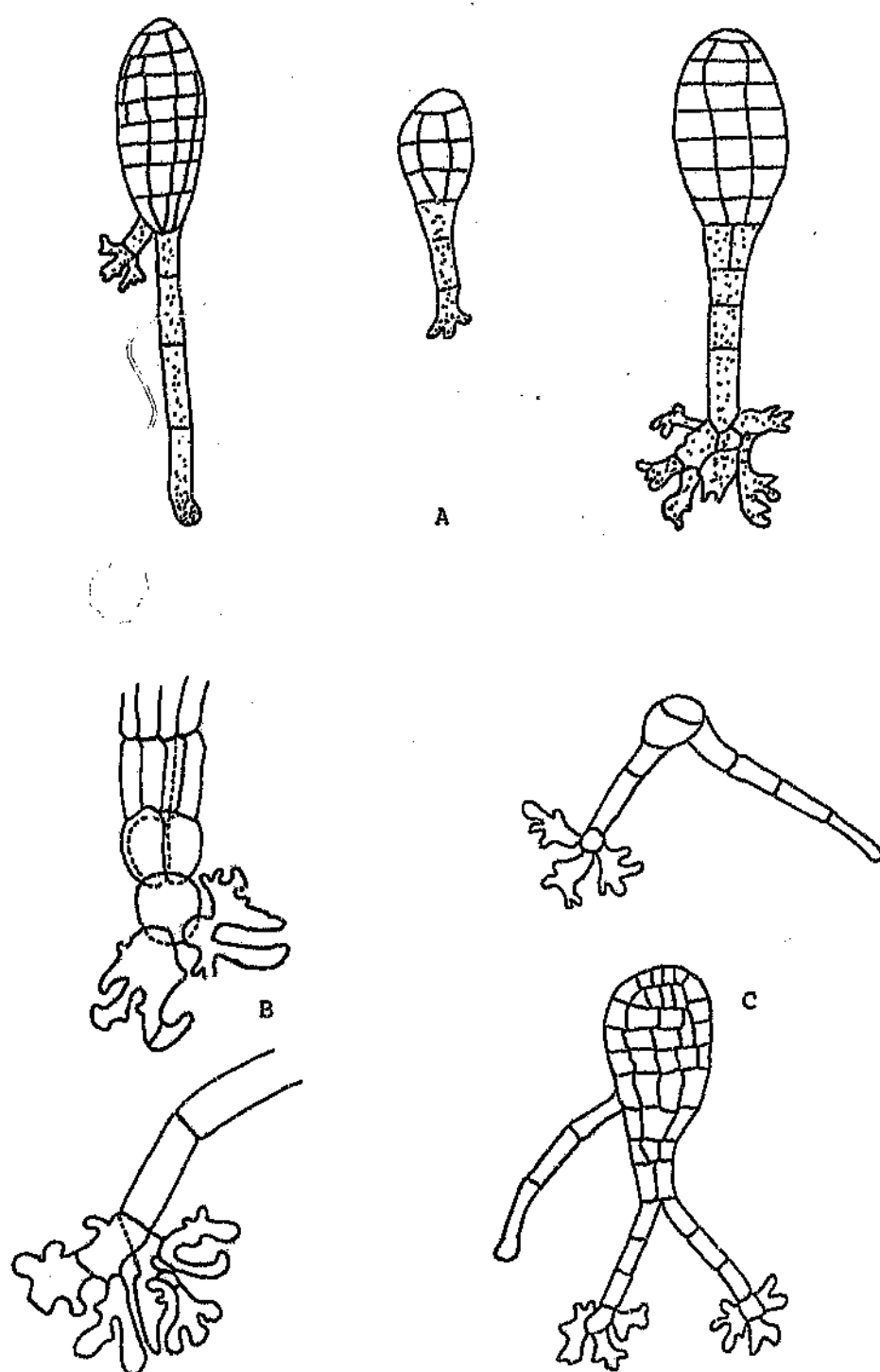


Figure 70: Diagram showing the "jigsaw puzzle" terminal rhizoid proliferations as reported in Dictyota dichotoma (redrawn from Nishibayashi & Inoh., 1959. (A); Gaillard et al., 1986 (B)) and observed in D. longifolia (this study (C)).

4.12.3 Growth Rates of Sporelings at Different Temperatures

D. longifolia, as with most members of the Dictyotales, is found in tropical to temperate waters, where seawater temperatures are in the range of 15-25°C (Dawes, 1981). Temperatures lower or higher than these are rarely experienced. As it has been reported that the production of asexual spores is controlled by environmental conditions such as temperature (Dring, 1982), it can be expected that the optimal temperature range for spore production, germination and growth, would occur in this range. It has been reported that Dictyota dichotoma overwinters by having spores which do not germinate unless the temperature and photoperiod are optimal. Seasonality of spore production in D. longifolia is suspected, as spores were only produced on sections of lamina placed into culture in June. However, spores were recorded as being present from March to October in specimens from other regions (Chihara, 1963; Herbarium specimens). The growth study performed on the spores of D. longifolia showed that maximum growth of both the rhizoid and the thallus, occurred at 20°C and 25°C (thallus elongation was much slower than that of the rhizoids; Figs 65 & 66). Initially there was slight growth at temperatures lower than 20°C, but this ceased after the first three days. At temperatures greater than 25°C, there was an initial increase and then subsequent decrease in length due to necrosis (Figs 65 & 66).

Large numbers of tetraspores were produced by a single lamina and, although many do not germinate, prolific production may explain the clumped appearance of patches of D. longifolia in the field. Tetraspores may get caught in the mats of rhizoids and laminae of adult plants, and germinate without dispersal. This would result in a mixing of generations with gametophytes being attached to

the sporophyte plant. Alternatively, unreleased or unseparated spores may increase clump size. Another possible explanation for clumping has been observed in D. membranacea (Gaillard, 1977), in which it was reported that any cell of the germinating spore, including those of the rhizoids, were capable of vegetatively producing plantules and that this may account for the very localised distribution of the plants. D. longifolia was not observed to produce more than one plantule from each tetraspore and the new thalli were only observed to be produced from the spore, not from the sporeling rhizoid. However, isolated rhizoids from the holdfast of D. longifolia are capable of producing plantules vegetatively (this study; Section 4.10.6; Pl. 27, A-L), as has been reported for D. divaricata (Tokida *et al.*, 1953). This may be another contributing factor to the clumping of individuals in natural stands.

4.13 MORPHOMETRIC AND STRUCTURAL SUMMARY

Polygonal graphs were compiled to display a summarised comparison of the various morphometric and structural aspects of D. longifolia, from different wave exposure sites, measured in this study. Mean values from the whole study period were used to compile the graphs (except for 4.13.3).

4.13.1 Morphometric Summary

The polygonal graph (Fig. 71) comparing the various morphometric results obtained for the sites, indicates that the ranking of the sites with respect to wave action was correct. It is obvious from the graph that high wave exposure greatly affected most of the morphological aspects measured. It is interesting to note that the highest wave exposure site (H+) showed considerably

higher values for most of the features measured. The distinction between the low wave activity sites and the intermediate wave exposure site (I) is not always clear, however it does appear that the ranking of L2 and L+ should have been reversed, as many of the L2 measurements are greater than those of the L+ site. It appears that extremely high wave exposure has the greatest effect on the morphological aspects measured, with intermediate and low wave exposure not affecting the results to such a degree. The morphological aspects of D. longifolia could be used to give a reasonably accurate indication of the wave exposure of the shore however, it must be remembered that many of these characters vary considerably with season.

4.13.2 Structural Summary

The polygonal graph (Fig. 72) is compiled from various structural aspects of D. longifolia from the different wave exposure sites. It appears that the structural aspects of the thallus are far less related to the degree of wave exposure experienced, than the morphological features. It would seem that only the extremely low wave exposure site (L1) displayed a consistent position in the ranking. This site consistently showed the lowest values for those aspects displayed on the graph. There is no apparent pattern in the other sites. It appears that the structural aspects measured in this study are not useful as biological exposure indicators. It must be remembered that in many of the structural aspects that were measured, the methods used had fundamental limitations. The structural aspects were also influenced by season.

4.13.3 Seasonal Variation

As an indication of the seasonal variation in morphology and structure in D. longifolia, a polygonal graph (Fig.

73) was compiled to show the measurements for the two extreme study sites (L1 and H+) at the beginning and end of the study period (ie March is the end of the growing season, and October in the beginning). It is clear from this graph that at both extremes of the season, the high wave exposure site has higher values for the aspects included in the graph, than the low wave exposure site (L1). For the H+ site, there does not seem to be a trend in variation of the measurements. However, the marked difference in lamina length is clear. It is surprising that the other lamina features do not show a similar difference. In the case of the low wave exposure site, it is clear that the variation does not follow the pattern of the H+ site, but that the March readings are greater (in nearly all the cases) than the October measurements. The most important point that can be drawn from this graph is that, although there is considerable variation in most of the morphological and structural aspects examined in this study, the trend in seasonal variation is not consistent in sites experiencing different wave exposure.

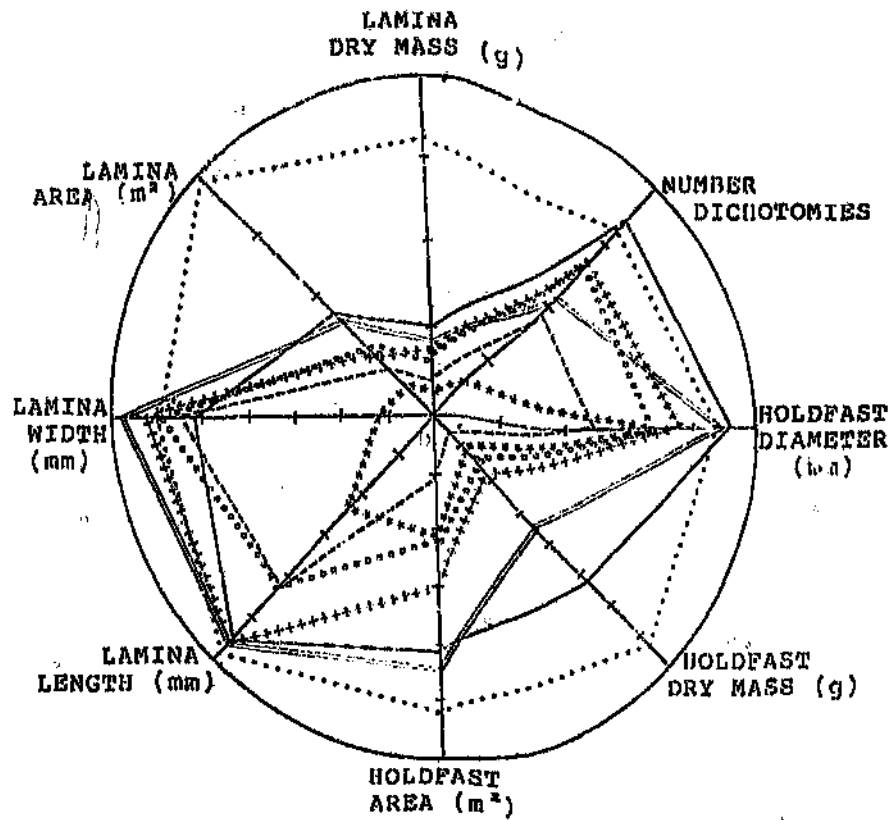
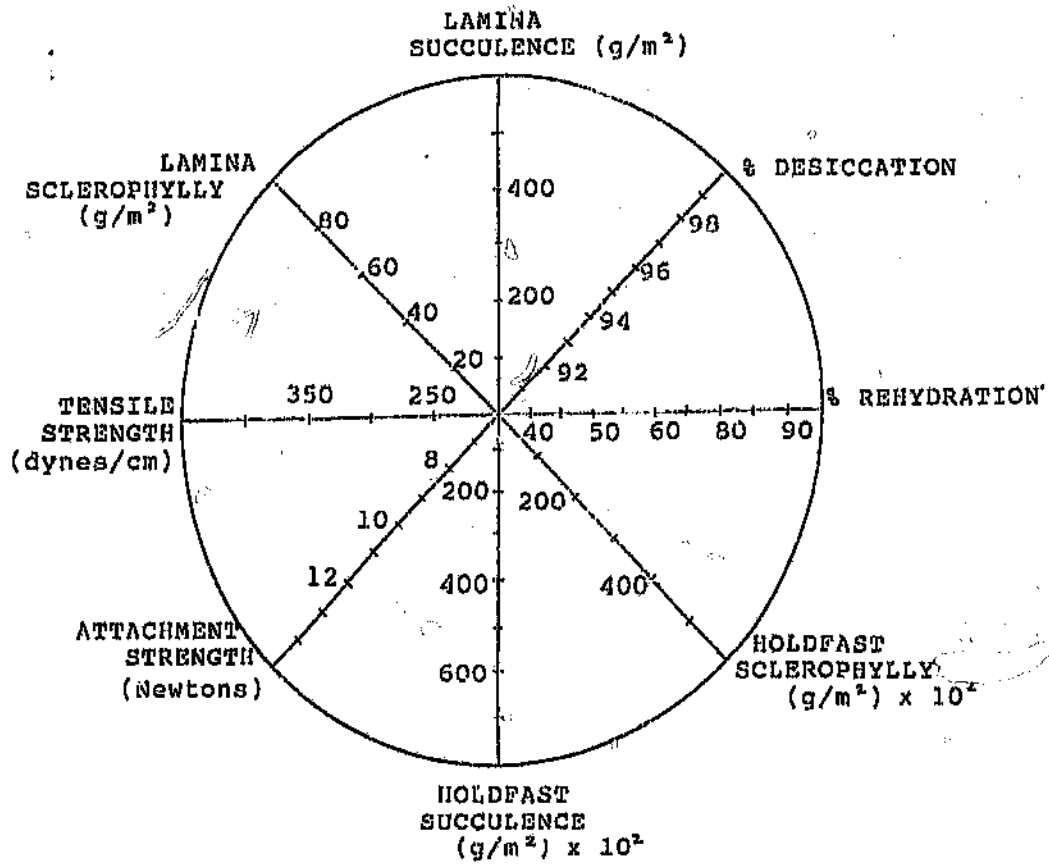


Figure 71: Polygonal graph to represent an inter-site comparison of some of the morphological features of *D. longifolia* measured in this study.

SCALE



KEY

L1	*****
L2	oooooooooooo
L+	-----
I	+++++
I+	=====
H	=====
H+	

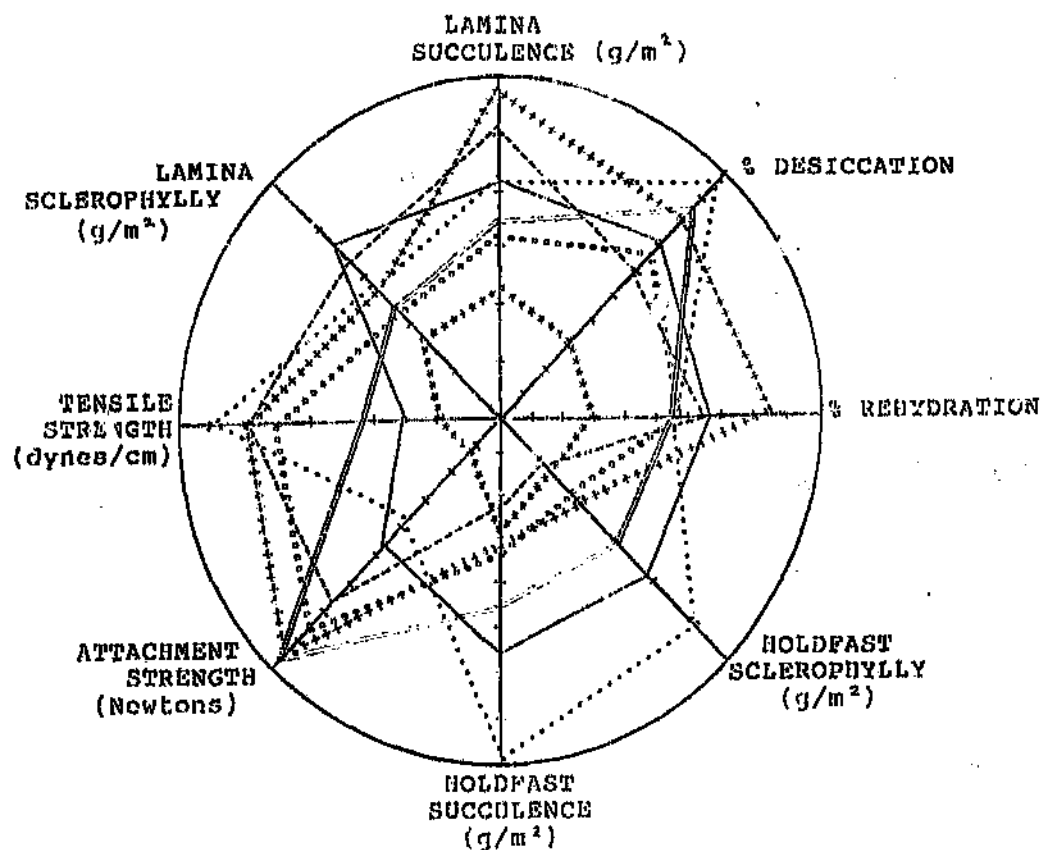
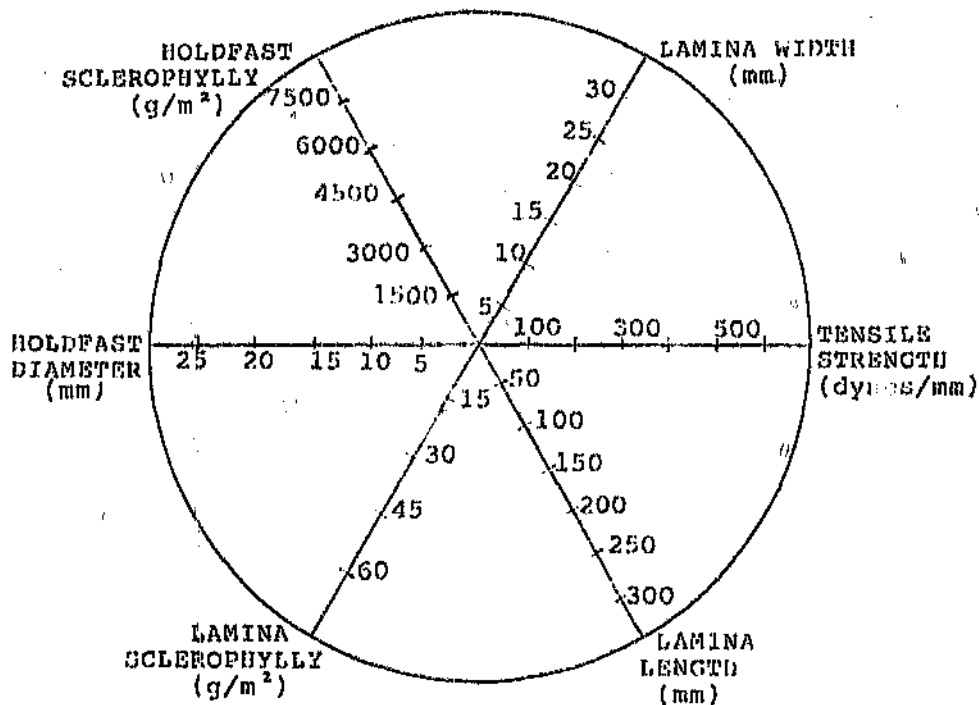


Figure 72: Polygonal graph to represent an inter-site comparison of some of the structural features of *D. longifolia* measured in this study.

SCALE



KEY

LOW WAVE EXPOSURE SITE (L1):

March:

October:*****

HIGH WAVE EXPOSURE SITE (H+):

March:

October:.....

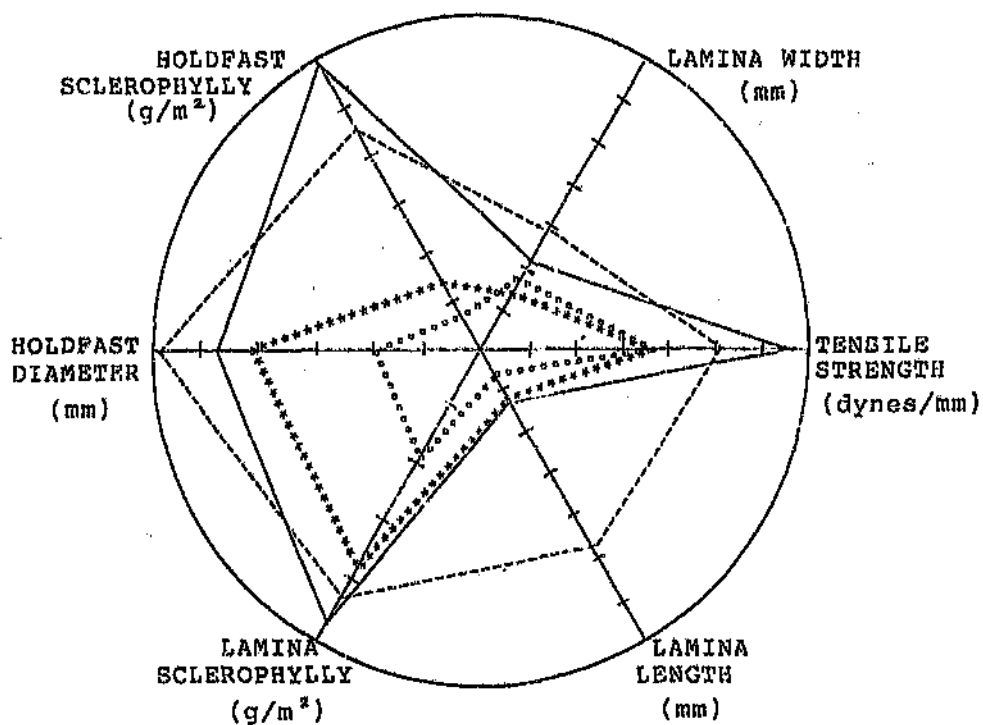


Figure 73: Polygonal graph to represent seasonal variation in some of the morphological and structural features measured in *D. longifolia*.

5 CONCLUSIONS

The aim of this study was to investigate the brown alga Dictyopteris longifolia (Phaeophyta, Phaeophyceae, Dictyotales), with special reference to the effect that exposure to waves has on the morphology, structure and reproduction of the plant.

The species occurs in a variety of intertidal conditions on the east coast of the southern African subcontinent, although the northern and southern limits of distribution on this coast were not determined (Section 4.2). The strap-shaped, dichotomously branched brown alga is commonly referred to as D. longifolia and, although its formal description is outstanding, is believed to be the new species which the late Professor G. F. Papenfuss intended to publish (Section 4.1.2).

Various methods of measuring wave exposure were assessed (Section 4.3). The results of the methods used in this study, in those sites experiencing wave exposure at low tide (ie wave number, strength and the dissolution of Lifesaver sweets), correlated well with the subjective ranking of the sites (ie the H+ site measurements indicated the highest wave exposure, followed by H and I+; Sections 3.3.1 and 3.3.2). However, it was concluded that a technique involving equipment which could remain at the site throughout the tidal cycle, and thus measure wave exposure in those sites which lack wave exposure at low tide, would be optimal, eg the dissolution method using plaster of paris blocks (Section 4.3).

Sand abrasion (Section 4.4) and deposition (Section 4.5) were observed to vary considerably and are believed to be important factors in determining the morphological condition of D. longifolia. Sand and particulate matter suspended in the water column is available to cause

abrasion and influence the light conditions of the microenvironment, eg reduction in light penetration. Although it was originally presumed that the sand content of the water would be found to be related to the degree of wave exposure, it appears that it is rather a function of the topography of the shore surrounding the study site. For example, the high wave exposure site (H) had the lowest amount of suspended sand which could be explained by the large rock to the seaward side of the site and on which the waves broke (Fig. 3, B). The water washed over a large area of rock, thus depositing the sand, prior to reaching the study site. Sand deposition was observed to be considerable in some study sites, and the morphological measurements recorded in the intermediate wave exposure site (I) were attributed to the protection against drift, herbivory and abrasion provided by continual sand cover. For example, the laminae in the sand inundated, intermediate site (I) were observed to be longer and healthier than those of plants in the other sites, at certain times of the year (Section 3.6). Unfortunately, the sand trap method used to measure this physical feature was inadequate (Section 3.5), and attention needs to be paid to developing an easier and more accurate measurement of sand deposition.

Variation in the size and form of the holdfast (Section 4.7.1) and lamina (Section 4.7.2) of D. longifolia were determined, and the results for the sites compared. These measurements included holdfast diameter, area and wet and dry mass, as well as lamina length, width, area, wet and dry mass, dichotomy number and the number of small and large laminae. There was considerable seasonal variation in morphological attributes over the study period, as well as variation between sites. The trends in morphological variation appear to be related to the degree of wave exposure experienced, with larger plants occurring in areas of higher wave exposure (Section

4.13). The holdfast measurements indicate that the low wave exposure sites had the least prominent holdfast (lowest diameter, area and mass), and the higher wave exposure sites had the larger, more robust holdfasts indicating greater effort in the production of an attachment organ (Section 3.7.1). The intermediate wave exposure sites displayed intermediate measurements for the holdfast. The measurements of the mean maximum lamina length (Section 3.6) indicated that there were seasonal fluctuations in lamina length of D. longifolia, with the longest laminae being produced in summer (Fig. 17). Following the summer months (from March), the laminae were observed to degrade until regrowth and regeneration was initiated in spring, ie September (these patterns were altered in the intermediate wave exposure sites (I) which was frequently inundated by sand; Pl. 6, J-L). Most of the other lamina measurements indicated a similar trend to that observed for the holdfast, with the laminae from the lower wave exposure sites being smaller, narrower and less robust than those in the more wave exposure sites. These trends were observed for lamina width (L1 8.21mm and H+ 12.53mm), lamina area (L1 0.002345m² and H+ 0.007301m²) and mass (wet, L1 0.583g and H+ 9.133g; dry, L1 0.0864g and H+ 1.639g). The low wave exposure site (L1) also had a significantly lower ($P < 0.001$) mean dichotomy number per lamina (0.267) than the other sites, with the high wave exposure sites (H and H+) having the highest number of dichotomies (1.738 and 1.672, respectively). The dichotomy number does, however, seem to be related to the lamina length and may thus vary seasonally (Figs. 30 & 33). There does not seem to be any trend in lamina number with respect to wave exposure. It would appear that in D. longifolia, increased wave exposure results in increased growth, probably due to the increased nutrient and gas availability. However, before the morphological features of D. longifolia measured in this study could be used to suggest a biological exposure

index, the patterns of seasonal variation would have to be determined and taken into account.

Structural attributes of the experimental organism were also measured, and an inter-site comparison performed. These measurements included sclerophylly and succulence of the lamina and holdfast, tensile and attachment strength, desiccation and rehydration potential. There appears to be a great deal of variation in these attributes, both seasonally and between sites. The tensile strength of the laminae showed no marked trend with respect to wave exposure, other than the low wave exposure site (L1, 349.95 dynes/mm) having a significantly lower ($P < 0.001$), and the highest wave exposure site (H+, 524.87 dynes/mm) having the highest tensile strength (Section 3.8.1). Attachment strength lacked any trend with respect to wave exposure, with the intermediate wave exposure sites (L2, L+, I and I+) having significantly ($P < 0.001$) higher attachment strength than the extreme wave exposure sites (L1, H and H+; Section 3.8.2). There was also little pattern in the lamina sclerophylly and succulence measurements, other than the low wave exposure site (L1) having significantly lower ($P < 0.001$) values than the other sites (Section 3.8.3). Holdfast sclerophylly and succulence, however, did display an increase in relation to increased in wave exposure. Desiccation and rehydration rates also do not appear to be related to wave exposure (Section 3.8.4). A number of the methods used to determine structural aspects, displayed fundamental problems and these need to be addressed before a conclusion can be drawn on the effect of wave exposure on the structural attributes of D. longifolia.

The microscopic investigation of the anatomical composition of D. longifolia indicated that, although there was some cell differentiation, the cell

organisation of this species is not as complex as that reported for some other brown algae. The presence of elongated midrib cells with pores in the walls, suggests that some form of longitudinal transport or translocation occurs. The characteristic apical pit contains the longitudinal dividing meristematic cells and is lined by two different layers of material (Section 3.9.1). The wing is composed of a number of layers of large, thin-walled, irregular cells (number depends on the age of the lamina), and is covered on both sides by a layer of smaller, rectangular epidermal cells. The margins of the lamina are thickened and are composed of smaller cells than the wings (Section 3.9.2). The midrib is centrally placed and prominent. It develops from the apical cells and is thicker in more mature regions. The cells of the midrib are regular, brick-shaped and thick walled (Section 3.9.3). The midrib develops a meristoderm and gives rise to the multicellular, branched rhizoids in the basal regions. The rhizoids become long and entangled and form the holdfast mat. Tufts of colourless hairs grow from pits on the lamina surface and are thought to be involved in nutrient uptake (Section 3.9.7)

D. longifolia, in the field, was frequently observed to display significant amounts of regeneration following damage. It is believed that a high regenerative potential is an important survival strategy for D. longifolia, particularly in high wave exposure areas. Regeneration occurred readily in culture from various sections of the lamina, holdfast and rhizoids (Section 3.10). The process of regeneration was similar to that described for other brown algae (Section 4.10.3), in that a single cell (from the lamina surface or from the rhizoid) became swollen and dense, divided and differentiated into a lamina with an apical pit, rhizoids and a midrib.

Although sexual reproduction was not observed to occur prolifically in the field, some material bearing sexual structures was collected. From the studies performed on this material, it appears that sexual reproduction and the related structures produced in this species are similar to those reported for other Dictyotalean species (Fig. 60). Sexual reproduction is believed to have a lower success rate in areas of high wave exposure, where tetrasporogenesis and vegetative propagation play an important role.

The production of tetraspores was observed to occur prolifically on material from all the sites studied. A study of the processes involved indicated that tetraspore production, germination and morphogenesis in D. longifolia is similar to that in other Dictyotalean species (Fig. 69), with only minor differences such as the presence of a single stalk cell and a cuticle in D. longifolia. Once the raised tetraspore mother cell had divided into four tetrahedrally arranged spores, the spores were released and germination was initiated. The latter process usually began with the division and elongation of a primary rhizoid, followed by the development of another rhizoid or the thallus. An investigation of the effects of temperature range on germination of spores, indicated that the optimal temperature for germination was 20-25°C.

The intertidal environment at Palm Beach exerts a number of stresses and forces on the inhabitants of the zone. The brown alga, D. longifolia responds to these stresses in a number of different ways which may include variation of morphological, structural and reproductive characters.

STUDIES ON THE BROWN ALGA DICTYOPTERIS LONGIFOLIA
(DICTYOTALES), WITH SPECIAL REFERENCE TO THE
EFFECTS OF WAVE ACTION

VOLUME 2

NATALIE LYNN BLACKMORE

APPENDIX 1: Provasoli's Enriched Seawater (PES
(Provasoli, 1968)

Stock Solutions (in 100ml of distilled H ₂ O)	ml stock to be added
NaNO ₃ 35g/100ml	8
Na ₂	
Glycerophosphate 5g/100ml	8
Vitamin B ₁₂ 1mg/100ml	8
Thiamine 50mg/100ml	8
Biotin 0.5mg/100ml	8
Tris Buffer	200
Trace Elements	200

made up to

1000ml

Tris Buffer:

Fe (as EDTA 1:1 molar): $\text{Fe}(\text{NH}_4)_2(\text{SO}_4) \cdot 6\text{H}_2\text{O}$

351.mg/500ml

Na₂EDTA

300mg/500ml

Trace Element Solution: (in 100ml distilled water)

H ₃ BO ₃	1.14g
FeCl ₃	29.4mg
MnSO ₄ ·7H ₂ O	203.7mg
ZnSO ₄ ·7H ₂ O	22.0mg
CoSO ₄ ·7H ₂ O	4.8mg
Na ₂ EDTA	1.0g

APPENDIX 2: Germanium Dioxide

GeO ₂	100mg
KOH	4-6 pellets
Distilled water	3ml.

Boiled in a zirconium or polypropylene vessel until GeO₂ is in solution (approx. 15 mins).

Add 10-12 KOH pellets if necessary.

Adjust pH to 8.0 with 2N HCl..

Add distilled water to make 25ml of stock (4mg GeO₂/ml).

Dilute to 200ml and use 25ml/l.

APPENDIX 3: 0.1M Na Cacodylate Buffer

$(\text{CH}_3)_2(\text{AsO}_2\text{Na})$ 16g

Double distilled water to make 1000ml

Adjust pH to 7.2 - 7.4 by addition of drops of concentrated HCl. Store in refrigerator.

**APPENDIX 4: Spurr's Low Viscosity Epoxy Resin
(Harper, 1983)**

Ingredients	Standard	Long life
ERL 4206	10g	10g
DER 736	6g	5g
NSA	26g	26g
S ₁	0.4g	0.2g
pot life	2 days	7 days

The long life Spurr's resin (Harper, 1983) requires a longer polymerisation time than does the normal recipe (18 and 12 hours respectively). It is also more brittle and harder than the normal resin. Care must thus be taken to prevent shattering during the trimming and sectioning processes.

APPENDIX 5: Stains for Transmission Electron Microscopy.

1) Uranyl Acetate

1g uranyl acetate is made up to 50ml with distilled water. The flask is kept light tight due to the sensitivity of the stain.

2) Lead Citrate

1.33g lead nitrate $\text{Pb}(\text{NO}_3)_2$ is combined with 1.76g sodium citrate $\text{Na}_3(\text{C}_6\text{H}_5\text{O}_7) \cdot 2\text{H}_2\text{O}$ in 30ml distilled water and shaken well (lead nitrate becomes lead citrate).

8ml fresh NaOH is added and made up to 50ml with distilled water.

Turbidity may be removed by centrifugation.

3) Staining Process

A petridish is lined with dental wax and filtered drops (through a millipore filter) of uranyl acetate are placed onto it. The grids are inverted onto these drops and stained in darkness for 15 minutes.

Pellets of NaOH are enclosed in the second petridish to remove CO_2 .

Filtered drops of lead citrate are placed onto the dental wax in the second dish.

The grids are washed well in distilled water and then inverted onto the lead citrate for a further 15 minutes.

The grids are washed in 0.02N NaOH followed by distilled water before being dried.

APPENDIX 6: DATA

WATER MOVEMENT (Section 3.3)

Wave Action

a) Wave Strength

Site	L1	L2	L+	I	I+	H	H+
Mean (N/m ²)	-	-	-	-	-	355.6588	539.4911
Standard Deviation	-	-	-	-	-	209.5831	281.0404
Sample Number	-	-	-	-	-	30	57

b) Wave Number

Site	L1	L2	L+	I	I+	H	H+
Mean (number/min)	-	-	-	-	5	7.0833	16.7
Standard Deviation	-	-	-	-	0.816496	1.296363	0.989949
Sample Number	-	-	-	-	3	12	11

Water Motion

a) Lifesaver Sweet Dissolution

Site	L1	L2	L+	I	I+	H	H+
Mean (g/min)	0.1271	0.157164	0.174905	0.15139	0.189015	0.349353	0.41894
Standard Deviation	0.04309	0.033707	0.075635	0.021792	0.093197	0.02736	0.088258
Sample Number	9	9	10	9	10	10	9

b) Plaster Block Dissolution

Site	L1	L2	L+	I	I+	H	H+
Mean (% loss)	58.0869	42.43929	46.14003	22.4912	46.46515	61.86759	68.94019
Standard Deviation	6.19906	3.821027	11.66194	-	14.41673	11.04235	-
Sample Number	2	5	5	1	5	4	1

SAND CONTENT OF WATER (Section 3.4)

Site	L1	L2	L+	I	I+	H	H+
Mean (g/100ml)	0.05721	0.06185	0.071564	0.088035	0.043701	0.047364	0.101126
Standard Deviation	0.02232	0.00265	0.006002	0.033193	0.003906	0.029087	0.04477
Sample Number	46	12	19	30	19	34	39

SAND DEPOSITION (Section 3.5)

Site	L1	L2	L+	I	I+	H	H+
Mean (g)	300.88	-	-	347.033	-	326.2166	354.6633
Standard Deviation	10.859	-	-	8.869548	-	49.9235	22.83962
Sample Number	3	-	-	3	-	3	6

MAXIMUM LAMINA LENGTH OF THE POPULATION (Section 3.6)

March							
Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	64.225	-	-	-	-	204.656	354.98
Standard Deviation	33.19	-	-	-	-	110.09	188.827
Sample Number	42	-	-	-	-	32	50

April							
Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	44.4125	-	-	151.333	-	157.2985	229.744
Standard Deviation	20.2	-	-	67.33	-	76.32	101.79
Sample Number	30	-	-	27	-	28	47

May							
Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	16.6	-	-	177.3665	-	109.941	104.508
Standard Deviation	9.156	-	-	81.45	-	74.66	41.7
Sample Number	15	-	-	37	-	34	61

July							
Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	44.29	-	49.4	195.4	94.167	74.261	61.098
Standard Deviation	21.8	-	16.84	104.92	42.04	31.29	28.81
Sample Number	31	-	25	15	30	23	51

September							
Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	50.381	98.6	113.2	204	135.677	69.235	51.117
Standard Deviation	34.18	43.18	49.78	47.39	72.37	31.15	18.7
Sample Number	20	31	25	6	31	42	60

October							
Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	54.375	96.814	130.524	159.611	150.485	69.826	57.375
Standard Deviation	24.83	56.29	51.91	59.55	72.48	37.02	22.69
Sample Number	24	43	21	18	30	23	48

MORPHOMETRY (Section 3.7)

Features of the Holdfast

a) Holdfast Diameter

Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	15.8	15.7	12.95	18.75	22.2333	23.2333	21.85
Standard Deviation	4.41814	2.8	2.75	0.75	0.997775	5.292972	7.774799
Sample Number	25	31	27	26	36	42	56

b) Holdfast Area

Site	L1	L2	L+	I	I+	H	H+
Mean (m ²)	0.00022	0.000223	0.00013	0.000302	0.000442	0.000418	0.000516
Standard Deviation	9E-05	3.78E-05	4.78E-05	4.51E-05	6.98E-05	8.41E-05	0.000361
Sample Number	25	30	28	24	36	41	53

c) Holdfast Wet Mass

Site	L1	L2	L+	I	I+	H	H+
Mean (g)	0.84778	0.865722	0.372439	1.192106	2.726527	3.842743	5.54725
Standard Deviation	0.47221	0.292041	0.206139	0.048794	0.705107	1.675963	6.296589
Sample Number	25	31	27	26	36	42	56

d) Holdfast Dry Mass

Site	L1	L2	L+	I	I+	H	H+
Mean (g)	0.44666	0.472798	0.208987	0.793103	1.737797	2.552811	3.675489
Standard Deviation	0.29853	0.160634	0.120527	0.110136	0.522115	0.977474	4.274647
Sample Number	25	30	28	24	36	41	53

Features of the Lamina

a) Lamina Length

Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	46.191	86.82772	83.7531	112.6815	113.9552	113.6776	118.2855
Standard Deviation	9.49151	21.68067	6.10605	0.5565	15.44263	58.57134	79.21833
Sample Number	79	93	87	87	112	131	158

b) Lamina Width

Site	L1	L2	L+	I	I+	H	H+
Mean (mm)	8.21	12.75	12.5	13.15	13.7	12.0333	12.525
Standard Deviation	1.24956	1.05	0.7	0.05	2.182984	0.805836	1.640693
Sample Number	79	93	87	87	112	131	158

c) Lamina Area

Site	L1	L2	L+	I	I+	H	H+
Mean (m ²)	0.00234	0.005629	0.003653	0.005023	0.007341	0.007301	0.020989
Standard Deviation	0.00106	0.001548	0.000698	0.000332	0.001949	0.004786	0.028894
Sample Number	25	30	28	24	36	41	53

d) Lamina Wet Mass

Site	L1	L2	L+	I	I+	H	H+
Mean (g)	0.58304	1.890099	1.456708	2.032364	2.590434	2.947458	9.132947
Standard Deviation	0.28589	0.850854	0.182288	0.544798	0.850668	1.785521	12.01749
Sample Number	25	30	28	24	36	41	53

e) Lamina Dry Mass

Site	L1	L2	L+	I	I+	H	H+
Mean (g)	0.08642	0.277172	0.191383	0.29101	0.355442	0.508193	1.63888
Standard Deviation	0.04003	0.154391	0.033063	0.083043	0.116539	0.336811	2.401742
Sample Number	25	30	28	24	36	41	53

f) Dichotomy Number - Total

Site	L1	L2	L+	I	I+	H	H+
Mean (number)	0.26667	1.291731	0.955669	1.328869	1.093974	1.737968	1.671764
Standard Deviation	0.12086	0.352337	0.073316	0.233631	0.49556	1.218784	1.236606
Sample Number	79	93	87	87	112	131	158

g) Dichotomy Number - March

Site	L1	L2	L+	I	I+	H	H+
Mean (number)	0.17647	-	-	-	-	3.461538	3.652174
Standard Deviation	0.51281	-	-	-	-	2.134529	1.154701
Sample Number	17	-	-	-	-	13	23

h) Dichotomy Number - October

Site	L1	L2	L+	I	I+	H	H+
Mean (number)	0.18605	1.644068	1.028986	1.5625	1.6	0.8875	0.534884
Standard Deviation	0.38914	0.987425	1.141713	1.116286	1.134087	0.806129	0.67682
Sample Number	25	30	28	24	36	41	53

i) Percentage Laminae without Dichotomies

Site	L1	L2	L+	I	I+	H	H+
Mean (%)	57.9727	19.1675	37.0915	18.22917	33.76263	16.20277	29.8666
Standard Deviation	30.6068	7.303091	1.797386	15.10417	19.81475	10.72631	21.25085
Sample Number	79	93	87	87	112	131	158

j) Lamina Number Less than 5mm

Site	L1	L2	L+	I	I+	H	H+
Mean (number)	6.4	3.88	5.005	6.28	7.04	5.04	5.4
Standard Deviation	2.86124	0.07	0.805	1.12	2.282513	2.202543	1.785525
Sample Number	25	31	27	26	36	42	56

k) Lamina Number Greater than 5mm

Site	L1	L2	L+	I	I+	H	H+
Mean (number)	16.8433	18.55	12.4	16.6	23.2333	14.8333	12.6825
Standard Deviation	9.23636	4.75	2.8	3.4	4.970133	5.067763	8.59746
Sample Number	25	31	27	26	36	42	56

STRUCTURAL PROPERTIES (Section 3.8)

Tensile Strength

a) Tensile Strength - Total

Site	L1	L2	L+	I	I+	H	H+
Mean (Dynes/mm)	349.946	477.8319	500.6245	497.8499	413.8855	372.2087	524.87
Standard Deviation	14.2167	92.45665	13.86175	44.22145	27.616	147.3367	86.13128
Sample Number	23	45	39	64	39	39	48

b) Tensile Strength - March

Site	L1	L2	L+	I	I+	H	H+
Mean (Dynes/mm)	334.802	-	-	-	-	317.0155	509.7818
Standard Deviation	99.3282	-	-	-	-	188.1459	234.4934
Sample Number	13	-	-	-	-	12	23

c) Tensile Strength - October

Site	L1	L2	L+	I	I+	H	H+
Mean (Dynes/mm)	346.065	570.2886	486.7628	453.6285	379.2213	573.8095	669.6879
Standard Deviation	72.7695	242.5241	179.7679	216.5215	172.8227	163.0213	234.2619
Sample Number	6	27	31	48	25	21	18

Attachment Strength

a) Attachment Strength - Total

Site	L1	L2	L+	I	I+	H	H+
Mean (Newtons)	7.07233	13.5886	12.8736	14.504	14.609	10.6315	9.8245
Standard Deviation	2.07433	2.14041	2.31637	7.9787	1.281	1.94515	4.1405
Sample Number	18	31	27	20	26	32	30

b) Attachment Strength - September

Site	L1	L2	L+	I	I+	H	H+
Mean (Newtons)	9.14667	11.44818	15.19	-	13.328	8.686363	5.684
Standard Deviation	5.09747	5.692414	3.205663	-	6.576961	6.534379	3.655019
Sample Number	3	11	5	-	5	11	10

c) Attachment Strength - October

Site	L1	L2	L+	I	I+	H	H+
Mean (Newtons)	4.998	15.729	10.55727	14.504	15.89	12.57666	13.965
Standard Deviation	2.83015	3.76663	3.548011	7.978728	4.725561	3.247946	4.856935
Sample Number	15	20	22	20	21	21	20

Sclerophylly

a) Lamina Sclerophylly

Site	L1	L2	L+	I	I+	H	H+
Mean (g/m ²)	33.8053	43.7206	67.99868	55.83715	46.13817	74.71776	58.88457
Standard Deviation	4.34528	4.345276	5.405022	11.10497	9.637083	10.99628	11.28964
Sample Number	25	30	28	24	36	41	53

b) Holdfast Sclerophylly

Site	L1	L2	L+	I	I+	H	H+
Mean (g/m ²)	1344.996	1858.918	1230.215	2004.78	3046.873	3919.782	5085.762
Standard Deviation	432.353	432.3528	377.4704	334.2028	846.8412	349.7225	3291.856
Sample Number	25	30	28	24	36	41	53

Succulence

a) Lamina Succulence

Site	L1	L2	L+	I	I+	H	H+
Mean (g/m ²)	231.815	316.9802	520.8263	570.6883	343.8575	423.1356	422.2757
Standard Deviation	15.2648	15.26479	77.56139	100.6699	77.17438	37.31845	98.83651
Sample Number	25	30	28	24	36	41	53

b) Holdfast Succulence

Site	L1	L2	L+	I	I+	H	H+
Mean (g/m ²)	2779.84	3488.626	2253.644	3109.021	4459.07	5674.927	7974.564
Standard Deviation	583.296	583.2964	538.5042	20.38445	456.949	456.9225	4693.254
Sample Number	25	30	28	24	36	41	53

Desiccation

Site	L1	L2	L+	I	I+	H	H+
Mean % Loss (5min)	21.3841	14.04071	14.16361	14.06371	13.78221	21.2222	10.21064
Standard Deviation	5.26877	4.443468	1.49716	1.306517	1.078672	9.068059	1.734726
Mean % Loss (10min)	33.5666	24.3958	26.27913	25.51171	25.53714	22.16533	18.31567
Standard Deviation	5.78355	4.497049	3.34131	3.190519	2.538081	8.255148	2.73338
Mean % Loss (15min)	44.966	32.98289	36.11622	36.64488	43.4347	33.0438	25.40393
Standard Deviation	6.12882	5.762787	4.246878	3.184821	10.13299	11.39766	3.395197
Mean % Loss (20min)	60.2775	39.90027	46.55379	46.10778	43.81231	41.80799	31.31841
Standard Deviation	13.0985	7.793518	5.074529	3.722173	1.175973	12.40804	3.284506
Mean % Loss (25min)	61.6908	46.25862	55.87551	55.21915	52.78348	49.88765	37.0561
Standard Deviation	5.91384	9.020596	5.303974	4.157577	0.176643	13.15846	4.036225
Mean % Loss (30min)	63.9385	51.24194	63.06372	63.78594	60.29129	56.77273	42.04281
Standard Deviation	8.81068	8.841032	5.626295	6.269968	0.790868	13.50816	4.947685
Mean % Loss (35min)	70.4922	55.79788	69.09016	69.33858	66.60831	62.78703	46.08489
Standard Deviation	6.95859	9.308824	5.711181	5.660694	1.416211	13.12811	5.225714
Mean % Loss (40min)	74.8415	57.92199	73.46397	74.41631	72.17578	67.39214	50.9924
Standard Deviation	7.67605	8.619503	22.31708	6.042888	1.685626	12.72139	5.776457
Mean % Loss (45min)	76.4262	62.55266	76.4244	77.88405	76.1477	70.70371	54.54363
Standard Deviation	7.54918	7.962895	5.821019	6.13056	1.661878	12.39865	6.329765
Mean % Loss (50min)	80.442	65.37521	79.1689	80.62364	79.97754	73.42141	57.89832
Standard Deviation	7.40165	7.327111	5.768598	6.075075	1.798755	12.04641	6.83838
Mean % Loss (55min)	82.0813	67.84495	81.09759	82.80002	82.63804	75.76074	60.75314
Standard Deviation	7.57367	6.939228	5.68763	5.853222	1.714766	11.69805	7.078975
Mean % Loss (60min)	82.5996	70.14756	82.87474	84.67503	84.617	77.7696	67.13975
Standard Deviation	7.70196	6.52581	5.6994	5.420811	1.470057	11.38078	33.02384
Mean % Loss (70min)	86.4401	75.11229	85.46694	89.97592	89.22424	81.78699	73.23496
Standard Deviation	8.16255	5.388374	5.540819	6.652901	1.650692	10.04035	3.092572
Mean % Loss (80min)	88.2903	78.08638	87.41575	90.89322	91.46992	84.02944	77.1918
Standard Deviation	8.56174	4.875568	5.696515	4.356122	1.432756	9.577991	2.873987
Mean % Loss (90min)	89.3926	80.73078	88.89811	91.23589	93.09928	85.81853	80.44878
Standard Deviation	8.66798	4.07228	5.847009	3.724035	0.958212	8.987725	2.997141
Mean % Loss (100min)	90.3659	82.8943	90.19148	92.43123	94.35858	87.36956	83.51863
Standard Deviation	8.67421	3.405574	5.87934	3.166533	0.610598	8.486068	2.99732
Mean % Loss (110min)	91.1335	85.01965	91.41419	93.50067	95.42456	88.90293	86.30201
Standard Deviation	8.93254	2.855472	5.640311	2.667398	0.425496	7.808732	2.873215
Mean % Loss (120min)	91.8784	86.84825	92.3859	94.39268	96.2853	90.29018	88.79598
Standard Deviation	9.04955	2.409462	5.414655	2.318539	0.353727	7.137796	2.879032
Mean % Loss (150min)	92.5042	90.49311	94.10689	96.1355	97.68816	92.86849	93.30899
Standard Deviation	9.16248	1.27343	4.965569	1.24023	0.366	5.657469	2.777677
Mean % Loss (180min)	92.8422	92.87559	95.0273	97.12864	98.33865	94.51618	96.44428
Standard Deviation	9.12056	0.619378	4.304238	0.503841	0.572484	4.259087	3.334088
Mean % Loss (210min)	90.4274	94.42812	95.5522	97.59972	98.55579	95.4291	98.01073
Standard Deviation	8.79334	0.337153	3.537869	0.2633	0.671014	3.343866	3.539611
Mean % Loss (240min)	93.1035	95.57624	95.85955	99.04517	98.6695	96.41058	99.30406
Standard Deviation	9.07093	0.457418	2.832663	1.556077	0.710323	2.346162	3.890386
Mean % Loss (270min)	94.7221	97.13726	95.98223	98.07906	98.72472	96.87124	99.80038
Standard Deviation	9.05656	0.514957	2.438924	0.240987	0.721843	1.93649	4.04788
Mean % Loss (300min)	93.1114	96.78528	96.01915	98.07566	98.68597	97.11771	99.94276
Standard Deviation	8.97414	0.524783	1.52391	0.27178	0.785781	1.733845	4.173131
Number Samples	3	3	3	3	3	3	3

Rehydration

Site	L1	L2	L+	I	I+	H	H+
Mean (%)	49.9244	64.5776	67.48338	77.81559	64.09452	68.57964	63.93955
Standard Deviation	8.823	4.631	1.916	4.884	4.2	2.68	1.15
Sample Number	3	3	3	3	3	3	3

REGENERATION (Section 3.10)

Apical Tip Elongation Rates

Day	0	5	11	18	27	34	41
Tip 1 Length (mm)	0	1.5	4	5	6.5	7	10.5
Tip 2 Length (mm)	0	1	3.5	5	8	9	13.5
Tip 3 Length (mm)	0	2	4	5	5.5	6.5	7.5
Tip 4 Length (mm)	0	1	3	3.5	3.5	5	8.5
Tip 5 Length (mm)	0	0.5	1.5	3	4	9	11

TETRASPOROGENESIS (Section 3.12)

Spore Thallus Elongation Rates

	2	4	6	8	13	20
10°C - length (mm)	0.00567	0.003333	0.003333	0.008	0.005667	0.004667
Standard Deviation	0.01627	0.01672	0.014907	0.02151	0.017452	0.02125
15°C - length (mm)	0.00533	0.028	0.036	0.010333	0.001333	0.015333
Standard Deviation	0.03313	0.041451	0.0511	0.030214	0.020669	0.021554
20°C - length (mm)	0.03067	0.067	0.0871	0.095	0.126667	0.149667
Standard Deviation	0.04357	0.047216	0.037094	0.059251	0.048421	0.055972
25°C - length (mm)	0.05267	0.079333	0.101667	0.103667	0.12	0.135667
Standard Deviation	0.03658	0.041931	0.031883	0.050773	0.049221	0.047727
30°C - length (mm)	0.03533	0.046667	0.054	0.053333	0.058	0.041667
Standard Deviation	0.0314	0.03134	0.028821	0.026575	0.03559	0.02345
35°C - length (mm)	0.003	0.008667	0.007	0.007	-	-
Standard Deviation	0.02108	0.023627	0.021523	0.021367	-	-
Sample Number	30	30	30	30	30	30

Spore Rhizoid Elongation Rates

Day	2	4	6	8	13	20
10°C - length (mm)	0.01267	0.016667	0.012667	0.009333	0.008	0.039333
Standard Deviation	0.05554	0.055602	0.032221	0.067168	0.051511	0.046885
15°C - length (mm)	0.04	0.077	0.07	0.085	0.109	0.154333
Standard Deviation	0.06551	0.073899	0.101902	0.100158	0.085664	0.107439
20°C - length (mm)	0.15733	0.315667	0.474	0.608667	0.662	0.801333
Standard Deviation	0.0879	0.09922	0.096629	0.148071	0.186555	0.278181
25°C - length (mm)	0.21033	0.373	0.534667	0.533	0.662667	0.641
Standard Deviation	0.07265	0.132357	0.119981	0.185935	0.185234	0.185547
30°C - length (mm)	0.09	0.123333	0.113333	0.073667	0.023333	0.085667
Standard Deviation	0.05604	0.065802	0.089572	0.059044	0.079183	0.060218
35°C - length (mm)	0.019	0.016333	0.02	0.018333	-	-
Standard Deviation	0.05892	0.069219	0.047405	0.06642	0.061454	-
Sample Number	30	30	30	30	30	30

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PLATE 1

Sites at Palm Beach, Natal where D. longifolia was observed growing under varying degrees of wave exposure.

- A D. longifolia growing in a calm pool in the upper regions of the shore.
- B A highly wave exposed site at Palm Beach where D. longifolia was observed to grow prolifically.
- C D. longifolia left exposed to the air in areas of extreme wave activity.
- D Highest wave exposure site (H+) composed of a long wave exposed bed of rock (Fig. 3, A for map).
- E Site of high wave exposure (H) where the area in which D. longifolia was observed growing was partially protected by a large rock (Fig. 3, B for map).
- F Site of high, intermediate wave exposure (I+) consisting of a raised pool heavily washed by waves from the deep waters on the far side (Fig. 3, C for map).
- G The sandy gully which experienced intermediate wave exposure (I; Fig. 3, D for map).
- H The higher, low wave exposure site (L+) consisting of a raised pool interconnected with other pools (Fig. 3, E for map).
- I-J Two lowest wave activity sites consisting of raised pools far back on the beach (L2 and L1; Fig. 3, F & G for maps).

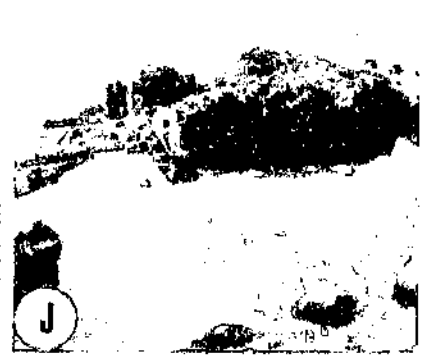
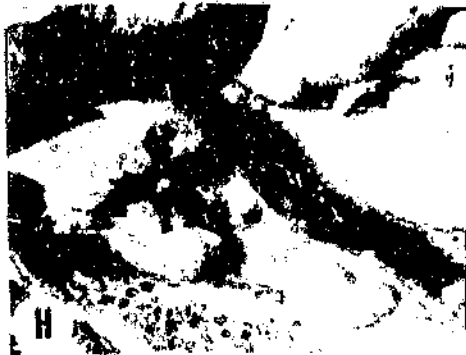
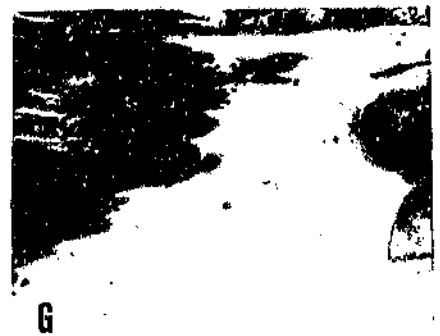
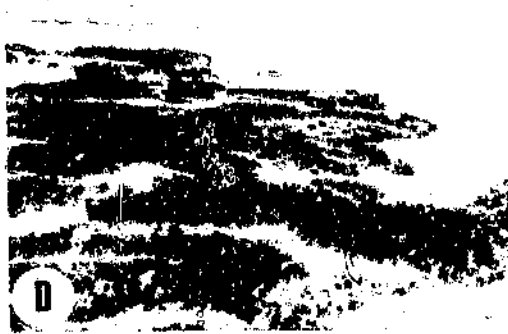
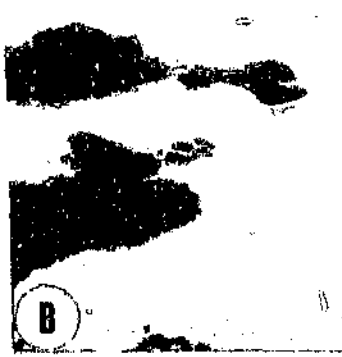
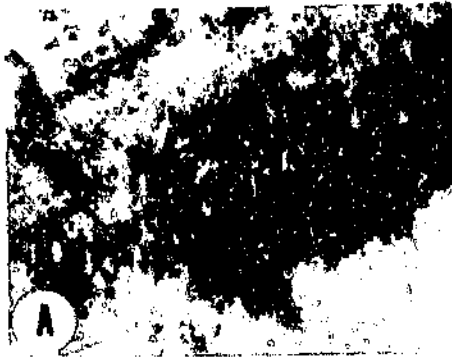


PLATE 2

Methods used to measure environmental conditions and aspects of the structure of *D. longifolia*.

- A Modified dynamometer in which the wave force was determined by measuring the extent of the stretched elastic band, using a spring balance.
- B Structure of the dynamometer showing the drogue (d), the cable tie (c), elastic band (e) and the head of the tie (h) threaded onto the tie.
- C The dissolution technique using "Lifesaver" sweets attached to a wire coat hanger to determine water motion.
- D-E The round, boiled sweets of various flavours, characterised by a central hole and known as "Lifesavers".
- F The dissolution method of measuring water using a plaster of paris block fastened to a well attached tuft of seaweed such as *Celidium*.
- G The ice-tray (t) used to ensure the consistency of the plaster of paris blocks.
- H Structure of the block (b) attached to a cable tie (c) by an embedded piece of wire (w).
- I The tensilmeter constructed according to Martens and de V. Booysen (1968).
- J-K A diagram to show the procedure of tensile strength measurement. A piece of plant was attached between the two clamps (c) of the tensilmeter. The balance (b) read the mass of the top clamp only in J, while in K the balance measured the mass of the clamp and the force exerted on the plant just prior to its breaking.

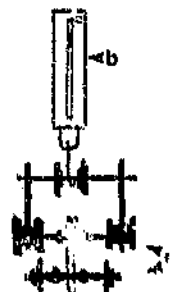
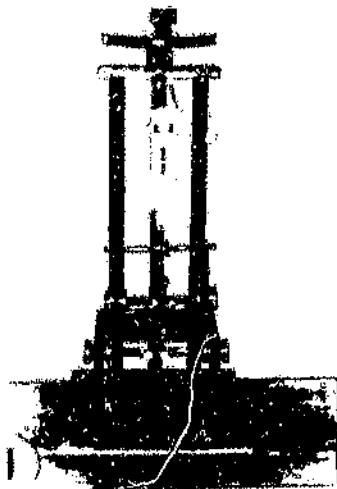
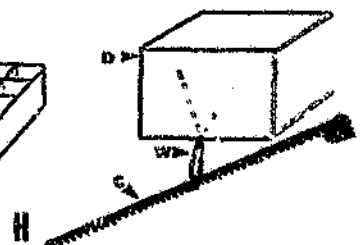
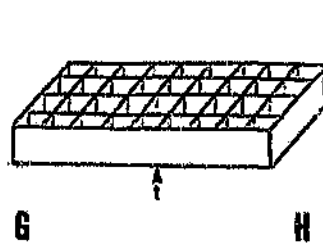
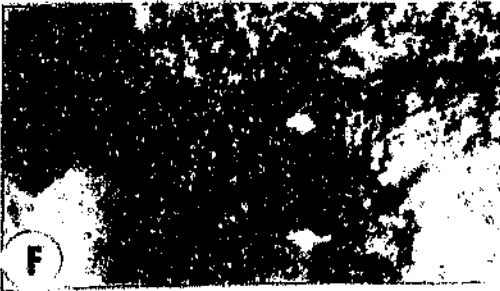
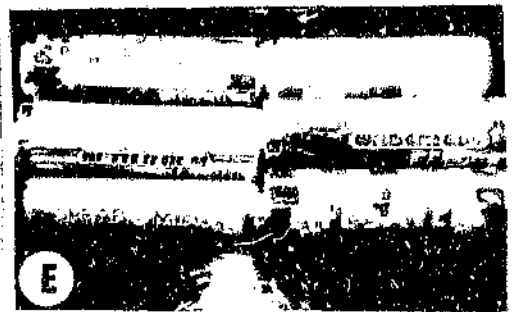
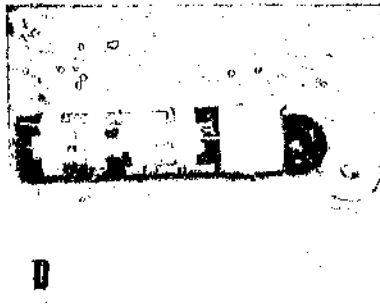
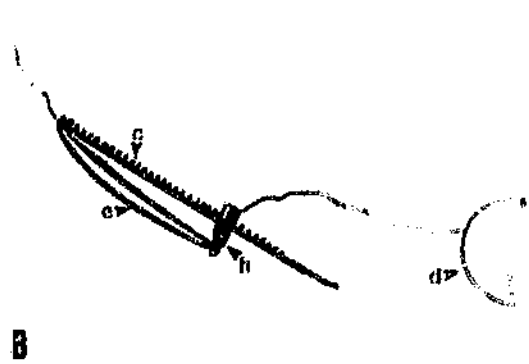
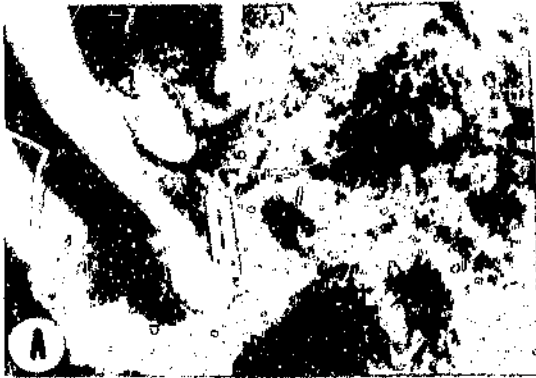


PLATE 3

Methods used to measure environmental conditions and aspects of the structure of *D. longifolia*.

- A Adaption of the plucking meter for firmly attached plants (attached by cable tie).
- B Plucking meter for normally attached plants (attached by a clamp).
- C Structure of the plucking meter showing the clamp (c), the elastic band (e) and the ruler (r) used for the measurement of force.
- D The sand trap in the field, showing the pipes filled with sand.
- E Structure of the sand trap showing the brick (b), the pipes (p) and the wire used to secure the pipes into the brick (w).
- F Structure of the pipe arrangement showing the securing wire (w), the PVC pipe (p) and the piece of cloth attached over the bottom of the pipe (c).
- G The dehydration experiment comprising individual stands and an oscillating electric fan.
- H The large plants were attached to the under side of the shelf above the arrangement.
- I The structure of the stand comprising a petridish (d) and the glass rod uprights (s).
- J The aerated, plastic 2l bottles arranged on a shelf in a walk-in growth chamber.
- K A plastic dish consisting of 6 wells and used for the culture of plant segments.
- L Whole plants were kept in tanks (t) and 250ml flasks (f).

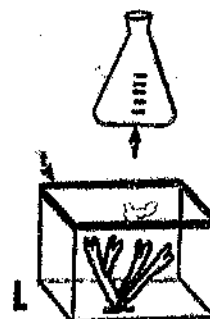
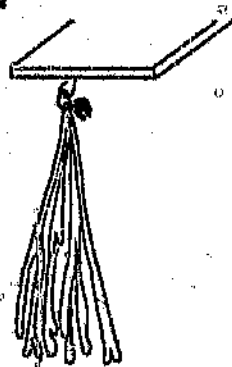
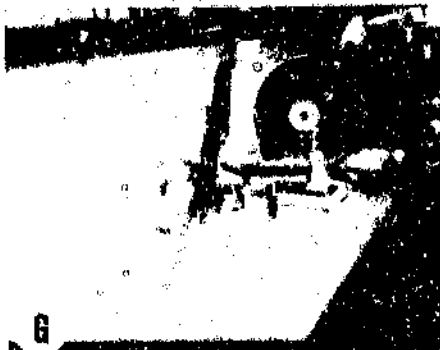
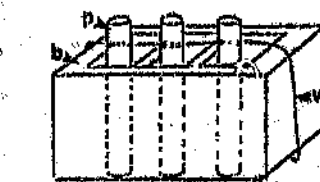
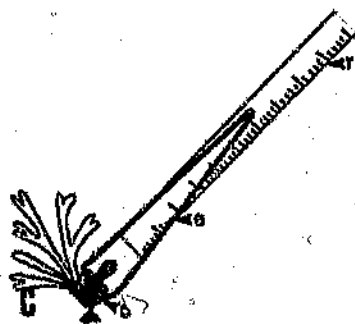


PLATE 4

General morphology of D. longifolia.

- A The entire plant is composed of a number of laminae attached to a holdfast.
- B The perennial holdfast gives rise to new laminae.
- C-D The holdfast is composed of numerous intertwined rhizoids and may give rise to many laminae.
- E-G The intertwined, multicellular rhizoids of the holdfast showing the rounded growing tip and the branched nature.
- H The rounded growing tip with a high density of granular material concentrated in the terminal end of the cell.
- I Rhizoid production at the base of the midrib where the lamina wing has been removed due to abrasion and herbivory.
- J The well developed rhizoids on the midrib at the base of the lamina.
- K SEM section through the base of the lamina showing the rhizoids produced from the midrib meristoderm.
- L Rhizoid production from the midrib in an area near the apex of the lamina where the lamina wing had been abraded.

Scale bar = 100 μ m, except K = 200 μ m

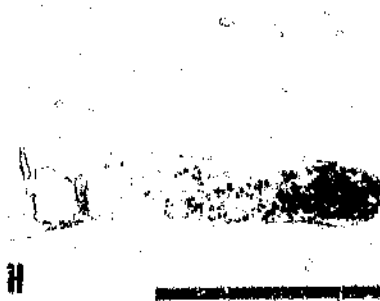
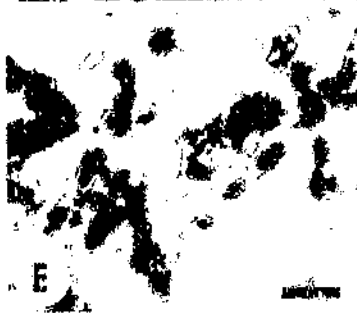
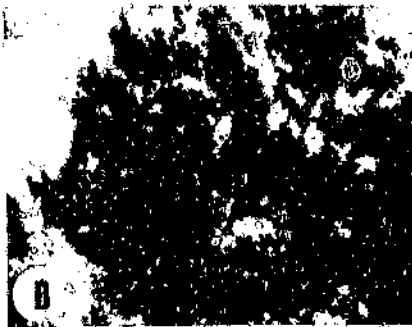


PLATE 5

General morphology of *D. longifolia*.

- A-B The flat, strap-like laminae are dichotomously branched and have a prominent midrib and a sunken, apical meristematic region.
- C Cross-section through the midrib at the lamina tip.
- D Cross-section through the midrib near the base of the lamina. There is a small amount of rhizoid production from the epidermis in this midrib region.
- E Lower regions of the lamina exhibiting rhizoid production from the remains of the midrib.
- F Cross-section through the base of the lamina where the rhizoids are well developed and the lamina wings are absent.
- G-H Cross-section through the thickened margin of the lamina wing tip. Note the small cells on the outer periphery of the thickened margin.
- I SEM of the meristematic cells found in a sunken pit at the apex of the laminae.
- J The apical pit showing the elongated meristematic cells and the layer of protective material.
- K Spores found in patches on the surface of the lamina wing away from the midrib.
- L Antheridia scattered on the surface of the lamina wing.
- M-N Clumps of multicellular hairs produced from pits on the surface of the lamina.
- O Detail of the multicellular hairs.

Scale bar = 100 μ m, except C, D, F, G and H = 200 μ m

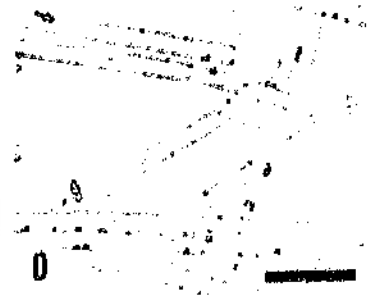
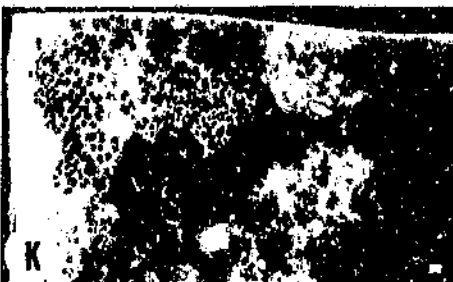
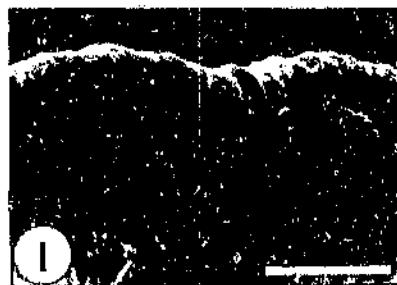
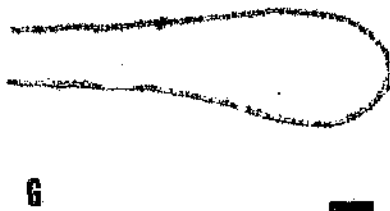
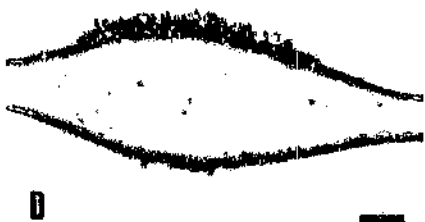
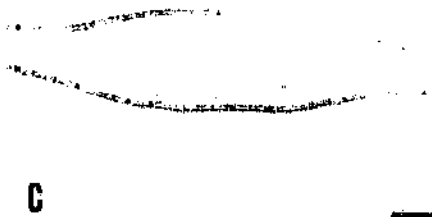


PLATE 6

Sand deposition in some of the sites at Palm Beach,
Natal.

- A-E An individual D. longifolia plant experiencing various degrees of sand inundation, from completely exposed to almost totally covered.
- F-I The intermediate wave activity, sandy gully site (I) under varying degrees of sand cover, from being a deep pool to total sand inundation.
- J-L The highest wave exposure site (H+) showing varying degrees of sand inundation from a total absence of sand to heavy sand inundation.

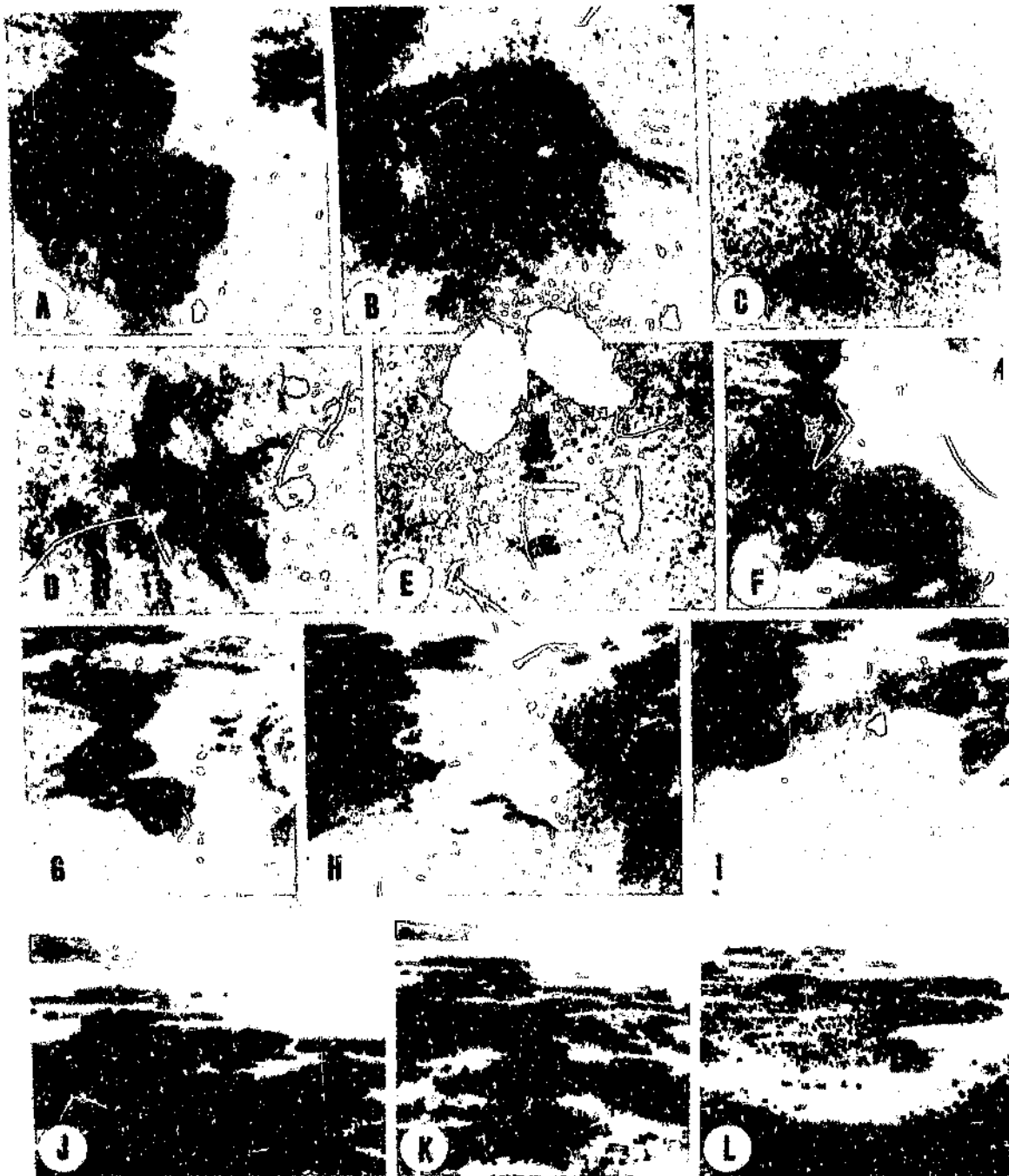


PLATE 7

Detail of the apical region of *D. longifolia* laminae.

- A-B The apical pit (arrow) positioned at the tip of the dichotomously branched lamina.
- C-D Young laminae lacking the sunken pit but having some meristematic cells in the apical region (arrows).
- E SEM of a young lamina lacking the apical pit but exhibiting the elongated, apical cells.
- F-G More mature apical tips, lacking the sunken pit but exhibiting the characteristic, longitudinal cell division (arrows).
- H SEM of a mature apex exhibiting the sunken pit and the longitudinal cells.
- I-K The apical pit showing the elongated cells in different stages of division (small arrow = completely divided, large arrow = beginning division). The exterior layer of material covering the apical pit is also visible.
- L The early stages of a dichotomy showing the initial development of two meristematic centres.
- M A more advanced dichotomy showing two completely separated meristematic pits.

Scale bar = 25 μ m

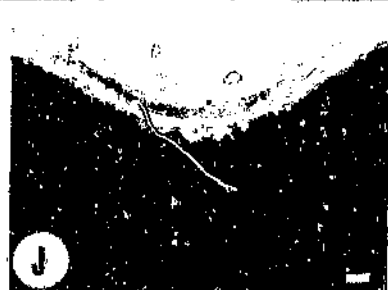
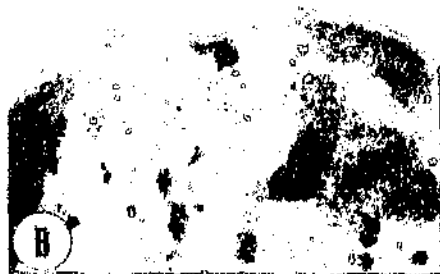


PLATE 8

Detail of the layer lining the sunken, apical pit of
D. longifolia.

- A-C The sunken, apical pit exhibiting the thick,
exterior bilayered region lining the region
(arrows).
- D Detail of the layer lining the pit showing the
inner, thinner, more dense layer and the thicker
layer which is thought to be mucilaginous .

Scale bar = 100 μ m

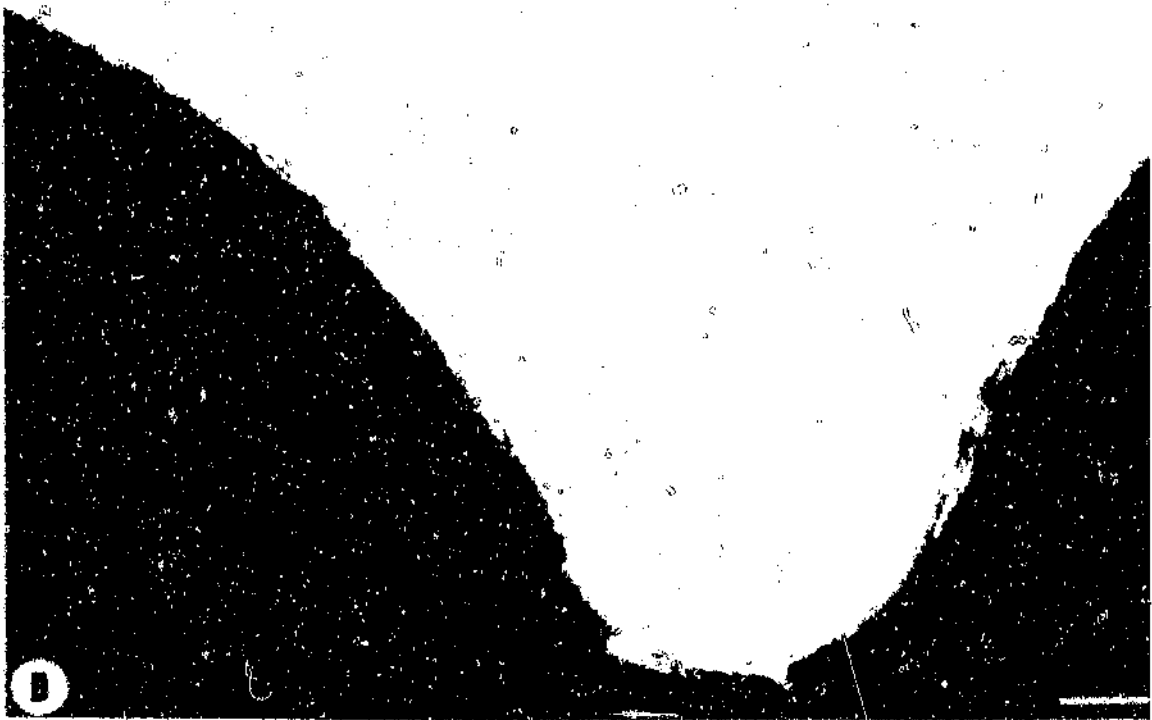


PLATE 9

Detail of the structure of the wing of *D. longifolia*.

- A-B Thickened region along the outer margin of the wing.
- C-E SEM sections through the thickened region on the outer edge of the wing.
- F Detail of the thickened area showing the region of smaller cells lying under the epidermal cells.
- G Cross-section through the wing of a young lamina exhibiting only two layers of wing cells, besides the epidermal layers.
- H A more mature, young lamina with more layers of cells in the wing.
- I SEM section of a young lamina having two layers of wing cells besides the epidermis.
- J Cross-section of a mature, multilayered lamina wing.
- K-P Various views of the thin walled, irregularly-shaped wing cells.

Scale bar = 50 μ m

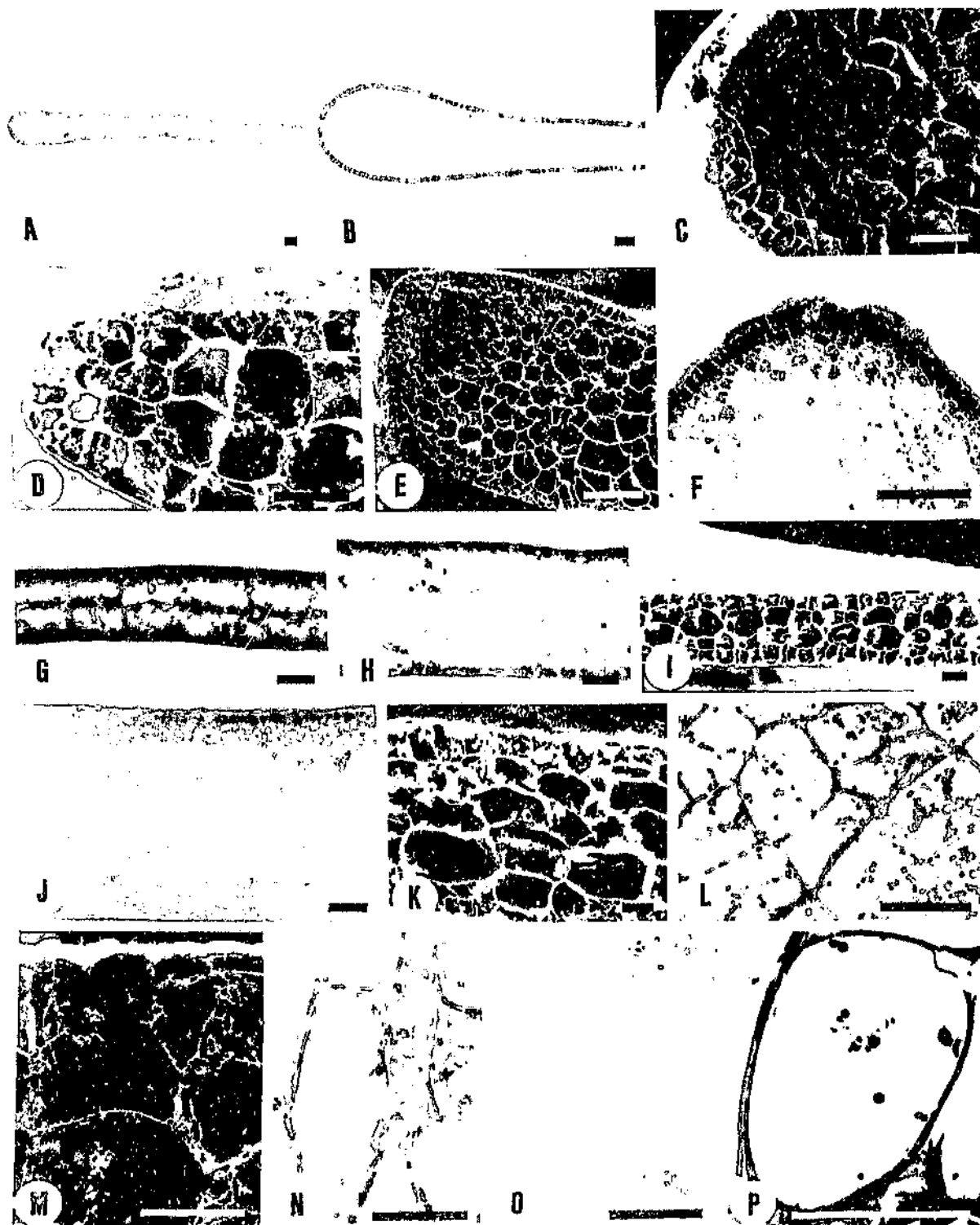


PLATE 10

Sections through various regions of the lamina midrib of *D. longifolia*, from the tip to the base of the plant.

- A-C Sections through the midrib at the tip of the lamina showing the thin epidermal layer, thin-walled central cells and the lack of peripheral protrusions. The wings are intact.
- D-E Sections through the midrib further down the lamina showing a thicker, denser epidermal layer, thick-walled central cells and a lack of peripheral protrusions. This region has intact wing tissue.
- F-G Sections through the midrib in a region where the development of the protruding rhizoids begins.
- H-J Sections near the base of the lamina showing the midrib region with longer, protruding rhizoids. The meristodermal layer is clearly visible between the midrib cells and the rhizoids. The wing tissue is still intact.
- K-M Sections through the stipe region indicating the decay of the wing tissue (arrow), the decrease in the size of the midrib region and the elongation and intertwining of the rhizoids.
- N-O Sections through the holdfast region showing the total absence of wing tissue, the small amount of midrib tissue and the entangled mat composed of the elongated rhizoids.

Scale bar = 100 μ m, except C = 85 μ m, A, D, G, K, I, N and M = 200 μ m

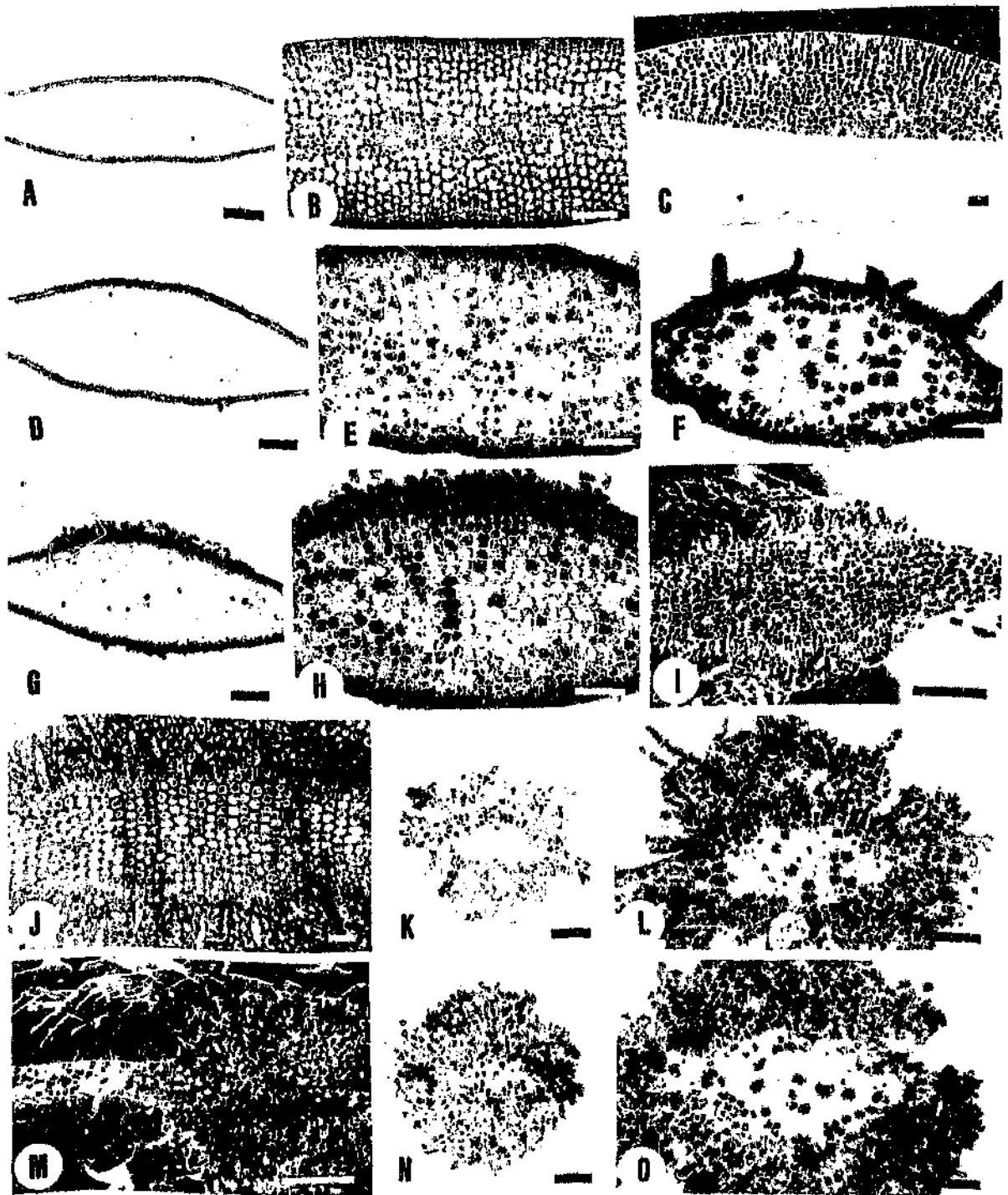


PLATE 11

Detail of the cross-section of cells from the midrib region of D. longifolia.

- A-H Cross-sections of the cells of the midrib region, showing their cuboidal shape and thick walls.
- I-J TEM sections of the cells of the midrib with the extremely thick ($4\mu\text{m}$) walls evident.
- K-L TEM photographs showing detail of the thick multilayered walls of the midrib cells.

Scale bar = $5\mu\text{m}$

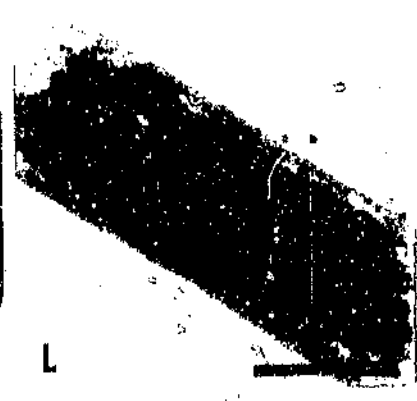
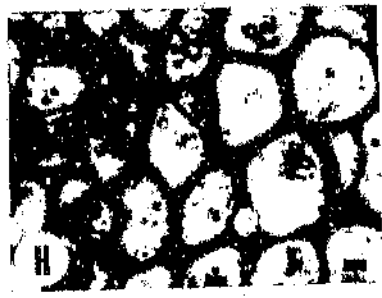
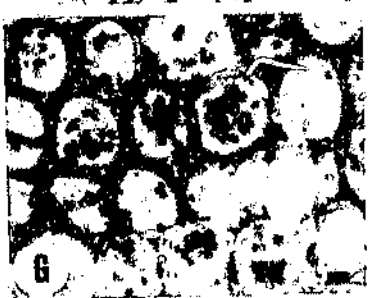
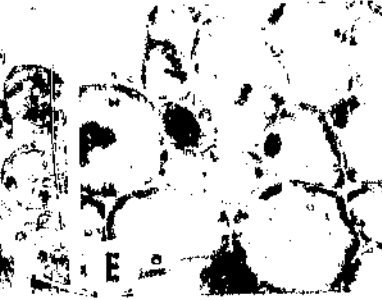
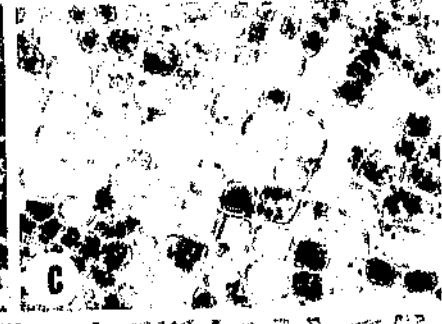
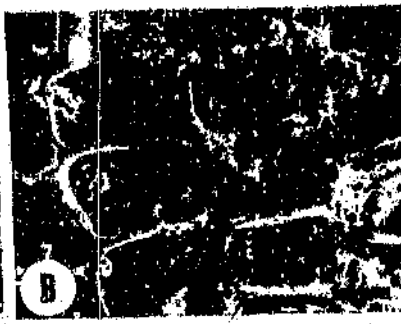
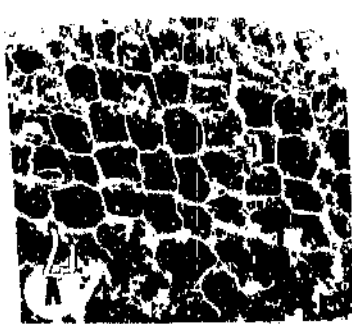


PLATE 12

Detail of the longitudinal-sections of cells of the midrib region and sections of the cells of the epidermis.

- A** Longitudinal-section through a region of the stipe which is lacking in wing tissue but has rhizoids. The elongated midrib cells can clearly be observed.
- B-D** Longitudinal-sections through the midrib showing the long, narrow cells characteristic of this region.
- E-G** Detail of the elongated cells of the midrib showing the pits in the side walls of the cells (arrow).
- H-K** Cross-section through a region of the midrib showing the cuboidal, thick-walled cells of the midrib region and the small, dark, rectangular cells of the single epidermal layer.
- L** Cross-section of the wing showing the irregular wing cells and the layer of rectangular epidermal cells.
- M** Longitudinal-section through the midrib region showing the elongated central cells and the single layer of small, dark, rectangular epidermal cells.

Scale bar = 50µm

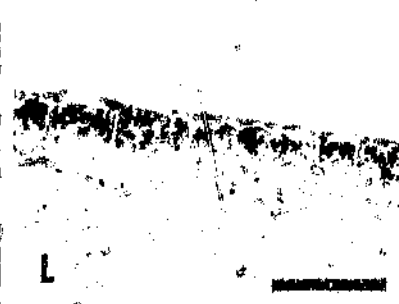
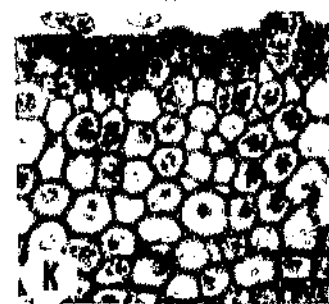
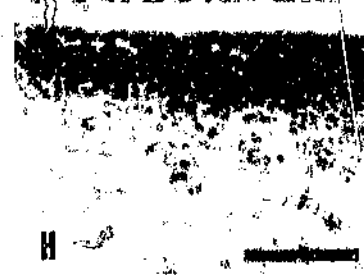
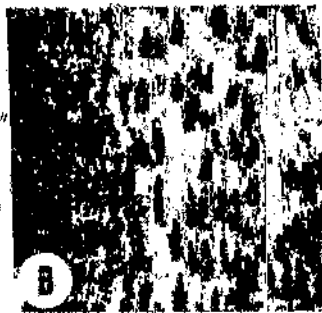
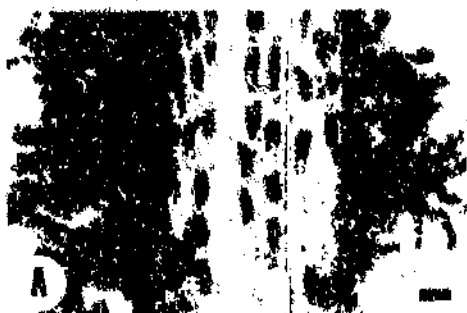


PLATE 13

Detail of the rhizoid-producing meristoderm and related structures found in the midrib region of D. longifolia.

- A The initial stages of rhizoid production from the meristodermal region.
- B-F Detail of the more advanced stages of rhizoid production showing the multicellular rhizoids and the layer of dividing meristodermal cells.
- G Detail of the meristodermal layer showing the dividing meristomatic cells at the base of the rhizoids.
- H TEM showing the thick layer of material covering the initial stages of the rhizoid production.
- I TEM of a rhizoid in the initial stages of formation.
- J-L Detail of strange dense-staining structures (arrows) frequently observed between the newly produced rhizoids and the meristematic layer.

Scale bar = 50 μ m

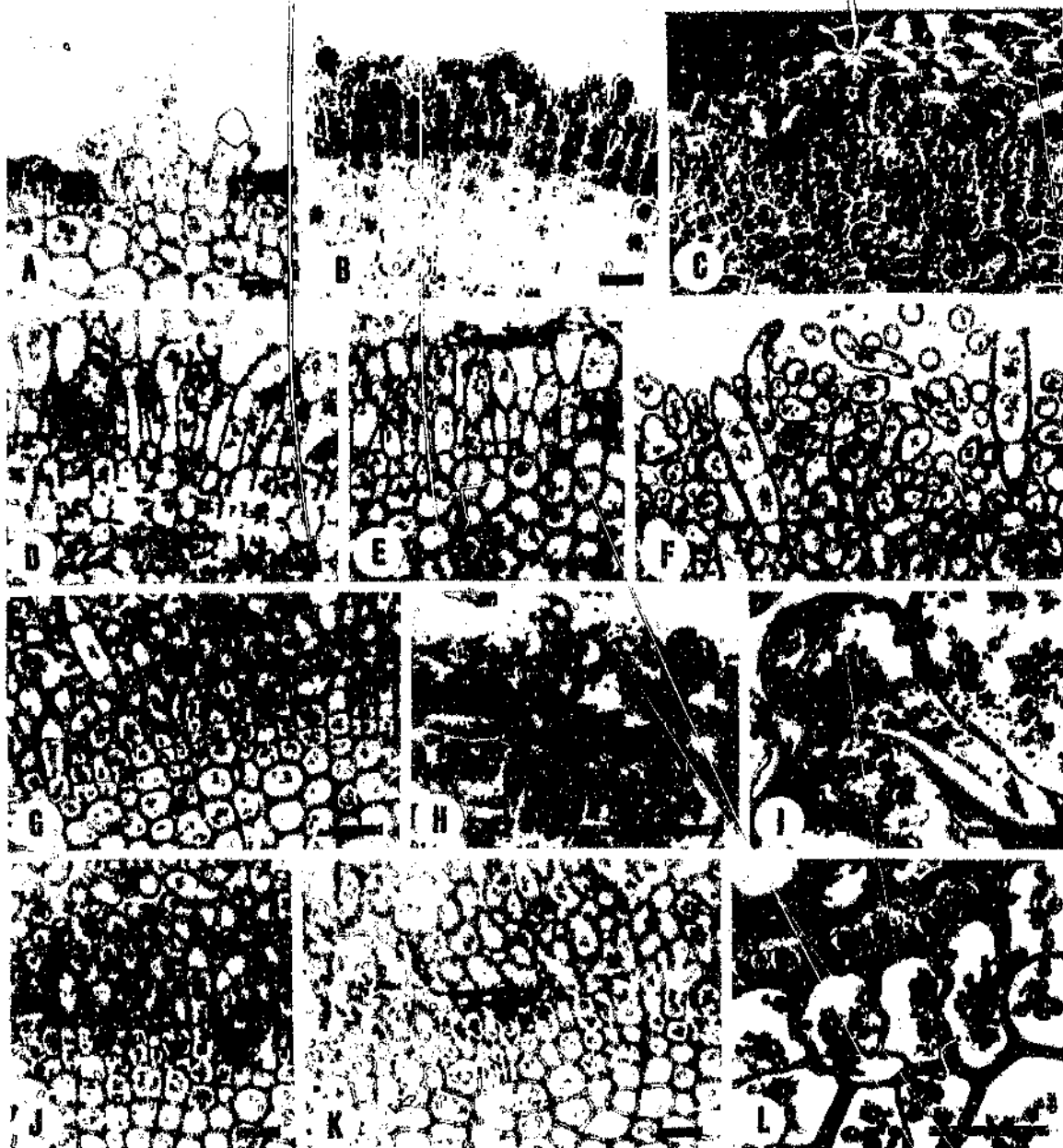


PLATE 14

Surface view of epidermal cells from different regions of a lamina of D. longifolia.

- A-B A surface view of a young lamina showing the more elongated cells in the central region, which eventually develop into the midrib.
- C Some of the elongated cells in the centre exhibit longitudinal division (arrows).
- D The elongated cells of the midrib are darker in colour and can be observed on the left, while the lighter, irregular wing cells can be observed on the right.
- E The elongated midrib cells can be observed closer to the top of the photograph, with the wing cells at the bottom.
- F Elongated midrib cells.
- G The different cell shapes with the elongated midrib cell (small arrow) and the irregular wing cells (big arrow).
- H Wing cells dividing (arrows) in different directions.
- I Highly irregularly shaped wing cells.
- J-L Wing cells with different concentrations of chloroplasts, from different regions of the lamina.

Scale bar = 50 μ m

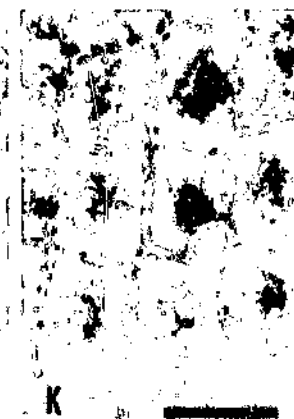
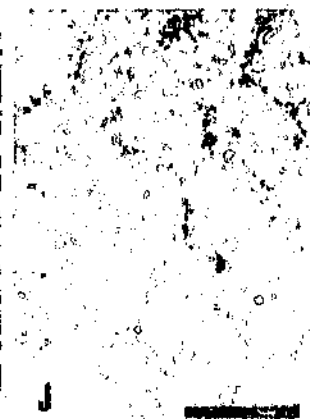
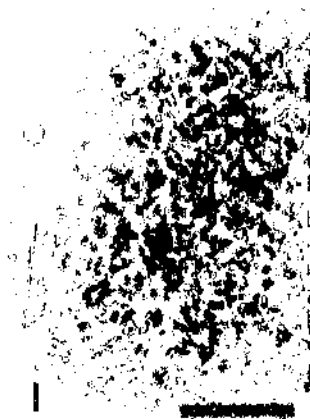
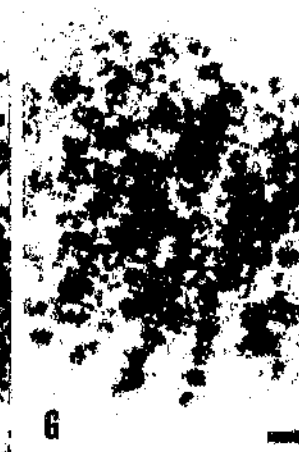
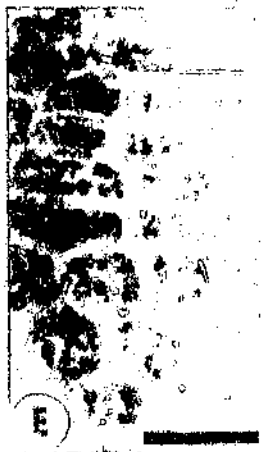
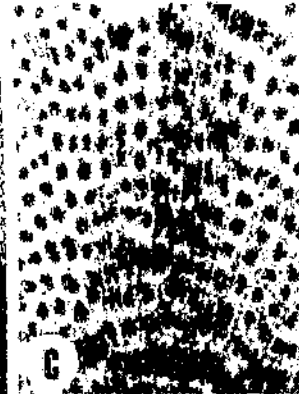
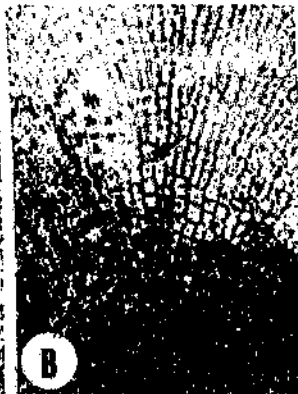


PLATE 15

Detail of the rhizoidal holdfast structure of *D. longifolia*.

- A-B** The holdfast composed of a mat of entangled rhizoids giving rise to the laminae.
- C** Cross-section through the holdfast region showing the proliferation of rhizoids from the central midrib region, which lacks any wing tissue.
- D** Surface view of the base of a lamina showing the rhizoids developing from the midrib. The rhizoids are small nearer the apex of the lamina and increase in length closer to the base.
- E-G** Surface views of the midrib region from near the apex towards the base, showing increasing rhizoid length.
- H-J** Sections through multicellular rhizoids.
- K-L** Detail of the multicellular, branched rhizoids.
- M-N** An example of the structure of the majority of rhizoid tips showing the rounded growing tip and the concentration of organelles in the terminal region.
- O-P** Detail of a more infrequently observed bulbous rhizoid tip which appeared to be involved in attachment.

Scale bar = 100 μ m; except C = 200 μ m



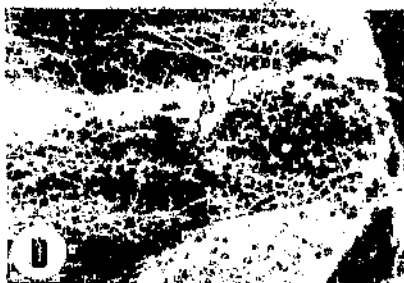
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B



C



D



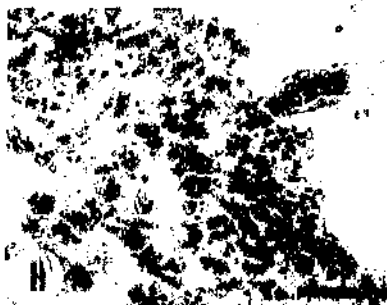
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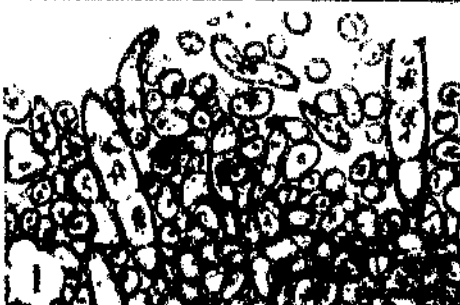
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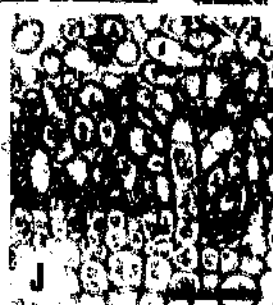
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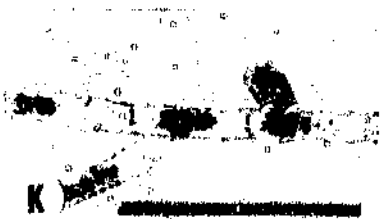
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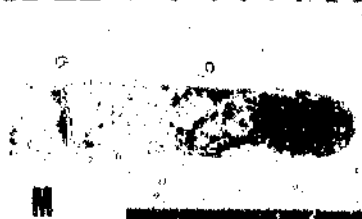
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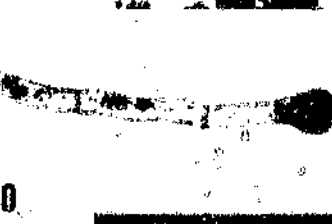
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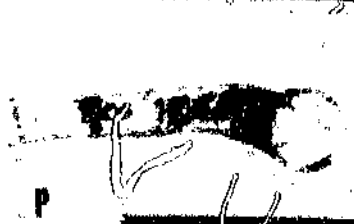
M



N



O



P

PLATE 16

Surface hairs from laminae of *D. longifolia*.

- A-B Surface view of multicellular hairs on the lamina surface.
- C-D Sections through the multicellular hairs showing the pit on the lamina surface into which the bases of the hairs are sunk.
- E-F Old or deformed hairs occasionally observed in sections.
- G-K SEM of the hairs from the early stages of production to a mature, fully protruded clump of hairs. The multicellular nature of the hairs is clearly visible.
- L-N Structure of the thin-walled, multicellular hairs showing some organelles and the large, brown structures causing indentation of the walls (arrows).
- O Detail of the terminal cell of the hair having a blunt ended tip.
- P Sequence of the cells from the point of attachment, where the cells are small and densely packed with organelles, to nearer the apex of the hair where the cells are large and relatively empty, with most of the organelles present in the central region.

Scale bar = 50 μ m



PLATE 17

Other Structural Observations and Associations of
D. longifolia.

- A View of the lamina surface showing regular structures growing on the surface.
- B-D Detail of the hair-like tufts observed growing at regular intervals on the surface of some laminae.
- E-G Damage caused by what is believed to be a fungus (arrows) growing on the lamina and causing some degradation.
- H A red filamentous alga (arrow) growing epiphytically on the holdfast.
- I-J Tufts of a filamentous brown epiphyte found on the lamina, and detail of its reproductive structure.
- K Section through a red epiphyte from the lamina of D. longifolia.
- L-M Cross-section through a red epiphyte showing the lack of any visible penetration of the host.
- N-O Epidermal sloughing observed in culture and believed to be involved in the removal of epiphytes.
- P Detail of what is believed to be an epiphyte on the sloughed epidermis.
- Q-R The nest and body structure of the polychaete Pseudonereis variegata frequently found living on D. longifolia.
- S Large bites out of the lamina, believed to have been made by a feeding fish.

Scale bar = 50 μ m

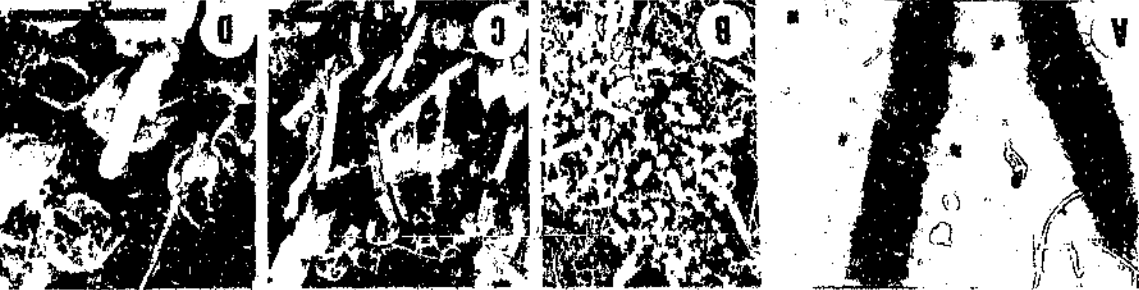
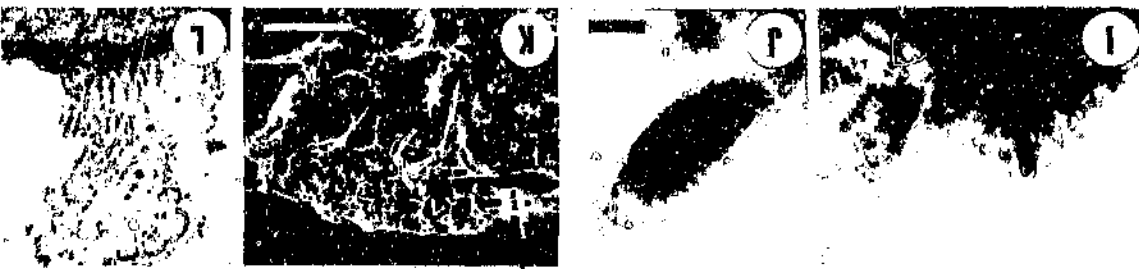


PLATE 18

Degeneration and regeneration of *D. longifolia* in the field.

- A Degeneration of the basal wing tissue is a natural annual procedure occurring mainly in winter.
- B Removal of the laminae tips occurred due to herbivory.
- C A highly abraded plant showing most of the laminae reduced to the midrib region. The extent of the degeneration is thought to be a result of sand abrasion as well as senescence and herbivory.
- D-F Plants showing degeneration of the lamina material, with E showing the laminae reduced to the midribs (arrow).
- G-H Thalli exhibiting regeneration of new laminae from the damaged tips.
- I-J Plants in the field exhibiting regeneration from the damaged laminae tips.
- K A plant in the field showing the remaining old, abraded laminae reduced to midribs (big arrow), and the new laminae regenerating from the original holdfast clumps (small arrow).
- L New laminae regenerating from an old holdfast clump lacking any remaining abraded laminae.

Scale bar = 50 μ m

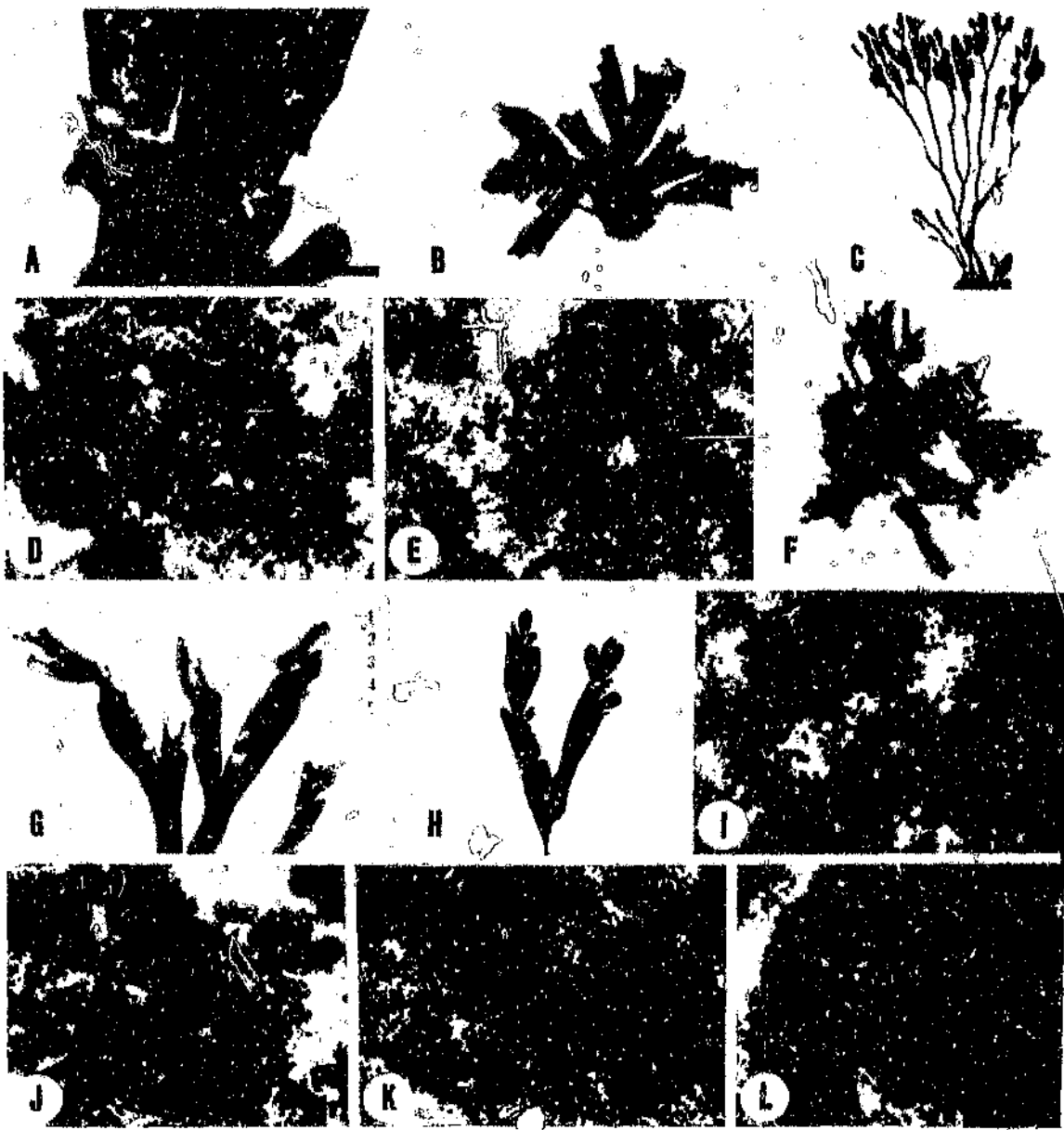


PLATE 19

Regeneration from lamina sections of D. longifolia.

- A Section of the lamina across the wing and including the midrib did not exhibit regeneration.
- B Section across the laminae but including the midrib and a small section of wing tissue did not show any regeneration due to the high degree of epiphytism resulting from the growth medium.
- C A similar section to that in B, but kept in filtered seawater exhibited some regeneration from the midrib region after three weeks in culture.
- D-F Detail of the initial regenerated material showing both regenerated rhizoids and laminae-like structures, without any well developed laminae forming.
- G-J Various stages of the regeneration of laminae (at three day intervals) from the cut edge around the midrib region of a lamina.
- K A mature regenerated laminae showing rhizoids at the base (arrow).
- L Some cut edges produced an undifferentiated callus consisting of a few protrusions of tissue which did not develop further.

Scale bar = 100 μ m

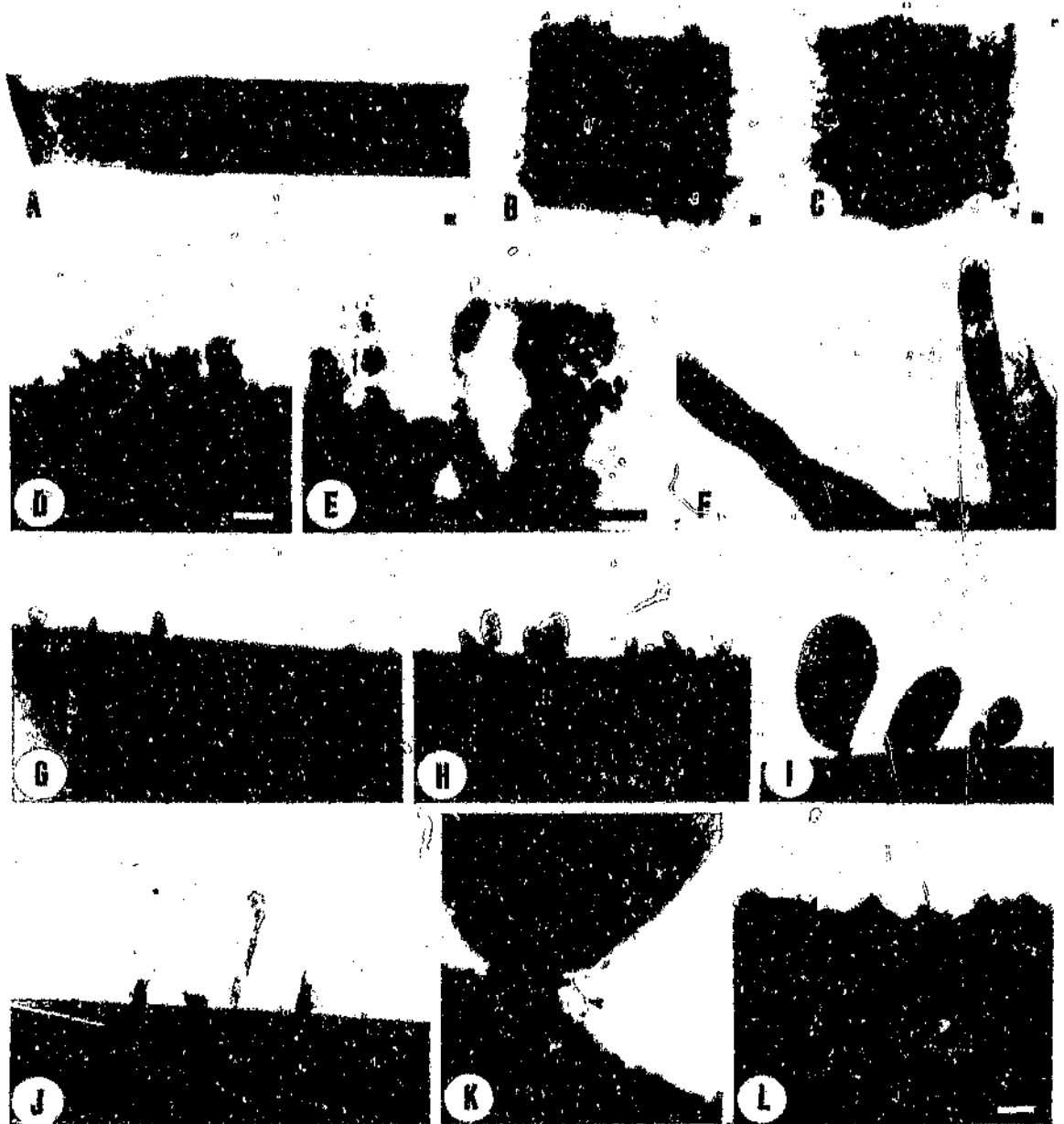


PLATE 20

Regeneration from different sections of the lamina of
D. longifolia.

- A-C A sequence of elongation of a removed lamina apex (at weekly intervals), which elongated without showing any regeneration of new laminae.
- D-E Two apical sections which had the tips damaged and subsequently developed regenerated laminae from the basal region, ie in the opposite direction to that of the original growth (after a three week period).
- F An apical section which exhibited regeneration of new laminae from both the apical and basal regions.
- G-H The apical section of a dichotomously branching lamina tip, showing an undamaged tip and regeneration from the base only.
- I-K Sequential stages in the regeneration of laminae from the cut edge of the apical region (taken at five day intervals), where the apical tip had been excised by a V-shaped section being removed.

Scale bar = 1000 μ m



PLATE 21

Regeneration from various sections of the lamina of
D. longifolia (taken at weekly intervals).

- A Sequence of new lamina regeneration from sections across the lamina, including both margins and the midrib.
- B Sequence of growth of the apical tip of an entire lamina, with a horizontal cut made across one wing and through the midrib.
- C-D Sequence of lamina regeneration from the apices of sections of dichotomizing laminae which had the apical tips removed with straight horizontal cuts.
- E Sequence of lamina regeneration from a complete lamina, with the apical region removed with a V-shaped cut.
- F Sequence of growth of the apex of a complete lamina with a horizontal cut made across one wing and through the midrib.

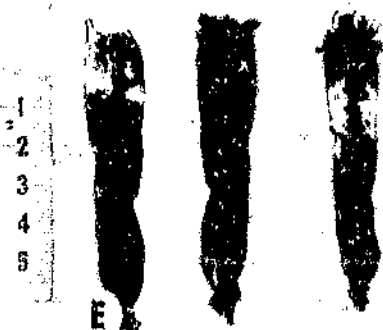
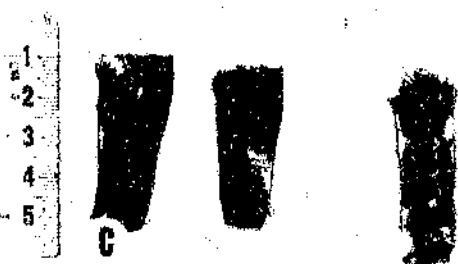
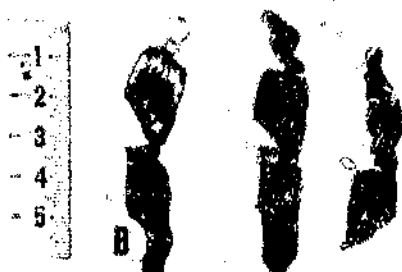
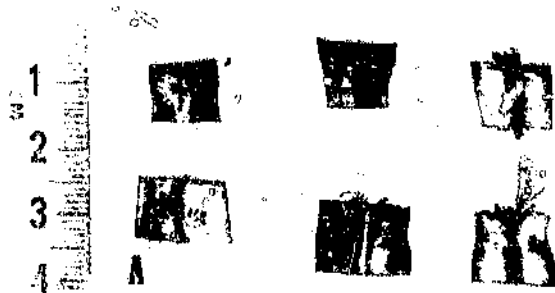


PLATE 22

Sequence of development (at three day intervals) of a single lamina regenerating from the cut surface of a lamina section of D. longifolia.

A-E Sequence of development of the initial outgrowth of tissue which developed into the regenerated lamina.

F-I Sequences of further development of the lamina showing the development of the apical pit and the surface differentiation of cells of the midrib region.

J A mature regenerated lamina developing a dichotomy.

Scale bar = 100 μ m

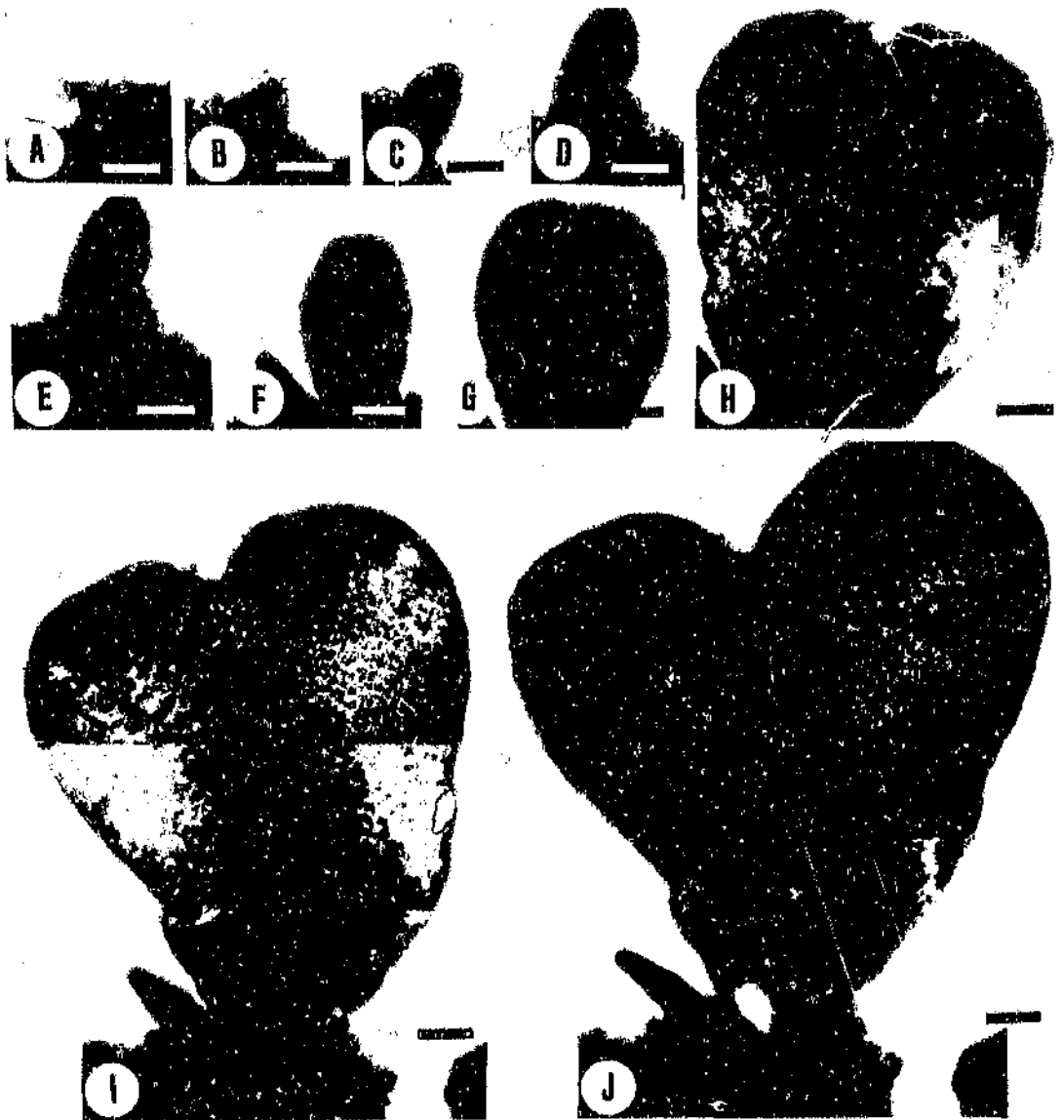


PLATE 23

SEM studies on stages of lamina regeneration from the cut edge of a lamina section of *D. longifolia*.

- A-D Sequence of development of the initial stages of regeneration which developed on the cut surface.
- E-G Early development of the laminae showing the thick, elongated apical cells.
- H-I Advanced stages of the developing laminae.
- J Apical region of a developed lamina showing the dividing, elongated, apical, meristematic cells.
- K-L Large, developed laminae growing from the cut edge of the original lamina.
- M Fully developed laminae exhibiting apical pits and having rhizoids growing from the bases of the laminae.
- N Initial stages of the development of the rhizoids from the lamina base.
- O The apical pit of a developed lamina showing the elongated, apical, meristematic cells in the pit.
- P-S Stages of development of the rhizoids of the lamina from the initial stage of a small protrusion on the surface, to fully developed, long rhizoids.

Scale bar = 25 μ m; except H, K, N, O, P, Q, R, S = 100 μ m

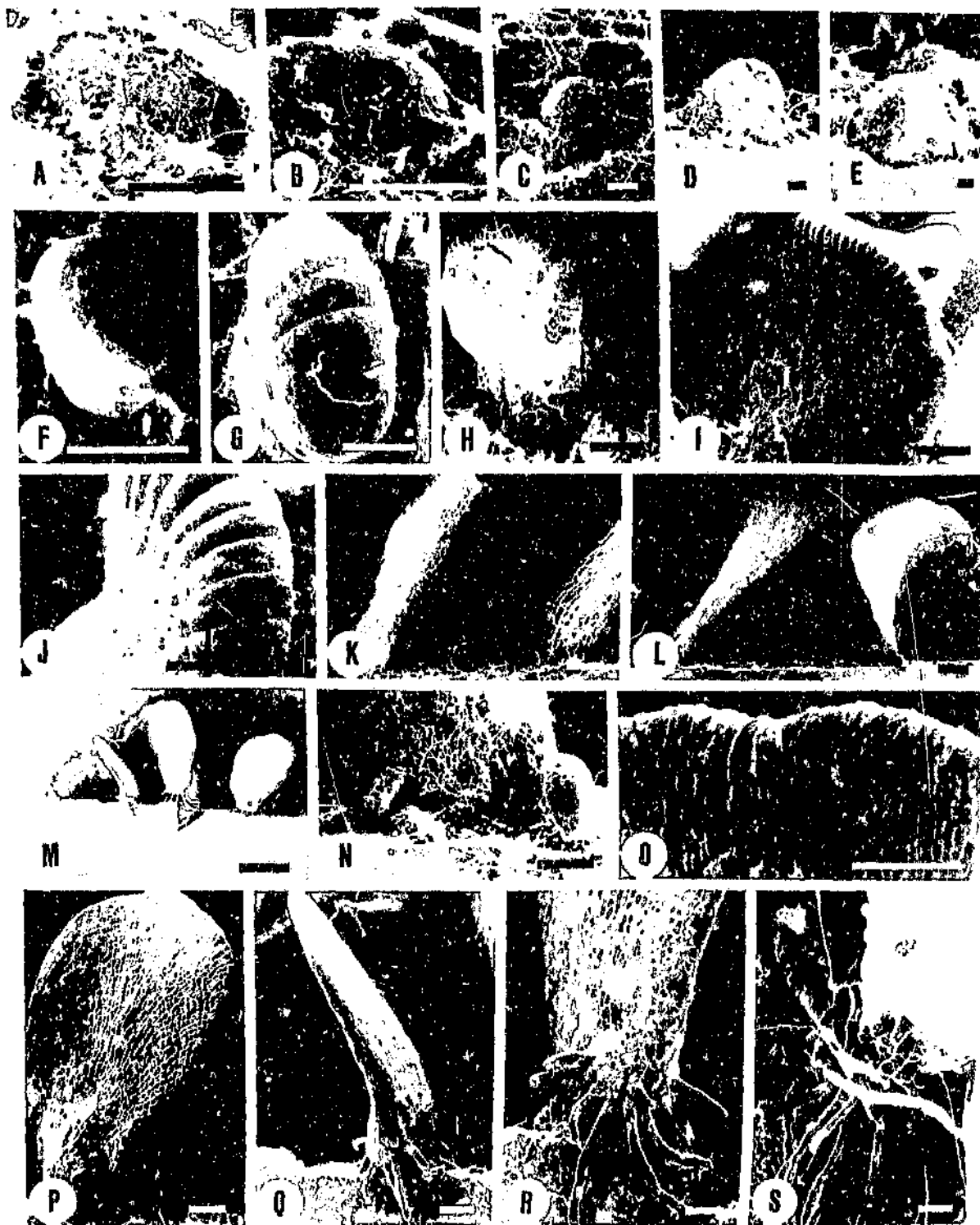


PLATE 21

Sections through various stages of development of regenerated *D. longifolia* laminae.

- A-D Sections through recently cut laminal edges showing how the thallus cells heal, the organelles collect in an undamaged cell on the cut edge, and the cell begins to protrude outwards. It is interesting to note the walls remaining of the damaged cells.
- E-G Stages in the development of a dividing protrusion (arrow) on the cut edge of the lamina. A single protrusion seems to dominate over the other protrusions in an area.
- H-K Sections through developed, regenerated laminae.
- L Developed, regenerated lamina showing the presence of a rhizoid (arrow).

Scale bar = 100 μ m

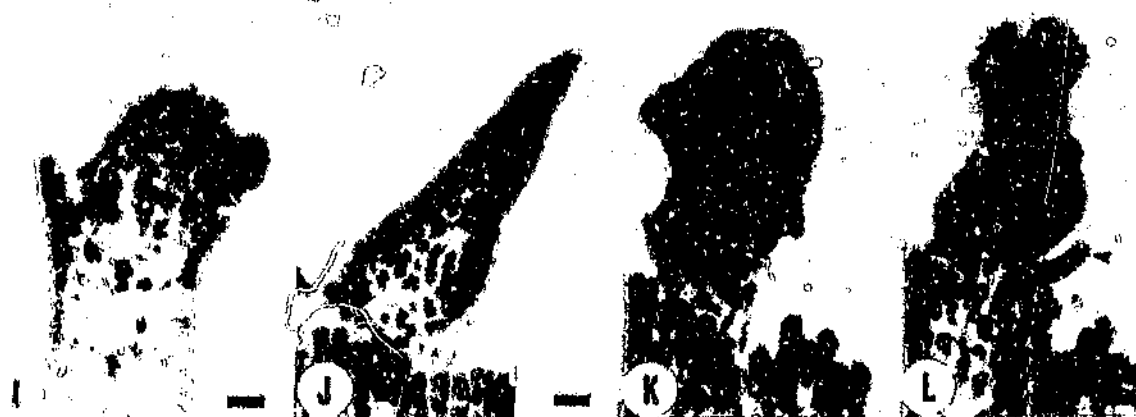
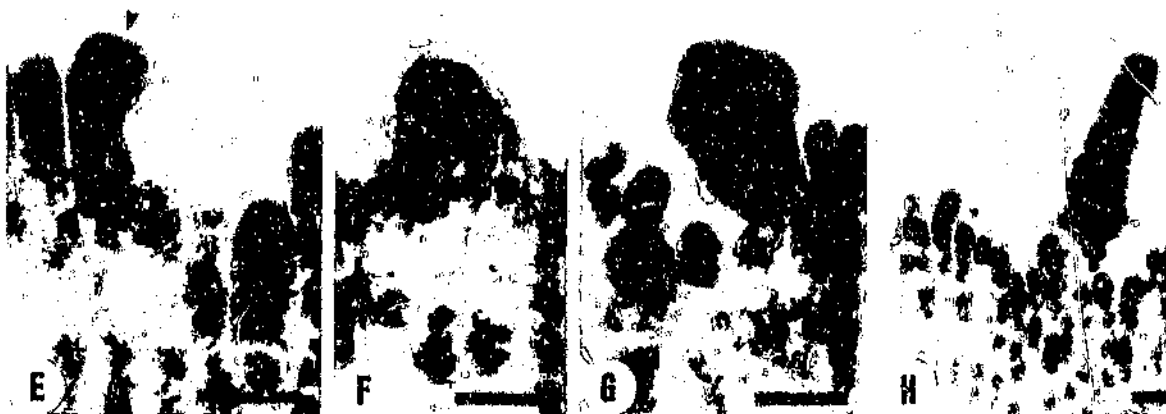


PLATE 25

Stages of the abnormal development of new laminae from the undamaged surfaces of young laminae in D. longifolia.

- A New laminae developing from the undamaged base and apex of a sporeling.
- B Laminae developing on the undamaged surface of a regenerated lamina removed from the parent lamina.
- C Laminae developing from an abnormal apical outgrowth of a sporeling. .
- D-E Developing laminae on the surface of the original, removed laminae.
- F-H SEM studies of the early stages of development of laminae from the surface of a young lamina, showing the initial protrusion of undivided tissue.
- I-L Stages in the growth of multicellular laminae.
- M-P Abnormal, lamina-like and rhizoidal outgrowths on the new laminae, produced from the surface of an undamaged lamina.

Scale bar = 50 μ m

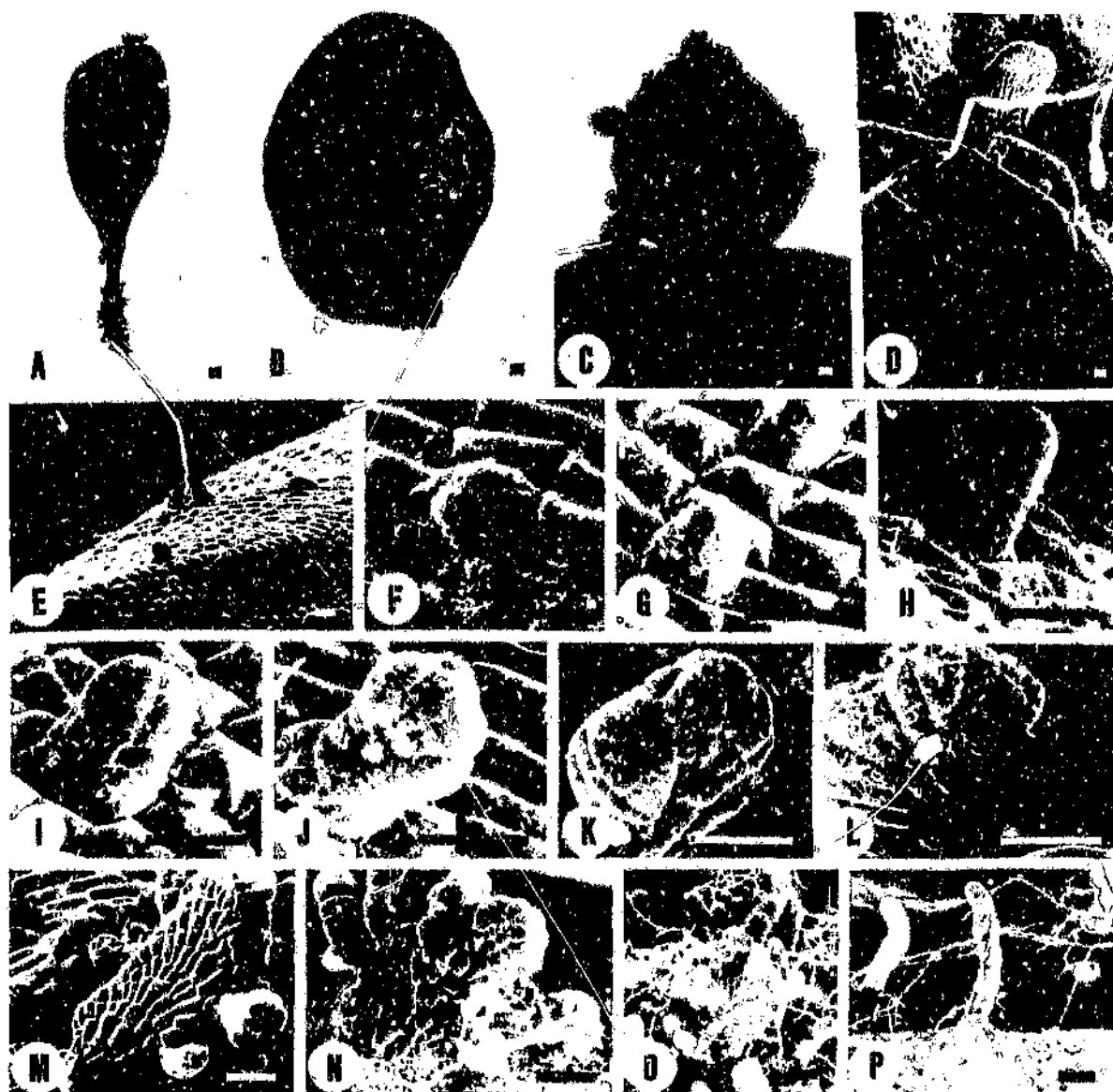


PLATE 26

Various aspects of regeneration of laminae from the holdfast of D. longifolia.

- A A plant in the field regenerating new laminae from the rhizoidal clump.
- B-F Regenerating holdfasts kept in culture in a small dish of filtered seawater.
- G Section through a holdfast, showing the rhizoid producing midrib region and a section through the new lamina.

Scale bar = 100 μ m

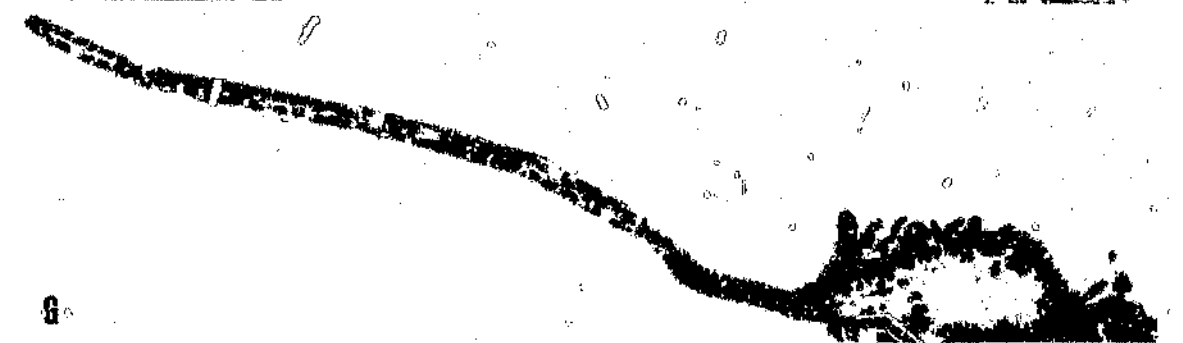
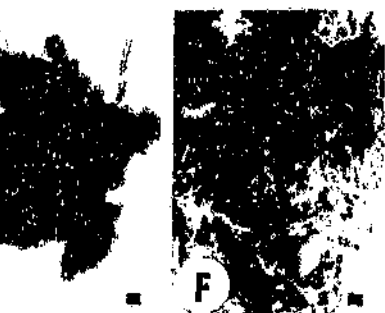
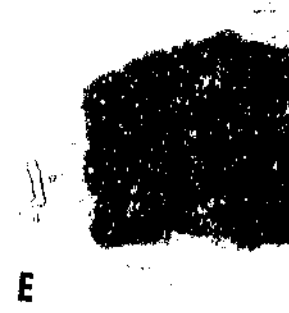
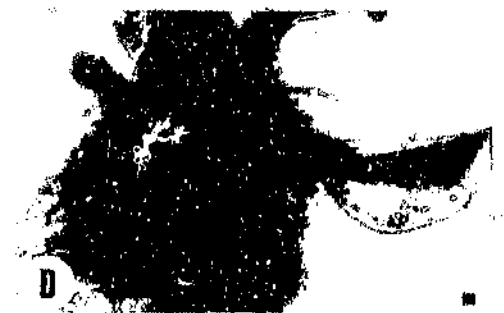
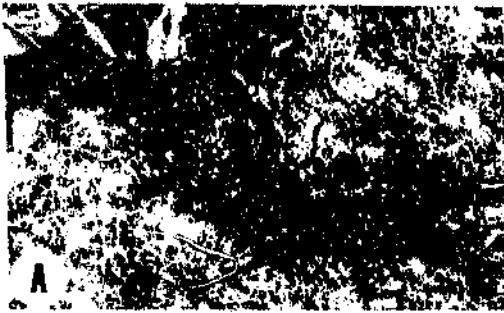


PLATE 27

Regeneration of new laminae from sections of rhizoids from the holdfast of D. longifolia.

- A Portion of a rhizoid showing the newly developed lamina.
- B-K Stages in the development of new laminae from sections of rhizoids.
- L Advanced, regenerated lamina showing the apical pit and a clump of hairs.
- M-N Laminae lacking an apical pit showing the dividing apical cells.
- O Omitted
- P SEM of a lamina, regenerated from a section of rhizoid and exhibiting the apical pit and rhizoids developing from the base.

Scale bar = 150 μ m; except H = 75 μ m



PLATE 28

Sexual structures of *D. longifolia*.

- A-C Surface views of the antheridia, showing their scattered distribution on either side of the midrib on material collected during summer.
- D-G Sections through the initial stages of the development of the antheridia.
- H-I Sections through the mature antheridia.
- J Surface view of what is interpreted as an oogonium.
- K-L Sections through what is interpreted to be the immature oogonia.

Scale bar = 100 μ m

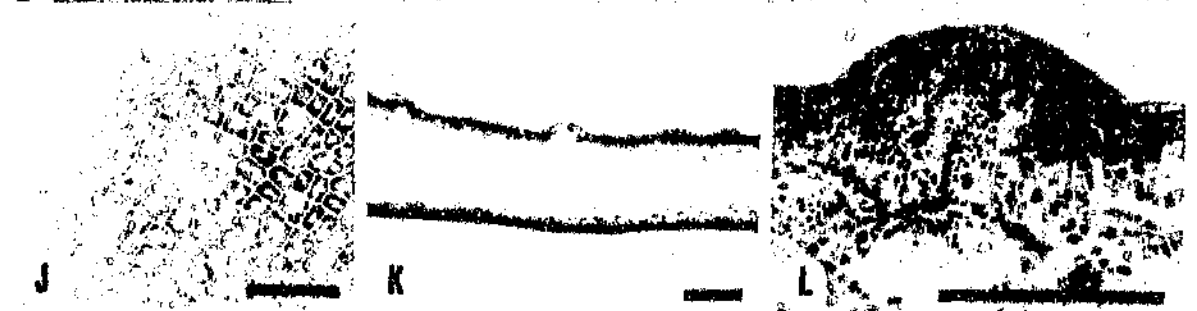
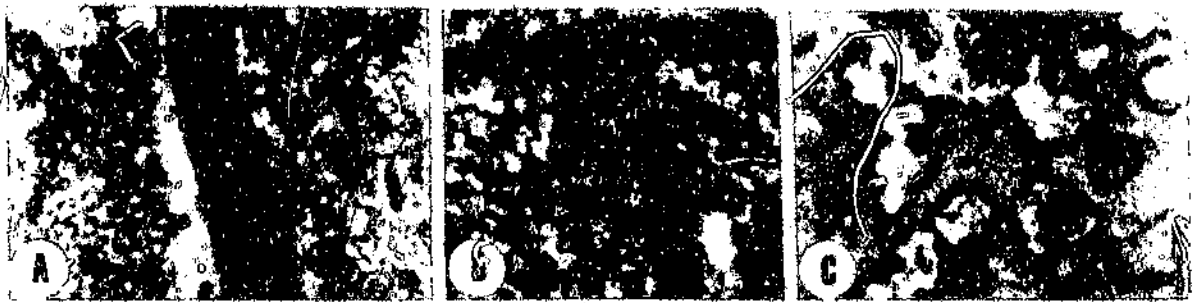


PLATE 29

Surface view of the development of the asexual tetraspores in *D. longifolia*.

- A-B Surface view of the lamina, showing the distribution of the spores in patches on the lamina wing of material collected in June.
- C Section through a spore-producing laminal section, showing spores produced on both surfaces of the lamina.
- D-E Surface views of various stages of spore development.
- F The undivided spore mother cell.
- G-H The first division (arrow) which divides the spore mother cell into two.
- I The second division (arrows) which divides the spore mother into four tetrahedrally arranged spores.
- J-K The tetrahedrally arranged spores separate, and some begin to produce a rhizoid while still attached to the others in the tetrad.
- L The development of the rhizoids from spores, still attached to the lamina surface and in the tetrahedral arrangement, is believed to be due to the lack of water motion in culture.

Scale bar = 100 μ m

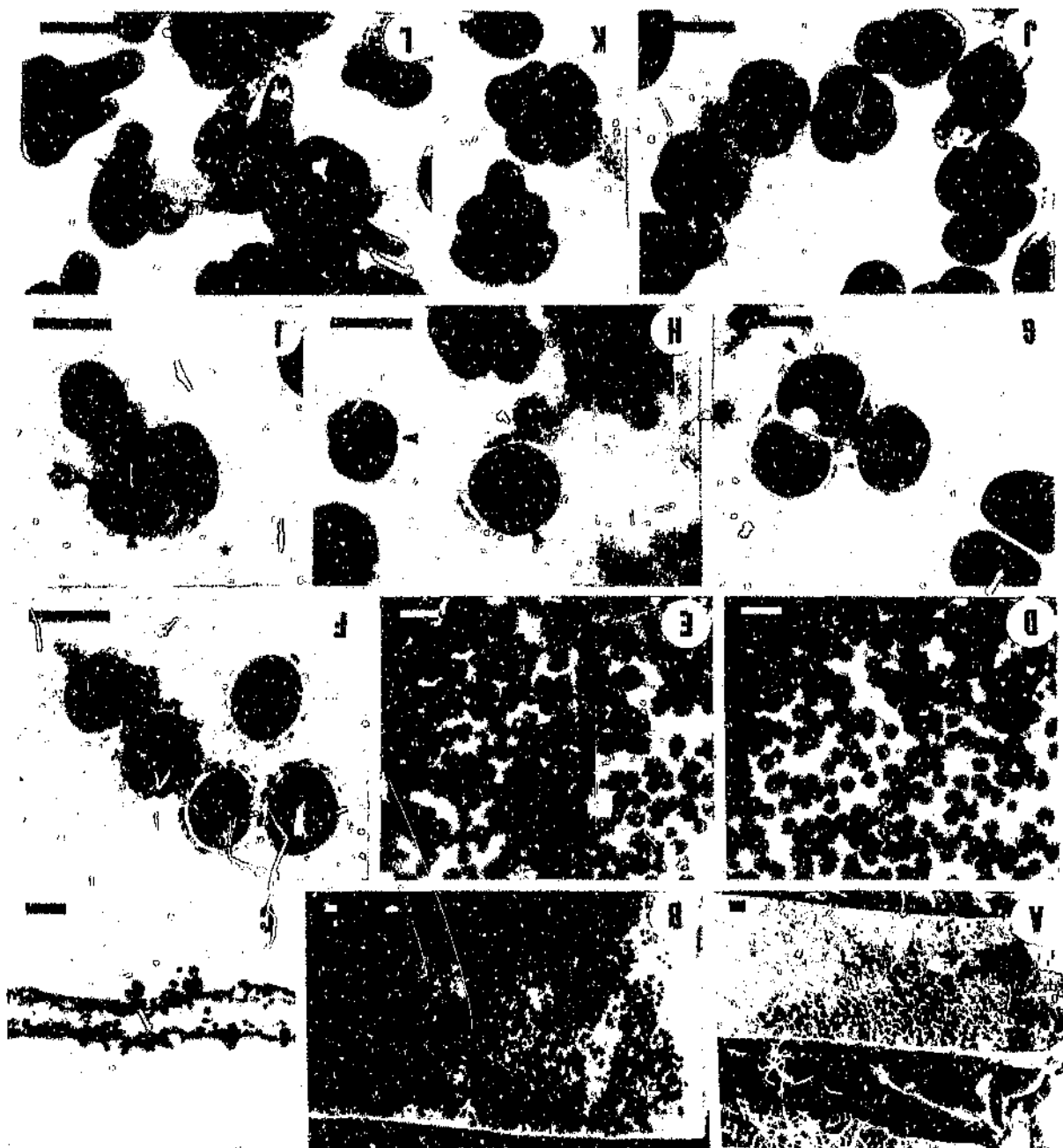


PLATE 30

SEM of the lamina surface showing various stages of tetraspore development and germination in *D. longifolia*.

- A-B The surface of the lamina showing various stages of spore development.
- C-G Stages of the development of the tetraspores from a single, small raised spore mother cell to the tetrahedrally arranged tetraspores.
- H-J Tetrasporangia, showing the apical opening that develops for the release of the spore.
- K A spore released from the sporangium.
- L Germinating spores showing long rhizoids.
- M The development of the original spore into a multicellular structure which eventually forms the lamina of the sporeling.
- N-O Germination of spores in culture occurred while the spores were still attached to the lamina of the parent plant.
- P A germinating spore developing a second rhizoid.
- Q Some spores germinated in the tetrad with the rhizoids becoming intertwined.
- R-S Some rhizoids germinated with the original spore still embedded in the sporangium and the rhizoids developing outwards.

Scale bar = 50 μ m

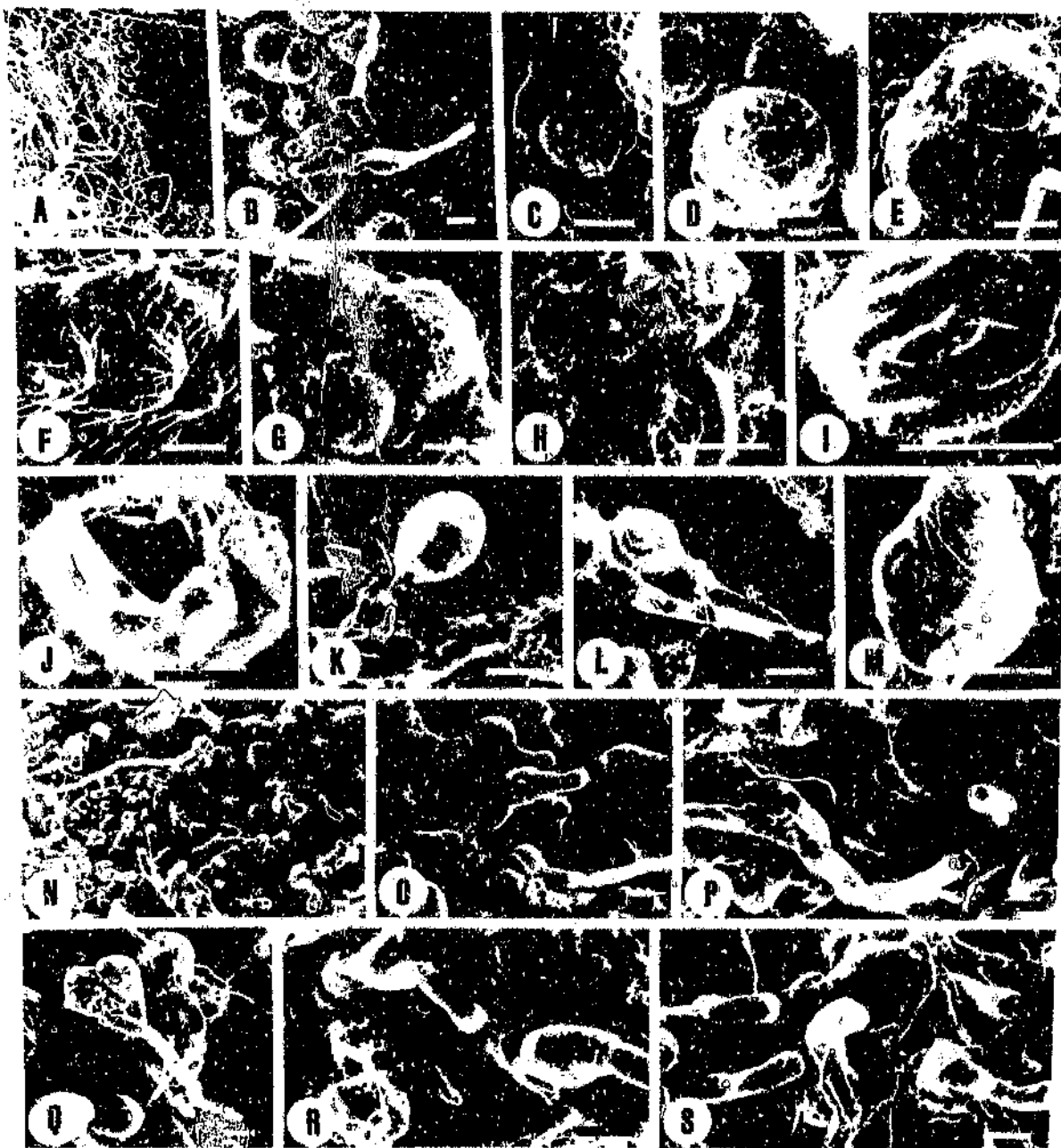


PLATE 31

Sections through laminae of D. longifolia showing the stages of development of the tetraspores.

- A Formation of the spore mother cell beneath the surface of the lamina.
- B-C Early stages of tetrasporangial protrusion, showing the raised cuticle (small arrows) and the epidermal cells extending up the sides of the protrusion (big arrow).
- D-E Developed tetrasporangia showing increased protrusion.
- F-H Mature spore mother cells prior to meiotic division and clearly showing the single stalk cell (arrows).
- I Section through the lamina showing various stages of spore formation and release.
- J Unreleased tetraspore germinating whilst still within the tetrasporangium.
- K Four unreleased tetraspores germinating whilst still attached to the tetrasporangium and to each other.
- L-O Vacated tetrasporangia following the release of the tetraspores, clearly showing the single stalk cell that remains.

Scale bar = 50 μ m



PLATE 32

Tetraspore germination and development in D. longifolia.

- A-C Initial development of a rhizoid protrusion from a tetraspore which underwent fluorescent marking (with calcofluor) shortly after release.
- D A tetraspore shortly after release and prior to any rhizoid development.
- E-F Tetraspores with rhizoidal protrusions developing but prior to the division into a rhizoidal and a thallus cell.
- G A tetraspore just after the initial division into a thallus and rhizoidal cell.
- H-K The development of the sporeling showing the elongation and increase in cell number of the primary rhizoid.
- L Well developed tetraspores with multicellular rhizoids, developing while still attached in a tetrad.
- M A sporeling with a well developed, multicellular rhizoid.
- N-P Sporelings exhibiting the early stages of development of a second rhizoid and some development of the thallus cell.

Scale bar = 100µm

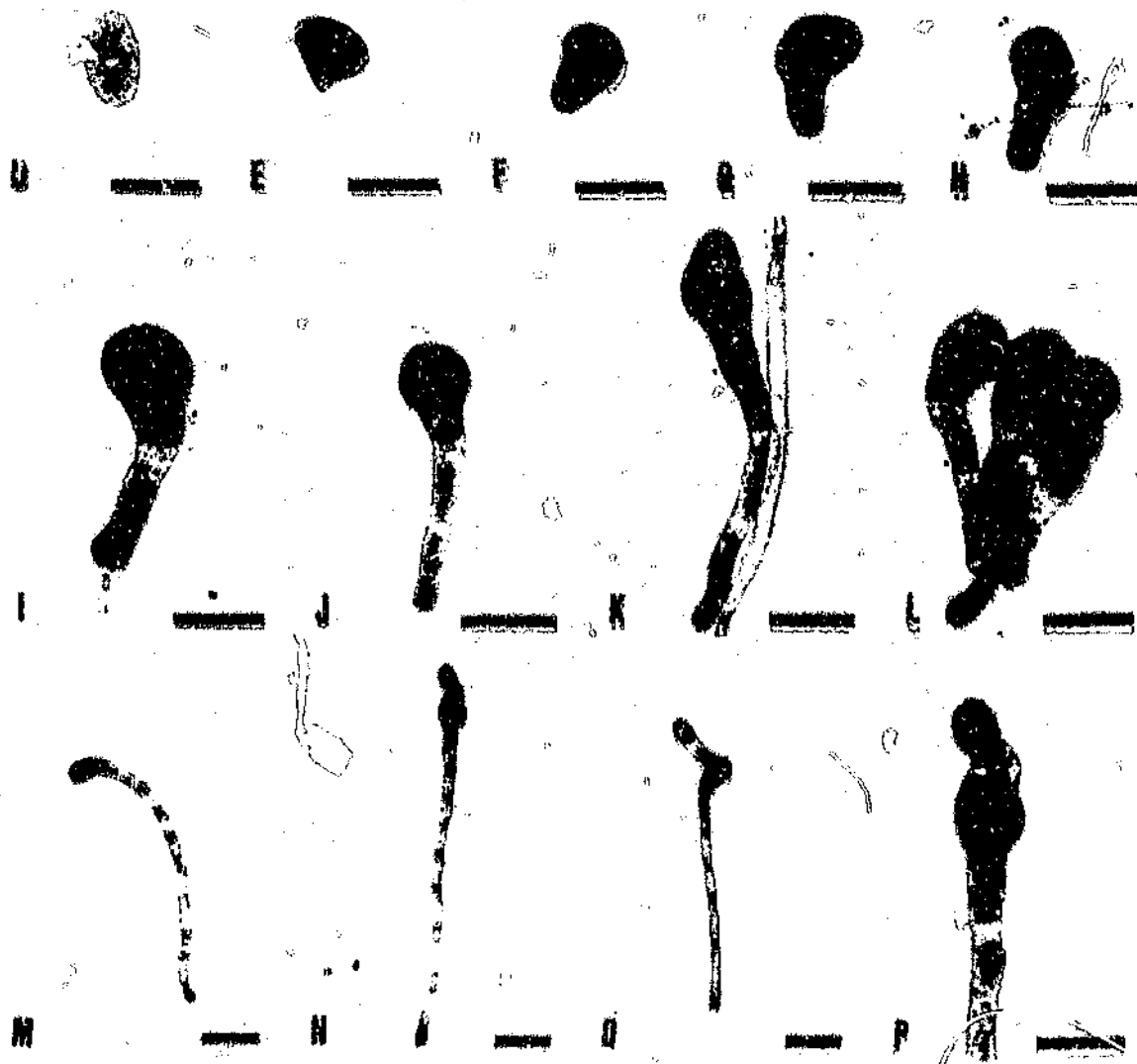
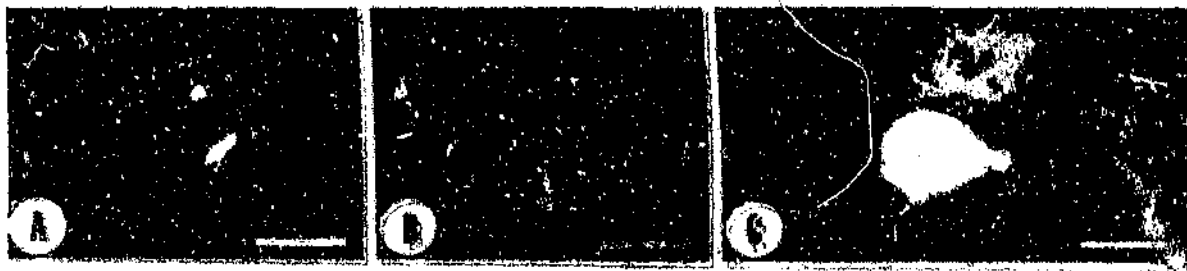


PLATE 33

Development of the juvenile gametophyte of D. longifolia.

- A Sporeling showing early development of the second rhizoid and development of the thallus.
- B Sporeling with two well developed rhizoids and the initial stages of thallus development.
- C Detail of the initial stages of thallus development from a sporeling having two well developed rhizoids.
- D-E Multicellular thallus in the early stages of development.
- F-G Juvenile gametophyte showing dividing, meristematic cells at the apex.
- H-J Juvenile gametophytes with multiple rhizoids, multicellular, well-developed thalli, and clumps of hairs.
- K A fully developed juvenile with multiple rhizoids, an apical pit and the initial signs of surface differentiation of the cells of the midrib region.

Scale bar = 100 μ m



PLATE 34

Abnormal development of D. longifolia spores from 20°C cultures.

- A A well developed thallus with an under developed rhizoid.
- B-C Thalli which developed into more globular structures and developed a "jigsaw puzzle" shaped rhizoid tip.
- D-F Tetraspores with stunted rhizoids and exhibiting the "jigsaw puzzle", aseptate terminal outgrowths.
- G A "normal" rhizoid tip.
- H A rhizoid tip showing the aseptate, lobed "jigsaw" shaped protrusion common in the 20°C cultures.
- I A highly lobed example of the terminal protrusion.
- J-K Another abnormality observed in the cultures kept at 20°C, with the thallus and the rhizoids being deformed.

Scale bar = 50µm



Author: Blackmore Natalie Lynn.

Name of thesis: Studies on the brown alga Dictyopteris longifolia (Dictyotales), with special reference to the effects of wave action.

PUBLISHER:

University of the Witwatersrand, Johannesburg

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