The Development of Costaria, Undaria, and Laminaria.

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With Plates LIII-LV.

QUITE recently, Drew¹ has discussed the behaviour of the spores of *Laminaria*, and concluded that they are gametes and not zoospores. This diverges somewhat widely from the view hitherto held by eminent botanists for many years. Yet I hope his observation has revealed the truth, as there seem to occur in nature other cases which may be more easily explained by granting the fusion of two spores of Laminariaceae. For instance, *Hirome undarioides*, Yendo, stands as an intermediate form between *Undaria pinnatifida*, Sur., and *Laminaria radicata*, Kjellm., in its habit, texture, and propagating organs. An explanation of the genetic relationships between them may be facilitated if hybrids of Laminariaceous species have been proved possible.

Whatever the spores in the sori of Laminariaceae may be, and whatever sort of evolution takes place during germination, 'the full development from spore to adult has not yet been studied for any member of the Laminariaceae.'² Thuret³ briefly described and beautifully figured some embryonal stages of *Saccorhiza bulbosa* some sixty years ago; and this is the only direct evidence we have with reference to the sporelings of the Laminariaceae. Barber, Setchell, Reinke, Foslie, McMillan, Griggs, and others who have traced the stages of development in various members of the Laminariaceae have started from much later stages than Thuret described. Among these authors Setchell gives the most important account as regards the details concerning the development of the internal structure. As the result of the studies of these botanists we are led to believe, though without exact evidence on many particular points, that most members of the Laminariaceae are simply rows of cells at the beginning; that they then become monostromatic, and add the new layers of cells at the lower middle part of the lamina; that the simple

¹ Drew: Reproduction and Early Development of *Laminaria digitata* and *L. saccharina*. Ann. of Bot., xxiv, No. 93, 1910.

² Setchell: Post-embryonal Stages of the Laminariaceae. Univ. of Cal. Public., vol. ii, No. 4, 1905.

³ Thuret: Recherches sur les Zoospores des Algues. Ann. des Sci. Nat., Bot., 1850.

Laminaria-like frond increases in its length by intercalary growth, or, as Thuret calls it, by stipo-frondal growth, and adds to its thickness by the formation of cortex and medulla.

The present writer has had opportunities for years of collecting and examining the early stages of development of various species of Laminariaceae on the coasts of Japan. In most cases the mode of development of these members coincided with what we had reason to expect. Among them *Costaria Turneri* has supplied especially favourable material for investigation, and the results of the study proved interesting. The present paper is prepared to elucidate the development of this species in detail, as well as of *Undaria pinnatifida* and *Laminaria* sp., referring to some parallel accounts of other genera previously studied.

I must not miss this opportunity of expressing my hearty thanks to Dr. D. H. Scott for so kindly taking the trouble of looking over the manuscript and proofs. It is due to this that the present writer has been able to publish his paper on the opposite side of the globe.

I. COSTARIA TURNERI.

Costaria Turneri is an inhabitant of the North Pacific at low-water mark, descending to several fathoms of depth. It is found abundantly on the coasts of northern Japan, especially that of the Hokkaido Island (Yesso). In the vicinity of the Otaru Harbour, on the west side of the island, the plant begins to appear late in December. Numerous young fronds are found on rocks as well as on *Sargassum Thunbergii*, *Rhodomela Larix*, and some others which abound about there. These epiphytic specimens usually lose their anchorage as the fronds grow larger, and only those on rocks can survive to attain to their maturity. For the purpose of searching for the youngest individuals of the species, *Rhodomela Larix* serves as an especially suitable host. The latter is, at this season of the year, covered with *Sphacelaria*, *Ulothrix*, *Bangia*, &c., and the spores of *Costaria* seem to seek their resting-places among the filamentous Algae. Several young shoots of *Costaria* are usually found growing together at a point. An examination of such points under a dissecting microscope generally reveals a number of minute fronds of much earlier stages. I shall first treat of the embryonal stages and then trace the more advanced forms.

Embryonal Stages.

It is a rather puzzling matter to give an exact definition of the embryonal stage in the life-history of Algae. The term can by no means be applied with clear limitations as in animal embryology. For Laminariaceous plants Setchell¹ includes in the embryonal stages the development

¹ Setchell: Post-embryonal Stages of the Laminariaceae. Univ. of Calif. Public., Botany, vol. ii, 1905, p. 1.

from the germinating spore till the simple Laminarioid frond is completed, with its various medullary, cortical, and epidermal tissues. Reinke¹ insists upon the term 'embryonal stages' for all those before sorus-formation. In the present paper the term is taken as by Setchell, but a little extended; viz. from the sporeling up to the time when all the organs (the sorus excepted) found in matured plants have been indicated, though in a primitive state.

The youngest stage of *Costaria Turneri* that I could find was a confervoid body measuring about 70μ in length (Pl. LIII, Fig. 1). It was a simple filament of seven cells disposed in a row. The cells were cylindrical without any marked constrictions at the septal points, and the length was nearly equal to the diameter. The apical cell was more or less elongated compared with the rest, and was slightly swollen, with a round head. Chromoplasts were present in each cell, filling up nearly the whole room in the terminal cell, but rather poor in the others. The basal part of the confervoid body could not be examined in a satisfactory manner, as this portion was entirely hidden in the interwoven filaments of *Sphacelaria*, *Ulothrix*, &c. Judging, however, from observations on the later stages, it is very likely that the lowermost cell of the confervoid body is elongated into a long siphonal tube penetrating the felty substratum.

The growth of the confervoid body in length results from successive divisions of the apical cell in transversal planes perpendicular to the axis of the filament.

Areschoug² described the sporelings of *Chorda tomentosa* as becoming simple or branched monosiphonous filaments. Similar sporelings have been observed by Williams³ in certain members of the Laminariaceae, and by Okamura⁴ in *Leathesia*. Kützing⁵ delineated three very young stages of *Laminaria saccharina* growing in association. In his figure he indicated the confervoid, branching bodies at the base of a young plant. He does not mention them as young stages of the plant, remarking simply: 'Conferva-artige Fäden, welche den protonematischen Bildungen der Moose ähnlich sind.' It is very probable, however, that he regarded these bodies as the primary stage of the plant jointly illustrated with them. These facts might suffice to convince us that various brown Algae of three dimensions are at the beginning confervoid. In *Saccorhiza bulbosa*, according to observations by Thuret,⁶ the monosiphonous filament does not branch at all, and ceases to add to its own length after there are half a dozen cells in a row.

The zoospores of *Costaria Turneri* are freed from the mother frond late

¹ Reinke: Studien zur vergleichenden Entwicklungsgeschichte der Laminariaceen, 1903, p. 11.

² Areschoug: Observationes Phycol., iii, p. 15, Tab. I, Fig. 1.

³ Williams: Nature, vol. lxii, p. 613.

⁴ Okamura: Icon. of Japan. Algae, vol. i, No. 4, Pl. XVIII, Figs. 10-12.

⁵ Kützing: Phycol. Generalis, p. 345, Pl. XXIV, I, Fig. 5.

⁶ Thuret: l. c., Pl. XXX, Fig. 10.

in autumn or early in winter. If they germinate within a short time after liberation, the confervoid body observed must itself have passed through a resting stage of several weeks. Or, if the confervoid body had only just been formed as the result of germination, the spore must have had a certain period of rest. I am rather inclined to believe that the zoospores must pass through a resting period without germinating. The actual occurrence of this has been verified by Williams.¹ Okamura² reported on *Undaria pinnatifida* that its spores germinated in July, as he observed at Omori, near Tokyo, shortly after the liberation of the zoospores. In Tokyo Bay, the young blades of that species are first seen late in autumn or early in winter. If so, the filamentous sporelings of *Undaria* must have spent a few months in developing into a minute frond. Drew's recent observation that the gametospores produce several sporophytes after a complicated process adds a new and quite different case to those already recorded. His view, however, important as it is, requires further proof before universal acceptance.

In the next stage, the apical cell of the confervoid body no longer divides in a transverse direction, but by a longitudinal septum through the middle point. The longitudinal division extends downwards, leaving a few basal cells in the initial state. The result is a linear-spathulate lamina constructed with two rows of cells in a single layer, with the monosiphonous stipe attached to the lower end. An exactly similar stage has been illustrated by Thuret³ in *Saccorhiza bulbosa*.

Another longitudinal division takes place in the cells of the lamina by two planes parallel to the first division-plane. The apical two cells, resulting from the primary division, do not divide in this case. As a consequence, each terminal cell is now seated upon the two newly formed cells. Thus the lamina becomes practically composed of four rows of cells disposed in a single layer.

The second division above described begins its action in the cells next to the apical pair. The process goes on downwards, segment after segment, till it reaches the basal one upon the stipe.

Successive divisions proceed, after the secondary division has been completed. They take place in two directions, the one parallel to the sagittal plane and the other passing through the middle of each segment, and perpendicular to the other. In any case, the two contiguous cells which are seated beneath the apical pair and embrace the axis of the lamina divide one step further than the rest. The lamina in these stages eventually becomes obovate in outline, the broadest part being at about the level of the two cells just mentioned.

Figs. 1-5, Pl. LIII, illustrate the various stages of development referred to above, all carefully drawn by the aid of Abbe's reflecting camera. The

¹ Williams: l. c.

² Okamura: Botanical Magazine, Tokyo, vol. xv, No. 163, 1900, p. 230.

³ Thuret: l. c.

geometrical figure (Fig. 18) is diagrammatized from this series. From the diagrammatic figure it may be easily understood that the growth of the embryonal lamina of *Costaria Turneri* results from the division of the two initial cells situated side by side beneath the apical cap. This mode of cellular arrangement is rather disturbed in *Saccorhiza bulbosa*, judging from the figure given by Thuret,¹ and in *Undaria* and *Laminaria* as described below.

The cells which constitute the monosiphonous stipe elongate as the lamina extends, to a length much exceeding the diameter. At the same time they divide longitudinally and transversely, quite irregularly, to form a cylindrical stipe. The resulting cells are poor in chromatophores, and those in the lower part are entirely devoid of them. From the basal cells of the stipe, a few rhizoidal filaments are given off, in a manner reminding us of the root-hairs of a land plant (Fig. 5). Two forms answering to such a stage have been illustrated by Kützing² in *Laminaria saccharina*; in them, the terminal cells are shown in regular transverse zones, but their longitudinal arrangement is not in any apparent order.

When a plant has attained about 2 mm. in length, the monostromatic lamina becomes distromatic. The process is first carried on at the point which corresponds to the transitional region in an adult frond. The division of the cells is by a simple plane passing through the middle points between the two surfaces of the lamina. Hence, in the cross-section of a lamina at this stage, the sister cells of the two layers are exactly facing one another.

At this stage the cells at the transitional region undoubtedly play the part of a meristem, although the apical cells multiply as well. The activity of the latter, however, is gradually retarded as the blade is extended by the so-called stipo-frondal growth. Most former writers, if not all, seem to have omitted to recognize the apical growth of the sporelings of Laminariaceae, and hence the crucial stage in the mode of growth has not been hitherto considered. So far as I am aware, Reinke³ is the only one who, arguing from the figures given by Thuret, has remarked that the embryonal blades of Laminariaceae extend at first by cell-division in all parts of their area, and that afterwards the intercalary growth is localized in the transitional region.

While the lamina becomes two-layered after the monostromatic stage, the stipe becomes gradually thicker. Cross-sections show many polygonal cells compactly but irregularly arranged without any remarkable distinction in their size. The boundary between the distromatic lamina and the polysiphonous stipe lies, of course, at the transitional point.

When the stipe has become cylindrical the rhizoidal filaments are copiously given off from its basal point (Fig. 14). Each filament is simply

¹ Thuret : l. c.

² Kützing : l. c., p. 345, Tab. XXV, I, Fig. 5.

³ Reinke : Studien zur vergleichenden Entwicklungsgeschichte der Laminariaceen, 1903, p. 8.

an elongation of an epidermal cell without any septum throughout the whole length. This is somewhat different from the case which Kützing¹ has illustrated in *Laminaria saccharina*. Griggs² found tufts of filamentous strands at the base of *Lessoniopsis littoralis* which measured about 1.1 mm. in length. He has not remarked on the finer structure of the strands. The filaments, as the plant grows on, add to their number, resulting finally in a cluster of conical shape in general outline—the primary haptere. This process agrees in a striking manner with what has been observed in *Chorda* and *Punctaria*. Strömpfelt's³ description of the formation of the primary haptere of *Laminaria* is in some points inapplicable to our case.

Soon after the blade has extended its area by the stipo-frondal growth and its greater part has become distromatic, another layer of large parenchymatous cells makes its appearance. This layer originates from the transitional point between the blade and the stipe. So far as my researches extend, it has no direct genetic relation with the already existing two layers. In other words, the cells which constitute the new layer are generated at the transitional point from the internal cells of the polysiphonous stipe. As a striking analogy, I cannot help mentioning, superfluous as it may seem, the mesoderm formation in the primary stage of an animal embryo.

Fig. 21, Pl. LIV, shows a cross-section through the upper part of the four-layered area of a frond about 1.5 cm. in total length. About the point *a* the axis passes; the right half and the left monostromatic marginal part are not shown in the figure. About *b* we clearly find the new layer interposed between the older two. The cells composing the latter still correspond to one another in their position, though somewhat more disturbed than before. Those of the new layer are quite different in size from those of the two older layers, and the septa are not at all related. At the point *c* we find a distromatic portion without any layer interposed, and about *d* the lamina in the initial state. In the middle of the frond, the new layer is again split into two; each cell of one layer has its double in the other, showing that the two facing layers are sisters. These two new layers initiate both the cortex and the medulla in more advanced stages, as will be explained hereafter. Hence I prefer to assign the name 'precortical layers' to them for the sake of convenience.

Fig. 20 shows the cross-section of the same frond through the apex of the tristromatic area. Here we see the terminal cell of the new layer penetrating the apical portion of the distromatic area.

¹ Kützing: l. c., Tab. XXV, I, Fig. 5.

² Griggs: Juvenile Kelps and the Recapitulation Theory. American Naturalist, vol. xviii, No. 506, 1909, p. 10.

³ Strömpfelt: Untersuchungen über die Haftorgane der Algen. Bot. Centralbl., Bd. xxxiii, 1888, p. 398.

Longitudinal sections of fronds at a similar stage of development have revealed that the constituent cells of the precortical layer are isodiametrical, but much flattened. The length and the breadth are 3-4 times as large as those of the pre-existing cells, but the height is nearly alike. The relative sizes of the cells of the three layers may also be recognized by observing such fronds in surface view after being stained and clarified *in toto*.

When the lamina has attained to 5-7 mm. in length, its general outline becomes lanceolate or elliptical-lanceolate with tapering base and acute apex. The length of stipe varies according to the place where the plant is growing. Those found among the caespitose filaments of *Sphacelaria* or such-like Algae naturally have the stipe longer (Figs. 6-10, Pl. LIII).

Kuckuck¹ has delineated a cross-section of a frond of *Laminaria* apparently corresponding to the above-mentioned stage. He has not given an explanation in full of what he has delineated. But his illustration suggests a conception diverging too widely from what I have observed on my material. I reproduce here the figure given by him (Fig. 22, Pl. LIV). Others besides myself might suppose from this figure that the middle layer is the primary one, and that the peripheral layers have been formed on both surfaces of the initial layer.

The process of gradual increase of the cell-layers is essentially the same in the blades of *Costaria*, *Undaria*, and *Laminaria* treated in the present paper. They agree in the formation of the peripheral or epidermal layers, as they may be termed, previously to that of the precortical layer. And so far as I have observed in Dictyotae, Zonariae, Punctariae, &c., which have one or more layers of parenchymatous cells between the two single epidermal layers, the formation of the latter from the former is a view hardly to be accepted.

The multiplication or the addition of layers has its centre practically at the transitional region. The process extends more rapidly in the longitudinal than in the transverse direction. The boundaries between the successive layers may be readily traced by observing such a lamina under a low power of the microscope after the specimen has been stained and clarified by a suitable method. Fig. 13, Pl. LIII, shows diagrammatically a frond which measures about 1.5 cm. in total length. In *Costaria* the formation and interpolation of the tertiary layer follows directly after the formation of the distromatic layers. The genuine distromatic structure is therefore in most cases able to be traced along the outer margin of the tristromatic area. Generally speaking, the boundaries of the different numbers of layers form concentric lines parallel to the periphery of the lamina, converging towards the transitional region.

Comparing the blades at these various stages of development, the

¹ Kuckuck: Bemerkungen zur marinen Algenvegetation von Helgoland. Wiss. Meeresuntersuch., N. F., Helgoland, 1906, p. 250, Fig. 19.

monostromatic part first formed seems to have never decreased in its area, nor does the distromatic, &c. In other words, the areas of simpler structure do not add any complexity to the tissue by the later development except for the extension in area. The additions of new elements always commence in the transitional region.

Close examination under a higher power of the microscope shows, however, that the boundaries are not in straight lines, but very irregularly serrated. Setchell¹ mentions a similar condition in the youngest fronds of *Saccorhiza dermatodea*. Besides, there are many small areas detached from the principal part, but with a similar addition of layers. This is especially the case for the distromatic layer. Such oases must have resulted from an abnormal meristematic activity retained in the cells of the monostromatic area. Fig. 16, Pl. LIII, illustrates a part of the lamina under such a condition, the shaded part signifying a di- or tri-stromatic area; Fig. 17 shows one of the oases still more magnified. The irregularity of the border line is due to the fact that certain cells in a group—areoles of cells as it were—which have been derived shortly before from the same mother-cell are simultaneously divided into two layers. Fig. 19 shows a part of Fig. 16 under a high power.

Kützing² seems to have observed a similar structure in an embryonal blade of *Laminaria saccharina*. He remarks: 'Man bemerkt, dass an einigen Stellen die Randzellen sich in kleine Kügelchen aufgelöst haben, die je 4 und 4 zusammenstehen (Exanthem?).' He seems to have regarded the areolar cells as having a pathological origin. I am rather inclined to suppose, if I may be allowed the suggestion, that his specimens had the epidermal cells plasmolysed.

In *Costaria Turneri* the apical portion of the blade remains in its monostromatic state for a considerable time. I found several specimens measuring 3-4 cm. in length, with the three costae already formed, which still had the apical region in a single layer of cells.

Similar stages of development—polystromatic lamina with monostromatic apex—have been recorded by Kützing, Kuckuck, Reinke, Setchell, Griggs, &c., in *Laminaria saccharina*, *L. ephemera*, *Saccorhiza dermatodea*, *Alaria esculenta*, &c. The present writer has collected many specimens of *Undaria* and *Laminaria* with a similar structure. Hence, it may be safely stated that most members of the Laminariaceae have once passed through such a stage during their life-history.

In *Costaria Turneri*, some species of *Laminaria*, and certain others, the apical growth seems to continue, however, in a slighter degree than before, even after the greater part of the blade has become polystromatic. It

¹ Setchell: Concerning the Life-history of *Saccorhiza dermatodea*. Proc. of Amer. Acad. of Art and Sc., 1891, p. 182, Figs. 1 and 2.

² Kützing: l. c., p. 345.

is some time after the formation of all the ribs that we find the lamina of *Costaria Turneri* with an eroded apex. Griggs¹ states that *Hedophyllum sessile* measuring 2.3 mm. in length had already 'several' layers of cells in the middle region and towards the base, but with a monostromatic edge. In *Lessoniopsis littoralis* measuring about 1.1 mm. in length he also found its lamina already 'several' layers of cells thick, even at the edge. Of the latter specimen he remarks: 'It hardly seems possible that there could have been any remnant of the one-layered lamina which had not been transformed into the many-layered adult blade.' In this respect he mentions *Cymathere* as the opposite case, 'in which a large portion of the embryonic lamina is not changed, but continues to grow and persists until the plant is more than 20 cm. long.' As regards the 1.1 mm. specimen of *Lessoniopsis* he does not state whether the apex had been eroded or not. Judging, however, from his figure, the apical portion is clearly worn away. Still, his remark above quoted remains open to question unless the apex of the lamina had been proved to be persistent. Putting aside this questionable case as exceptional, there is ample reason to conclude that in Laminariaceae the monostromatic area of the blade is sooner or later atrophied without developing into complex tissue.

Setchell² and McMillan³ give the name 'midrib' to the thickened area which runs longitudinally in the blades of *Saccorhiza* and *Pterygophora* respectively. In the present paper the area is mentioned under the name of meridional region in order to distinguish it from the true midrib. McMillan remarks that this area makes its first appearance in *Pterygophora*, when the plant has grown to several centimetres in height. So also in the case of *Laminaria* sp., as is described below. But in *Costaria Turneri*, the primary midrib is first seen as a longitudinal elevation in the polystromatic transitional region when a frond has attained 1 cm. in the total height (Fig. 6). To the naked eye, however, it is not yet sharply defined from the adjacent region. Transverse sections through such points reveal the first step in the formation of the midrib as a few parenchymatous cells aggregated beneath the precortical layer of the ventral side. I mean by 'ventral' the surface with the midrib elevated. The dorsiventrality of the lamina of *Costaria* is thus begun at an early stage of development.

After the primary midrib has been formed and the frond has attained about 1.5 cm. in length, the lateral ribs begin to come out, one on each half of the lamina. The new ribs are shorter than the primary one already in existence and are elevated on the dorsal surface. The three are parallel to one another for the greater part of their length, but gradually converge

¹ Griggs, l. c.

² Setchell: Concerning the Life-history, &c., p. 182.

³ McMillan: Observations on *Pterygophora*. Minnesota Botanical Studies, 2nd series, Part VI, 1902, pp. 725-6.

in the transitional region and finally unite together at the base of the blade.

Fig. 24, Pl. LIV, is drawn with the aid of Abbe's reflecting camera from a cross-section at the transitional region of a frond about 12 mm. in total length. The three ribs are clearly shown. The essential part of the ribs is built up of the subcortical cells, which are much more increased in number than in the other parts. The epidermal layer is a single sheet of cells, now anticlinally elongated.

The figure shows at the same time how the medulla is generated. The two layers of the precortical cells are separated one from the other by the intervening space filled with a gelatinous matrix. The latter substance is undoubtedly secreted from the precortical cells. As a consequence, the cell-ends facing the gelatinous matrix become convex by their own turgescence. The hyphal cells are now generated from some of the precortical cells on the side towards the space. At the time when the hyphae are just formed, they contain, as in the cortical cells, a small number of chromoplasts. It is, however, in the later stages that the hyphae fill up the medulla as a compactly interwoven filamentous tissue.

When a blade with the hyphae just formed is observed from the surface under a low power, they are seen as delicate veinlets traversing longitudinally the polystromatic area (Fig. 15, Pl. LIII). Their course has been very difficult to trace, owing, no doubt, to the fact that they run freely through the gelatinous matrix. This was also the case in *Undaria*. In *Laminaria* the two precortical layers remained in close contact for a considerable time after the hyphal cells had been well developed (Figs. 44-6, Pl. LV). More precise accounts of the formation of hyphae will be therefore given in a later chapter. It is noteworthy, however, that in some specimens of *Costaria* measuring 10 cm. or more, the upper part of the four-layered area remained without the hyphal cells.

Soon after the formation of the three ribs, a row of tiny bullations begin to attract our attention on both sides of the midrib (Fig. 10, Pl. LIII). The lamina continues its stipo-frondal growth, adding new bullae successively below. The bullation of *Costaria Turneri* is not a simple over-extension of the lamina at certain points. From the beginning it is an elevation and depression occurring regularly and alternately, and parallel to one another. They are slightly transversely stretched at right angles to the adjacent ribs. At a somewhat more advanced stage an end of the elevation—depression on the other surface—bends at right angles and parallel to the rib. The depression adjacent to the elevation also bends in like manner, but at the opposite end and in the opposite direction to fit the former. The process will be more easily understood by a glance at the illustration, than by imitating an enunciation by Euclid (Figs. 11, 12). Briefly speaking, the bullation reminds us of a sort of carved fretwork. These bullations

are undoubtedly due to the quicker growth of the area adjacent to the ribs, while the latter elongate at a less speed. Yet the characteristic regularity of the bullating process deserves special attention.

A similar bullation is to be seen in the young blades of *Laminaria cichorioides* and several others, and still more strikingly in the whole life of *Kjellmaniella* (*Laminaria*) *gyrata*. The bullation found in the blades of *Laminaria bullata* and its forms comes out at a later period of life and is rather of a secondary nature.

When a frond has reached a total length of 3-4 cm. another rib begins to appear in each marginal area. It is at first indicated by the formation of bullae along the external side of the lateral ribs (Fig. 11). The newly formed external ribs are elevated towards the ventral surface, i.e. similar to the midrib; they converge downwards with the already existing ones to meet together at the base of the lamina. After the new ribs have been completed, one more row of bullations makes its appearance along the external side of each rib (Fig. 12).

When the five ribs have been completed we generally find the monostromatic apex of the lamina more or less worn away. But the distromatic area may be still seen remaining in the upper portion of the lamina even after that.

The first appearance of cryptostomata takes place in the area between the first three ribs, after the bullation has begun to attract our notice. The seats of the hairs in such an area are more or less depressed below the surrounding epidermis, as shown in Fig. 26, Pl. LIV, but never so deeply as to be called pits even in an adult frond. The depression appears to be due to the fact that the cells in this area neither increase in diameter nor divide tangentially, while the surrounding epidermal cells are multiplying actively to extend the lamina.

In examining the earlier stages of the cryptostomata we find a group of epidermal cells almost simultaneously elongated in height and each finally septated (Fig. 25). I could never detect a special cell which corresponds to the so-called initial cell commonly occurring in the cryptostomata of Fucaceae.¹

The slight depression and the lack of the initial cell in the cryptostomata of *Costaria* are characters parallel to those of *Alaria*.² Exact similarity is found in *Undaria*, as will be seen below (p. 705). Comparing these members of the family with *Adenocystis*³ and *Saccorhiza*⁴ we might with safety come to the conclusion that the cryptostomata in Laminariaceous species are different from those of Fucaceous Algae in the mode of formation.

¹ Simons : A Morphological Study of *Sargassum filipendula* Bot. Gaz., vol. 49.

² Murray : On the cryptostomata of *Adenocystis*, *Alaria*, and *Saccorhiza*. Phyc. Mem., x, 1893.

³ Ibid,

⁴ Ibid.

Setchell¹ has found small clusters of hairs in *Saccorhiza dermatodea*, not only in the area of complex structure but also in the monostromatic part of the blade of some young specimens. In *Costaria*, the simplest structure provided with them, so far as I could ascertain, was not less than four layers of cells thick (Fig. 27, Pl. LIV). Before the three ribs have been marked out, no indication of cryptostomata could be found either in the four-layered area or in the transitional region of more complex structure. I am inclined to think from this fact that the cryptostomata are formed in all parts of the blade, though there may be differences in structure, after a plant has attained to a certain stage of development.

The primary haptere, after being formed in the manner before described, remains simple until the first three ribs have appeared. When the bullations begin to attract our notice, new rhizines are given off in a radiating manner above the primary one. These rhizines follow the growth of the frond to a certain extent, but mostly remain in the simple state. The new whorls of rhizines above the old ones grow and ramify to play the important part of the adult holdfast.

Post-embryonal Stages.

The appearance of the last pair of ribs may be taken as an indication that the embryonal stage of the plant has ended. At this stage, indeed, all the characters of the species that might be found in an adult frond are manifested, though in a primitive state.

The further development of the fronds after this stage is practically in the internal structure. Every element which makes up the blade, stipe, and holdfast gradually adds to its thickness and becomes more complicated. The external characters undergo but little change except that the size of the frond gains in an enormous degree. The fronds which measure 10–15 cm. at the end of December will attain to a total length of as much as 1.5 metres by the beginning of April. Among the minor changes in the external characters, the appearance of the longitudinal furrows on the stipe and the gradual change in the shape of the base of the lamina are to be mentioned.

As I remarked several years ago,² the general outline of the blade of a Laminariaceous plant undergoes gradual change by age. The important change is in the transitional region. Those species with a round or even cordate base of the lamina in the adult have, in a majority of cases, a cuneate or acute base while yet young. So also in the case of *Costaria*, as shown in Figs. 11, 12, Pl. LIII, and Fig. 29, Pl. LV. After a blade has been furnished with the five ribs, it begins to add to its length at a

¹ Setchell : Concerning the Life-History of *Saccorhiza*, p. 182.

² Yendo : Three New Marine Algae from Japan. Bot. Mag., Tokyo, 1903, vol. xvii, p. 101.

considerable speed, the breadth not following the growth in the same ratio. Late in spring we find many narrowly lanceolate blades, 30–50 cm. in length and 3–4 cm. in breadth, with the base gradually attenuating towards the stipe. At the beginning of summer the growth in length seems practically to have ceased in the blades and the increase in breadth becomes remarkable. The wearing away of the terminal portion of the blade proceeds downwards. As in other costated species the membranous part decays off one step further than the ribs. Finally the general outline of the blades become ovate with a broad cordate base (Fig. 29, Pl. LV).

At the stage when the growth in length of the blade becomes somewhat slow, a number of longitudinal ridges and furrows make their appearance on the stipe. They run longitudinally from the transitional region and disappear before reaching the holdfast. In dried specimens they are liable to be mistaken for the wrinkles caused by shrinking of the stipe on drying. The ridges have undoubtedly a certain connexion with the ribs in their position, but there seems to be no apparent rule in their relation. The intercostal area, however, becomes narrow at the transitional region and is always continued into one of the furrows. The ribs themselves have a furrow on each at the base of the blade. Some of the furrows are continuous for the whole way, but others are discontinuous (Fig. 29).

The cross-sections of the furrowed stipe show the arrangement of the subcortical cells in a peculiar manner. In general, the parenchymatous cells are arranged radially, as in other members of the Laminariaceae. Towards the depressions, however, the cell-rows gradually converge and in the elevations they diverge (Fig. 31). In the latter case the cell-rows do not radially split to increase their number fastigiately, but each cell below the anticlinal point is much stretched tangentially, as shown in Fig. 31. What makes it necessary to have such a peculiar construction in the stipe is at present beyond our comprehension. For the purpose of mechanical strength the structure of the ridges seems to be hardly expedient. Barber¹ has called attention to the fact that the ridge peculiar to the stipe of *Saccorhiza bulbosa* does not result from a rapid multiplication of the cortical cells, but from their increase in size. I mention this here as a curious coincidence in such widely different cases.

Harvey² described a perforated specimen of *Costaria Turneri* as a special form, calling it *forma pertusa*. It is, however, a rather aberrant case to find a frond of *Costaria Turneri* at an adult stage without any perforation. Generally speaking, a few holes are completed when a frond has attained some 20 cm. or so, and gradually increase in number as the blade extends. In the area above the transitional region, the holes are especially numerous, but in the upper portions of the blade new holes may also make

¹ Barber : Development of *Laminaria bulbosa*. Ann. of Bot., vol. iii, No. 9, p. 52.

² Harvey : Characters of New Algae, &c. Proc. of Amer. Academy, vol. iv, 1859, p. 329.

their appearance. The number of holes varies very much according to the habitat of the plant; in some cases there is a considerable number and in others only a few.

The mode of formation of the holes is essentially similar to that in *Agarum Turneri*, which has been studied by Humphrey.¹ In *Costaria*, however, the points of formation are not elevated on one side so remarkably as in *Agarum*. In a majority of cases one surface is slightly depressed and the other much more deeply (Fig. 28, Pl. LIV). The tissue at this point, with both surfaces thus drawn together, is gradually atrophied. The epidermal layer of the less depressed surface lasts longer than the other, so that a round, milky-white remnant of membrane may be often still found stretching over a small hole. The healthy borders of the two epidermal layers come together as the atrophied tissue melts away, and finally the scar is entirely healed. The youngest holes visible to the naked eye measure about 2 mm. in diameter. They are widened as the blade extends and may reach often as much as 1 cm. in diameter.

At the beginning of a post-embryonal stage the five ribs are evenly distributed in the lamina, dividing the entire breadth into six longitudinal strips. But in more advanced stages the marginal regions are far wider than the other intercostal areas and the lateral two ribs are more approximated to one another than to the midrib (Fig. 29, Pl. LV).

II. UNDARIA.

Embryonal Stages.

The early stages of development of *Undaria*, from the filamentous sporelings until about 2 mm. in total height, are in the essential points similar to those of *Costaria*. The cellular arrangement, however, so far as the specimens in my hands have shown, is not so regular as in the latter case. Even in the blades comparable with the stage shown in Fig. 4, Pl. LIII, the whole arrangement of cells could hardly be schematized in a simple geometrical figure. A frond measuring 0.9 mm. in total height, with a very short stipe and roundish blade—aberrant from the normal shape—had the cells in an especially disturbed condition.

The precortical layer makes its appearance when a plant has attained 1.7 mm. in total height. The mode of formation of this layer is quite similar to that in the case of *Costaria*. The tristromatic area, so far as any difference can be made out, is extended longitudinally, while attaining comparatively less width.

The young fronds a few centimetres high of *Costaria* and *Undaria* are hardly separable one from the other by the naked eye. But in *Undaria* as

¹ Humphrey: On the Anatomy and Development of *Agarum Turneri*. Proc. of Amer. Academy, 1886.

soon as the blade has attained to the length of 7.5 mm. or more, a conspicuous number of mucilage glands may be clearly seen under a hand lens. As an exceptional case I found a frond with the blade about 2 cm. in length and the midrib running half of its whole length—without the slightest doubt of its being *Undaria*—in which no gland could be detected.

The glands are far more numerous in the embryonal blades than they are in the youngest ligules of a more developed stage. They are denser in the marginal region than in the middle of the blade and the transitional region. Along the margin of a blade about 2.5 cm. in length I counted 120 glands in a square millimetre, taking both surfaces together.

The formation of the glands takes place after the hyphal structure has appeared in the meridional area above the transitional region. But when it has commenced its work, the glands are generated in the two-layered as well as in the more complex area (Fig. 34, Pl. LV). Hence, the formation of the glands is related to the age of a plant and not to the structure. In other words, the glands are formed after the epidermal layer has attained to a certain stage of development. An analogous case has been pointed out in the formation of cryptostomata in *Costaria*.

In my former paper¹ I have remarked that each glandular cell, as a rule, originates from a single cortical cell which is in contact with the epidermal layer. In the majority of Laminariaceae, the peripheral layers of the blade have distinct features from those of the underlying tissue in the cellular arrangement and in the cell-contents. In my use of the term 'cortical cells' I follow the practice of many algologists and mean the cells which constitute the layers interposed between the epidermal layers and medulla. It is a well known fact, however, that in the stipes the peripheral cells are hard to distinguish from the underlying layer, as the former give rise to the latter by the formation of tangential walls. German botanists include the whole portion of such tissue, in the stipes as well as in the blades, which has nothing to do with the hyphal cells, under the name 'Rinde'. Setchell² applies the term 'limiting layer' to the peripheral portion of the 'Rinde'. This layer is characterized by having its cells much smaller than those of the underlying layer. In a young blade which has a single layer of large parenchymatous cells between the well defined epidermis and medulla, he calls the interposed layer 'cortex'. And, in a more complex structure, he applies the term 'outer cortex' to the layers of small cells beneath the epidermis, and 'inner cortex' to those of large parenchymatous cells near the medulla. The outer cortex in his sense is nothing but the 'limiting layer' minus the epidermis. Barber³ also noticed in the stipes of *Saccorhiza bulbosa* that the peripheral two layers are constructed of much smaller

¹ Yendo: Mucilage Glands of *Undaria*. Ann. of Bot., vol. xxiii, No. xcii, 1909, p. 621.

² Setchell: Concerning the Life-history of *Saccorhiza*, p. 200.

³ Barber: l. c., p. 53, Fig. 11.

cells than the deeper-seated layers. He seems to believe all the layers to have originated from the same meristematic one, and he regards the above-mentioned differences as indicating that the growth of the stipe by formation of new cells is exceedingly slow.

In the young blade of *Undaria* I have noticed the transverse division of the well-defined epidermal cells in a plane parallel to the surface. The daughter-cells form a discontinuous stratum of cells under the epidermis; they are nearly equal in size to their mother-cells and much smaller than the pre-existing cortical cells. The latter are precortical cells or their derivatives. As the epidermis of the blade is a layer well defined from the beginning, the name 'limiting layer' cannot be applied to the resulting layers of *Undaria* without modifying Setchell's conception. The name 'Rinde', again, when applied to the tissue of the blade, comprises two distinct parts, one originating from the precortical and the other from the epidermal layers. Similarly the 'cortex' comprises the cells interposed between the epidermis and the medulla whatever may be the difference in their origin. The distinction of the cortex into outer and inner layers as proposed by Setchell in the case of the blades of *Saccorhiza* comes near to separating the tissues according to their origin.

Considering the origin of the glandular cells with reference to these conceptions, it may be advisable to modify my former statement concerning this point, as follows:—Each glandular cell, as a rule, originates from a subepidermal cell which has been generated from the epidermal cell above it.

The cryptostomata are produced from the epidermal cells after the glands have appeared. Their number is far less than that of the glands. On examining the mode of development of the cryptostomata, I cannot find any essential difference from what has been seen in *Costaria*, *Alaria*,¹ and *Saccorhiza*.² At the start, the position of the hairs is at the depth of one epidermal cell and is slightly depressed below the surrounding level. There is no special initiating cell comparable with that characterizing the Fucaceous cryptostomata (Fig. 35, Pl. LV).

The young blade of *Undaria* increases in area, adding the glands and cryptostomata proportionately. The appearance of the rachis takes place after the blades have attained at least 4 cm. in length. The primary rachis is constructed by cell-aggregation along the median line of blade. The origin of the cells is similar to that in the case of *Costaria*, but on both sides instead of one. The rachis is, of course, more sharply defined near the transitional region and gradually evanescent above. Such a stage of the plant is hardly distinguishable from the young lamina of *Alaria*, unless the presence of glands is taken into account.

¹ Murray: l. c., Plate XVI, Fig. 5-7.

² Murray: l. c.

Post-embryonal Stages.

The appearance of the four organs, rhizines, glands, cryptostomata and midrib, may be taken as marking the end of the embryonal stages of *Undaria*. The formation of pinnules and sporophylls remains to be accomplished before the individual is adult.

The indications of the pinnules are seen as minute lateral ligules on both sides of the base of the blade (Fig. 32). These ligules are shifted upwards, increasing more or less in size, as the blade grows at the transitional region. The result is the dentation of the blade margins near the base. New ligules are successively given off below the older ones as the plant grows larger and larger (Fig. 33). Full-grown adult plants have the blades 1.5-2.0 feet long and 6-9 inches broad. The ligules follow the growth of the blade, extending more in the transverse than in the longitudinal direction of the frond, to form the pinnules characteristic of the species. The sinuses between the adjacent pinnules are round, and in some forms they are very deep, approaching near the midrib, while in others they are comparatively shallow. It is clear from these facts that the extension of the ligules takes place in the entire area from the very tip down to the midrib. If the meristematic tissue were limited to the area in the transitional region near the midrib, the ligules should remain as dentations along the margin of the blade without adding to their size; and if it were situated in the ligule proper, the sinuses must reach down to the rib.

At the time when the primary ligules begin to appear, the cylindrical stipe becomes gradually compressed. In a middle-aged frond it is ancipitous, with prominent margins. The cross-sections of such a stipe show the medullary layer in a narrow strip bridging the space between the marginal ridges. The greater part of the section consists of thick-walled quadrangular cells, disposed in rows radiating from the medullary slit.

The sporophylls are practically over-extensions of the marginal ridges. As a plant approaches maturity, the marginal ridges extend in width as well as in length. The rate of growth in length of the sporophyll is far quicker than that of the stipe, which is often negligible at this stage. The undulation of the sporophyll naturally results. The matured *Undaria* has its stipe almost covered by the ruff-like foldings from both sides. As a rule, the extension is gradually propagated upwards from the point of its commencement. The point of commencement of the extension varies according to the locality where the plant grows. In the northern form, which has an enormous length of stipe, it is localized at the basal part of the stipe; in the short-stiped southern form the upper portions of the sporophylls are confluent with the base of the lamina. Moreover, in the southern form, sterile ligules from the margins of the sporophylls are generally found,

which is never the case in the northern. From these variations we may distinguish three forms of *Undaria pinnatifida*, Sur., thus:—

f. *typica*.

= *Undaria pinnatifida*, Sur. Illustr. Alg. du Japon, p. 77, Pl. VI–VII.
Ditto; Alg. Jap., Pl. X.

f. *distans*, Miy. et Okam.; in Okamura, Nippon Sōrui Mei, i, p. 128.

= *Alaria pinnatifida*, Harv. Charact. of New Algae (Proc. Amer. Acad., vol. iv, 1859), p. 329.

= *Ulopterix pinnatifida*, Kjellm.; in Kjellm. et Peters, Om Japans Lam., p. 275, Pl. XI.

= *Undaria distans*, Miy. et Okam. Report on Fisheries of Hokkaido, vol. iii, p. 57, Pl. XXVI.

Stipite longitudinem laminae profunde pinnatifidae subaequante, sporophyllis ad basin stipitis limitatis, majoribus, nudis.

Notice.—The present form has once been mentioned with specific rank by Miyabe, but afterwards as a form by himself and Okamura jointly. In both cases the diagnosis has been incompletely given, in Japanese only. I hope these authors will publish their discoveries in full detail in a form universally accessible. The Japanese characters are, unfortunately for us, unfamiliar to scientific circles. The present writer feels obliged to mention the manuscript names.

f. *narutensis*.

Stipite brevissimo, sporophyllis pauci-undulatis lamina confluentibus e margine ligulas steriles proliferentibus.

III. LAMINARIA.

According to Miyabe,¹ there are three species of *Laminaria* in the vicinity of Otaru Harbour, viz. *L. ochotensis*, Miy., *L. religiosa*, Miy., and *L. cichorioides*, Miy. The former two are so nearly related that we very often meet with specimens to which either description may be applied equally well. In the sterile, and even more so in the young fronds, the specific distinction is almost impossible.

In April, 1910, I collected numerous sporelings of a *Laminaria* at the Marine Station of Oshoro, near Otaru. The specimens may be either *L. religiosa* or *L. ochotensis*, but I cannot tell to which species they belong, for the reason above stated.

An examination of the sporelings showed close agreement in various points with the results obtained by many former observers on various species of Laminariaceae, as well as with the above statements on *Costaria* and *Undaria*. *Laminaria*, however, is separated from these two essentially by the presence of mucilage canals and the absence of cryptostomata

¹ Miyabe: *Laminaria* Industry. Report on Fisheries of Hokkaido, vol. iii, 1899, in Japanese.

and midrib. As it may not be uninteresting to compare these three members of the order, and as some points seem worth mentioning, a brief account of the early stages of development is given below.

Embryonal Stages.

In my collection the youngest specimen measured 0.45 mm. in total length, with a lanceolate monostromatic blade and short stipe. The transitional region was already three-layered, as seen under the microscope by varying the focus. Although I was not able to find the confervoid stage of the present species, I do not doubt that it may be similar to what has been observed in *Saccorhiza* by Thuret and in *Costaria* by myself.

A specimen measuring 1.62 mm. in total length is shown in Fig. 36, Pl. LV. The greater part of the blade, except a small area at the transitional region, is monostromatic. In the apical point we see the coaxial hyperbolic arrangement of cells still beautifully regular (Fig. 37). In more advanced stages when the blade has attained 4 mm. or more, the complex structure in the transitional region is highly developed. The primary hyphal cells traverse it longitudinally, having a vein-like appearance, anastomosing with the adjacent ones by short lateral branches. The minute structure of these cells, together with their relation to the precortical cells, is vividly seen in this species, by observing the blade *in toto* under a microscope. In *Costaria* and *Undaria* we could not trace the veinlets completely (Fig. 15, Pl. LIII). Fig. 45, Pl. LV, is drawn from a specimen with the frond about 2 cm. in total length. It is from about the middle part of the blade. In the lower portions towards the transitional region, the hyphae gradually become hard to trace, as the complexity of the structure makes the preparations less translucent. It will be recognized from this figure that room for the passage of the hyphae is sought in the intercellular spaces of the precortical cells. But this fact is more easily understood when observed in cross-sections of the blade at earlier stages.

Figs. 43 and 44 are cross-sections through the middle part and the transitional region respectively of a frond about 5 mm. in total length. In the former we see two hyphal cells in section at the meeting points of four rectangular precortical cells. An exactly similar figure has been drawn by Kützing¹ from a four-layered stage of *Laminaria saccharina*, though he does not give a full explanation of it. In the transitional region, which shows a more advanced state of the tissue, the two layers of the precortical cells are separated by the gelatinous matrix interposed between them. The hyphal cells are no longer compressed in the intercellular spaces, but have a free medium around them. They terminate at the external limit of the four-layered area, finally joining on to a comparatively small precortical cell.

¹ Kützing: Phyc. Gen., Pl. XXIV, I, Fig. 3.

The latter, as in the case of *Costaria* above alluded to, result from the division of the pre-existing cells. The lower limit of the hyphal strands runs into the complex tissue of the transitional region. Judging from these facts, the hyphal cells seem to be added to the distal ones at the transitional region. They elongate to follow the extension of the surrounding area, keeping their original diameter. Hence, it may be understood that the primary septa of the hyphal filaments, at least in the embryonal stages of the blades, do not result from the division of the already completed hyphal cells. At a later period new hyphal cells may grow out as branches of the inner cortical cells, or the older cells may multiply by formation of septa. It is very interesting to note that the junctions of the hyphae are mostly at the intercellular spaces of the precortical cells; and that the expansion of the terminal portion of the cell, to form the so-called trumpet cell, is already to be seen at such an early period of development.

Taking the results obtained in *Costaria* and *Undaria* into account, it will be clearly seen that the sporelings of the Laminariaceous Algae start at first from a simple cell-row, then become monostromatic, distromatic, and so on, and finally proceed to the complex structure with hyphal tissue in the medulla. This accords satisfactorily with the conclusions arrived at by former investigators. One thing, however, remains to be remarked about the sclerenchymatous cells of *Saccorhiza dermatodea* which were termed 'tubular cells' by Setchell.¹

Setchell² describes, in a very young blade of *Saccorhiza dermatodea*, a layer of the tubular cells interposed between the two epidermal, or, as he calls them, limiting layers. These tubular cells are, according to him, an important element of the medulla in the blade and stipe. He further describes a plant which has the first set of hapteres well developed. In it, at the tip of the blade, he finds 'a well-defined limiting layer on each surface, and within this, on both sides, a cortical layer of a single series of cells, and in the centre the medulla, represented by a few scattered tubes'.³ He has nowhere given any decisive information relating to the origin of either the tubular cells or the cortical cells. But it is possible to understand from what he describes in various parts of his paper, that he regarded them both as having originated from the epidermal layers. It naturally follows from his statements that the medullary elements at the beginning, and the cortical at the next stage, are generated from the primary epidermal tissue.

The same writer attributes the origin of the hyphal cells to the ramifications of the inner cells of the two- or three-layered cortex. This leads us to suppose that in *Saccorhiza dermatodea* the hyphal cells are developed at a somewhat later stage than in our plants.

As in the case of *Costaria* and *Undaria*, the blades of the present

¹ Setchell: Concerning the Life-history of *Saccorhiza*, p. 195.

² Ibid.

³ Setchell: l. c., p. 204.

Laminaria, even after they have attained to several centimetres in length, still keep their primitive structure. In a blade of 5–6 cm. in length we usually have the apical portion in a monostromatic state, and the greater part of the area in the four-layered condition. The diagrammatic figure showing the boundaries of the different numbers of strata is represented in Fig. 39, Pl. LV. Compare this with Fig. 13, Pl. LIII, which is of *Costaria*. Only in the transitional region do the precortical layers leave some spaces between them filled with a gelatinous matrix; they are in close contact in the remaining area. The meridional area can only be distinguished from the marginal when a blade has attained 10–12 cm. in length. In the younger stages the marginal parts of course have a more simple structure when compared with the middle. Still, we can by no means regard the latter as the indication of the meridional area.

In most Japanese forms of *Laminaria*, the meridional area is much thicker than the marginal regions. It has, in some species, a different structure when compared with the latter. For example, the meridional area of some species is provided with double layers of lacunae while there is a single layer in the marginal regions. Still more remarkably, the meridional area is depressed on one surface and elevated on the other. Along each side of the area, in *Laminaria ochotensis*, there is a narrow canaliculation which dies out near the transitional area. In some species the meridional area is comparatively narrow, and in others much broader. The cross-sections of a blade, therefore, give a bilaterally symmetrical undulating figure, characteristic of the species (Fig. 46, Pl. LV). Actual observation of the growing plants reveals that the depressed meridional area is always turned towards the source of light unless disturbed by an external mechanical force. The appearance of sori mostly begins on the shaded side, and is often limited to it. Thus in the blade of *Laminaria*, at least in the Japanese forms, there is a dorsiventral differentiation.

The dorsiventrality of the blade in the species under consideration is indicated in the transitional region when a plant has attained 2 cm. in total length. The one side, probably the future under-side, is elevated, while the other remains flat (Fig. 38). The characteristic canaliculation, however, becomes recognizable in much more advanced stages, viz. after a blade has attained 50–70 cm. in length. In some individuals two rows of dimples with regular intervals appear on both sides of the meridional area, no doubt owing to the difference in the speed of growth of the two areas. The canaliculations are not really distinct until the dimples have disappeared.

The differentiation in the internal structure of the stipe is first to be noticed when a plant has attained 4–5 cm. in total length. The medulla is not sharply delimited from the inner cortex, but may be more or less distinguished by the cellular arrangement. The loose anastomosing structure of the hyphal cells is limited to the base of the transitional region (Fig. 38).

In a primary stipe which is a few millimetres in length, the medulla is quite wanting. As the meristematic point lies in the transitional region, and as the hyphal cells are generated after the precortical layers have been formed, the lack of the medullary tissue in the primary stipe is to be expected. Barber,¹ speaking of the stipe of *Saccorhiza bulbosa*, states that in the portion below the ridge and in the hapteres there is no formation of the hyphal tissue. Setchell² noticed also in a young frond of *S. dermatodea* the presence of the hyphal cells at the transitional point only.

The primary root of a plant measuring about 2 cm. in total length is round and disc-shaped with a diameter of about 1 mm. (Fig. 40, Pl. LV). The periphery is still felty at this stage. When a frond has attained the height of 7 cm. or so, the disc-shaped root extends horizontally, forming a haptere or scutellum with an uneven surface and a few shallow notches on the margin (Fig. 41). The periphery is now thick and rounded, and is undoubtedly constructed of a compact tissue of minute cells. Indications of the future rhizines may be seen as insignificant outgrowths around the point just above the primary haptere. These rhizines quickly elongate, the primary haptere extending as well, first horizontally, but soon bending downwards to form the primary holdfast (Fig. 42). The further development consists in the addition of new whorls of rhizines above the older ones, the diameter of the stipe and rhizines increasing at the same time.

The part of the primary stem in which the medulla was absent is practically lowered down as the stipe elongates, and becomes buried within a part of the axis of the holdfast. And this part decays away before long with the primary haptere. Hence, in an adult form, no part of the stipe is devoid of medulla.

The two species of *Laminaria* above mentioned are characterized by the constant presence of lacunae in the stipe as well as in the lamina. In these, the lacunae are situated close along the periphery and are regularly arranged, with narrow intervals between one another.

A search for the lacunae in young specimens gave a negative result. In a specimen with the total height 54 mm., maximum breadth of blade 21 mm., and diameter of stipe 2 mm., no indication of the lacunae could be seen in the whole length of the plant. The younger specimens of course were devoid of them. These searches have been carried out by making sections at every millimetre of the frond, and also by staining, *in toto*, in aqueous solution of aniline blue. The blade of *Laminaria*, suitably fixed beforehand, and preserved in alcohol, is dipped in aniline blue (after Ranvier) for half an hour; then washed thoroughly in 70% alcohol. The lacunae only are then stained a deep blue. Thus the presence and the distribution of the lacunae may be satisfactorily demonstrated.

The specimens collected in July and August, which had the stipes

¹ Barber: l. c., p. 54.

² Setchell: l. c., p. 197.

3.5-4.5 mm. in diameter, are provided with well-developed lacunae. But in a specimen collected late in June the lacunae are generally narrow and slit-like, although their number may be quite as great as in the August specimens. Unfortunately, I have no set of specimens from April to June, and so am unable to trace the exact stage of the plant when the lacunae begin to appear. It is a fact, however, that the lacunae in our species are not formed until the frond has attained a considerable height. The period when the first-year plant has ceased its quick growth in length and begun to add to its width may probably be the time of lacunae-formation.

GENERAL CONCLUSIONS.

1. The earliest stage of development of the sporelings of the Laminariaceae investigated is a confervoid body growing by a single apical cell. The confervoid body becomes monostromatic in the next stage, with a monosiphonous stipe. The growth of the monostromatic blade is initiated by the two cells situated side by side at the same level beneath the apical cell, the axis of the blade passing between the two cells.

2. The monostromatic blade becomes distromatic at its base; the monosiphonous stipe becomes polysiphonous at the same time. A new meristematic tissue begins to appear at the transitional region between the blade and the stipe.

3. The growth in length as well as in breadth is due, at a certain period, to both the apical and the stipo-frondal growth. The apical growth is gradually retarded, and finally ceases. Erosion of the apex of the blade follows next.

4. A single precortical layer of large parenchymatous cells is generated at the transitional region between the already-existing two layers. The former soon becomes two-layered, and adds to the number of its layers later on. Additions of layers of cells are, as a rule, limited to, and begin at, the transitional region.

5. The hyphal cells are generated as the precortical layer becomes doubled, and the expansion of their distal ends into a trumpet shape takes place at the intercellular spaces.

6. The rib and the meridional region are formed by special thickening of the cortical layers. The dorsiventrality of the lamina, if it exists, is indicated simultaneously with the formation of such parts.

7. In *Undaria* the mucilage glands are developed at an early stage, but in *Laminaria* the appearance of the lacunae does not take place before the blade has attained to a considerable length.

8. The cryptostomata in the Laminariaceae are not generated from a single initial cell. Each hair has its origin in an epidermal cell of equal value, except that those in the middle develop earlier than the peripheral cells.

EXPLANATION OF PLATES LIII–LV.

Illustrating Professor Yendo's paper on *Costaria*, *Undaria*, and *Laminaria*.

Figs. 1–31. *Costaria Turneri*.

PLATE LIII.

Fig. 1. Filamentous stage of a sporeling; the basal portion unknown, as it was hidden in a tuft of *Elachista*. $\times 450$. From a fresh specimen.

Figs. 2–4. Further advanced stages. $\times 450$. From fresh specimens.

Fig. 5. More advanced stage with root-strands just formed; the stipe has become polystromatic. $\times 150$.

Figs. 6–10. Stages from the beginning of the appearance of the midrib up to the formation of the three ribs. The shaded area shows the di- and poly-stromatic portion, and the non-shaded area the monostromatic. All in nat. size.

Figs. 11 and 12. Five ribs formed; the characteristic bullation is especially conspicuous along the midrib. Nat. size.

Fig. 13. A diagrammatic figure showing the boundaries of the variously layered areas; *a*, *b*, *c*, *d*, *e*, mono-, di-, tri-, tetra-, poly-stromatic respectively.

Fig. 14. Primary root of a frond measuring about 5 mm. in total length. $\times 150$.

Fig. 15. A frond before formation of the midrib; the outer area without shading is monostromatic, in which, however, oases of distromatic spots are scattered. Observe the irregularly toothed boundary of the polystromatic area. The hyphae are also seen as anastomosing, longitudinally running veinlets in the polystromatic area. $\times 15$.

Fig. 16. The upper half of the blade shown in the preceding figure more highly magnified.

Fig. 17. One of the small distromatic oases, showing the irregular cell-division; the underlying cells are shaded, with finer outlines. $\times 220$.

Fig. 18. Schematic figure reduced from Fig. 4, showing the hyperbolic arrangement of cells; *a*, *a*, the two initiating cells.

PLATE LIV.

Fig. 19. A part of Fig. 17 still more highly magnified; areoles of the epidermal cells, which have lately divided from a common mother-cell, are defined with thicker walls. The shaded area signifies the distromatic part; in this, the irregularity of the boundaries between the monostromatic and the distromatic is seen to be related to the areoles. $\times 220$.

Fig. 20. Cross-section of blade of a young plant about 1.5 mm. in total length, through the apex of tristromatic area; in the middle a primary cortical cell is seen. $\times 240$.

Fig. 21. Cross-section of the same lamina through the upper part of the four-layered area; about *a* the axis of the lamina passes. The areas with different numbers of cell-layers are seen with remarkable regularity. $\times 240$.

Fig. 22. Reproduction of a figure delineated by Kuckuck. The figure is said to show a cross-section of a blade of a young *Laminaria*. $\times 150$.

Fig. 23. Diagrammatic figure showing longitudinal section of a blade with the primary medulla formed.

Fig. 24. Cross-section of the transitional region of a plant with the blade about 12 mm. in length. $\times 100$.

Fig. 25. Cr ss-section of a blade with the three ribs just formed, to show the origin of the hairs. $\times 450$.

Figs. 26 and 27. Cross-sections of blade of a plant about 10 cm. in total length, through points about 1 cm. from the base and 2 cm. from the apex of the blade respectively. From a fresh specimen. $\times 450$.

Fig. 28. Cross-section of a blade through a hole in course of formation. $\times 25$.

PLATE LV.

Fig. 29. Lower portion of an adult frond. *p*, the perforations. Nat. size.

Fig. 30. Cross-section of the stipe at a point about 1 cm. from the base of the blade. $\times 2$.

Fig. 31. A part of the above, to show the structure of the ridges and furrows. $\times 54$.

Figs. 32-5. *Undaria pinnatifida* f. *distans*.

Figs. 32 and 33. Young blades with the midrib and the ligules formed. Cryptostomata are frosted over the blade except at the transitional region and on the midrib. Nat. size.

Fig. 34. Cross-section of blade of a plant about 6 mm. in total length, to show the 'Anlage' of three mucilage glands in the distromatic area. $\times 450$.

Fig. 35. Cross-section of blade through a young cryptostoma. $\times 450$.

Figs. 36-46. *Laminaria* sp.

Fig. 36. An embryonal frond with polystromatic transitional region. $\times 36$.

Fig. 37. The apex of the same. $\times 240$.

Fig. 38. Cross-section of the basal portion of blade of a plant about 2 cm. in total length. About a is the axis of the blade. $\times 240$.

Fig. 39. A diagrammatic figure to show the boundaries of variously layered areas; a, b, c, d, e , mono-, di-, tri-, tetra-, poly-stromatic area respectively.

Fig. 40. The simple primary root from a plant about 2 cm. in total height. $\times 10$.

Fig. 41. The same, from a plant about 7 cm. in total height; the 'Anlagen' of the rhizines are seen as small wart-like protuberances near the scutellate root. $\times 10$.

Fig. 42. A more advanced stage of the same, from a frond about 20 cm. in total height. $\times 5$.

Figs. 43 and 44. Cross-sections of middle and transitional region respectively of a blade measuring about 4 mm. in length. $\times 450$.

Fig. 45. A portion of four-layered area with hyphal cells seen from the surface by varying the focus. The small cells at the right hand show the epidermis; large cells, the precortical layer; the shaded cells, the hyphal filaments. The left upper side is the limit of the four-layered area. $\times 240$.

Fig. 46. Cross-section of blade of *Laminaria ochotensis* at middle part of its whole length. Nat. size.

19x220

25.

20.

24.

19 x 220

21.

25.

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