

Studies of South African Phaeophyceae. I. *Ecklonia maxima*, *Laminaria pallida*, *Macrocystis pyrifera*

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STUDIES OF SOUTH AFRICAN PHAEOPHYCEAE. I. ECKLONIA MAXIMA, LAMINARIA PALLIDA, MACROCYSTIS PYRIFERA¹

George F. Papenfuss

THE PRESENT paper is the first of a short series dealing with the development in culture of certain South African Phaeophyceae. The forms treated in this account are representative of three of the five families of the order Laminariales, viz., Alariaceae (*Ecklonia maxima*), Laminariaceae (*Laminaria pallida*), and Lessoniaceae (*Macrocystis pyrifera*). The results obtained agree with those of other investigators of this order. For the pertinent literature reference should be made to the papers of Kylin (1933), Hygen (1934), and Kanda (1936). The papers of McKay (1933) and Hollenberg (1939) contain valu-

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The writer wishes to express his appreciation to Professor R. S. Adamson for placing at his disposal the facilities of the botanical laboratory of the University of Cape Town where this study was made during the years 1935-1939, and to Professor Harald Kylin for granting the facilities of the botanical laboratory of the University of Lund where most of the manuscript was prepared. Dr. M. A. Pocock kindly prepared the photographs reproduced in this paper. During the course of the study, financial assistance was obtained from the following sources: the James Buchanan Johnston Scholarship of the Johns Hopkins University, a University Research Scholarship of the Research Grant Board of South Africa, and a grant from the Carnegie Corporation of New York provided through the University of Cape Town.

able information on the process of fertilization, and the former author gives a good account of the chromosomal cycle in the life history of *Pterygophora californica*.

METHODS.—The culture methods followed were those used by Kylin (1933) and others. Fertile parts of the plants were kept out of water for several hours or over night in covered glass jars. Pieces of the material were then placed in glass dishes containing filtered sea water and slides arranged on end along the sides of the dishes. After a period ranging from about thirty minutes to several hours, depending upon the number of zoöspores that had become attached to the slides, the latter were removed, all spores wiped from the one surface and the edges, and filtered sea water poured over the slides in order to wash off as many diatoms as possible. The slides were then placed on end in glass tumblers containing the nutrient solution,² the surface containing the spores facing the side of the tumbler. The tumblers were covered with glass dishes and placed in front of a southeast window in an unheated basement room, precaution being

² The culture fluid used was the one employed by Schreiber (1930). It consists of: NaNO₃, 0.1 gr.; Na₂HPO₄, 0.02 gr.; distilled water, 50.0 cc.; sea water, 1,000.0 cc.

taken that they were at no time exposed to direct sunlight. The nutrient solution was not renewed except when the cultures were kept for many months. In certain instances distilled water only was added at intervals to replace the water lost by evaporation. Desired stages of the sporelings were fixed in position on the slides with Flemming's weak solution for a period of five to ten minutes. The fixative was removed by rinsing the slides in sea water. A few drops of glycerine were then added to the slides and the lat-



Fig. 1. *Ecklonia maxima*, habit of plant, about 1/20 nat. size.

ter kept in covered boxes for several weeks to allow the glycerine to become concentrated. Cover-glasses were then placed on the slides and the latter sealed and stored for future study. In such preparations the sporelings retain their normal form and most of their color; no staining is necessary unless it is desired to study the cytology of the plantlets.

ECKLONIA MAXIMA (OSBECK) PAPENF.—*General remarks.*—This plant has been known for a long time as *Ecklonia buccinalis*, but it was recently pointed out by Papenfuss (1940) that the specific name *maxima* has priority.

The known South African distribution of *E. maxima* extends from Port Nolloth on the west coast

(Bright, 1938) to a place, Papenkuilsfontein, about six miles west of Cape Agulhas on the south coast, where the writer found it growing in abundance in 1937. This distribution is not continuous, however, for the species is absent, or is represented only by occasional stunted individuals, along the northern and the greater part of the western shores of False Bay. The absence or scarcity of *E. maxima* in this region is owing no doubt to the high sea temperatures that prevail there during the summer months.³ Isaac (1938), who has studied the temperature conditions of the South African coastal waters, states (p. 25): "It is safe to assume that, where more or less normal sized *Ecklonia buccinalis* grows, the mean annual temperature does not exceed about 14.6°C." The high temperature conditions that eliminate *E. maxima* from the flora of the northern and western parts of False Bay are apparently less marked or do not obtain along the central and southern parts of the eastern shore of this bay and in consequence the species reappears at certain stations along this coast, starting at the mouth of the Steenbras River, and extends eastward beyond False Bay as far as the locality near Cape Agulhas referred to above.⁴

In addition to South Africa, *E. maxima* has been reported from the following parts of the world: St. Paul Island in the southern ocean (Grunow, 1867), Tristan da Cunha (Kolben, 1719), Falkland Islands (Bory, 1826), Chile (Postels and Ruprecht, 1840).

The presence of *E. maxima* at St. Paul is not improbable, as this island has a number of other marine algae in common with South Africa. The occurrence of the species at any of the other localities is extremely doubtful, however. The record for Tristan da Cunha is based on Kolben's (1719, p. 298) statement that the plant was observed floating in the vicinity of the island during his voyage to South Africa in 1705. It is not clear from Kolben's account, however, that he actually was near Tristan da Cunha. According to Dr. E. Baardseth, algologist of the recent Norwegian expedition to Tristan da Cunha, the species does not occur at the island (personal communication). The record for Falkland Islands is based on the plant that Bory (1826, p. 594) described as *Laminaria flabellum*, a species that he (Bory, 1828, p. 99) later considered as a variety of *E. maxima*. Certain subsequent authors have also regarded *L. flabellum* Bory as being identical with *E. maxima*, but Hooker (1845, p. 160) and others are doubtful of the correctness of this interpretation. The Chilean record of Postels and Ruprecht (1840, p. 3) is based on specimens that were secured from the drift. Judging from their figure (plate 11), it seems very doubtful that the plant is *E. maxima*. The figure shows a specimen in which the pinnae are split

³ For a discussion of the factors that cause these high temperatures in this part of False Bay, see Isaac (1937a, pp. 658-659).

⁴ De Toni (1889, p. 790; 1895, p. 358) refers to a specimen of *E. maxima* in Herb. Kew that came from Algoa Bay. If this record is correct the specimen must have been obtained from the drift, as *E. maxima* does not grow in this region.

longitudinally to the base into several segments, a feature that I do not recall having seen in *E. maxima*.

In the juvenile state, the thallus of *E. maxima* consists of a simple, somewhat elongated, blade borne on a stipe. In slightly older stages pinnae develop along both margins of the blade, as will be seen from the youngest specimen in figure 1. The pinnae are initiated in the meristematic region at the base of the

The sori form broad elongated patches on both surfaces of the pinnae. Fertile plants were obtained during all months of the year but March, for which month the writer has no field data on this species.

Development of gametophyte.—The zoöspores like those of most other Laminariales lack an eyespot and exhibit no phototactic response. In this connection, it is of interest to note that in the laminarian

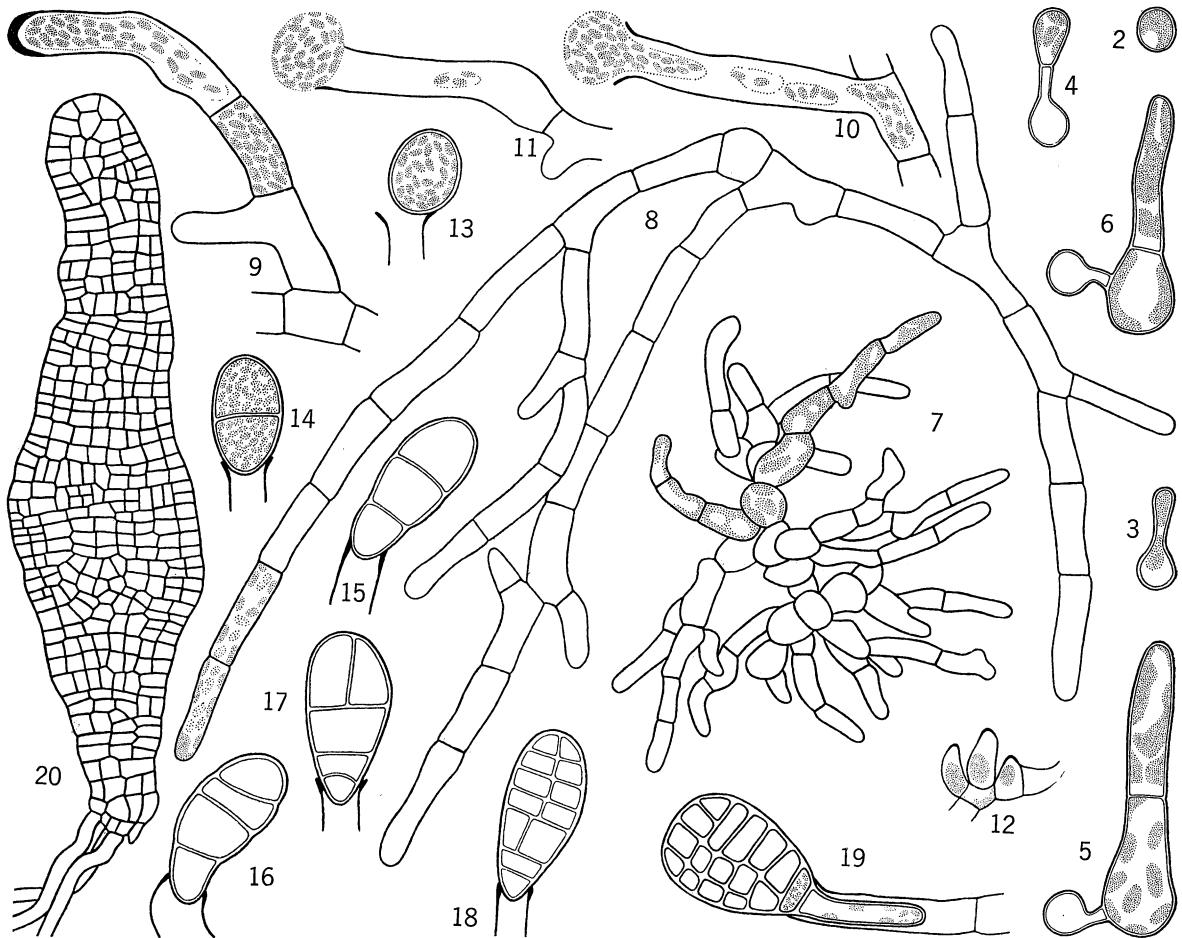


Fig. 2-20. *Ecklonia maxima*.—All figures are camera lucida drawings of plants grown in nutrient solution.—Fig. 2. Rounded zoöspore, $\times 990$.—Fig. 3. Gametophyte, 1 day old, $\times 990$.—Fig. 4. Same, 3 days old, $\times 990$.—Fig. 5. Same, \varnothing , 15 days old, $\times 990$.—Fig. 6. Same, σ , 15 days old, $\times 990$.—Fig. 7. Same, σ , 25 days old, $\times 650$.—Fig. 8. Same, \varnothing , 25 days old, $\times 440$.—Fig. 9. Oögonium with cytoplasm in an early stage of contraction, $\times 440$.—Fig. 10. Extrusion of egg, $\times 440$.—Fig. 11. Extruded egg, $\times 440$.—Fig. 12. Cluster of antheridia, one antheridium empty, $\times 990$.—Fig. 13. Zygote, $\times 440$.—Fig. 14-20. Stages in development of sporophyte. Fig. 14-19, $\times 440$. Fig. 20, $\times 290$.

primary blade and are progressively shifted upward by elongation of the latter. Later the distal portion of the primary blade is worn away and the pinnae become aggregated in a dense cluster immediately above the transition region (fig. 1), the older pinnae continually wearing away and new ones being initiated. In older plants, the stipe becomes hollow and its terminal portion becomes inflated, forming a large float. Mature plants may attain a length of seven meters or more from base of stipe to tips of longest pinnae.

Eisenia arborea the zoöspores show no reaction to light even though they possess an eyespot (Hollenberg, 1939).

After a period of motility ranging from a few minutes to several hours, the zoöspores come to rest, assume a rounded form, and secrete a wall about themselves (fig. 2). Germination sets in shortly afterward and in cultures that are twenty-four hours old many germlings may have well-formed germ tubes, and the single chromatophore may have divided once (fig. 3). As development continues, the chromato-

phores and most of the cytoplasm migrate into the terminal portion of the germ tube; and in cultures that are three days old this portion of the tube usually has been delimited by a cross wall from the spore case (fig. 4). At this time the chromatophores usually have undergone further division. During the succeeding seven to ten days, growth is more or less limited to enlargement, few additional cells being formed. In cultures that are fifteen days old, it is possible, however, to distinguish between female

tension which serves as the apical portion of the oögonium (fig. 10). The oögonia are readily recognizable by their dense content and by the fact that the cytoplasm pulls away from the wall. When mature the egg is extruded through a rupture that arises at the apex of the oögonium (fig. 10). A small amount of cytoplasm frequently remains in the oögonium. The extruded egg forms a spherical naked protoplast at the mouth of the oögonium (fig. 11), where it usually remains in position. The chromatophores

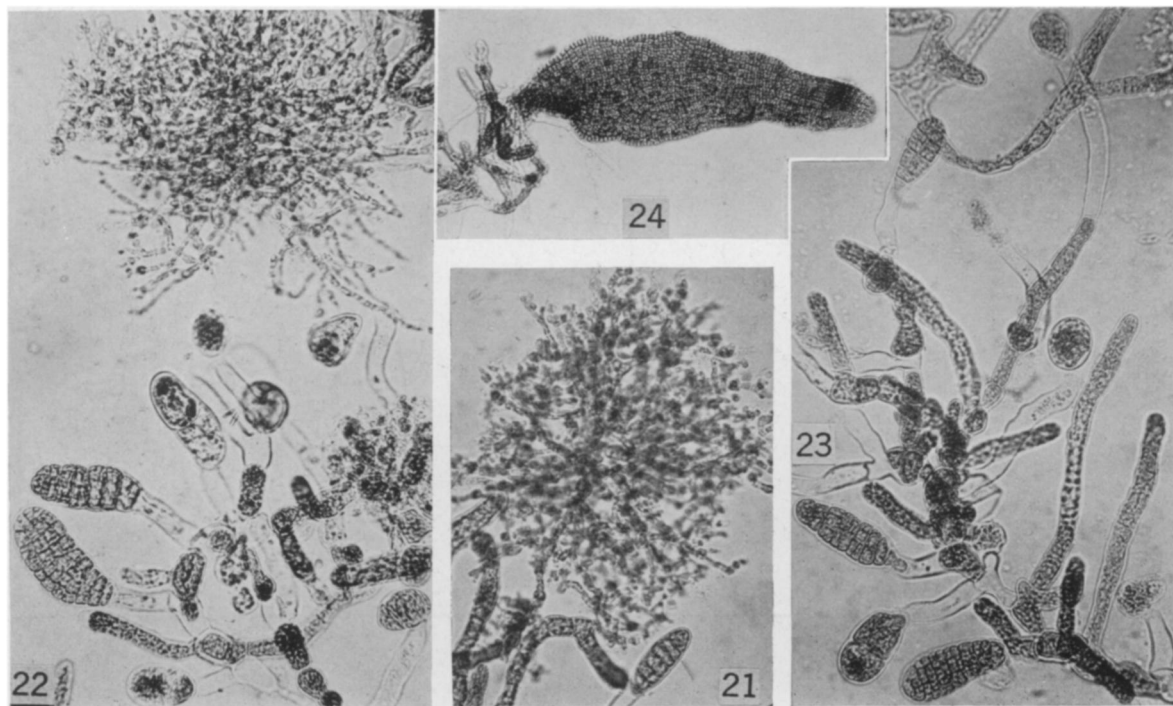


Fig. 21–24. *Ecklonia maxima*.—Photomicrographs of plants grown in nutrient solution.—Fig. 21. Male gametophyte, with portion of female at the lower end, $\times 200$.—Fig. 22. Male and female gametophytes, and several young sporophytes, $\times 200$.—Fig. 23. Female gametophyte with young sporophytes, $\times 200$.—Fig. 24. Young sporophyte, $\times 85$.

(fig. 5) and male (fig. 6) gametophytes, the female plantlets being of a greater diameter than the male. Not infrequently male gametophytes of this age may have formed the first branch and consist of a total of six cells. Subsequent growth continues at a comparatively rapid rate and in cultures that are twenty-five days old the male and female plantlets have assumed the form shown in figures 7 and 8, respectively. In male gametophytes of this age, the cells, especially the terminal ones, generally contain fewer and larger chromatophores than do those of the female plantlets. At this stage the first signs of the differentiation of reproductive organs, especially of the oögonia, may be observed; and in cultures that are thirty-five days old young sporophytes may already be present, although reproductive organs and sporophytes are usually not formed in abundance until the gametophytes are forty to fifty days old.

The oögonia (fig. 9) develop from terminal or from intercalary cells. When an intercalary cell is transformed into an oögonium it forms a lateral ex-

of the egg retain their identity and can be recognized during the entire maturation period of the egg (fig. 9–11).

Male gametophytes (fig. 21, 22) differ from female ones in being slenderer and much more profusely branched. The antheridia (fig. 12) are formed in clusters at the tips of the branches or as outgrowths from intercalary cells. Young antheridia may be distinguished from vegetative cells by their denser cytoplasmic content. As the antheridium matures, the cytoplasm withdraws from the wall and appears as a homogeneous brownish matrix. Each antheridium apparently forms but one spermatozoid.

Development of sporophyte.—Fertilization of the egg was not observed but the first noticeable change which presumably follows this process is the formation of a wall about the zygote (fig. 13). The zygote then elongates and ultimately divides transversely (fig. 14). The next few walls are also in a transverse plane (fig. 15, 16). Longitudinal walls then set in, starting at the terminal end (fig. 17, 18), and

as a result growth takes place in two planes, giving rise to a somewhat elongated monostromatic sporophyte (fig. 23). The plantlet shown in figure 19 has formed its first rhizoid. At times a second rhizoid may have been formed at this stage but usually it is formed considerably later. The rhizoids are always nonseptate and are usually unbranched; branched rhizoids were but rarely observed. The chromatophores present in a young rhizoid later degenerate.

The young sporophytes become distromatic at a comparatively early stage. The first cells to divide periclinally are those in the basal region, the part

prevail in these regions during the summer months (cf. Isaac, 1937b, p. 146).

In addition to South Africa, *L. pallida* has been reported from St. Paul Island in the southern ocean (Grunow, 1867, p. 51); the Canary Islands, the Atlantic coast of Morocco, the coasts of Portugal and northwestern Spain, and the southwestern part of the Mediterranean (cf. Dangeard, 1936, p. 101; Feldmann, 1934, p. 13). The plants from St. Paul probably are of this species, but those from the north-eastern Atlantic and the western Mediterranean have been shown by French algologists to be of a distinct

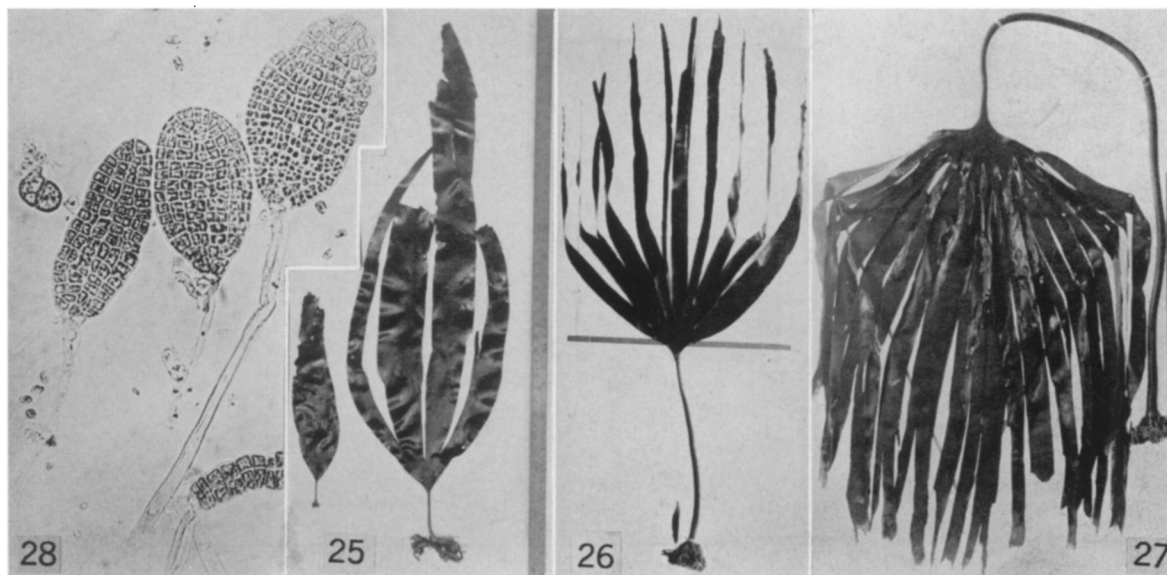


Fig. 25-28. *Laminaria pallida*.—Fig. 25-27. Stages in development of macroscopic phase of sporophyte.—Fig. 28. Young sporophytes of plants cultured in sea water. Fig. 25, about 1/12 nat. size. Fig. 26, about 1/33 nat. size. Fig. 27, about 1/30 nat. size. Fig. 28, $\times 200$.

destined to form the stipe. The sporophytes shown in figures 20 and 24 had already become distromatic in the basal region.

The development of gametophytes and young sporophytes described above is that which occurs during spring and summer. During winter months the gametophytes are considerably slower in attaining sexual maturity. This is in agreement with the findings of several other investigators of the Laminariales.

LAMINARIA PALLIDA GREV. EX J. AG.—*General remarks.*—The binomial *Laminaria pallida* is a MS. name of Greville under which the species was first described by J. Agardh in 1848.

The known South African distribution of *L. pallida* extends from the southwestern part of the Cape Peninsula to Port Nolloth (Bright, 1938) in the northwestern part of the Cape Province. The species increases in relative frequency towards the north (Isaac, 1937b; Bright, 1938), in which direction there is a gradual decrease in sea temperatures. The absence of the species along the east coast of the Cape Peninsula and points farther east is undoubtedly associated with the higher sea temperatures that

species which was described by La Pylaie in 1824 as *Laminaria ochroleuca* (cf. Hamel, 1931-1939, p. 303).

In the juvenile state *L. pallida* consists of a simple blade (fig. 25). The blade splits longitudinally at an early stage into several deep segments (fig. 25, 26) which, as growth continues, in turn become divided. In the mature state (fig. 27), the plant may attain a length of about 5 meters. Fertile plants were obtained during all months of the year but March, for which month the writer has no data. The sporangia form extensive sori on both surfaces of the segments of the blade. The histology of the sporophyte of *L. pallida* has been studied by Dangeard (1936).

Development of gametophyte.—In structure and behavior the zoöspores agree with those of *Ecklonia*. Stages in the development of the gametophytes and sexual organs are shown in figures 29 to 36. In *Laminaria pallida* the spore case is but seldom cut off by a cross wall from the germ tube, as in *Ecklonia* (compare fig. 4 to 6 and 31, 32). The plantlets do not usually become fertile until they are at least one month old; but at times, as shown in figure 34, sexual

organs develop on younger gametophytes. In older plants the antheridia occur in clusters, as in *Ecklonia*. The oögonia develop, as in *Ecklonia*, from intercalary as well as terminal cells of the female gametophytes (fig. 35).

Development of sporophyte.—The early stages in the development of the sporophyte will be seen from figures 37 to 42 and 28. In many sporophytes of the stage shown in figure 42, or even in less advanced ones, the basal cell will have formed the first rhizoid. Additional rhizoids are formed later from

coming fertile. The gametophytes in the sea water cultures were much smaller, however, than those in the nutrient solution. The sporophytes, on the contrary, appeared normal as will be seen from those of *L. pallida* shown in figure 28. The further development of the sporophytes was soon arrested, however, and they finally died without having attained as advanced a stage as did those developing in nutrient solution. The early development of reproductive organs in sea water cultures is undoubtedly owing to a starvation effect.

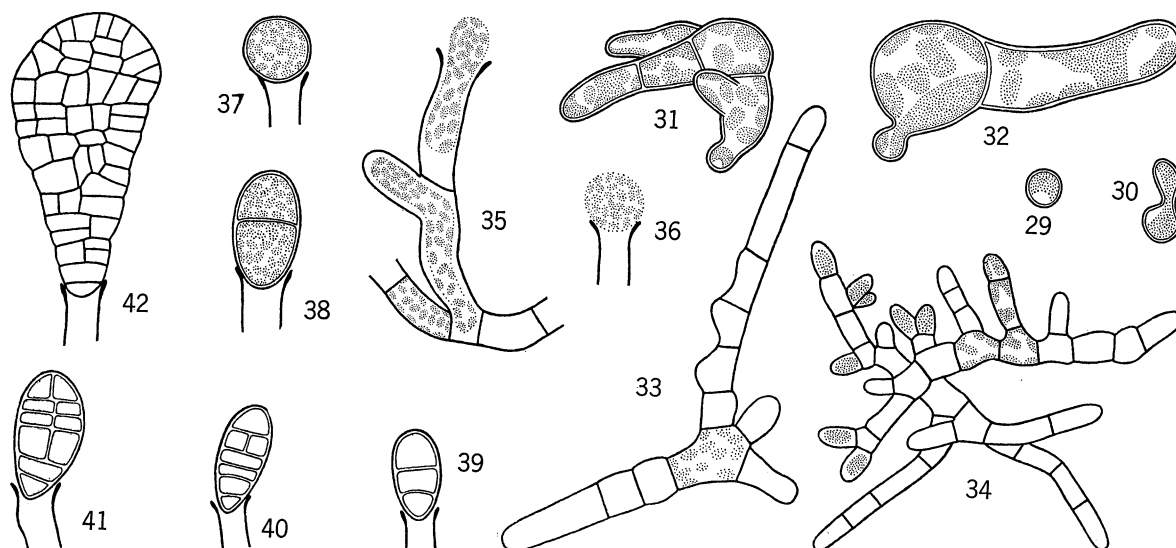


Fig. 29-42. *Laminaria pallida*.—All figures are camera lucida drawings of plants grown in nutrient solution.—Fig. 29. Rounded zoöspores, $\times 990$.—Fig. 30. Gametophyte, 2 days old, $\times 990$.—Fig. 31. Same, ♂, 14 days old, $\times 990$.—Fig. 32. Same, ♀, 14 days old, $\times 990$.—Fig. 33. Same, ♀, 25 days old, $\times 440$.—Fig. 34. Same, ♂ with antheridia, 25 days old, $\times 650$.—Fig. 35. Portion of female gametophyte with two oögonia, one in the process of extrusion, $\times 440$.—Fig. 36. Extruded egg, $\times 440$.—Fig. 37. Zygote, $\times 440$.—Fig. 38-42. Early stages in development of sporophyte, $\times 440$.

other cells in the basal region. As in *Ecklonia*, the rhizoids are nonseptate and but rarely branched. The young sporophyte shown in figure 42 had become distromatic throughout its basal half.

In connection with the development of gametophytes and young sporophytes, it is of interest to note that Harries (1932, p. 925), working on *Laminaria digitata*, *L. saccharina*, and *L. Cloustoni*, found that "... no growth occurs where the initial supply of sea water is not renewed and nutrient materials are not supplied." In the present study it was found, however, that the gametophytes of both *Laminaria pallida* and *Macrocystis pyrifera* will become fertile in sea water alone. Thus, for example, on October 29, 1935, four cultures were made of zoöspores from the same parent plants of *L. pallida* and *M. pyrifera*. In two of the cultures the fluid consisted of sea water only while nutrient materials were added to the other two. The vessels were placed next to one another some distance away from a window and the fluid was not changed. In the sea water cultures, sporophytes had been formed in both species after twenty-five days (November 23, 1935), while the gametophytes in the nutrient solution as yet showed no sign of be-

coming fertile. In the course of this study it was found that in certain nutrient solution cultures of all three species, the gametophytes form but few reproductive organs or remain entirely sterile. Thus, a culture of *L. pallida* that was started on November 20, 1935, was still growing actively on December 3, 1936, when it was discarded, without having become fertile. Other cultures made during the same month and year formed reproductive organs. In another culture of *L. pallida* that was started on May 14, 1936, a few sporophytes had developed after twenty-seven days (June 10) but no additional sex organs were formed, and the culture was finally discarded on December 3, 1936. In none of these cultures was the nutrient solution renewed; only a small amount of distilled water was added from time to time to replace the water lost by evaporation.

These results are comparable to those obtained by Hollenberg (1939, p. 38), who states: "When gametophytes of *Eisenia arborea* in the cultures once take on an elongate sterile form, I have been unable to induce the formation of sex organs, although I have tried low temperatures (2-3°C.) and changes

in light intensity as well as changes in nutrient concentration."

MACROCYSTIS PYRIFERA (L.) C. AG.—*General remarks.*—This plant has attracted the attention of naturalists and navigators since early times (cf. Hooker, 1845, p. 157). The species was described by Linnaeus in 1771 from specimens that were collected by König on his voyage to India. The source of König's plants, as given by Linnaeus, is "*Mare Aethiopicum*." Setchell (1932) attributes this name to certain Antarctic islands, but Papenfuss (1940) recently pointed out that according to old maps it applies to that part of the Atlantic which lies opposite Africa from the coast of Guinea southward.

fera in South Africa, it becomes evident that the area of distribution is limited to a comparatively small region lying approximately between latitudes 33° 24'S. and 34° 8'S. According to data presented by Isaac (1937a), the minimum and maximum annual sea temperatures of this region may be taken as varying between approximately 12° and 16°C. In consideration of the fact that in Antarctic regions *M. pyrifera* thrives at temperatures much lower than these (cf. Setchell, 1932, p. 446) and that along the west coast of South Africa there is a gradual decrease in sea temperatures from south to north, it would be expected that the species would extend northward for a considerable distance beyond Das-

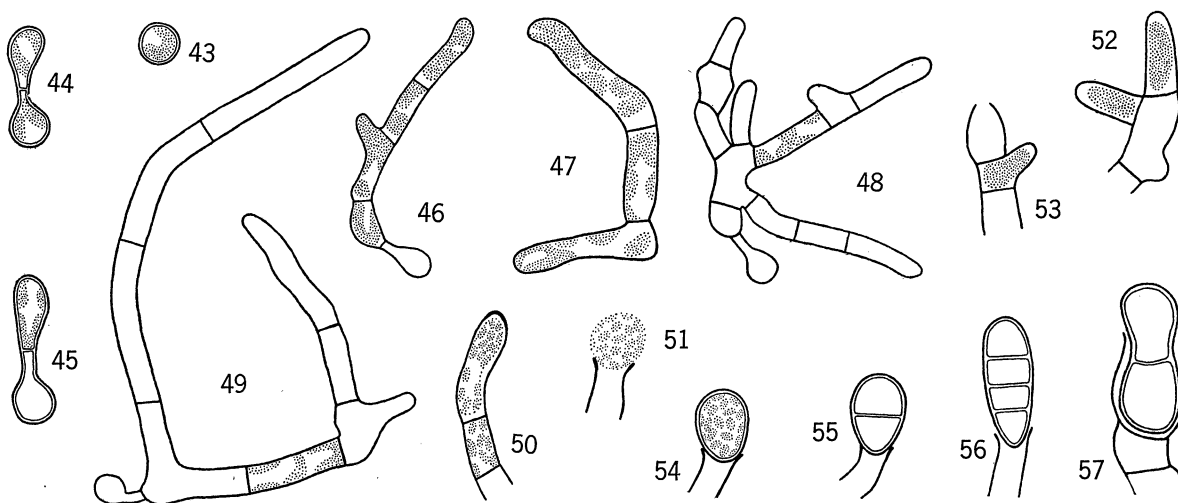


Fig. 43-57. *Macrocyctis pyrifera*.—All figures are camera lucida drawings of plants grown in nutrient solution with the exception of figure 57, which is of a plant grown in sea water.—Fig. 43. Rounded zoospore, $\times 990$.—Fig. 44. Gametophyte, 5 days old, $\times 990$.—Fig. 45. Same with spore case emptied of cytoplasm, 5 days old, $\times 990$.—Fig. 46. Same, ♂, 17 days old, $\times 650$.—Fig. 47. Same, ♀, 17 days old, $\times 650$.—Fig. 48. Same, ♂, 25 days old, $\times 650$.—Fig. 49. Same, ♀, 25 days old, $\times 650$.—Fig. 50. Immature oogonium, $\times 440$.—Fig. 51. Extruded egg, $\times 440$.—Fig. 52, 53. Antheridia, $\times 990$.—Fig. 54. Zygote, $\times 440$.—Fig. 55-57. Early stages in development of sporophyte, figure 57 showing a sporophyte developing within the oogonium from an unextruded egg, $\times 440$.

As is well known, *Macrocyctis pyrifera* has an extensive distribution, which has been discussed and mapped by Setchell (1932). As will be seen from Setchell's account this area is inhabited in part by a second species of *Macrocyctis*, *M. integrifolia* Bory.

The South African distribution of *M. pyrifera* is limited to the southwestern part of the Cape Province, extending from the Olifants River in the north to Cape Point in the south (i.e., approximately between latitudes 31° 42'S. and 34° 20'S.). It is likely, however, that the Olifants River record (Drège, 1843, pp. 107, 200) is based on a specimen that was cast ashore, in which event the northernmost known record of occurrence would be Dassen Island (Isaac, 1937b, p. 142). The southernmost locality, Cape Point (Delf and Levyns, 1926, p. 503), also requires confirmation. The species does, however, occur at Slangkop, a station in the central west coast of the Cape Peninsula. Assuming then that Dassen Island and Slangkop are the northernmost and southernmost limits of occurrence, respectively, of *M. pyri-*

sen Island. As yet there is no evidence, however, to support this supposition.

In South Africa *M. pyrifera* is a shallow water plant, inhabiting localities that are protected from the full force of the waves. The plants are much shorter than those recorded from certain other parts of the world and probably never exceed 15 meters in length, a dimension in excess of any of the specimens seen by the writer.

The morphology of the sporophyte of *M. pyrifera* has been the subject of a number of studies, the most important recent ones being those of Skottsberg (1907) and of Setchell (1932).

Fertile plants were obtained by the writer during all months of the year with the exception of April and June. This gap is filled, however, by Delf and Levyns (1926), who obtained fertile specimens during April, and by Levyns (1933), who secured some in June.

In South African plants, the sori seem to be confined to the smooth or but slightly wrinkled pinnae of

the basal short branches, whereas in the Falkland Islands, Skottsberg (1907) observed sori also on the wrinkled pinnae of long branches. The sori are formed on both surfaces of the pinnae and may occupy extensive areas or occur as isolated patches.

Development of gametophyte.—The development of the gametophyte and the early stages of the sporophyte have been studied previously by Brandt (1923), Delf and Levyns (1926), and Levyns (1933). None of these studies was complete, however, and certain statements required substantiation. Brandt misinterpreted the oögonium and referred to it as a proembryo.

In structure and behavior the zoöspores agree with those of *Ecklonia*. According to Delf and Levyns

As stated in the section on *Laminaria pallida*, the gametophytes when cultured in sea water become sexually mature within twenty-five days. Levyns (1933) obtained young sporophytes in a sea water culture that was seventeen days old (June 8–25). Gametophytes grown in nutrient solution are slower in attaining sexual maturity. In such cultures the writer has observed the differentiation of oögonia thirty-seven days after the culture was started (during spring), while in a culture that was forty-four days old reproductive organs were abundant (fig. 58) and sporophytes had been formed.

Development of sporophyte.—The development of the young sporophyte (fig. 54–56, 59) is in accordance with that of other members of the order. In

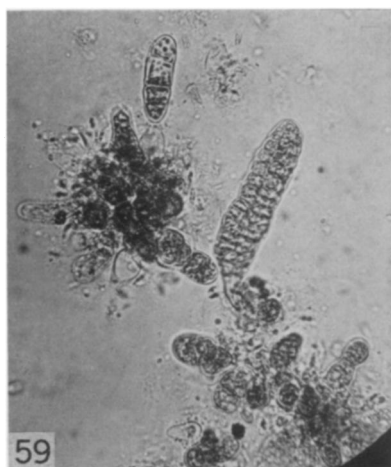


Fig. 58, 59. *Macrocyctis pyrifera*.—Fig. 58. Male and female gametophytes, the latter with extruded eggs, of plants cultured in nutrient solution, 44 days old, $\times 200$.—Fig. 59. Gametophytes and young sporophytes of plants cultured in sea water, 25 days old, $\times 200$.

(1926), the zoöspores of *Macrocyctis pyrifera* appear to be of two sizes; but the writer, in agreement with Levyns (1933), found them to be of the same size.

Stages in the development of the gametophytes and sexual organs are shown in figures 43 to 53 and 58. In the majority of gametophytes the spore case is emptied of cytoplasm, as shown in figure 45, but not infrequently this cell remains functional (fig. 44). The oögonia and antheridia are formed as in *Ecklonia*.

The statements of Delf and Levyns (1926) regarding the sexual nature of the gametophytes are contradictory. In their figures 1a and 1b are shown plantlets that were believed to be male and female gametophytes, respectively, while on page 505 they state: "The empty thick-walled cells at the base of the young sporophyte (fig. 2) seem to indicate a bisexual gametophyte. . . ." These authors obviously mistook empty oögonia for empty antheridia. Brandt (1923) makes no reference to male gametophytes, while Levyns (1933) describes and figures them correctly.

figure 57 is shown a two-celled sporophyte which was formed from an egg that had not been extruded from the oögonium. The retention of the ripe egg in the oögonium is an abnormal condition that was frequently observed in plants cultivated in sea water only and is probably associated with the general lack of vigor of such plants. In this connection attention may be drawn to the statement of Levyns (1933, p. 352) that: "In *Macrocyctis* the egg is fertilized within the oögonium, and the process of extrusion takes place *after* the zygote has been formed." The writer's observations indicate that Levyns, who had sea water cultures only, was misled in believing that the retention of the ripe egg in the oögonium represents the normal condition in *Macrocyctis*. Moreover, her conclusion that extrusion occurs after fertilization is probably based, judging from her figures, on observations of different eggs—some that were not extruded, some that were partially extruded, and others that were completely extruded. The writer's sea water cultures showed similar stages but the presence of young sporophytes within the oögonia (fig. 57) indicates that an unextruded egg remains in the oögonium even

after fertilization. With respect to the undischarged eggs, it is highly probable, however, that a rupture of the oögonial wall precedes fertilization and that the spermatozoid enters through this break. The body lying next to the partially extruded egg in Levyns' figure 8 probably does not represent the remains of the spermatozoid, as the author believes, at least not the one which fertilized the egg, since it has been shown by McKay (1933, pl. 14, fig. 2) and by Hollenberg (1939, fig. 22-25) that the spermatozoid completely coalesces with the egg during fertilization.

Finally, it may be noted that *Chorda Filum* is the only member of the Laminariales in which the ripe eggs are known to be normally only partially extruded from the oögonium (Kylin, 1933; Kanda, 1938). *Chorda*, however, differs from other Laminariales also in several other features, such as in the formation of hairs and of septate rhizoids by the young sporophytes.

SUMMARY

Ecklonia maxima, *Laminaria pallida*, and *Macrocystis pyrifera* inhabit the colder west coast waters of South Africa, *E. maxima* being the only species

of the three that extends eastward beyond the Cape of Good Hope.

The geographical distribution of *E. maxima* and *L. pallida* is discussed, and it is pointed out that St. Paul Island in the southern ocean is probably the only authentic extra-South African station for these species.

Fertile sporophytes of the three species were secured during all seasons of the year. The development of the gametophytes and the young sporophytes is similar to that described for other Laminariales.

In agreement with the observations of Levyns (1933) and in contrast to those of Delf and Levyns (1926), it was found that the zoöspores of *Macrocystis* are not of two distinct sizes.

In nutrient solution cultures the eggs of *M. pyrifera* are extruded from the oögonia, indicating that the retention of the egg in certain oögonia of plants cultured in sea water only is an abnormal condition and not a characteristic feature of this species, as was believed by Levyns (1933).

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PARASITISM AMONG THE CHYTRIDS ¹

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FUNGUS PARASITES of other fungi are fairly common in nature, but parasitism between closely related genera and species is comparatively rare. This is particularly true in the order of simple fungi known as the Chytridiales where only a few cases of parasitism have been found. Up to the present time only nine species parasitic on other chytrids have been reported, as is shown by the following list:

Olpidiopsis (?) *Sphaeritae* comb. nov. on *Sphaerita endogena* (Dangeard, 1889).

Pleotrachelus paradoxus on *Rhizophidium distinctum* (Petersen, 1905).

Tylochytrium dangeardii comb. nov. on *Saccomyces dangeardii* (Serbinow, 1907).

Phlyctochytrium Synchytrii on *Synchytrium endobioticum* (Köhler, 1924).

Rozella Polyphagi on *Polyphagus Euglenae* (Sparrow, 1936a).

R. maximum on *Chytridium Polysiphoniae* (Sparrow, 1936b).

Rozella sp. on *Rhizophlyctis rosea* (Ward, 1939).

R. Cladochytrii on species of *Cladochytrium* and *Nowakowskiella* (Karling, 1941).

R. Endochytrii on *Endochytrium operculatum* (Karling, l.c.).

All of these species are parasitic on chytrids, which in turn parasitize amoebae, algae, and higher plants or live saprophytically in dead vegetable debris. Of the nine species listed above, none attack hosts which belong to the same genus as the parasite, and only one, *T. dangeardii*, occurs on a host within the same family. Two of the parasites are extramatrical, eucarpic, and rhizidial, while the remainder are intramatrical, holocarpic, and *Olpidium*-like. To this latter group may now be added another species of *Rozella* which has recently been found in *Rhizophlyctis petersenii*.

Rozella is of particular interest to pathologists because all of its species are parasites of higher Oomycetes and chytrids and cause local hypertrophy or septation of the host hyphae. Although species of this genus have been recognized for more than a half century, very little is known about their development within the host. Nonetheless, students of *Rozella* divide the species into two groups on the basis of their development within the host and the reactions induced. Species in the so-called "sporangium-group" cause marked local hypertrophy of the host hyphae, and each thallus forms a single sporan-

gium or resting spore. In the "septigena-group" the thallus or plasmodium is reported to segment and give rise to a linear series of sporangia which mature in basipetal succession. The presence of the parasite also causes slight hypertrophy and leads to the formation of cross walls in the host hyphae, whereby the successive sporangia are separated from each other. However, no conclusive cytological data have been presented to support these distinctions. Cornu (1872) reported that after entry into the host the zoospores become indistinct and obscure but form a plasmodium in the center of host hyphae. While he found no conclusive evidence to support his view, he nevertheless believed it more plausible that the successive sporangia in *R. septigena* originate by fragmentation of the plasmodium than from multiple infection in basipetal succession. Fischer (1882) asserted that in the *R. septigena*, the type species of the "septigena-group," the parasite loses all individuality as its protoplasm mixes with that of the host and forms a plasmodium, which, however, eventually consumes the host constituent. At maturity this plasmodium divides into a number of portions which become permanently separated through the formation of cross septa by the host. Later, each portion forms one sporangium which completely fills the delimited segment of the host hypha. While it is true that the parasite usually becomes largely invisible in the relatively dense protoplasm of the host and gives the appearance of having fused with the latter, neither Fischer nor subsequent workers have clearly demonstrated its miscibility with the host protoplasm. Dangeard's (1890) figures of thalli from fixed, sectioned, and stained material, however, suggest that the host protoplasm is consumed completely by the time the thalli are mature.

Likewise, it is not certain whether the plasmodium develops from a single zoospore or is formed by the union of several protoplasts within the hosts. Butler (1907) upheld the latter view from his study of species in the "sporangium-group" but did not support it by cytological data. Furthermore, the development of the wall around the mature parasite in both groups is not clearly understood. Following Cornu's early description of the process, all students of *Rozella* have reported that as the sporangium wall of the parasite develops, it becomes fused so closely with that of the host that the two are indistinguishable and cannot be separated. While this type of development seems to occur, its successive stages have never been described or figured. In addition, our knowledge

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