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On the Gametophytes of Some Japanese Species of Laminariales V.

By

TIYOITI KANDA

In the third publication on the same line of research as this, the writer has discussed the distribution of Japanese Laminariaceous plants. As to the distribution they are divided roughly into two series of forms. The one is a cold current form, to which belong the following ten genera; *Thalassiophyllum, Streptophyllum, Pleuropterum, Cymathaere, Arthrothamnus, Alaria, Kjellmaniella, Agarum, Costaria* and *Laminaria,* being inhabitants of the northern colder seas, such as the Pacific coast of Hokkaido and the Kuriles, Okhotsk coast of the Kuriles and Saghalien, and the Japan Sea coast of Saghalien, Hokkaido and north-eastern parts of Korea. The other is a warm current form which includes the following five genera; *Eisenia, Ecklonia, Eckloniopsis, Undaria* and *Chorda,* being inhabitants of the southern warmer seas, such as the Pacific coast of Honsyū (the main island of Japan), Sikoku and Kyūsyū, and the Japan Sea coast of Honsyū and Kyūsyū. All the species of the cold current forms are limited to the coasts of Hokkaido, Saghalien and the Kuriles all to the northward of Tugaru Strait, which lies between Honsyū and Hokkaido, with the exception of some species which extend as far south as the coast of Miyagi Prefecture, and northeastern coast of Korea. Among the species belonging to the cold current form, following 24 species are supposed to be distributed chiefly on the coasts belonging to the Boreal District which is represented by the area including the greater part of the Kuriles, Saghalien and eastern parts of Hokkaido. They are *Laminaria longipes* BORY., *L. taeniata* POST. et RUPR., *L. subsimplex* MIYABE et NAGAI, *L. dentigera* KJELLM., *L. platymeris* DE LA PYLAIE, *L. yezoensis* MIYABE, *L. sachalinensis* MIYABE, *L. sikotanensis* MIYABE et NAGAI, *Cymathaere fibrosa* NAGAI, *C. triplicata* (POST. et RUPR.) J. AG., *C. japonica* MIYABE et NAGAI, *Streptophyllum spirale* (YENDO) MIYABE et NAGAI, *Arthrothamnus kurilensis* RUPR., *A. bifidus* (GMEL.) J. AG., *Thalassiophyllum Clathrus* POST. et RUPR., *Alaria fistulosa* POST. et RUPR., *A. praelonga* KJELLM., *A. macroptera* (RUPR.) YENDO, *A. dolichorhachis* KJELLM., *A. ochotensis* YENDO, *A. tenuifolia*

SETCH., *A. taeniata* KJELLM., *A. angusta* KJELLM., *Pleuropterum paradiseum* MIYABE et NAGAI and *P. fasciculatum* YAMADA.

In the summer of 1941, the writer visited the North Kuriles for the purpose of studying the life history of these Laminariaceous plants growing there. While staying in the North Kuriles for about 45 days, the writer has surveyed the coasts of Paramusiru and Simusyu Islands, and determined the maturation period of the Laminariaceous plants, and made the ecological research of the marine algae. At Suribati Bay, where the Kitatisima Branch Office of the Fisheries Experimental Station of Hokkaido, and many factories of some Fishing Companies are located, the writer has cultured the zoospores of *Alaria angusta* KJELLM. In the summer of 1942, the writer again visited the Islands, and stayed at Suribati Bay for about 40 days. This time the culture experiments were made at the office building of the Kitatisima Branch Office of the Fisheries Experimental Station of Hokkaido, until the 26th of August, when the resident official of that station has leaved the Island, and the station was shut. Henceforth the writer has moved into the room of office building of Kitatisima Suisan Co. Ltd., by the courtesy of Mr. S. KITIKAWA, the chief of Suribati Districts Branch of that company, and the culture experiments were continued at that place, until the latter part of September, when the writer left the Island.

In the present paper there are described the results of culture experiments with the gametophytes and the young sporophytes of six species of Laminariaceae growing on the coast of Suribati Bay, viz. *Laminaria subsimplex* MIYABE et NAGAI, *L. taeniata* POST. et RUPR., *Streptophyllum spirale* (YENDO) MIYABE et NAGAI, *Alaria fistulosa* POST. et RUPR., *A. praelonga* KJELLM. and *A. angusta* KJELLM.

Before going further the writer wishes to express his sincere thanks to Professor Y. YAMADA for his kind guidance and criticisms in the course of the present study. Thanks are also due to the Hattori Hōkōkai, for the pecuniary aid which helped him in carrying out the present study. Acknowledgements are also due to Mr. S. TAKAYASU, ex-Director of the Fisheries Experimental Station of Hokkaido, and to Messrs. T. KINOSITA and T. TAKAHASI, members of that Station, for their kindness to place at his disposal the seat necessary for the cultures. Further the writer is also much indebted to Mr. S. KITIKAWA, chief of Suribati Districts Branch of the Kitatisima Suisan Co. Ltd., for his kindness offered him during his stay in the North Kuriles.

XVIII. *Laminaria subsimplex* Miyabe et Nagai

This species is one of the representative species of the genus *Laminaria* in the North Kuriles. According to the report by Dr. M. Nagai (1940), the distribution area of this plant is from the North Kuriles to as far south as Simusiru Island of the Middle Kuriles. It grows on rocks or stones in the lower parts of the littoral zone or upper parts of the sublittoral zone, forming a large association together with *Laminaria taeniata* and *Streptophyllum spirale*. The shape and size of the blade as well as those of the stipe vary with the locality, and the plants having narrow blade are somewhat similar to the wide form of *L. taeniata*, and those having broad and thick blade growing in somewhat quiet shallow waters are rather similar to *Streptophyllum spirale* (Fig. 1). It becomes soriferous early in August. It is supposed that the liberation of zoospores continues for fairly long period, perhaps till the end of winter, because many small young sporophytes of the present species less than several centimeters in length are growing on rocks intermingled with adult matured ones of more than several meters in total length, when the writer collected the material for the culture experiments in August. The sori appear at first at the middle

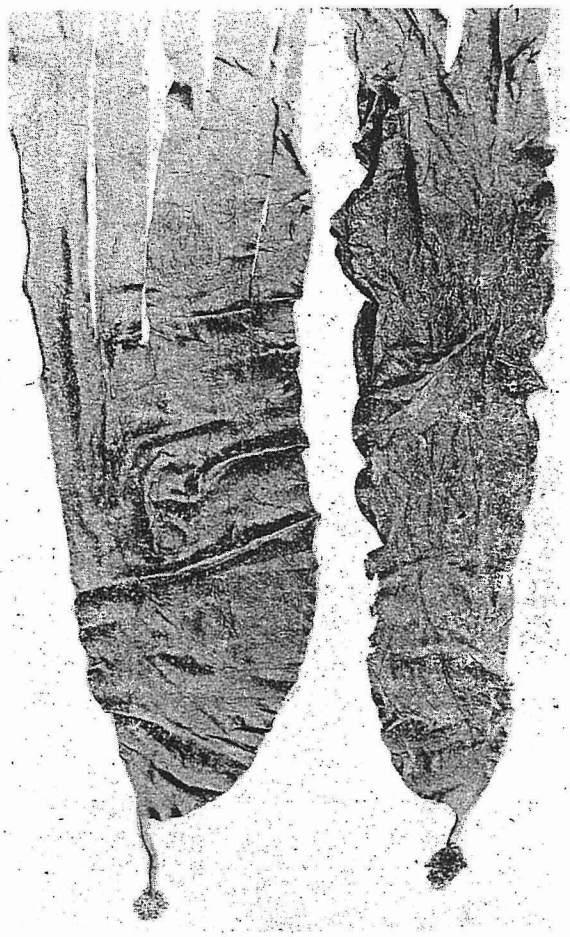


Fig. 1. *Laminaria subsimplex* Miyabe et Nagai. Habit of the plants, showing a digitate nature in blades.

portion on one side of the blade, forming a patch or patches with irregular outline. As the stages advance they increase their size in both directions upwards and downwards, till they cover the blade in broad area. The sori are formed on both surfaces when the plants reach full maturity.

The culture experiments were made twice in the summer of 1942. The first experiment was started on the 21st of August and the second one was on the 24th of the same month. The culture vessels were placed in a room with north-east exposure. But the culture-vessels were placed from time to time on the table in the shady outdoor, being prevented from a direct sunlight, for the prevention of the shortage of light intensity. Cultures were subjected to the fluctuation of air temperature, and no special considerations were paid for the regulation of the temperature of culture medium, though it ranged from 7°C to 17°C during the culture experiments. The temperature of sea water on the Suribati Bay coast ranged from 7.5°C to 10.5°C at this period. The fluctuation of 10°C of the temperature of culture medium was considered rather too much when compared with 3°C of temperature fluctuation of sea-water on the coast of Suribati Bay where the plants are growing in natural condition. The development of the gametophytes and young sporophytes were, however, very good in the present culture. The culture-medium was renewed every 5 days or a week and the culture-slides were washed carefully from time to time. Cultures were continued till the 23rd of September under these conditions when the writer left the Island. Some of these culture-slides were brought by steamer from Suribati Bay to Hakodate, and from Hakodate to the laboratory of the Institute of Algological Research at Muroran by rail, keeping them alive, where they were cultured till about the middle of October. Culture medium were renewed from time to time in the laboratory, but the temperature of the culture medium was not regulated, being exposed in the fluctuation of air temperature, ranging from 18°C to 21°C. The culture materials became gradually weakened from early in October, and they died completely by the 15th of the same month, when the writer gave up the experiment. It is supposed that the damage of these culture materials resulted from vigorous appearance of Protozoa and Diatom on the culture-slides which prevented the development of culture materials, as well as the elevation of temperature.

Zoospores and their Germination

The zoospore is pear-shaped when it is motile state, pointed at one end and rounded at the other, measuring about 8–9μ in length, 4–5μ in breadth;

it has two laterally placed cilia, one pointing forward measuring about 30–40μ in length, and the other pointing backward, being measured about 10μ. It has one chromatophore which fills the posterior part, one nucleus and some granular substances, but always lacks an eye-spot (Fig. 2, A). The zoospores are very active at first, but sooner or later their movement becomes slower; within 5–24 hours after the liberation of zoospores the majority of them assume a spherical form. They are invested with a membrane and become fastened to the slide-glass (Fig. 2, B). Soon after they have fastened to the slide, a germination tube grows out from the embryospore (Fig. 2, C). As the germination tube grows longer, the contents of the original cell migrates into this part, and within 48 hours a cross wall is formed so as to separate the distal end from the tube (Fig. 2, D–G). This distal end increases its diameter, and within 6 days, the cell division takes place in some sporelings. The gametophytes increase their sizes and some ones from 7 day culture, the diameter of cell is measured about 25μ in length and 10μ in breadth, being uni-cellular, while in others the diameter of cell is smaller being measured less than 8μ in breadth consisting of two or three cells at this stage. Later development shows that the former type of plants is the female gametophyte and the latter type is the male one (Fig. 2, H–M).

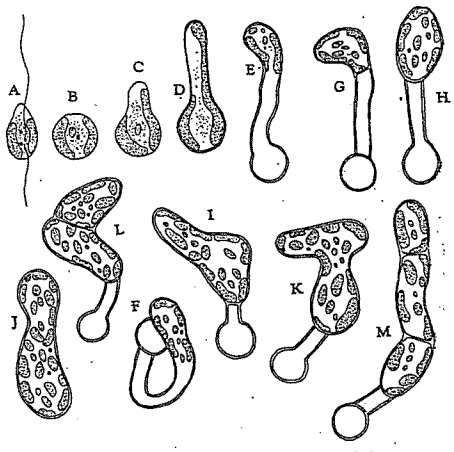


Fig. 2. *Laminaria subsimplex* Miyabe et Nagai. Zoospore and its germination. × 900. A. Zoospore in motile state. B. Embryospore. C–F. Development of the embryospore, from 6–24 hour culture. G–H. Sporelings from 2 day culture, showing the formation of transverse wall. I–K. Sporelings from 5 day culture. L–M. Sporelings from 7 day culture, showing the youngest stage of the male gametophytes.

Development of Male and Female Gametophytes

So far as the general appearances are concerned there is no striking characteristics in the male gametophyte of the present species. When the cultures are 10 days old, the male gametophytes reach maturation. Some of the apical cells, as well as intercalary, develop antheridia (Fig. 3, A–B). The content of the antheridial cell becomes paler in colour and more granular, and at last the cells assume a spherical form. The content of

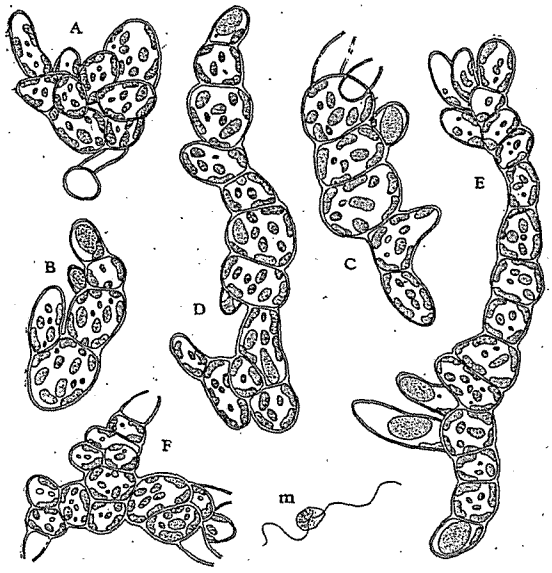


Fig. 3. *Laminaria subsimplex* MIYABE et NAGAI. Various forms of the male gametophytes. A. Mature male gametophyte from 10 day culture. B–F. Mature male gametophytes from 12–16 day culture. m. Male gamete in motile state. ×1000.

the antheridium is entirely used for the formation of a single male gamete (Fig. 3, C–E). At maturity the male gamete swims out from the opening at the apex of the antheridium, leaving an empty beak. The male gamete is ovate or rather round in shape measuring about 4μ in length. Two cilia of almost equal length, measuring about 10μ, arise from the lateral side of the body. Sometimes a pale remnant of chromatophores may be observed in it, but an eye-spot is always lacking (Fig. 3, m). The

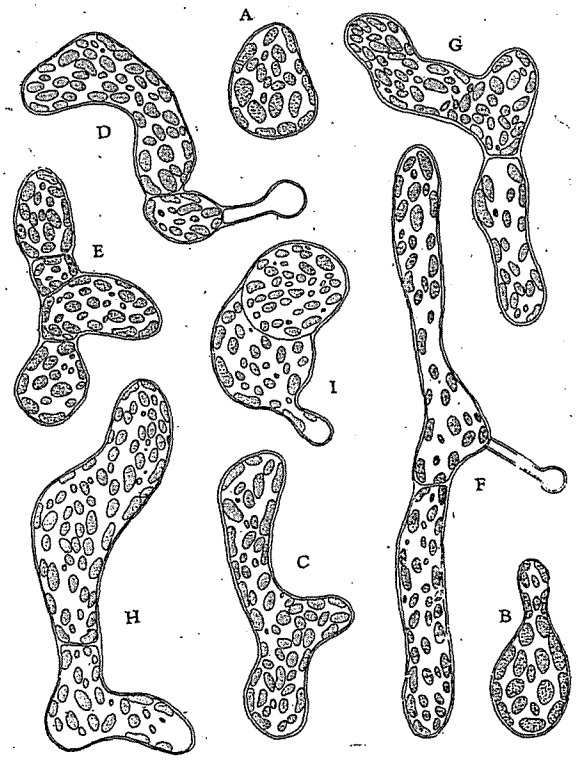


Fig. 4. *Laminaria subsimplex* MIYABE et NAGAI. Female gametophytes and mature oogonia. ×460. A–B. One-celled female gametophytes from 8 day culture. C–K. Female gametophytes from 10 day culture. L–P. Mature female gametophytes from 12 day culture.

liberation of male gamete from the opening of the antheridium was observed under microscope, and many male gametes swimming in the culture medium were observed on the slides.

Most of the female gametophytes of this species consists of only one or two cells, rarely more than 4 cells (Fig. 4). The shape and size of the gametophytes are very variable, being measured about from 15μ to 50μ in length, and from 8μ to 16μ in breadth (Fig. 4). Within 12 days the female gametophytes reach maturation, and develope oogonia. The oogonium cell is elongated, the chromatophores are divided into small pieces, and are crowded together at the apex. The contents of the oogonium become more and more liquefied, and it shows a strong internal pressure (Fig. 4, G–I). Then the egg is discharged through the opening at the apex, and remains attached there (Fig. 5, A).

Development of Young Sporophytes

The egg is spherical or elliptical in shape, covered with delicate plasma membrane. Fertilization with male gamete takes place at this stage, and then the first cell division occurs, increasing the thickness of the membrane (Fig. 5, B). The young sporophytes thus formed develop rapidly, and when the plants are 18–20 days old many of them develop one or more rhizoids from the cell at the base (Fig. 5, E). Further development of the young sporophyte is entirely similar to that of other Laminariaceous plants. As the growth of the sporophyte progresses, the upper part grows rapidly, forming a flat expanded blade (Fig. 6).

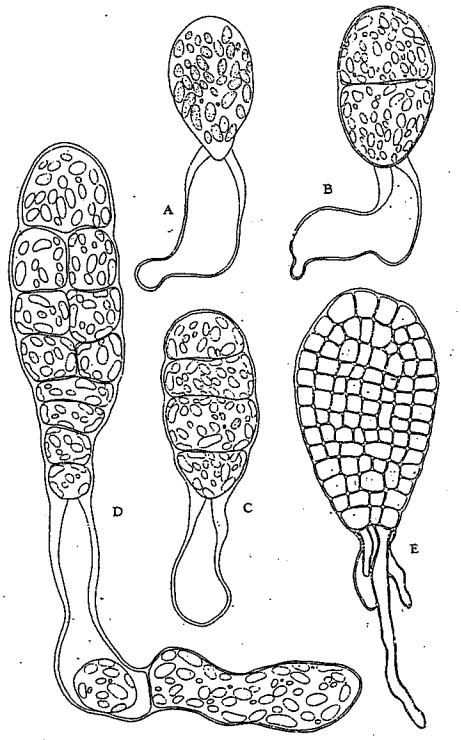


Fig. 5. *Laminaria subsimplex* MIYABE et NAGAI. Formation of egg-cells and the development of young sporophytes. ×670. A. Egg-cell resting at the tip of the oogonium, from 12 day culture. B. Two-celled stage of the young sporophyte, from 15 day culture. C–E. Further development of the young sporophytes, from 18–20 day culture. Rhizoids are produced from the cell in the lowest portion of the sporophyte.

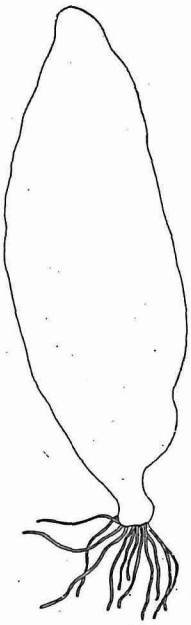


Fig. 6. *Laminaria subsimplex* MIYABE et NAGAI. Young sporophyte with flattened blade and numerous rhizoids. Differentiation of the blade and stipe is recognizable in the figure. ×100.

where the rhizoids are produced, becomes more and more thick, forming a disc-shaped expansion. From this expansion is produced the hapter, by means of which the plant gains permanent attachment to the substratum (Fig. 6).

When the plants are about a month old, the stipe is differentiated at the base of the frond (Fig. 6, A–B), and the lowest end of the stipe from

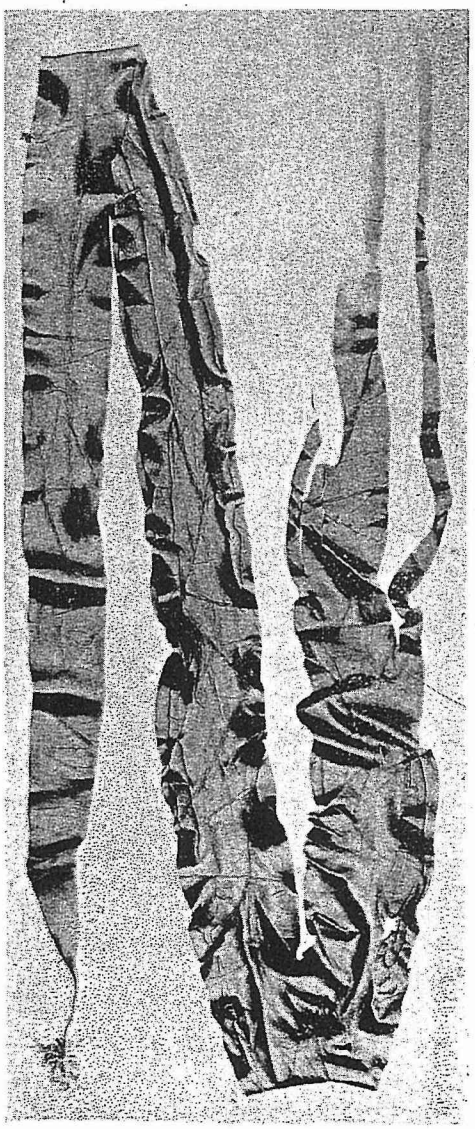


Fig. 7. *Laminaria taeniata* POST. et RUPR. Whole plant showing a digitate nature in the blade.

XIX. *Laminaria taeniata* POST. et RUPR.

This plant is also one of the representative species of the cold

current form of the Japanese *Laminaria*. It grows on rocks in the lower littoral or sublittoral zones being associated with *Laminaria subsimplex* MIYABE et NAGAI and *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. This plant is very variable in shape and size, and as stated above, the plant having wide blade is somewhat similar to the narrow form of *L. subsimplex*. On the eastern coasts of Paramusiru Island, these two species grow intermingled with each other. Therefore it is not easy to mark an exact demarcation between these two species which have an intermediate characters (Fig. 7).

As the material for the present culture study the writer selected the plant with as much typical form as possible. It becomes soriferous from the late summer to early autumn, being the same season as the maturation season of *L. subsimplex*. The mode of zoosporangium formation is entirely similar to that of *L. subsimplex*. The zoosporangia are produced at first on the middle portion of one side of the blade as a small patch with either round or irregular outline, and as the stages advance it grows larger towards both directions. When the plants are in full maturation the zoosporangia are observed on both surfaces, covering the greater parts of the blade, leaving a narrow sterile portion along the margin.

Cultures were made twice during the writer's stay in the North Kuriles from August to the latter part of September in 1942. The culture slides were brought to Muroran, keeping them alive. They were cultured carefully at the laboratory of the Institute of Algological Research at Muroran, but greater parts of these materials were seriously weakened when they arrived at Muroran, and died one after the other. Therefore the writer gave up this experiment in the middle of October.

Zoospores and their Germination

The zoospores are pear-shaped, measuring about 8–9μ in length, 4–5μ in breadth; they have two laterally placed cilia, one curved chromatophore, and some granular substances, the eye-spot, however, always lacking (Fig. 8, A). They swim actively at first, but sooner or later they become motionless. They lose their cilia before long, become spherical in shape, invested with a membrane and fasten themselves to the slide glass (Fig. 8, B). Soon after they have fastened to the slide glass, a germination tube grows out of the embryospore (Fig. 8, C–D). As the germination tube grows longer, the contents of the original cell migrate into this part, and within 4 days a cross-wall is formed so as to separate the distal end from the empty tube (Fib. 8, F). The first cell division in the newly formed cell

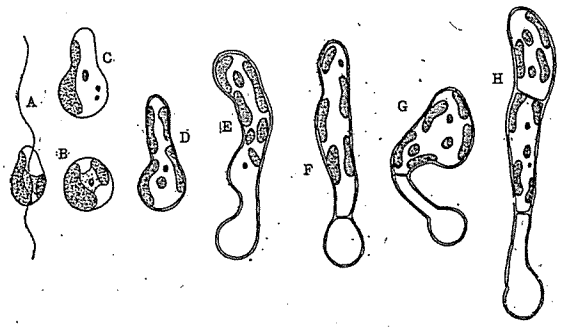


Fig. 8. *Laminaria taeniata* POST. et RUPR. Zoospore and its germination. ×510. A. Zoospore in motile state. B. Embryospore. C–D. Germination of the zoospore, from 12–24 hour culture. E. More advanced stage of the development, from 3 day culture. F–G. Sporelings from 4 day culture showing the formation of a wall, separating the germination tube and the distal part of the cell. H. Sporeling from 4 day culture. The first cell division takes place at this stage forming two-celled gametophyte.

was observed in plants of 4 day culture (Fig. 8, H). In the culture of seven days there is observed a striking increase in the size of the plants. At this time it is possible to distinguish two types of gametophytes.

Development of Gametophytes

As the accompanying figures show, the shape of the male gametophytes is almost similar to that of *L. subsimplex* (Fig. 9). The size of the cell constructing the male gametophyte as well as that of the whole body are, however, smaller than those of *L. subsimplex*. In 12 day culture the male gametophytes bear mature antheridia (Fig. 9, F–G). The liberation of male gametes from antheridia was observed under microscope. The shape and size of the male gamete are entirely similar to those of other species

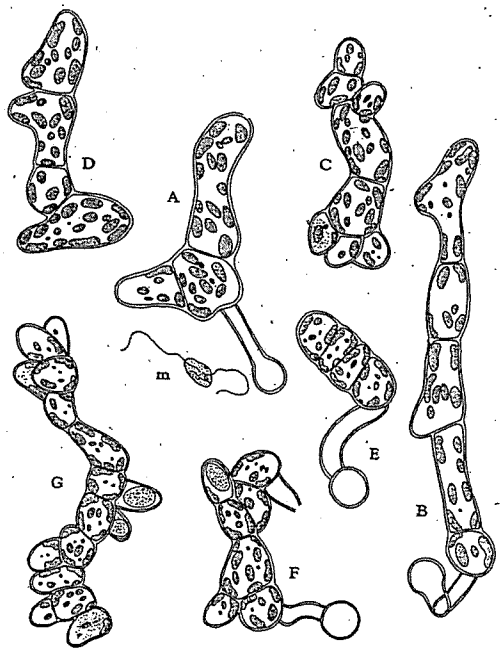


Fig. 9. *Laminaria taeniata* POST. et RUPR. Male gametophytes and male gamete, from 7–12 day culture. ×1000. A–C. Young male gametophytes from 7 day culture. D–E. Immature male gametophytes from 9 day culture. F–G. Mature male gametophytes, from 12 day culture. m. Male gamete in motile state.

of Laminariaceous plants (Fig. 9, m). When the male gametophyte reach maturation, the chromatophores of the antheridial cell become pale in colour, and whole contents assume a spherical form. The antheridial cell shows a strong internal pressure at this stage, and at maturity the wall of the antheridium bursts open at the apex, forming a beak, through which the male gamete comes out as if it were pressed. It has generally one or two pale coloured chromatophores, but always lacks an eye-spot (Fig. 9, m).

Most of the female gametophytes consist of only one or two cells (Fig. 10). General appearances of the gametophytes are very similar to those of *L. subsimplex*. When the plants are 9 days old, some gametophytes reach maturity (Fig. 11, A). The chromatophores in the oogonium cell are divided into small pieces having spindle-shaped form, and are crowded together with longitudinal arrangement (Fig. 11, A–C). At maturity the egg is forced out through the opening at the apex of the oogonium and remains attached there (Fig. 11, C–D). In the present species some of the female gametophytes develop upright oogonia, standing erect against the culture slide glass (Fig. 11, C). In other species of the Laminariaceous plants the opening through which the egg is forced out is formed at the terminal end of the oogonium cell, while in the present species some female

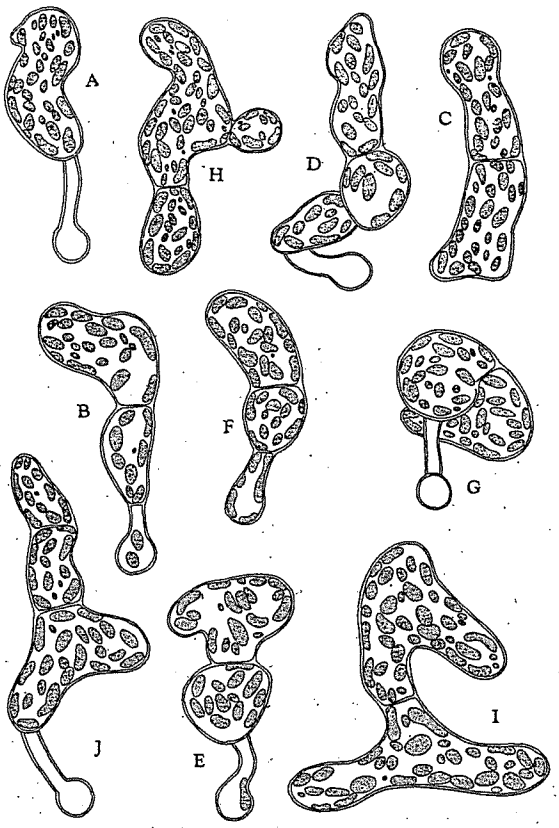
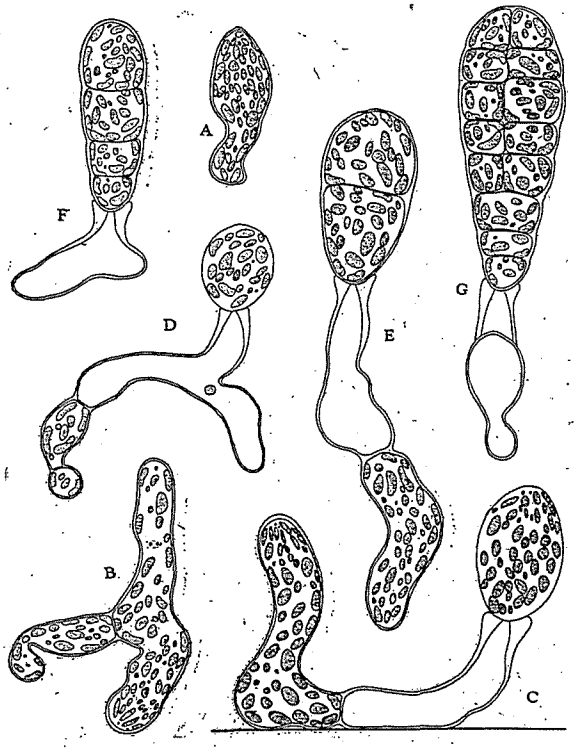


Fig. 10. *Laminaria taeniata* POST. et RUPR. Female gametophytes of various forms and various stages of the development. ×440. A–F. Female gametophytes, from 7 day culture. G–H. Young female gametophytes, from 9 day culture. I–J. More or less branched female gametophytes from 12 day culture.



gametophytes produce the opening at lateral side of the oogonium cell (Fig. 11, D).

Fig. 11. *Laminaria taeniata* POST. et RUPR. Development of oogonia, eggs and young sporophytes. ×520. A. Mature female gametophyte consisting of a single cell, from 9 day culture. B. Mature female gametophyte developing an oogonium, from 12 day culture. C. More or less diagrammatically figured female gametophyte, showing an oogonium which is standing erect. The ground line denotes the surfaces of culture slide. D. Development of egg-cell, from 12 day culture. E–G. Development of young sporophytes, from 12–14 day culture.

Development of Young Sporophytes

When the egg is fertilized the development of the sporophyte starts. In the 12–14 day culture the first cell division in the fertilized egg takes place (Fig. 11, E). Youngest stage of the sporophyte is a monosiphonous filament

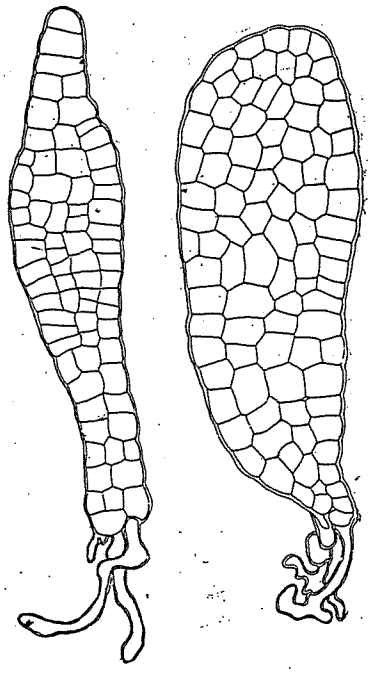


Fig. 12. *Laminaria taeniata* POST. et RUPR. Further development of the sporophytes: The shape of the sporophyte is very variable. The one is more or less slender in general appearance, while the other is rather broad. Rhizoids are formed from cells in the lowest portion of the sporophyte. About 40 day culture. ×230.

consisting of a row of several cells (Fig. 11, F), while in plants from 14 day culture, it was observed that the cell division takes place by the longitudinal walls (Fig. 11, G). The new sporophytes grow and develop many rhizoids at the base of the blade (Fig. 12). The speed of development is rather slow, and the shape of the sporophyte is highly variable. The one is more or less slender in general appearance, while the other is rather broad in breadth of the blade (Fig. 12). The free end of the rhizoid branches more or less, but the rhizoid is always destitute of any cross wall (Fig. 12).

XX. ***Streptophyllum spirale*** (YENDO) MIYABE et NAGAI

This species is a typical member of the cold current form of Laminariales, found growing on rocky shores in the lower littoral and upper sublittoral zones, being associated with *Laminaria subsimplex* and *L. taeniata*. It is distributed from the Bering Islands and Kamchatka to as far south as the Middle Kuriles along the Pacific coast, as well as the Okhotsk coast. The plant from the North Kuriles was described for the first time by YENDO in 1903, naming it as *Hedophyllum spirale* YENDO. After the issue of YENDO's paper, this plant was studied and discussed systematically by several authors, especially by MIYABE and NAGAI. In 1940, however, MIYABE and NAGAI established a new genus *'Streptophyllum'* taking *Hedophyllum spirale* YENDO as the type species, and now it stands as a monotypic genus.

When the plant is in early stage of development, the blade is simple,

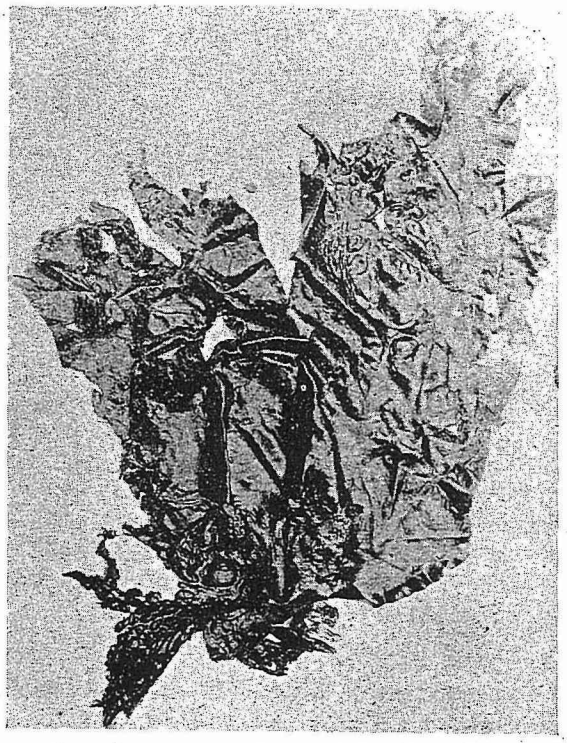


Fig. 13. *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. Habit of an old plant, showing roughly bullated blade, and decumbent base.

ovate and nearly plane, with two rows of bullae extending lengthwise. As the stages advance, the blade becomes broader and bullated, and it splits into several segments, begins the scrollings of both margins of the transition region. Then the meridional region of blade begins to decay downward to the base. The result is bifurcated stipe with one scrolled blade on each arm. It becomes soriferous in the same season as *Laminaria subsimplex* and *L. taeniata*.

The zoosporangia are produced at first on one side, being faced toward the substratum, as a small patch of irregular outline. Contrary to the fact that in *Laminaria subsimplex* and *L. taeniata* the zoosporangia are produced at first on the middle portion of the blade, in the present species they are commonly formed on the basal portion of it. As the stages advance they are produced on the other side, being faced heavenward, covering the greater parts of the blade always leaving a sterile portion along the margin.

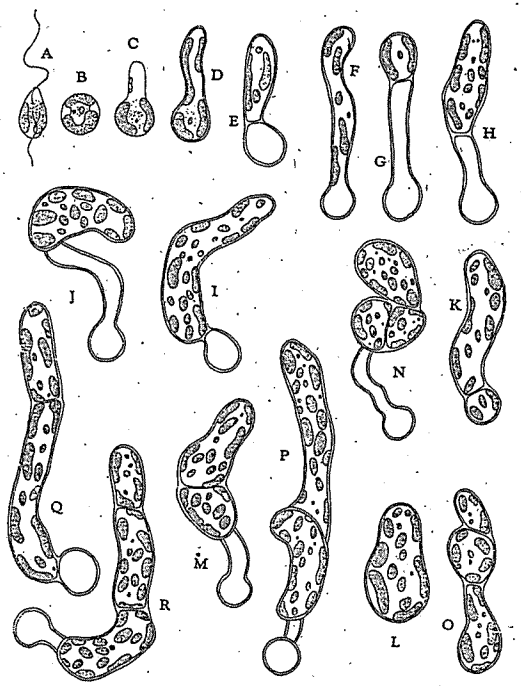


Fig. 14. *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. Germination of the zoospore and early stages of the gametophytes. ×448. A. Zoospore in motile state. B. Embryospore. C–D. Development of the germination tube; the contents of the cell migrate into this part. E–I. Sporeling from 2–5 day culture. The length of the germination tube is much variable. J–K. Sporelings from 5 day culture. L–M. Sporelings from 4–6 day culture. N–R. Earliest stage of the male gametophytes, from 4–6 day culture.

Zoospores and their Germination

The shape and size of the zoospores and the process of their development are entirely similar to those of *Laminaria subsimplex* and *L. taeniata* (Fig. 14). The zoospores swim actively at first, but sooner or later become motionless. They lose their cilia before long, become spherical in shape, invested with a membrane and fasten themselves to the substratum

(Fig. 14, B). Within 24 hours a germination tube grows out of the resting spore, and the contents of the original cell migrate into this tube (Fig. 14, C–D). The length of the germination tube of this plant is generally short, and some sporelings lack the tube at all (Fig. 14, E, I). Within 6 days two types of gametophytes may be distinguished. One type consists of only one or two cells, and later development shows that this type of plant is the female gametophyte (Fig. 14, L, M). The other type, however, consists of more than two cells at this stage. The diameter of each cell is smaller than that of the former, measuring about 6–8μ in diameter. This type of the gametophyte is male (Fig. 14, O, R).

Development of Gametophytes

As accompanying figures show, the shape and size of the male gametophytes bear a striking resemblance to those of *Laminaria subsimplex* and *L. taeniata* (Fig. 15). The male gamete is ovate in shape, measuring about 4.5μ in length. Two cilia of almost equal length, measuring about 12–18μ, arise from the side of the body. The chromatophores in the mature antheridium become pale in colour and gradually disintegrate. The male gamete liberated from the antheridium, therefore, possesses either pale chromatophores or granular substances only; the eye-spot, however, always lacking (Fig. 15, m).

Most of the female gametophytes of the present species consist of only one or two cells (Fig. 16, A–E).

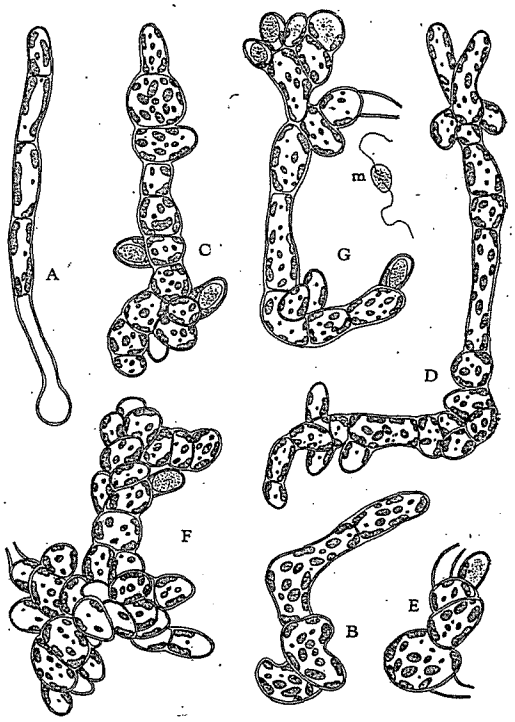


Fig. 15. *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. Various forms of the male gametophytes. ×486. A. Young male gametophyte consisting of a row of cells, from 5 day culture. B. Immature male gametophyte, from 8 day culture. C–G. Mature male gametophytes from 10–12 day culture; the tips of the branchlets divided forming the antheridial clusters. m. Male gamete in motile state, showing two cilia of almost equal length.

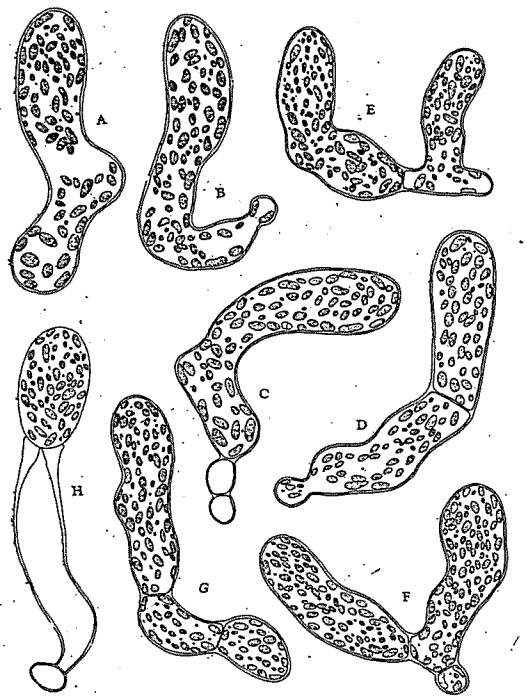


Fig. 16. *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. Female gametophytes, oogonia and eggs. ×680. A–C. One-celled female gametophytes; from 8–9 day culture. D–E. Two-celled female gametophytes from 8–9 day culture. F–G. Mature female gametophytes from 8–9 day culture. H. Egg discharged from uni-cellular female gametophyte, from 8 day culture.

coloured chromatophores, and in many cases a constriction makes appearance forming a small globule at the terminal end of the gametophytic cell (Fig. 16, B–D, F). The same fact as this was observed in the case of *Laminaria subsimplex*, though not so common as in this plant.

Development of Young Sporophytes

In the plants from 10 day culture the first cell division takes place and within 11 Within 8 days the female gametophytes reach maturation (Fig. 16, A–G). At maturity the egg is pressed out from the oogonium through the opening at the apex, and remains attached there (Fig. 16, H). The growth of the female gametophytes of this plant is very well and in some one-celled female gametophytes from 8 day culture the diameter of the cell is measured up to 70μ in length and 16μ in breadth. The cell is filled densely with deep brown

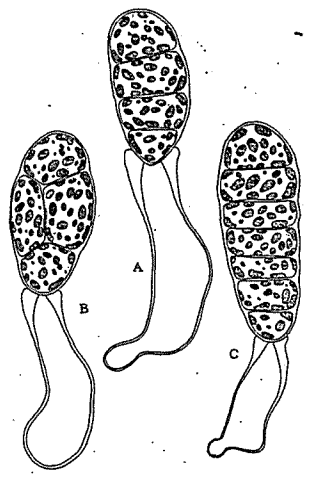


Fig. 17. *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. Development of the young sporophytes. ×680. A–B. Four cells stage of the sporophyte from 11 day culture. C. More advanced stage of the sporophyte, consisting of a row of several cells, from 12–13 day culture.

days after the liberation of zoospores 4 celled young sporophytes make their appearance (Fig. 17, A–B), and further development gives a filamentous sporophyte consisting of a row of cells (Fig. 17, C). As the development progresses, this filament gives rise to a flat expanded blade (Fig. 18, A–B). Rhizoids are produced out of the basal cell or cells (Fig. 18, A–B), and disc-shaped expansion, the initial of the secondary rhizoids, by means of which the plant gains a permanent attachment to the substratum is formed when the plants are about a month old (Fig. 18, B). Further development gives a blade with an aspect much resembling a round fan (Fig. 18).

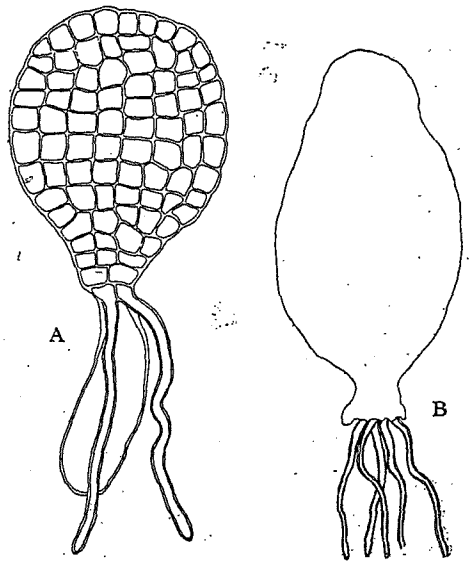


Fig. 18. *Streptophyllum spirale* (YENDO) MIYABE et NAGAI. Early stages of the sporophytes. A. Young sporophyte with rhizoids. General appearance of the blade is round; from 22 day culture. ×475. C. More advanced stage of the sporophyte, from 30 day culture. ×130.

XXI. *Alaria fistulosa* POST. et RUPR.

The present species is a typical member of Laminariaceae of the cold current form distributed in the Boreal Districts from the North Kuriles to as far south as Kusiro, Hokkaido, on the Pacific side, and at the southernmost point of Notoro peninsula of South Saghalien. The present species is the largest alga in Japan being measured up to 15–20 meters, growing gregariously on the stony or rocky bottom in a depth of 5–10 or more fathoms in the sublittoral zone.

It becomes soriferous in August, and the culture experiment of this species was started on the 21st of August. The zoosporangia are produced on both surfaces of the sporophylls, covering them entirely with the exception of narrow borders along the margin remaining sterile.

Development of Gametophytes

The zoospores are pear-shaped, about 9μ in length, have two laterally placed cilia, one curved chromatophore, one nucleus and some granular sub-

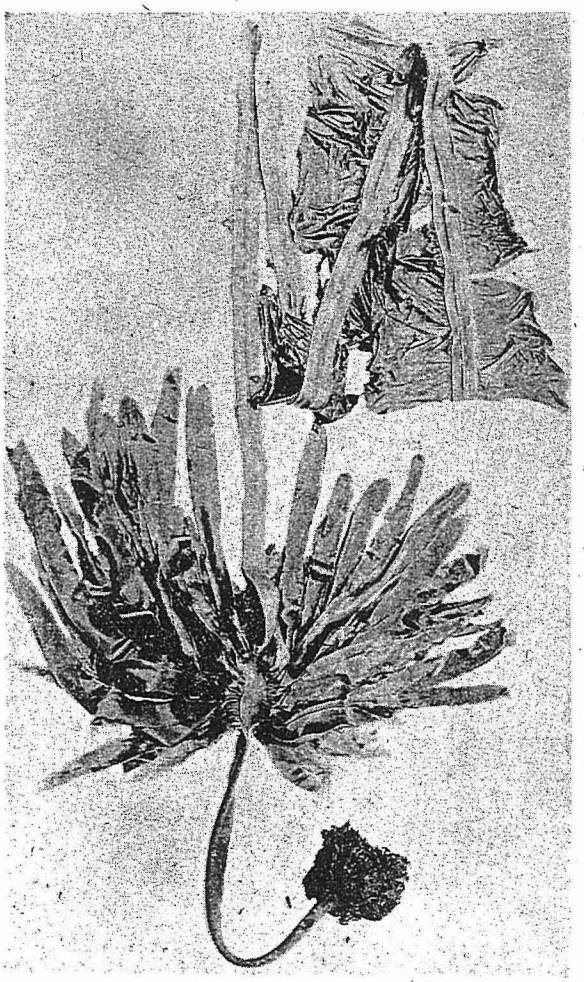


Fig. 19. *Alaria fistulosa* POST. et RUPR. Habit of the plant, showing large sporophylls and holdfast.

stances, but always lack an eye-spot (Fig. 20, A). Generally the germination tube is rather short in length (Fig. 20, G–H, J–L). When the plants are about 6–8 days old, two types of gametophytes may be distinguished (Fig. 20, L–Q, R–T). Though the male gametophytes are very variable in shape, so far as the shape and size of the male gametophytes are concerned, there was observed no striking differences, when compared with those of other members of *Laminaria* already studied. In the present species, however, the mature male gameto-

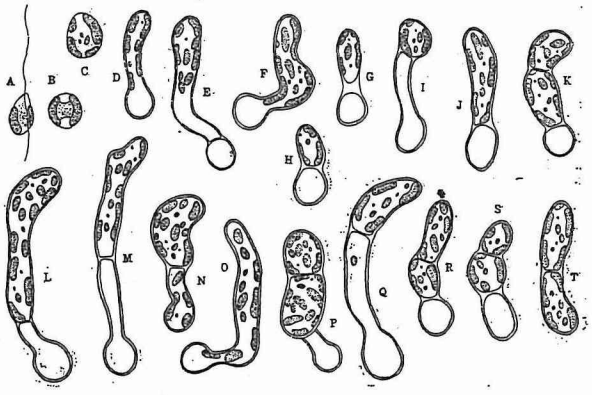


Fig. 20. *Alaria fistulosa* POST. et RUPR. Zoospore and its germination. ×480. A. Zoospore in motile state. B–C. Embryospore. D. Sporeling from 12 hour culture, showing the development of the germination tube. E–J. Sporelings from 5 day culture, showing the first transverse wall. The germination tubes are rather short in length. K. Sporeling from 5 day culture, showing the first cell division. L–Q. Early stages of the female gametophytes, from 6–8 day culture. R–T. Early stages of the male gametophytes consisting of two cells, from 6 day culture.

phytes were observed for the first time in cultures of 13 days old. Thus the development of the gametophytes is considerably slow. The male gamete bears a close resemblance to that of other members of Laminariales. t must be noted here that the eye-spot is always lacking in male gamete of the present species too (Fig. 21, m). The female gametophytes of this species are widely variable in shape, generally consisting of more than two cells. Some of the female gametophytes consist of several cells being branched irregularly, while the others are twisted or folded, standing erect against the surface of the culture slide (Fig. 22, N). From 13 to 16 days after the liberation of zoospores, the plants reach maturation. At the time of fruiting, the oogonium is elongated, the contents become dense, and the chromatophores are crowded together at the apex (Fig. 22, L).

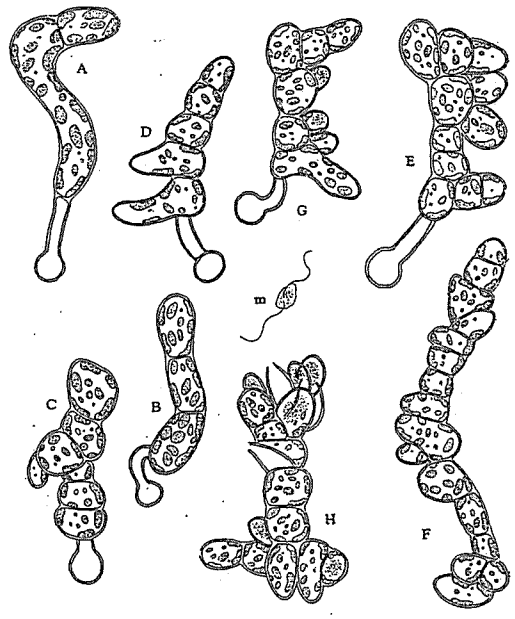


Fig. 21. *Alaria fistulosa* POST. et RUPR. Various forms of the male gametophytes. ×460. A–B. Male gametophytes from 8 day culture. C–D. Young male gametophytes from 13 day culture, consisting of few cells. E–F. Male gametophytes from 13–16 day culture in immature stage. G–H. Mature male gametophytes from 13–25 day culture. The tips of the branches are divided forming the antheridial clusters. m. Male gamete in motile state.

Development of Young Sporophytes

At maturity the egg cell is forced out through the opening at the apex of the oogonium and remains attached there (Fig. 23, A–B). Generally the whole contents of the oogonium cell are used for the formation of a single egg, while in the present species the egg is formed of a portion of the oogonium cell contents, and the rest portion of the cell contents remains in the empty oogonium cell, assuming a spherical form (Fig. 23, A–E). The first cell division in the fertilized egg cell may be observed in plants of 20 day culture (Fig. 23, C–D). Fig. 23, B. denotes the female gameto-

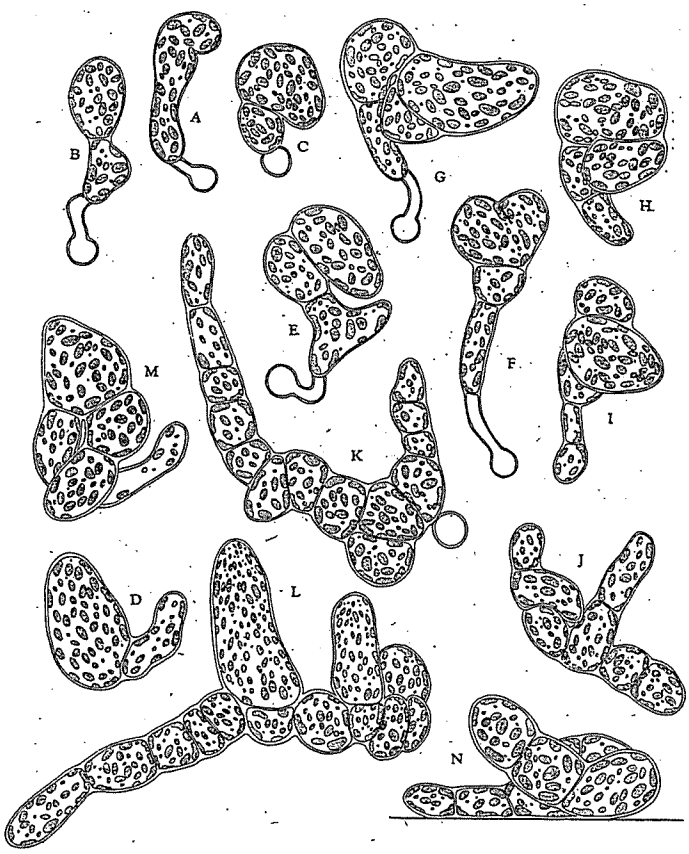


Fig. 22. *Alaria fistulosa* POST. et RUPR. Female gametophytes in various stages of the development. ×540. A. Very young female gametophyte from 13 day culture. B–C. Young female gametophytes consisting of two cells, from 13 day culture. D–F. More advanced stages of the female gametophytes, from 13–16 day culture. G–I. Female gametophytes showing a characteristic branching, from 13–16 day culture. J–K. Female gametophytes from 16 day culture. L. Mature female gametophyte from 24–25 day culture. M–N. Twisted female gametophytes. N. was figured diagrammaticaly, the ground line denotes the surface of the culture slide.

phyte developing two eggs. In the materials from 25 day culture a young sporophyte consisting of eight cells arranging in a row, developed from large female gametophyte, was observed, but it was impossible to trace the development beyond this stage. The formation of rhizoids and of flat expanded blade was not ascertained.

Though the cultures were carried out under the same condition and methods as those of *Laminaria subsimplex, L. taeniata* and *Streptophyllum spirale*, the development of the gametophytes especially the female ones was defective to a certain extent. It is supposed that the ecological nature, being the inhabitants of deep bottom of the sea, caused this defective growth of the gametophytes.

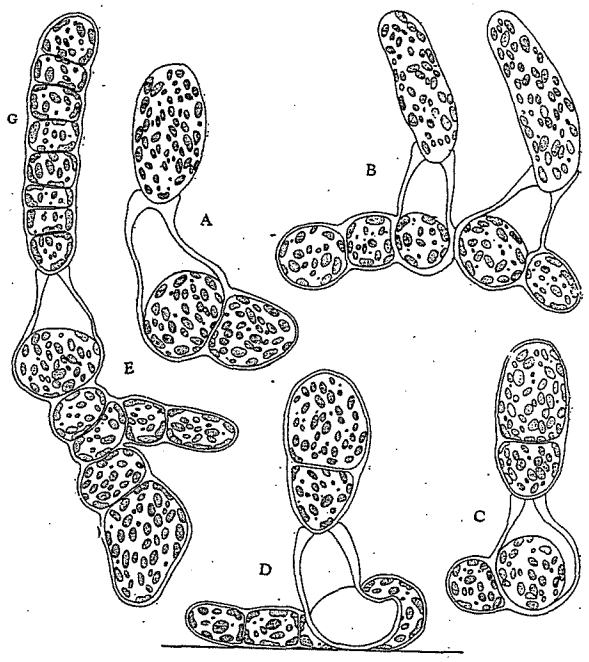


Fig. 23. *Alaria fistulosa* POST. et RUPR. Formation of egg-cells and the development of young sporophytes. ×520. A. Egg-cell developed from two-celled female gametophyte, from 16 day culture. Some portions of the contents of oogonium cell remain in the oogonium, assuming a spherical form. B. Two egg-cells developed from single female gametophyte. C. The first cell division in the fertilized egg, from 20 day culture. Remnant of the contents of oogonium cell assumes a spherical form in the empty oogonium. D. Diagrammatic figure showing the twisted female gametophyte. The ground line denotes the surface of the culture slide. E. Young sporophyte, from 25 day culture.

XXII.
Alaria angusta
KJELLM.

This species is also a typical member of the inhabitants of algae growing along the coasts of the North Kuriles. It forms a large association singly or in company with *Laminaria taeniata*, on rocky shore in the littoral zone, prefering the place where the surf is strong.

The distribution area of the present species in Japan is the Kuriles, the western coast of the southernmost point of Notoro peninsula of South Saghalien and Soya Strait.

Culture experiments were made once in the summer of 1941, and twice in the summer of 1942 at Suribati Bay. This species becomes soriferous from early in August, and the liberation of the zoospores occur without any difficulty. The zoosporangia are produced on both surfaces of the

Fig. 24. *Alaria angusta* KJELLM. Habit of an adult plant, showing narrow sporophylls.

sporophylls, covering the greater portion of them.

Zoospore and its Germination

So far as the shape, size and behavior of the zoospores are concerned, no remarkable difference was observed compared with those of other Laminariaceous plants studied.

They are ovate in shape, pointed at one end and rounded at the other, when they are active, measuring 8–9μ in length, 4.5μ in breadth; they have two laterally placed cilia, one pointing forward, as long as about 3–4 times the length of the body itself, and the other pointing backward, a little longer than the body. They have one curved chromatophore which occupies the posterior part, one nucleus and some granular substances, but always lack an eye-spot (Fig. 25, A). They are very active at first, but sooner or later their movement becomes slower; within 12 hours after the liberation of the zoospores the majority of them lose their cilia, assuming a spherical form, they are invested with a membrane and become fastened to the slide; a germination tube grows out from the embroyspore (Fig. 25, B–D). As the germination tube grows longer, the contents of the original cell migrate into this part, and within 2–3 days a cross wall is formed so as to separate the distal end from the tube (Fig. 25, E–F). The distal end increases in its diameter, then the first cell division takes place in the 4 days old plant (Fig. 25, H). Under favourable conditions, the male and female gametophytes are distinguishable in cultures from 7–8 days.

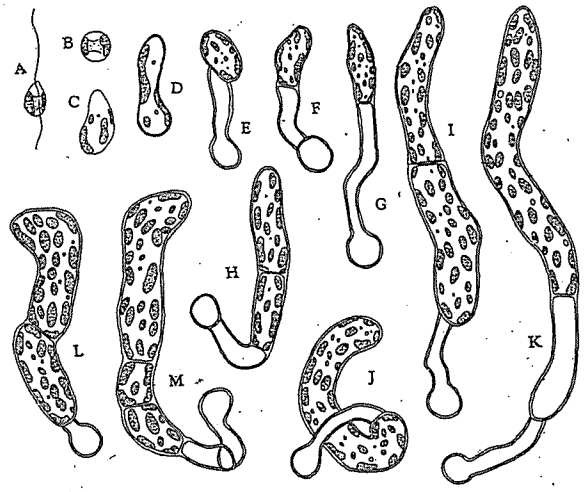


Fig. 25. *Alaria angusta* KJELLM. Zoospore and its germination. ×510. A. Zoospore in motile state. B. Embryospore. C–D. Germination of the embryospores, from 12–24 hour culture. E–G. Sporelings from 3–4 day culture. H. Sporeling from 4 day culture, showing the first cell division. I–M. More advanced stages of the germination, from 7–8 day culture.

Male Gametophytes and Male Gametes

As the culture progresses the male gametophytes increase in the number of cells more and more, and in the 8 day culture they form long filament with some branchlets (Fig. 26, A–B). As was figured in Fig. 26, C–D the male gametophyte develops vigorously, and the cells composing the filament are larger in size, and filled with deeper brown coloured chromatophores when compared with those of *Alaria fistulosa*. Generally the branchlets are produced on one side of the filament (Fig. 26, B–D). General appearance of the male gametophyte at this stage shows a noticeable characteristics. As the development advances the branching of the main filament becomes denser, and in plants of the 17–24 days culture, the male gametophyte form profusely branched clumps bearing mature antheridia and empty beaks in dense clusters at the tips of the branches (Fig. 26, C–D). As stated above, the branchlets are formed on one side of the main filament; general appearances of the male gametophyte, especially the mode of antheridium formation are very characteristic. The writer counted 23 antheridia developing in a single clump on the branchlet. At maturity the wall of the antheridium bursts open at the apex, forming a beak through which

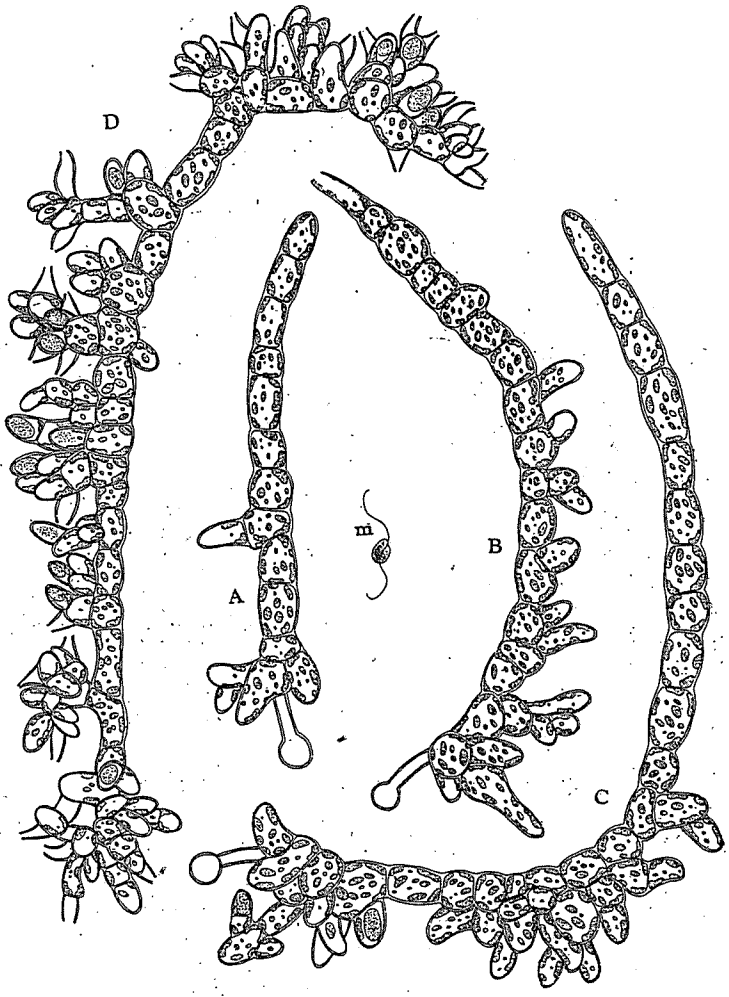


Fig. 26. *Alaria angusta* KJELLM. Various forms of the male gametophytes. ×480. A. Male gametophyte from 8 day culture. B. Well developed male gametophyte with characteristic branching, from 8 day culture. C. Immature male gametophyte from 15 day culture. D. Well developed male gametophyte consisting of fairly large number of cells, showing mature antheridia, from 17–24 day culture. The antheridial branchlets are formed on one side of the main filament. General appearance of the male gametophyte is very characteristic. m. Male gamete in motile state.

a mature male gamete swims out (Fig. 26, D). The male gamete is ovate or sometimes rather round in shape, measuring about 6μ in length. Two cilia of almost equal length measuring about 18μ arise from the lateral side

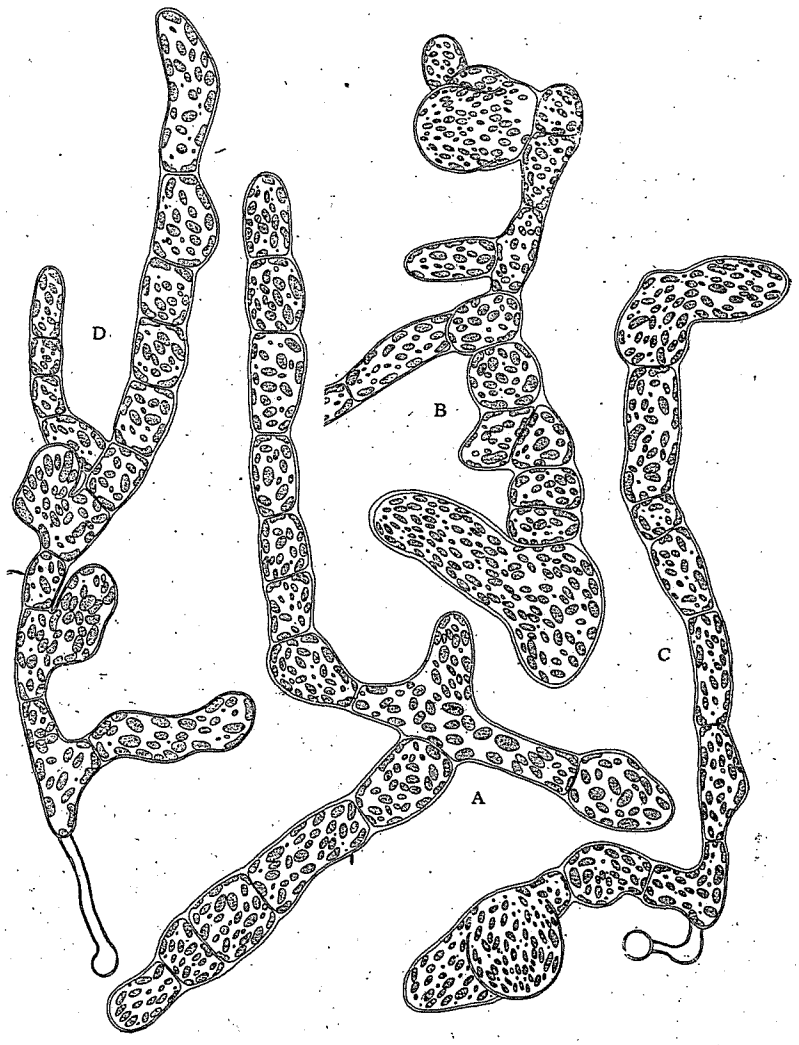


Fig. 27. *Alaria angusta* KJELLM. Female gametophytes and the development of oogonia. ×410. A. Immature female gametophyte from 10 day culture. The diameter of each cell is large, measuring about 45μ in length and 16μ in breadth, and the chromatophores are much denser and deeper in colour. General appearance of the branching is very characteristic. B–D. Mature female gametophytes developing oogonia, from 24 day culture. Oogonium is formed as an upheaval in the middle portion of the original cell. The chromatophores are crowded together at the apex of oogonium cell. General appearance of the female gametophyte and the shape of oogonium is characteristic.

of the body. It has one or two pale coloured chromatophores, but always lacks an eye-spot (Fig. 26, m).

Female Gametophytes and Oogonia

In the culture of 8 day the female gametophytes may be distinguished (Fig. 25, I–M). When the plants are 10 days after the liberation of zoospores a large immature female gemetophyte consisting of 13 cells, the diameter of which measured up to 45μ in maximum length, 16μ in breadth was observed (Fig. 27, A). As the development advances, the female

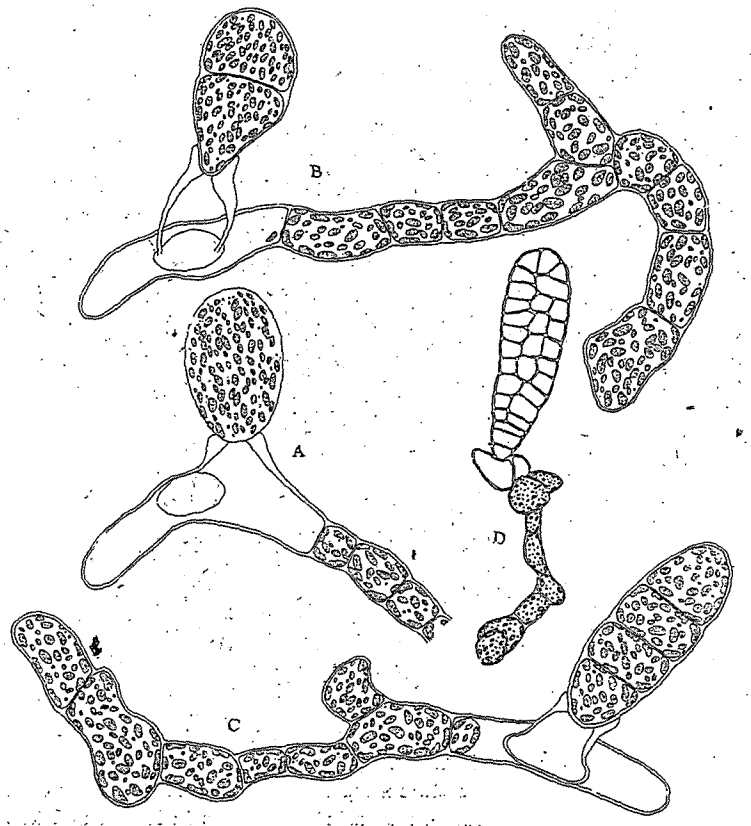


Fig. 28. *Alaria angusta* KJELLM. Female gametophytes, developing an egg-cell and young sporophytes. A. Female gametophyte showing the formation of egg-cell, from 24 day culture. × 670. B. The first cell division in the fertilized egg. The shape and general appearance of empty oogonium cell are very characteristic. × 670. C. Development of a young sporophyte, from 24 day culture. × 670. D. Further development of a young sporophyte from 24 day culture. × 320.

gametophytes increase in the number of cells, showing an irregular branching. When the female gametophytes are 24 days old, most of them reach maturity. One of the signs of the approach of maturity is the elongation of the oogonial cell. In the present species the oogonium is formed as an upheaval in the middle portion of the original cell (Fig. 27, B–D). This mode of oogonium formation is characteristic to the present species. The chromatophores at the apex of the oogonium are divided into small pieces, having a spindle shaped appearance, and are crowded together with longitudinal arrangement (Fig. 27, B–D).

Development of Young Sporophytes

At maturity the egg is forced out through the opening at the apex of the oogonium and remains attached there (Fig. 28, A). The egg is ovate or elliptical in shape, invested with thin plasma-membrane (Fig. 28, A). When the egg is fertilized the development of the sporophyte starts. In the 24 day culture the first cell division takes place at the right angle to the longitudinal axis of the egg (Fig. 28, B), and further development gives the sporophyte consisting of a row of several cells (Fig. 28, C–D). As the stages advance a flat expanded blade is formed (Fig. 28, D); the development of rhizoid, however, could not be traced. It must be noted here that the shape and appearance of the empty oogonium cell, at the apex of which

Fig. 29. *Alaria prealonga* KJELLM. An adult plant.

a young sporophyte remains attached are characteristic to the present species.

XXIII. *Alaria praelonga* KJELLM.

The present species is distributed rather widely from Bering Islands, Alaska, Kamtchatka to as far south as the Kuriles and the eastern coast of Hokkaido. It resembles *Alaria macroptera* (RUPR.) YENDO. On the coast of Paramusiru Island, these two species are growing very commonly intermingled with each other, on rocky shores in the lower littoral and upper sublittoral zones. Therefore much trouble was experienced by the present writer in forming an exact conception as to the limitation of the specific characters between this species and *Alaria macroptera* (RUPR.) YENDO. The plants having a typical characters were selected as carefully as possible by the writer as the materials for the present culture study.

Development of Gametophytes

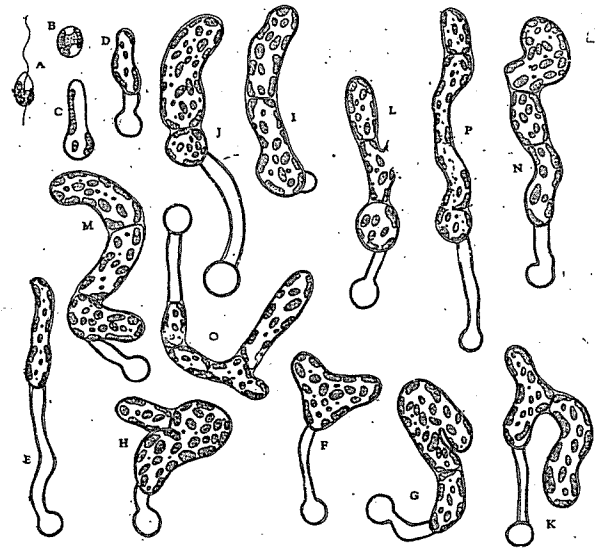


Fig. 30. *Alaria praelonga* KJELLM. Zoospore and its germination. ×590. A. Zoospore in motile state. B. Embryospore. C–D. Germination of the embryospore. E–F. Sporelings from 4–9 day culture. G–L. Two celled gametophytes from 7–9 day culture. M–N. Three-celled stages of the female gametophytes, from 9–13 day culture. O–P. Early stages of the male gametophytes, from 7–13 day culture.

The zoospores are pear-shaped, about 9μ in length, have two laterally placed cilia, one curved chromatophore, one nucleus and some granular substances, but always lack an eye-spot (Fig. 30, A). When the plants are 9–13 days old, two types of gametophytes may be distinguished (Fig. 30, F–P). As the accompanying figures show, there exists a strong resemblance in the shape and appearance of the gametophytes at this stage between the present species and *Alaria angusta* KJELLM. In

the present species the male gametophytes are more simple in shape than those of *Alaria angusta* KJELLM., and in certain materials a three celled male gametophyte bearing mature antheridium was observed (Fig. 31, B). As the development advances the male gametophyte increases in the number of cells forming a long filament with branchlets sparsely grown (Fig. 31, D–F). When they came to maturity the cell at the apex divides several times, producing a cluster of antheridia at the tip of branches. Later on any cell of the branches or main filament may become an antheridium. The whole contents of the antheridium are used for the formation of a single male gamete. At maturity the tip of the antheridium eventually splits open and the male gamete swims out, leaving an empty beak (Fig. 31, E–F). General appearance and shape of the male gametophyte differ to some extent from those of *Alaria angusta* KJELLM. The male gamete is ovate in shape when it is in motile state, but as the motion becomes slower it assumes a spherical form. There are two laterally placed cilia of almost equal length, measuring about 12–18μ in length. The contents of the male gamete is either almost pale in colour or pale yellowish due to the remnant of chromatophores in the antheridium cell. The eye-spot, however, is always lacking (Fig. 31, m).

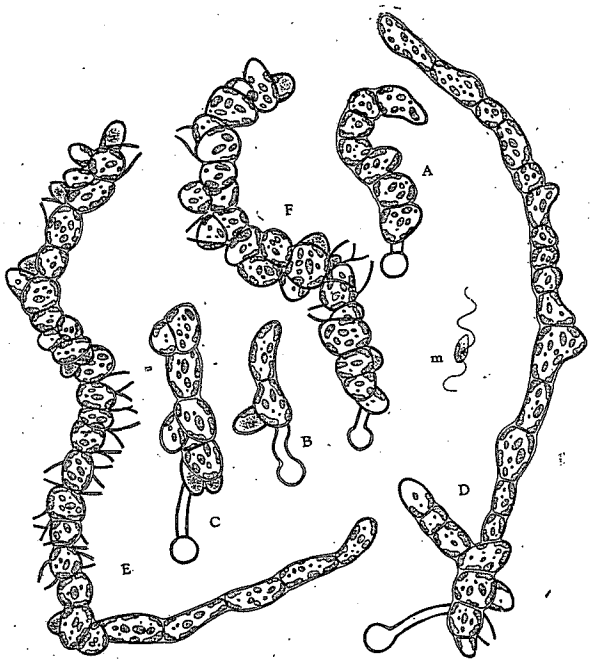


Fig. 31. *Alaria praelonga* KJELLM. Various forms of the male gametophytes. × 550. A. Immature male gametophyte, from 9 day culture. B–C. Mature male gametophytes, from 12 day culture. D–F. Well developed male gametophytes, from 12 day culture. m. Male gamete in motile state.

The shape and size of the female gametophytes are very variable; some one consists of one cell (Fig. 32, A), while the other consists of several

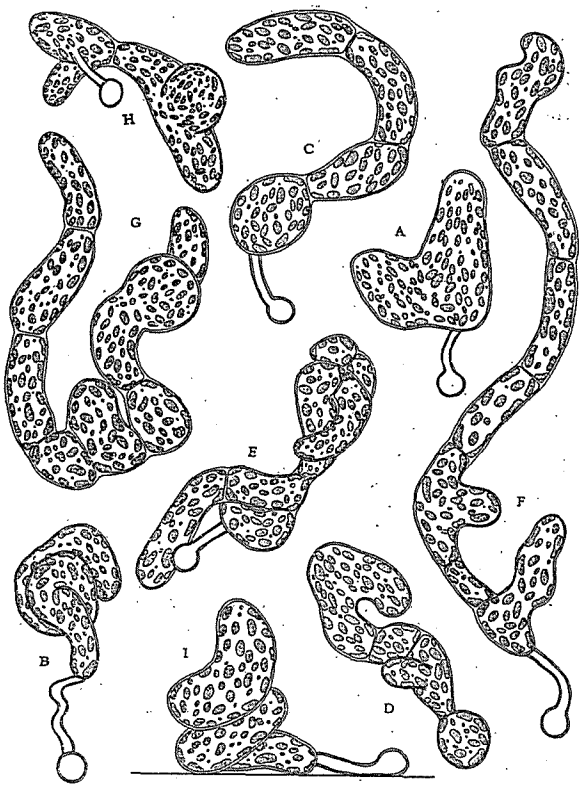


Fig. 32. *Alaria praelonga* KJELLM. Various forms of the female gametophytes, from 12–16 day culture. ×600. A. One-celled female gametophyte, from 12 day culture. B. Twisted female gametophyte. C–D. Female gametophytes consisting of more than three cells, from 12 day culture. E–G. Female gametophytes consisting of many cells, from 12–18 day culture. H. Mature female gametophyte, from 12 day culture. I. Twisted female gametophyte; ground line denotes the surface of the culture slide.

cells (Fig. 32, C–H); on the other hand some one develops into a very simple filamentous structure (Fig. 32, C), while the other forms a filament with irregular branching (Fig. 32, E–F), or spirally twisted (Fig. 32, B, I). The diameter of respective cells constructing the female gametophyte, as well as the total size of the gametophyte itself, are smaller than those of *Alaria angusta* KJELLM. Though the cultures were carried out under the same condition, the grade of development differs to a certain degree. It shows the fact that there exists a certain individuality in the shape and size of the gametophyte.

Within 12 days the gametophytes reach maturity (Fig. 32, H). At maturity the egg is pressed out through the opening at the apex of the oogonium cell and remains attached there (Fig. 33, A–D). As was observed in the female gametophytes of *Alaria angusta* KJELLM., the oogonium of the present species is formed as an upheaval in the middle portion of the oogonium cell (Fig. 32, H; Fig. 33, B–C). The shape as well as the size of the female gametophytes at this stage are characteristic.

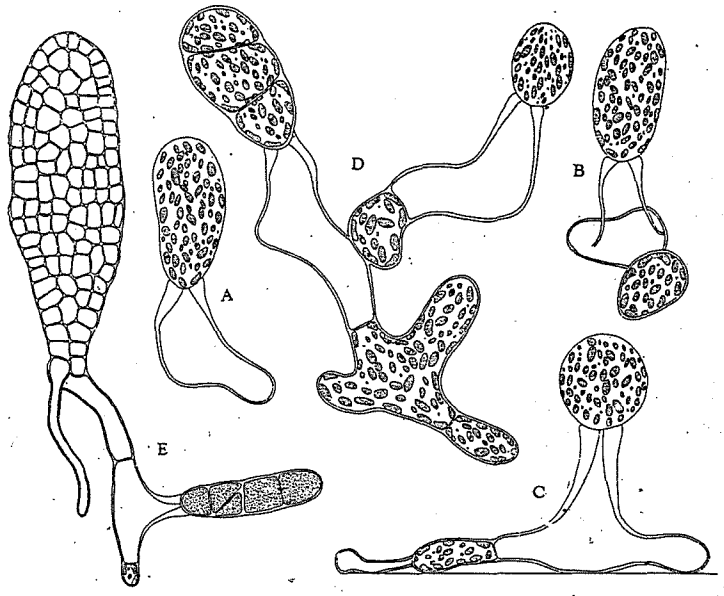


Fig. 33. *Alaria praelonga* KJELLM. Formation of eggs and development of young sporophytes. × 670. A–D. Various forms of eggs. C. Denotes the side view, standing erect on the surface of the culture slide. D. Development of an egg and young sporophyte consisting of three cells, from 25 day culture. E. Further development of the sporophyte producing a rhizoid, from 19 day culture.

Development of Young Sporophytes

The egg is ovate or spherical in shape and invested with delicate plasma membrane, and filled with dense brown coloured chromatophores (Fig. 33, A–D). When the egg is fertilized the first cell division takes place at a transverse direction. The young sporophyte grows rapidly, and in 19 day culture many of them develop rhizoid (Fig. 33, E). As the development of the sporophytes progresses the upper part grows rapidly forming a flat expanded blade.

Discussion and Summary

The purpose of the present paper is to offer the results obtained by the cultures of zoospores of six Laminariaceous plants, namely, *Laminaria subsimplex* MIYABE et NAGAI, *L. taeniata* POST. et RUPR., *Stretptophyllum spirale* (*Yendo*) MIYABE et NAGAI, *Alaria fistulosa* POST. et RUPR., and *A. praelonga* KJELLM., growing on the coast of Suribati Bay of Paramusiru

Island in the North Kuriles.

1. The life cycle and the gametophytic plants of these six species are essentially like those reported for other members of Laminariales, but in details there exist many characteristics to the respective species.

2. The presence of an eye-spot in the zoospores of Laminariaceae has been reported, hitherto, by four authors, namely, IKARI (1921) on *Laminaria religiosa* MIYABE; MYERS (1928) on *Egregia Menziesii* (TURN.) ARESCH.; MCKAY (1933) on *Pterigophora californica* RUPR.; HOLLENBERG (1939) on *Eisenia arborea* ARESCH.; but as previously reported by the present writer, he has never met with the zoospores bearing an eye-spot any Japanese species of Laminariaceae hitherto studied.

3. The writer was unable to confirm the presence of the eye-spots in the male gametes of these six species studied in the present culture.

4. The length of time necessary for the development of the gametophytes as well as the young sporophytes varies to a certain extent as the species and localities differ. There are also striking differences in the length of time necessary for the gametophytes to reach sexual maturity. As previously reported by HARRIES (1932), the shape and size of the gametophytes and the period of time taken for their full growth vary according to several conditions of the culture, such as temperature, intensity of light, amount of nutrient salt etc. Therefore the cultures must be carried out under various circumstances in order to determine the characteristic form and size of the gametophyte of any species or genus.

5. So far as the shape and size of the male gametophytes are concerned there exists a remarkable resemblance between *Laminaria subsimplex* MIYABE et NAGAI and *Laminaria taeniata* POST. et RUPR., while those of *Alaria angusta* KJELLM. and *Alaria praelonga* KJELLM. differ to some extent.

6. The male gametophytes of *Alaria angusta* KJELLM. grow into profusely branched filament, developing clumps of antheridia on the tips of branchlets, and in an extreme case a clump producing 23 antheridia was observed. In the present species the antheridial clusters are formed on the tips of the branchlets, while in *Alaria praelonga* KJELLM. the antheridial cells are apt to develop from the cells constructing the main filament.

7. The male gametophytes of *Alaria angusta* KJELLM. have a tendency of producing branchlets on one side of the filament.

8. The shape and size of the female gametophytes of *Alaria angusta* KJELLM. differ to a great extent from those of *Alaria fisculosa* POST. et RUPR. In the present species the oogonium is produced as an upheaval

in the middle portion of the oogonium original cell. The same nature as this was observed in the female gametophytes of *Alaria praelonga* KJELLM.

9. The female gametophytes of two species of *Alaria* are apt to develop into twisted form.

10. Though the cultures were carried out under the same condition and method, the growth of the gametophytes, especially the female ones of *Alaria fistulosa* POST. et RUPR. were defective to a certain extent. It is supposed that the ecological nature, being the inhabitants of deep bottom of the sea, caused this defective growth of the gametophytes.

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