Embryological Studies on *Pelvetia Wrightii* Yendo and *Fucus evanescens* Ag.

By

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(With 6 Text-figures and Plates II–IV)

Introduction

In his monograph on Japanese *Fucaceae,* Yendo (27) has enumerated 8 genera found in our country, namely, *Fucus, Pelvetia, Cystoseira, Cyctophyllum, Turbinaria, Coccophora, Sargassum* and *Ishige.* Recently Okamura (13) has added to them another genus *Hizikia.* Of these, four genera, *Sargassum, Coccophora, Cystophyllum* and *Hizikia,* which were considered by taxonomists to belong to the higher class of this family, have been hitherto investigated embryologically, especially concerning the mode of rhizoid formation, by Tahara (16, 18, 19), Okabe (12) and Inoh (4, 5, 6, 7).

The results obtained by these workers seem to suggest the following facts, (i) the number of primary rhizoids is proportionate to the size of the rhizoid cell, (ii) the size of the rhizoid cell is proportionate to the size of the egg, and (iii) the size of the egg is related to the complexity of the somatic constitution; species having larger eggs are more complex in their development and *vice versa.* It is regretful, however, that there are no detailed studies along the same line on *Fucus* and *Pelvetia* which are known to be of a taxonomically lower class of the family, although one can find in classic literature (21, 22, 14) some brief description of embryological development in certain species of these genera (*F. vesiculosus, F. serratus* and *P. canaliculata*). The present writer, then, aims to describe two species, *P. Wrightii* and *F. evanecens,* in respect to the mode of rhizoid formation, and to compare them with species hitherto investigated on this point. In addition to this, a brief account of the ovogenesis of these two species will be included in this paper.

Materials and Methods

At the adequate time of ripening of sexual cells, the writer visited

the Akkeshi Marine Biological Station in August, 1932, for *P. Wrightii,* and the Muroran Institute for Phycology in June, 1933, for *F. evanescens.*

As is well known, the liberation of sexual cells in *Sargassum, Coccophora* and *Cystophyllum* occurs simultaneously and periodically. In both *Pelvetia* and *Fucus,* however, the sexual cells are not liberated periodically. The sexual cells of conceptacles, when ripened, are discharged successively group by group.

For the study of the embryonal development, very thin hand sections of receptacles were made and stained with iron-aceto-carmine, in order to determine the degree of maturation of the receptacles. Then favorable materials were selected and cultured in small glass basins filled with natural sea water.

In *Sargassum,* the discharged eggs remain attached to the outer surface of the receptacle for several days and begin to develop there. When the rhizoid-cell division has been accomplished, they are detached from the receptacles. In the present case the matter is, however, quite different from the above. In the present two species, when the mature eggs are discharged from the conceptacles, they fall immediately to the bottom of the glass basin, and attach on the surface of the slides which were previously prepared, and then the embryo-development commences.

For the fixation of the embryos in both cases, Flemming's weaker solution prepared with sea water was used exclusively.

For the observation of the chromosomes in the oogonium in *Pelvetia Wrightii,* the following solution proved to give satisfactory results:

Stock solution of chromic acid (Sea water 98 c.c. saturated water solution of chromic acid 2 c.c.)	25 c.c.
Sea water	25 c.c.
2% Osmic acid	2.5 c.c.
Glacial acetic acid	2.5 c.c.

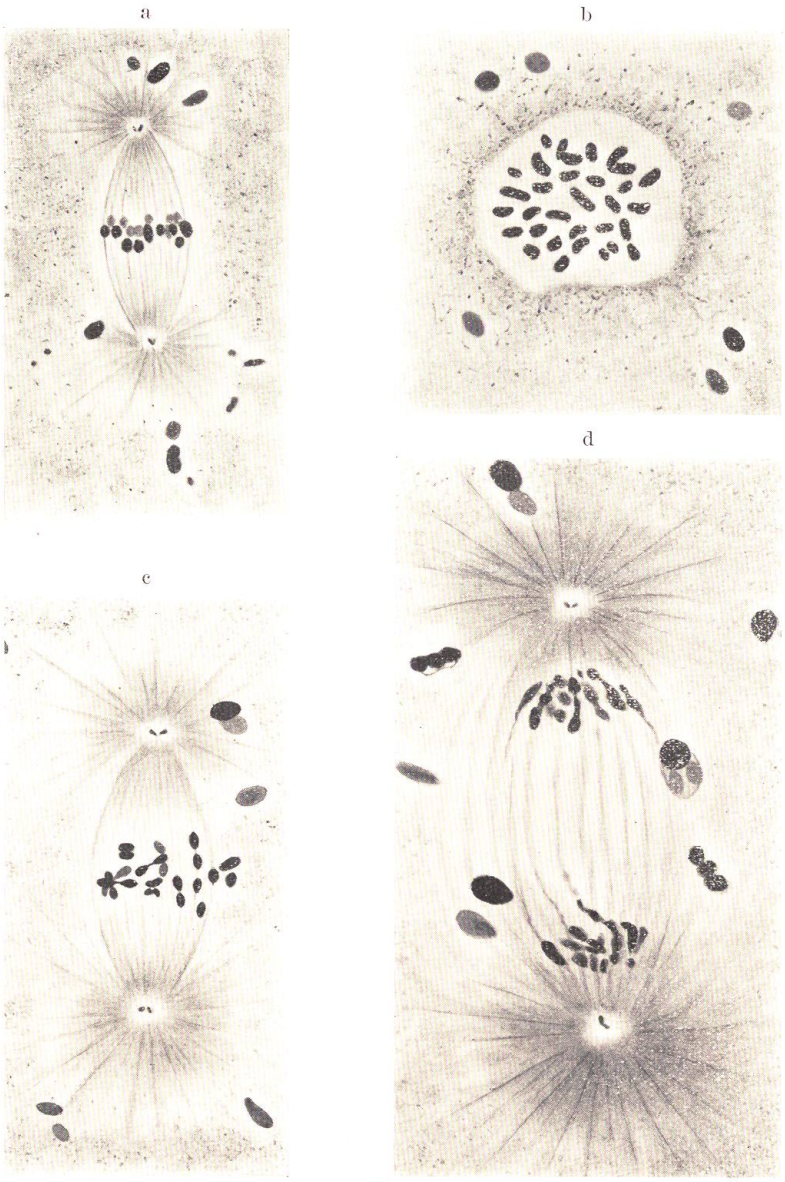
For the chromosomes of *F. evanescens,* Flemming's strong solution prepared with sea water was applied. The microtome sections, generally cut in 5–10 μ, were stained with Heidenhain's iron-alum haematoxylin.

Observations

I) *Pelvetia Wrightii* YENDO.

This species is one of the commonest algae in Hokkaido and is usually found in abundance on any rocky shore, forming a well-defined colony band, just below the highest level reached by the spring tide. The plants

are about 70 cm high and have a forked, flattened thallus attached to the rocks by a rounded disc.



Text-fig. 1. *Pelvetia Wrightii.* a, Metaphase in the second nuclear division (×2400). b, Polar view of the same (×3280). c, Anaphase (×3300). d, Telophase (×3300).

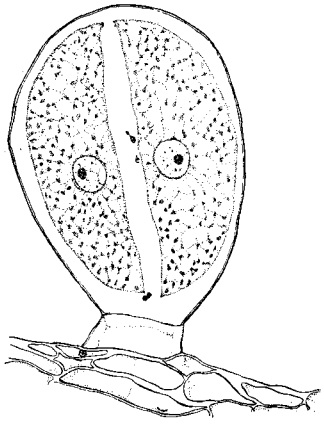
Receptacles are mostly simple in structure, but frequently bifurcated with wide angle. The plants is hermaphrodite and conceptacles contain antheridia, oogonia and paraphyses. They ripen in the vicinity of Akkeshi in about the end of August. In the present observations, the sexual cells were found to be liberated on the 24, 26 and 27th of August.

a) Ovogenesis.

The oogonium consists of a single cell and is situated on the tissue at the base of the conceptacle. It contains at first a single nucleus which divides later into eight as the result of three successive nuclear divisions.

In the metaphase of the second mitosis, 32 chromosomes are counted (Text-fig. 1, b) and at the opposite poles, two centrosomes are clearly seen, surrounded with radiate plasma striation (Text-fig. 1, a). The centrosome begins to divide at the end of metaphase. The divided bodies are first connected with each other, but they become completely separated at telophase (Text-figs. 1, c, d).

Of the eight nuclei in the oogonium, six begin to degenerate, and the remaining two are separated by the cell wall, running oblique or parallel to its long axis, forming two cells, each containing one nucleus which develops later to two ova (Text-fig. 2).



Text-fig. 2. *Pelvetia Wrightii*. The oogonium divided vertically into two ova (×410).

In *Pelvetia canaliculata* (16) however, the cell wall runs always transversely instead of longitudinally. Therefore *P. Wrightii* differs at least from *P. canaliculata* on this point.

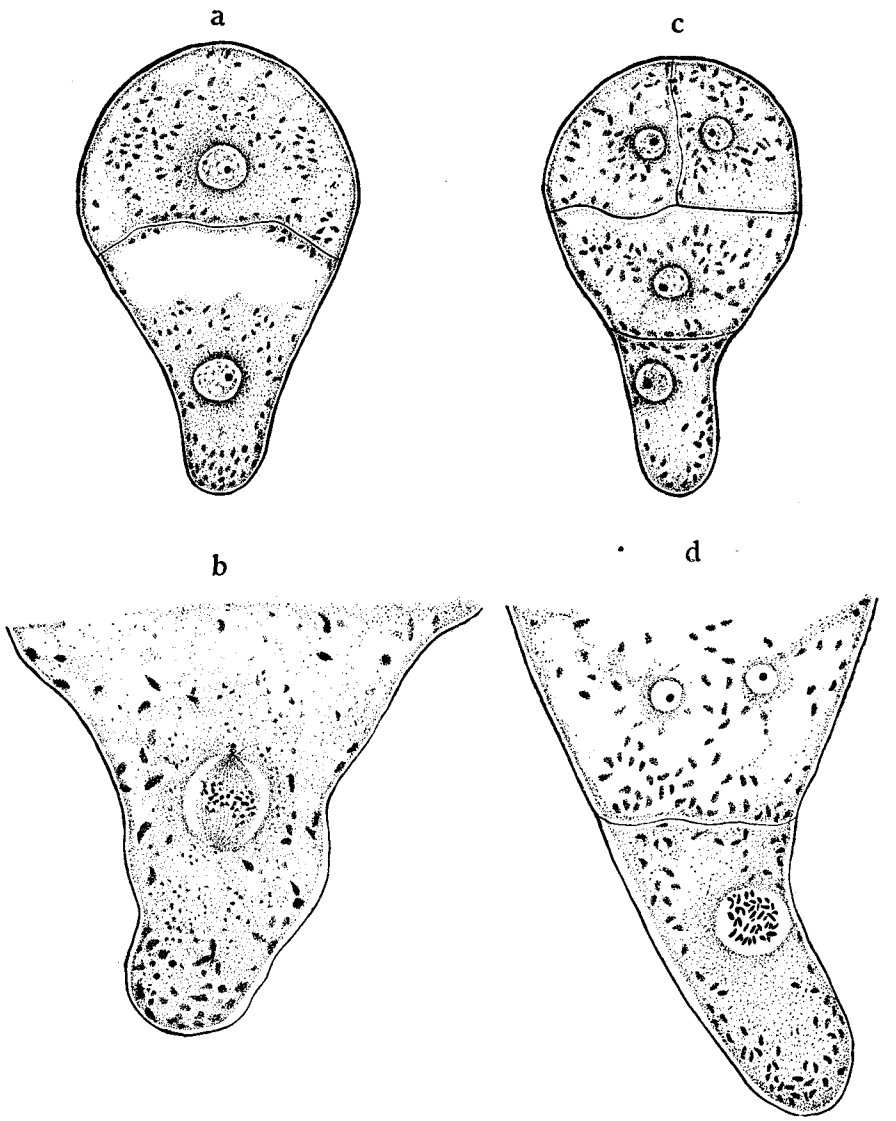
At these stages, the degenerated six nuclei are ejected from the ova into the septa, together with a small amount of cytoplasma. The small bodies seen in the vertical septum in Text-fig. 2, are some of these rejected nuclei.

b) Embryogenesis.

The egg discharged from the conceptacle is spheroid in shape. It has a single nucleus in the center of its body and chromatophores surrounding the nucleus. The diameter of the cell is measured as about 84 μ (Pl. II, Fig. 1).

After the fertilization, the first segmentation-wall runs transversely,

forming two cells (Pl.II, Fig. 2). Of these two, one nucleus begins to move to the periphery, and at the same time the embryo protrudes towards the same direction (Text-fig. 3, a). When the nucleus comes to the upper



Text-fig. 3. *Pelvetia Wrightii.* a, One nucleus beginning to move towards the distal end of the embryo (×480). b, Mitosis taking place in the corresponding nucleus (×950). c, The rhizoid cell being formed by the segmentation-wall, running parallel to the first one (×480). d, Mitosis in the rhizoid (×660).

part of the protrusion, the mitosis is commenced (Text-fig. 3, b) and the resulting nuclei are separated by a cell wall, running parallel to the first segmentation wall. The protruded cell forms the rhizoid cell (Text-fig. 3, c, d).

Later a single rhizoid develops from the rhizoid cell at one extremity of the embryo (Pl. II, Figs. 5, 6). As the development proceeds further, the rhizoid becomes made up of a few cells. At this stage, one or two cells of the upper part of the rhizoid are divided vertically into two or four cells and at the same time, its terminal part becomes bifurcated in several ways (Pl. II, Figs. 7, 8, 10, 11, a, b, c, d). Some of them form two rhizoids from one rhizoid cell at one extremity of the embryo (Pl. II, Figs. 6 a, 9).

Generally speaking, the embryo in the present species has at this stage either one rhizoid bifurcated at its terminal part or two rhizoids.

II) *Fucus evanescens* AG.

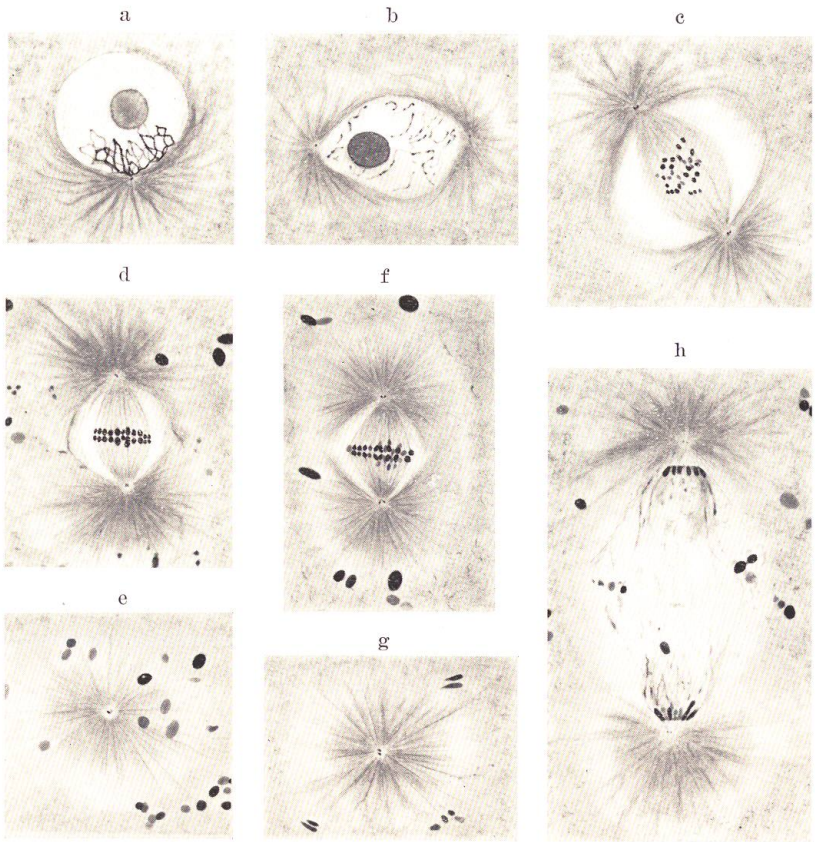
Along nearly the whole coast of Hokkaido, the present species is obtainable more or less. They grow on the rock at the high tide mark. The plants having receptacles are about 50–70 cm. high. By the position of vesicles, the present species is distinguished clearly from *F. vesiculosus*. This plant is hermaphrodite, antheridia, oogonia and paraphyses being formed in the same conceptacle.

They usually ripen on the coast near Muroran between late May and middle June. In the present observation, the sexual cells were found to be liberated on the 27th of May and the 5th of June.

a) Ovogenesis.

The cytological study on another species of *Fucus*, *F. vesiculosus*, has been already carried out by YAMANOUCHI in 1909. The present observation on the meiosis in the oogonium of *F. evanescens* seems to coincide with it in essential points. On the centrosome-division after metaphase, however, certain differences were noted between these two species; particular attention is then paid in the present paper to this point.

The large nucleus situated in the center of oogonium is seen surrounded closely by a multitude of chromatophores. At an early stage of synapsis, a small clear area at one side of the nucleus is seen, and in this area there is formed a centrosome which is surrounded by many striating plasms. Against this clear area is observed a small clump of chromatin threads in the nucleus (Text-fig. 4, a).



Text-fig. 4. *Fucus evanescens.* a, Synapsis. b, Late spireme stage. c, Early metaphase. d, Metaphase. e, Centrosome in the same stage. f, Meta-anaphase. g, Sister centromomes in the same stage. h, Telophase. (All figures, ×1375).

In these stages, a large nucleolus is present in the nucleus, but the chromophilous spherule which is described in the related genera, such as *Sargassum* (10) and *Coccophora* (20), was not observed.

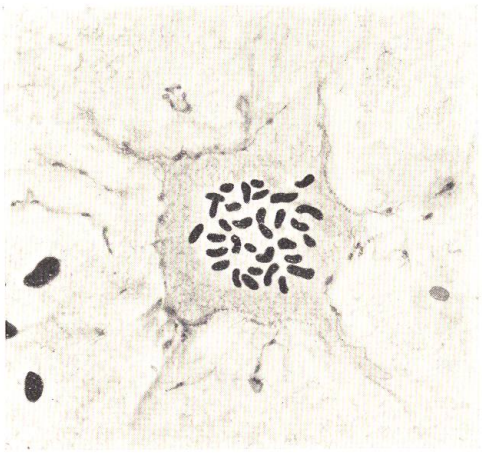
At the late spireme stage, another centrosome is visible at the opposite side of the first (Text-fig. 4, b).

In late diakinesis, 32 bivalent chromosomes are counted and at this stage, the spindle-fiber begins to appear from the two centrosomes (Text-fig. 4, c).

In the same manner as that of *Pelvetia Wrightii,* each centrosome begins to divide at metaphase. The new daughter centrosomes are first

connected with each other, but they become completely separated at telophase (Text-figs. 4, d, e, f, g, h).

Generally the radiated plasm striations of the centrosome in this species are more numerous and greater in length than those in *Pelvetia Wrightii*.



Texa-fig. 5. *Fucus evanescens*. Polar view of metaphase in the second mitosis. (×2750).

The two homotypic mitoses take place successively after the heterotypic one. At the metaphase of the first homotypic mitosis, 32 chromosomes are clearly counted (Text-fig. 5). As the result of three successive mitoses, the oogonium acquires eight nuclei.

In allied genera, namely, *Ascophyllum*, *Pelvetia* and *Sargassum*, four, six and seven of these eight nuclei, respectively, used to degenerate and the remaining nuclei develop into the egg-nuclei. But in *Fucus* all the eight nuclei are utilised, and result in the formation of 8 ova.

The manner of the egg-formation in the present species is the same as that of *F. vesiculosus* (21) and F. *serratus* (22).

As is well known, in the Fucaceous algae the sexual cells are liberated generally with some quantities of mucilage. The mucilage of this species is greater in quantity than that of *Pelvetia Wrightii*.

b) Embryogenesis.

The liberated egg is spheroid in shape and has a single nucleus in the center of its body, surrounding which chromatophores are seen. The diameter of the cell is measured as about 60 μ.

In the present species, successive stages of the embryo-development from the first segmentation to the complete formation of the rhizoid cell at one extremity of the embryo, occur nearly in the same manner as those in *Pelvetia Wrightii* (Pl. III, 1, 2, 9, 4) with some slight differences, however, in the manner of the rhizoid formation.

In a later stage, one rhizoid develops from the rhizoid cell at one extremity of the embryo. When the embryo-development proceeds further,

one rhizoid multiplies until it consists of a few cells (Pl. III, 6, 7, 8). But at this stage, the facts that a few cells of the upper part are divided vertically and that its terminal part becomes bifurcated in several ways as in *Pelvetia Wrightii,* are not observed in the present species. Though extremely seldom, as is shown in Pl. III, 9, 10 and Pl. IV, B, C, some abnormal embryos develop a rhizoid, the terminal part of which is bifurcated, or two independent rhizoids.

That the abnormal embryo develops two independent rhizoids as is shown Pl. IV, B, is generally thought to be due to the fact that in the early stage of the embryo development, the polarity of the embryo is determined abnormally by external factors, such as light, with the result that rhizoid cells are formed at two parts of the embryo, from each of which one rhizoid is to develop.

As above mentioned, the rhizoid formation in this species takes place in the most primitive manner within this family. A single rhizoid develops at one end of the embryo.

In a still later stage, rhizoids begin to develop from the cells adjacent to the rhizoid cell, and at further development the primary rhizoid becomes indistinguishable in appearance from the secondary ones (Pl. IV, D).

It is also noticed that at this stage, a few short hairs develop at the apical part of the embryo. They later become elongated and multicellular (Pl. IV, E, F, G, H).

Discussion and Conclusion

From the above observations, the mode of rhizoid formation in *Fucus evanescens* and *Pelvetia Wrightii* is more simple than in *Sargassum, Coccophora, Cystophyllum* and *Hizikia,* as suggested by the following features of embryonal development: i) the diameter of the liberated eggs in both the species is much smaller than in allied genera, *Cystophyllum* and *Sargassum*; ii) the rhizoid cells in these two species are only the protrusion of the embryo and later develop only one or two rhizoids, while in *Cystophyllum* and *Sargassum* the rhizoid cells are differentiated as specially lense-shaped ones and later divide into 4, 8, 16 or 32 cells, from each of which develops one rhizoid (4, 5, 12); iii) in *Fucus evanescens* young embryos develop a single rhizoid and in *Pelvetia Wrightii* one rhizoid which is bifurcated in its terminal part, or two rhizoids, whereas in *Cystophyllum* and *Sargassum* the embryo develop two or more rhizoids, namely, 4 in *C. hakodatense,* 8 in *S. hemiphyllum,* 16 in *S. enerve* and

32 in *C. sisymbrioides* (4, 5, 12).

According to THURET and BORNET (22), the young embryo of *Ascophyllum nodosum* develops a rhizoid which is bifurcated at its terminal part. This embryological similarity between *P. Wrightii* and *A. nodosum* seems to suggest that these two species are closely related to each other.

THURET reports also that in *P. cannaliculata* the oogonium is divided into two cells by the cell-wall running transversely, thus resulting in two ova, that the discharged eggs are still enclosed by the gelatinous inner wall of the oogonium, and that the embryo in an early stage develops four or more rhizoids, whereas in *P. Wrightii,* the oogonium is divided by the cell-wall running longitudinally or obliquely, the discharged eggs are not enclosed by the gelatinous wall, and the embryo develops only one or two rhizoids.

From the standpoint of embryonal development, it may be then presumed that *P. canaliculata* is closely like *Cystoseira barbata* (3) and *Cystophyllum hakodatense* (5), whose embryo develops four rhizoids, whereas *P. Wrightii* is closely related to *Ascophyllum nodosum.*

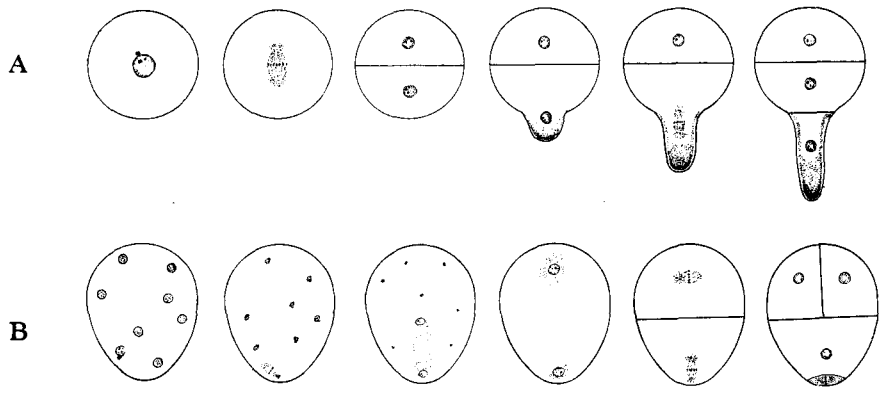
According to THURET's observations on the embryonal developments in *F. vesiculosus* and *F. serratus,* the rhizoid of the latter develops in a simmilar manner to that of *F. evanescens* and the embryo of the former usually forms a single rhizoid with some exceptions in which it is bifurcated at its terminal part.

From the above mentioned facts, it seems to be safely said that the embryonal development in the species hitherto investigated of this family, increases its complexity in the following order, viz., *F. evanescens, F. serratus, F. vesiculosus, A. nodosum, P. Wrightii, P. canaliculata, C. hakodatense, S. hemiphyllum, S. enerve and C. sisymbrioides.*

As already mentioned, the manner of embryonal development in *F. evanescens* and *P. Wrightii* differs greatly from that in *Cystophyllum* and *Sargassum.* For example, the comparison of *Pelvetia Wrightii* with *Sargassum enerve* (17) concerning the mode of rhizoid formation is made as in the following diagram.

As is shown above, the formation of rhizoid cell in the latter is more complex than in the former and in successive stages till the complete formation of the rhizoid cell, the embryos remain attached with gelatinous substances no the outer surface of receptacles.

The following table summarizes the writer's data concerning the size of discharged eggs and the number of primary rhizoids in the species hitherto investigated.



Text-fig. 6. Diagram of the comparison of A(*Pelvetia*) with B(*Sargassum*), concerning the mode or development of the liberated egg into the rhizoid cell formation. The rhizoidal portions are spotted.

TABLE I

Specific name	Form of egg	Diameter of egg cell	Number of primary rhizoids
Fucus evanescens AG.	Spheroid	60μ	1
Pelvetia Wrightii YENDO	„	84μ	1 or sometimes 2
Cystophyllum hakodatense YENDO	Ellipsoid	120μ× 80μ	4
Sargassum hemiphyllum AG.	„	125μ×103μ	8
Sargassum confusum AG.	„	210μ×140μ	8 or more
Sargassum patens AG.	„	218μ×177μ	16 or less
Sargassum piluliferum AG.	„	235μ×110μ	16 or less
Sargassum enerve AG.	„	250μ×235μ	16
Sargassum nigrifolium YENDO	„	264μ×236μ	16
Sargassum serratifolium AG.	„	272μ×202μ	16
Cystophyllum sisymbrioides AG.	„	321μ×229μ	32

Thus the data obtained in *F. evanescens* and *P. Wrightii* may be taken as further confirmation of the statement made in the previous papers (4, 5, 7) that the number of rhizoids is proportionate to the size of eggs and the size of eggs is related to the order of complexity of somatic constitution in Fucaceous algae.

The haploid chromosome number in both *F. evanescens* and *P. Wrightii* is 32 and is the same as that in other species of this family, viz. *Fucus vesiculosus, Coccophora Langsdorfii, Sargassum confusum, S. enerve, S. Horneri* and *Cystophyllum sisymbrioides* which were examined by YAMANO-

UCHI, TAHARA, SHIMOTOMAI, OKEBE and ABE (TOMITA) respectively (10, 11, 17, 20, 23, 24, 26), with the one exception of 16 (n) in *S. Horneri* reported by KUNIEDA (8).

The centrosomes are visible in ovogenesis of *F. evanescens* and *P. Wrightii,* as in *F. vesiculosus* (26), *C. sisymbrioides* (15), *S. enerve* (17) and *S. Horneri* (10, 11). Contrasted with this, in *Coccophora Langsdorfii* (20) and *S. confusum* (24), centrosomes are not visible.

Summary

A) *Pelvetia Wrightii* YENDO.

i. The haploid chromosome number of this plant is 32 and at metaphase of the second mitosis in oogonium two centrosomes are clearly seen at opposite poles.

ii. The oogonium cell is divided by the cell-wall running obliquely or longitudinally, forming two ova.

iii. The embryo of *P. Wrightii* develops in a manner strikingly similar with that of *Ascophyllum nodosum;* its young embryo has either one rhizoid which bifurcated at the terminal part, or two rhizoids. This mode of rhizoid development may suggest that this species is closely related to *Ascophyllum nodosum* and is of a more primitive form than *Pelvetia canaliculata, Cystoseira barbata* and *Cystophyllum hakodatense* in which the embryo is characterized by the formation of four rhizoids.

B) *Fucus evanescens* AG.

i. The haploid chromosome number of this plant is 32; at synapsis in the meiosis of oogonium, one centrosome is seen; at metaphase two centrosomes are visible at the opposite poles, and at telophase they have completely separated into two sister ones.

ii. The oogonium forms eight ova in the same manner as *F. vesiculosus* and *F. serratus* as observed by THURET.

iii. The embryo of this plant develops in the same manner as in *F. serratus;* its embryo in the early stages develops a single rhizoid and this rhizoid formation takes place in the most primitive manner within this family.

In conclusion, the writer wishes to express his thanks to Prof. H. MATSUURA and Prof. Y. YAMADA of Hokkaido Imperial University and Prof. M. TAHARA of Tôhoku Imperial University, for their valuable suggestions

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Explanation of Plates

Plate II

Representing sporeling development of *Pelvetia Wrightii* YENDO. All figures were drawn with the aid of Camera Lucida from fresh materials. Magnifications: 240 times.

Fig. 1. A discharged egg with a central nucleus and chromatophores surrounding the nucleus. Diameter 84 μ.

Fig. 2. First segmentation, forming two cells (24 hours after the oogonium liberation).

Fig. 3. Representing the terminal protrusion from one of the two cells (28 hours from the oogonium liberation).

Fig. 4. The second segmentation forming the rhizoid cell at one extremity (36 hours from the oogonium liberation).

Fig. 5. A rhizoid developing further, consisting of a few cells. (2 days from the oogonium liberation).

Figs. 6, 7. Further development. (3 days from the oogonium liberation).

Figs. 6a, 9. Abnormal embryo having developed two rhizoids at one extremity of the embryo.

Fig. 6b. Abnormal young embryo with a forked rhizoid.

Figs. 8, 10. An embryo with a rhizoid, the terminal cells of which show a bifurcatious condition. (5–6 days after the oogonium liberation).

Figs. 11a–d. Representing several conditions of bifurcatious branching at the terminal parts of the rhizoid. (5 days after the oogonium liberation).

Plates III and IV

Representing sporeling development of *Fucus evanescens* AG. All figures were drawn with aid of Camera Lucida from fresh materials. Magnification: Pl. III 1–8, 350 times. Pl. IV, A, B, C, D. 210 times, E, F, G, H. 115 times.

Plate III

Fig. 1. A discharged egg with a central nucleus and chromatophores surrounding the nucleus. Diameter 60 μ.

Fig. 2. First segmentation forming two cells. (24 hours from the oogonium liberation).

Fig. 3. Representing the terminal protrusion from one of the two cells (28 hours from the oogonium liberation).

Fig. 4. The second segmentation, forming the rhizoid cell at one extremity (36 hours from the oogonium liberation).

Fig. 5. Further segmentation of body cells.

Figs. 6, 7, 8. A rhizoid development further, consisting of a few cells (2 days from the oogonium liberation).

Figs. 9, 10. Abnormal embryos with a forked rhizoid. (2 days from the oogonium liberation).

Plate IV

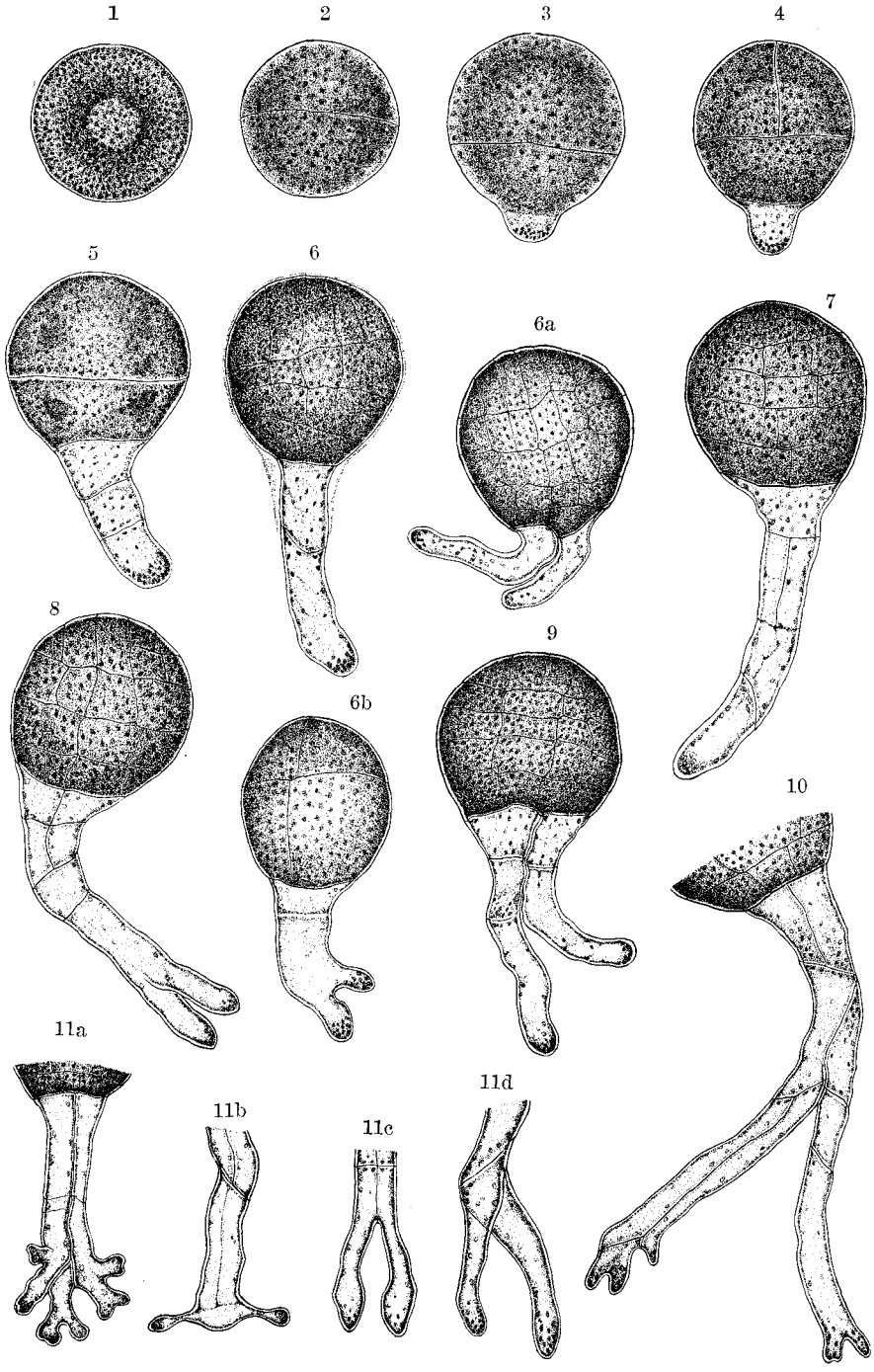
Fig. A. Representing the formation of the secondary rhizoid from the base of the primary rhizoid. (5 days from the oogonium liberation).

Fig. B. Abnormal development, two independent rhizoids being formed. (3 days from the oogonium liberation).

Fig. C. Abnormal development, one rhizoid branching into two at its base. (9 days from the oogonium liberation).

Fig. D. A later stage, in which the primary rhizoid becomes indistinguishable in appearance from secondary ones. (14 days from the oogonium liberation).

Figs. E, F, G, H. Representing successive stages of the development of secondary rhizoids and that of one or two hairs at the apical part of the embryo. (17 days from the oogonium liberation).



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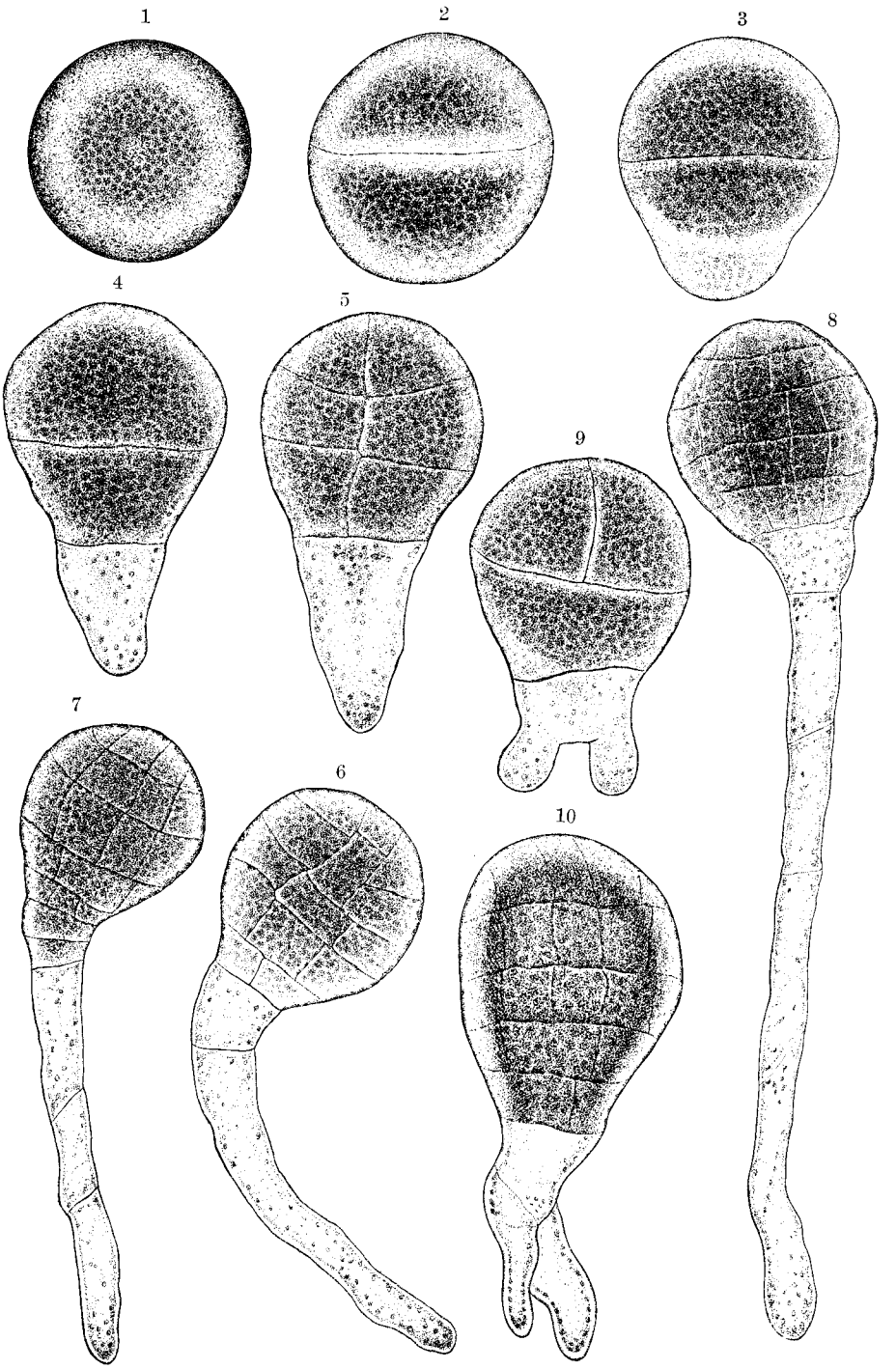

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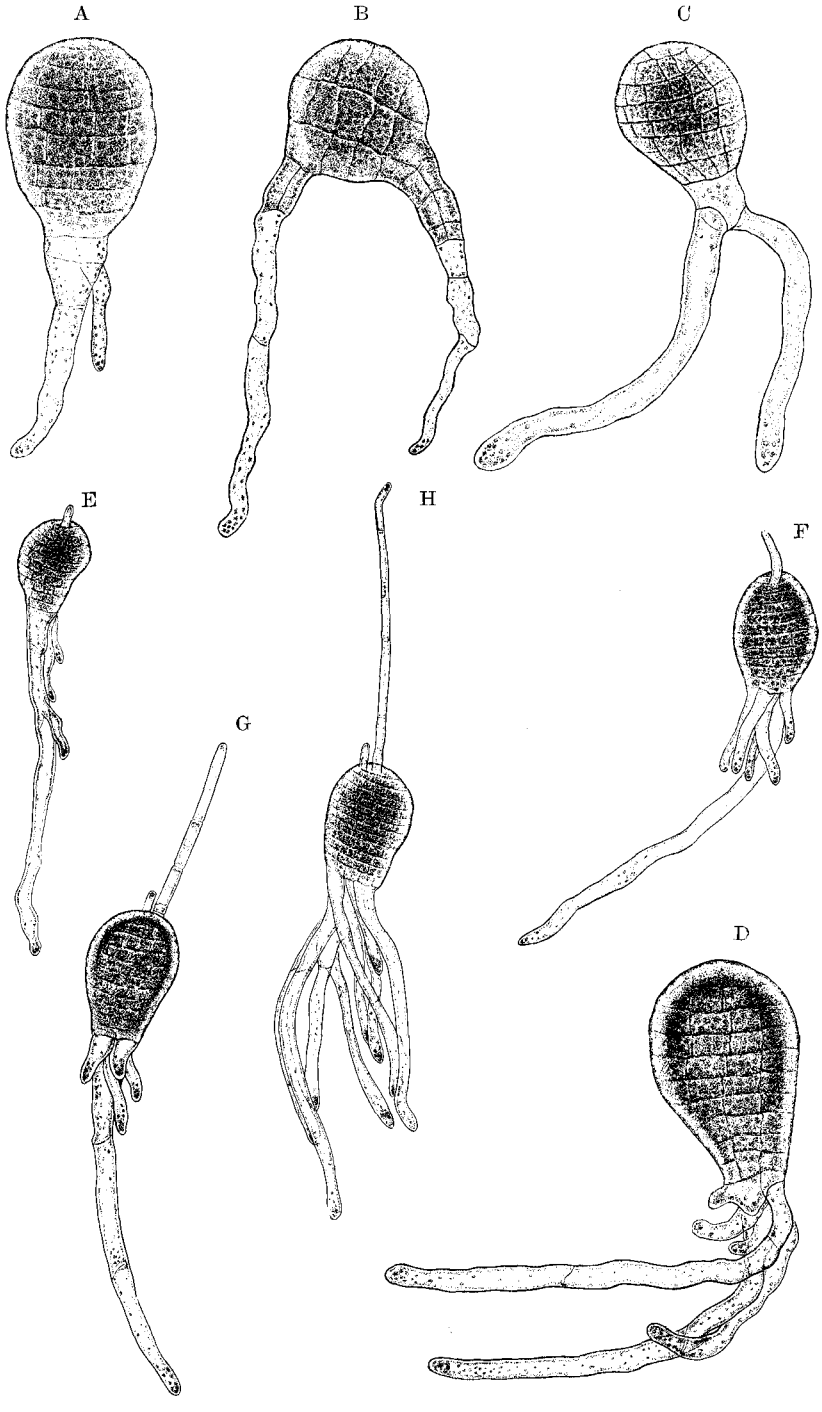

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