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A Study of the Male Reproductive Organ of the Florideae from Japan and its Vicinity*

By

NOBUO TAZAWA

Introduction

The Florideae which contains the vast majority of the Rhodophyta is at present grouped in six orders. These orders are mainly distinguished by details of reproduction, although vegetative features are commonly also of significance. The male reproductive organs of the Florideae are less known than either the female or the tetrasporic ones. The character of the male reproductive organ will throw light on the question of systematic relationships, since these have so far been mainly determined on the characters of the female and tetrasporic plants.

From 1953 to 1962 the writer has been systematically studying the male reproductive organs of the Florideae under the guidance of Prof. Y. YAMADA in the Botanical Institute, Faculty of Science, Hokkaido University. The present work was carried out to clarify in detail the development and structure of the male reproductive organs in some species of Florideae.

Sincere thanks are expressed to the writer's teacher, Professor Y. YAMADA for his kind guidance during the course of the present study and the use of the valuable material collected by him. His grateful thanks are also due to Professor Y. NAKAMURA for many helpful suggestions. Thanks are also due to Dr. Y. SAKAI, Dr. S. KAWASHIMA, and Mr. Y. TSUJI who gave him access to their collections.

Observations

Nemalion vermiculare SURINGAR

Pl. II, A; Fig. 1, C.

Material was obtained at Oshoro and Otaru, Hokkaido, in July 1953.

This species is monoecious. The spermatangial clusters are situated on the terminal cells of the assimilative filaments and appear as a branch-system, consisting

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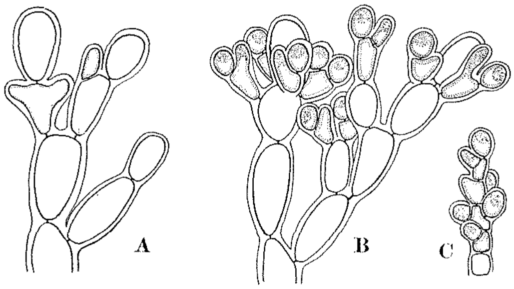

Fig. 1. Spermatangial clusters of *Nemalion*.
A–B. *Nemalion pulvinatum* GRUNOW, development of mother cells (A) and spermatangia (B).
C. *Nemalion vermiculare* SUR., showing formation of spermatangia.
A–C, ×800.

of usually four to six cells (Pl. II, A). The first step in the development of the male organ is the formation of an initial cell of the fertile branch-system. The initial cell originates from an apical cell of the assimilative filament. This initial cell cuts off a chain of four to six derivatives, each of which is a spermatangial mother cell. In early stages the spermatangial mother cell contains a well developed chromatophore. The sprmatangia appear as protuberances which arise from the distal end of the spermatangial mother cell (Fig. 1, C). As the spermatangial protuberance develops, the nucleus enters into nuclear division. After nuclear division one daughter nucleus enters the spermatangium, while the other remains in the spermatangial mother cell. Subsequently a wall completes the separation of the spermatangium. The newly produced spermatangium includes remains of a chromatophore.

Nemalion pulvinatum GRUNOW

Fig. 1, A–B.

Material was dried specimens which are preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is dioecious. The male organ usually forms irregular clusters on the distal ends of subterminal cells of the assimilative filaments (Fig. 1, B). The terminal cells of the assimilative filaments usually remain sterile but sometimes become fertile. The spermatangial mother cells first appear as protuberances which arise from the distal ends of the subterminal cells of the assimilative filaments. Subsequently cell walls complete the separation of the spermatangial mother cells (Fig. 1, A). Each spermatangial mother cell produces two or three spermatangia in the same way as in *N. vermiculare.*

Nemalion pulvinatum possesses the vegetative characters of the genus *Nemalion*. The chief differences between *N. pulvinatum* and the other members of *Nemalion* lies in the character of the male and the female organ (SEGAWA and OKAZAKI, 1941). In *N. pulvinatum*, the male organ forms irregular clusters around the shoulders of the subterminal cells of the assimilative filaments, whereas, in the other members of *Nemalion*, the spermatangial cluster appears as a branch-system which consists of several spermatangial mother cells. In *N. vermiculare* and *N. multifidum* (CLELAND, 1919), the spermatangial mother cell and the spermatangium include the chromatophore, while, in *N. pulvinatum*, no chromatophore was found. In the character of the male organ, *N. pulvinatum* is similar to *Dermonema frappieri* rather than the members of *Nemalion*. It is very questionable that *N. pulvinatum* belongs to the genus *Nemalion*.

Helminthocladia australis HARVEY

Pl. I, C; Fig. 2, A–B.

Material was obtained at Saga, Kochi Prefecture in April 1956.

This species is dioecious. The male organ forms head-like clusters on the terminal cells of the assimilative filaments (Pl. I, C). The spermatangial cluster appears as a branch-system which is composed of a number of short branchlets. The first step in the development of the male organ is the formation of initials of the fertile branchlets. These initials arise from the distal end of an apical cell of the assimilative filament. Subsequently each of initials divides usually to form a short ramified branchlet (Fig. 2, A), sometimes the initials, which arise from the subterminal end of the apical cell of the assimilative filament, produce only the spermatangial mother cells. Each cell of the fertile branchlet forms some sperma-

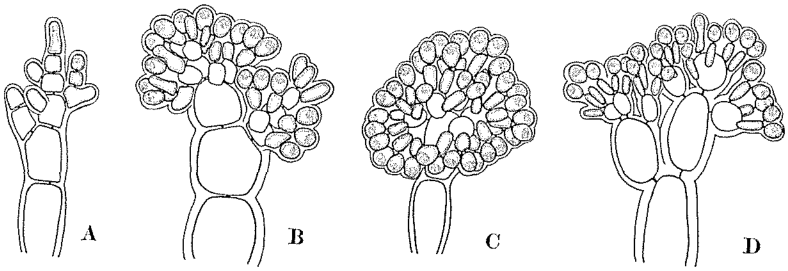

Fig. 2. Spermatangial clusters of *Helminthocladia*.
A–B. *Helminthocladia australis* HARV.; A, early stage in development; B, mature.
C. *Helminthocladia macrocephala* YAMADA.
D. *Helminthocladia yendoana* NARITA.
A–D, ×800

tangial mother cells, each of which is a colourless and forms one or two spermatangia (Fig. 2, B).

Helminthocladia macrocephala YAMADA

Fig. 2, C.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is dioecious. The male organ forms head-like clusters covering the terminal cells of the assimilative filaments (Fig. 2, C). The first step in the development of the spermatangial cluster is the formation of small fertile cells. These cells arise terminally and subterminally from the apical cell of the assimilative filament. They produce some spermatangial mother cells, each of which is colourless and forms one or two spermatangia.

Helminthocladia yendoana NARITA

Fig. 2, D.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is dioecious. The male organ forms hemispherical clusters on the apical cells of the assimilative filaments. The first step in the development of the spermatangial cluster is the formation of a small fertile cell. This cell appears as a protuberance which arises from the distal end of the terminal cell, occasionally the subterminal cell, of the assimilative filament. Subsequently a wall completes the separation of the small cell. This small cell produces radially some spermatangial mother cells, each of which forms one or two spermatangia (Fig. 2, D).

Liagora robusta YAMADA

Fig. 3, D.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is monoecious. The male organ forms a very loose group on the terminal cell of the assimilative filament (Fig. 3, D). Two or three spermatangial mother cells are directly produced from a terminal cell of the assimilative filament.

The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall. The spermatium is liberated through a narrow apical split in the spermatangial wall.

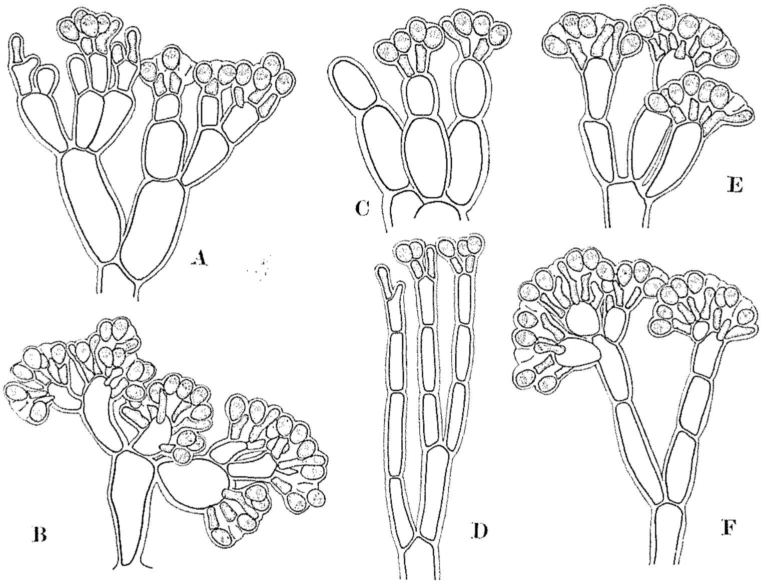

Fig. 3. Spermatangial clusters of *Liagora*.

A. *Liagora ceranoides* LAMOUR. f. *pulverulenta*.
B. *Liagora ceranoides* LAMOUR. f. *leprosa*.
C. *Liagora japonica* YAMADA.
D. *Liagora robusta* YAMADA.
E. *Liagora boninensis* YAMADA.
F. *Liagora orientalis* J. AG.
A–F, ×800.

Liagora japonica YAMADA

Fig. 3, C.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is monoecious. The male organ produces a small group on a terminal cell of the assimilative filament (Fig. 3, C). Two or three spermatangial mother cells arise directly from a terminal cell of the assimilative filament.

Liagora boninensis YAMADA

Fig. 3, E.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is dioecious. The male organ forms a small cluster on a terminal cell of the assimilative filament in corymbose manner (Fig. 3, E). Three to five spermatangial mother cells are directly produced from a terminal cell of the assimilative filament.

Liagora ceranoides LAMOUROUX

Fig. 3, A–B.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

According to YAMADA (1938) this species is divided mainly by the presence or absence of the proliferating ramuli into two forms, f. *pulverulenta* and f. *leprosa*. Both forms are monoecious and bear the male organ on the upper portion of the assimilative filament in nearly corymbose manner. The following differences are found, however, in detail of the structure of the spermatangial cluster.

In f. *pulverulenta* (Fig. 3, A) two or three (rarely four) spermatangial mother cells are produced on a terminal cell of the assimilative filament. As the result of this, the male organ develops in loose clusters on the assimilative filaments.

In f. *leprosa* (Fig. 3, B) the male organ forms dense clusters on the assimilative filaments, since five to eight spermatangial mother cells are formed on a terminal cell of the assimilative filament and, in addition, are formed on a small fertile cell which appears on a terminal cell of the assimilative filament.

Liagora orientalis J. AGARDH

Fig. 3, F.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is monoecious. The spermatangial cluster is found on the summit of the assimilative filament. The first step in the development of the spermatangial cluster is the formation of small fertile cells. Two or three small fertile cells arise from a terminal cell of the assimilative filament. Each and all of small fertile cells produce several sepermatangial mother cells, each of which forms one or two (rarely three) spermatangia. As the result of this, the male organ develops in somewhat dense clusters of corymbose manner on the top of the assimilative filament.

Liagora setchellii YAMADA

Fig. 4, A.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is ordinarily monoecious. The male organ produces dense clusters

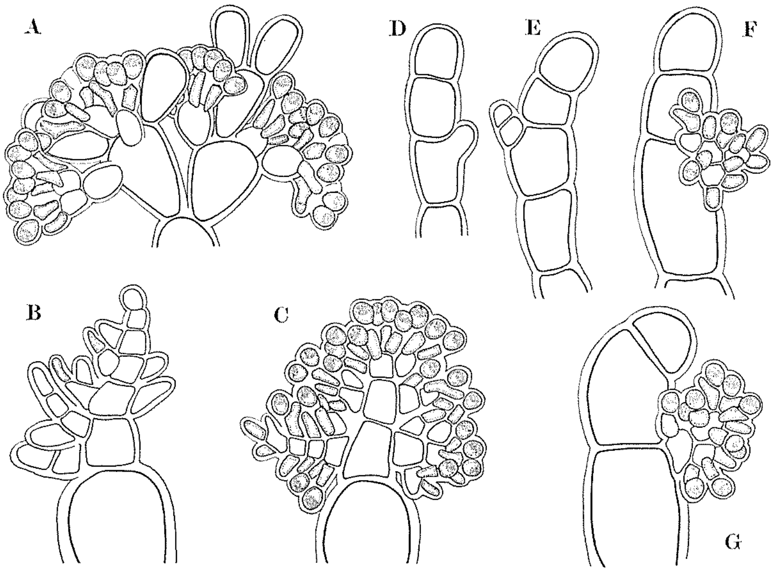

Fig. 4. Spermatangial clusters of *Liagora*.
A. *L. setchellii* YAMADA.
B–C. *L. farinosa* LAMOUR.; B, early stage in development.; C, mature.
D–G. *Liagora pinnata* HARV.; D–E, stages in development; F, young and G, mature.
A–G, ×800.

of corymbose manner on the upper portions of the assimilative filaments (Fig. 4, A). The first step in the development of the male organ is the formation of branchlets. The branchlets arise from cells near the distal end of the assimilative filament. Three to five spermatangial mother cells are formed from a cell of the branchlet. However, upper cells of the branchlets remain often sterile.

Liagora farinosa LAMOUROUX

Fig. 4, B–C.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is dioecious. The male organ appears as a densely packed spherical cluster on the terminal end of the assimilative filament. The first step in the development of the male organ is the formation of an initial cell of a branch-system. The initial cell arises from the distal end of a terminal cell of the assimilative filament. Subsequently the initial cell divides into several cells, which develop into the main axis of the spermatangial cluster. Each cell of the axis develop into a branch-system on all sides, the end cells of which bear several spermatangial mother cells (Fig. 4, B–C).

Liagora pinnata HARVEY

Fig. 4, D–G.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is monoecious. The male organ forms a densely spherical cluster on the third or fourth cell from the summit of the assimilative filament (Fig. 4, G). The first step in the development of the male organ is the formation of an initial cell of a branch-system. The initial cell first appears as a protuberance which becomes separated from the distal end of third or fourth cell from the summit of the assimilative filament (Fig. 4, D–E). Subsequently the initial cell develops into three or four fertile cells, each of which forms several spermatangial mother cells (Fig. 4, F).

Dermonema frappieri (MONT. et MILL.) BOERGESEN

Fig. 5, A–B.

The material used in this study was collected by Prof. Y. YAMADA at Hachijo Island in October 1952.

The fronds bear only one kind of sexual organ. The male organ forms small groups on the upper portions of the assimilative filaments (Fig. 5, B). One to three successive cells may be concerned in the production of the male organ. Usually the obovate terminal cell of the assimilative filament remains sterile, but in rare instances it become fertile. Sometimes the subterminal cell as well as the terminal cell remains sterile. The first step in the development of the male organ is the formation of spermatangial mother cells. These cells first appear as protuberances

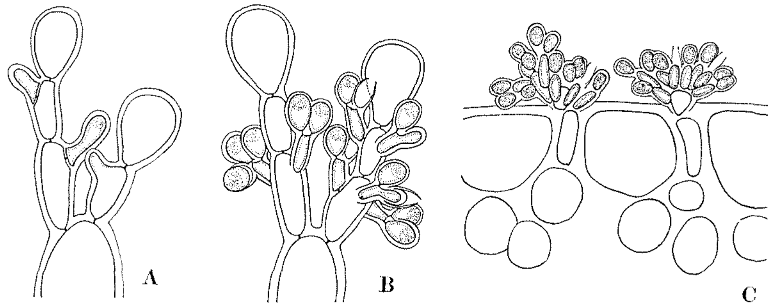

Fig. 5. Spermatangial clusters.
A–B. *Dermonema frappieri* (MONT. et MILL.) BOERGESEN ;
A, formation of spermatangial mother cells ; B, mature.
C. *Scinaia hormoides* SETCHELL ; vertical section.
A–C, ×800.

which arise from cells of the upper portions of the assimilative filaments (Fig. 5, A). Subsequently cell walls complete the separation of the spermatangial mother cell, each of which produces one to three spermatangia.

Scinaia hormoides SETCHELL

Pl. I, B; Fig. 5, C.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

This species is dioecious. The spermatangial clusters are borne as more or less hemispherical bodies covering the entire surface of branches of the male frond (Pl. I, B). Each of them is singly borne on a fertile thread, which arises from the pigmented end-cell of the cortex and grows among the vesicular cells. The fertile thread is composed of two or three cells. The terminal cell of this thread divides to give colourless, elongate cells, which produce a hemispherical cluster (Fig. 5, C). The cells so formed are spermatangial mother cells. One to three spermatangia arise from the distal end of the spermatangial mother cell.

Galaxaura elegans TANAKA

Pl. I, D.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male organ develops within deep and wide cavities scattered in the upper portion of the frond. The spermatangial cavities are nearly spherical in shape and measures about 250 μm in diameter. The female and the tetrasporic fronds of this species are wanting in the papillae on the exterior of them, but in the male frond, one- to three-celled papillae exist only near the aperture of the spermatangial cavities. The development and structure of the male organ are quite the same as those of *Galaxaura falcata*.

Galaxaura falcata KJELLMAN

Pl. I, E; Fig. 6, A–C.

Material was gathered at Katsu-ura, Chiba Prefecture in April 1956.

The male organ develops on the upper portions of branches of the frond. It is recognizable as deep spermatangial cavities, which are nearly spherical or rarely elliptical in shape and measures about 300 μm by 320 μm in size (Pl. I, E). The younger stage of the spermatangial cavity is found just below the apex of the branch. The first step in the development of the male organ is the formation of an initial cell of fertile threads. This initial cell arises from the outer cell of the central

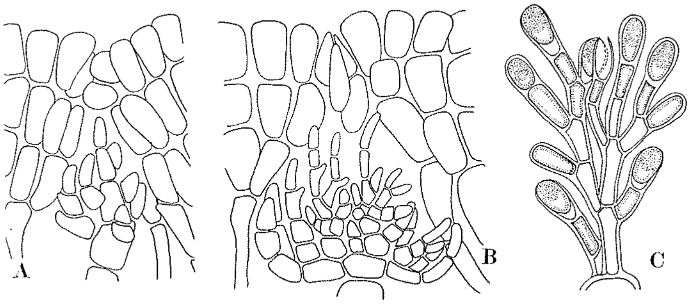

Fig. 6. Spermatangial conceptacles of *Galaxaura falcata* KJELLM.
A–B. vertical sections, showing two stages in development of a male branch-system.
C. male branch-system with spermatangia.
A–B, ×400; C, ×800.

frond-tissue and then divides to form a branch-system (Fig. 6, A–B). The thread which develops perpendicularly to the periphery of the frond from the initial cell becomes a main axis of a branch-system; the first laterals are borne on every side from the lower cells of the thread and produce secondary ones extending in the direction of the main axis. The secondary laterals develop into the axes of the second degree of the branch-system, each of which produces numerous small laterals. In the meantime, the fertile threads overgrown laterally are sunk within the cortex, as the neighbouring cortical threads grow out and are gradually calcified. The apical cells of the short and ramified laterals arising from each axis of the fertile branch-system are spermatangial mother cells (Fig. 6, C), each of which produces one to two spermatangia.

Galaxaura hystrix KJELLMAN

Pl. I, F.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male organ is produced within the cavities scattered on the upper portion of the male frond. The cavities are nearly spherical or ovate in shape and measure 200 μm to 300 μm in diameter. The development and structure of the male organ of this species are exactly the same as those of *G. falcata*.

Galaxaura papillata KJELLMAN

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male fronds are provided with one-celled papillae on the exterior of them, and the spermatangial cavities are scattered densely in the upper portions of them. The spermatangial cavity is nearly spherical or rarely pyriform in shape and measures 200 μm to 250 μm in diameter. The spermatangial cavity appears to be formed in a similar way to that of *G. falcata*.

Asparagopsis hamifera (HARIOT) OKAMURA

Pl. II. B; Fig. 7, D.

The material used in this study was collected by Prof. Y. YAMADA at Nada, Kôchi Prefecture in May 1954.

This species is dioecious. The spermatangial stand is borne on a hair-like lateral of limited growth (Pl. II, B) and develops in the same way as in *A. taxiformis*. The mature spermatangial stand is oblong in shape and 200–300 μm by 700–1,000 μm in size. The spermatangial mother cells arise from each surface cell in the swollen region of the male lateral. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has become swollen increasing in size, the spermatangium is cut off by the gradual ingrowth of the wall (Fig. 7, D).

Asparagopsis taxiformis (DELILE) COLLINS et HERVEY

Fig. 7, A–C.

Material was gathered at Sado Island in April 1956.

This species is dioecious. The spermatangial stand originates from a hair-like lateral consisting of a limited number of elongate axial cells. As the formation of the spermatangial stand is always preceded by the continual division of the pericentral cells (Fig. 7, C), the upper region of the male lateral develops in an obtuse and bladder-like form (Fig. 7, B). This swollen region is composed of

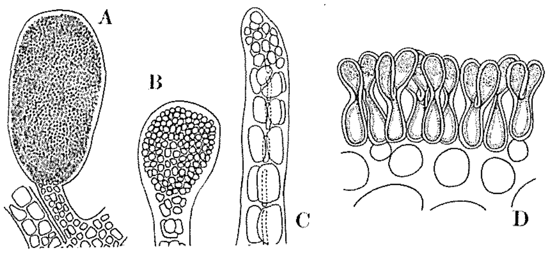

Fig. 7. Spermatangial stands.
A–C. *Asparagopsis taxiformis* (DELILE) COLLINS et HERVEY; A, mature; B–C, stages in development.
D. *Asparagopsis hamifera* (HARIOT) OKAMURA; cross section, showing formation of spermatangia.
A, ×80; B–C, ×243; D, ×800.

several rows of spherical cells, each surface cell of which divides to form spermatangial mother cells. The mature spermatangial stand is oblong in shape and 150–200 μm by 250–500 μm in size (Fig. 7, A).

Delisea fimbriata (LAMOUR.) MONTAGNE

Pl. II, C; Fig. 8, A–B.

The material used in this study was collected by Mr. Y. TSUJI at Shirahama, Shizuoka Prefecture in August 1958.

This species is dioecious. The male plants are similar in an outward appearance to the female and tetrasporic ones, but they may be distinguished by pale regions covering the surface of ramuli (Pl. II, C). These pale regions are spermatangial sori. The fertile ramuli are larger and thinner than the vegetative ones. In a sterile region, the outer layer of a ramulus consists of a single row of the cortical cells containing pigments, while, in a fertile region, the outer layer is composed of two cell rows, the spermatangial mother cells and the basal cells. The first sign of the formation of a sorus is initiated in an oblique division of superficial cells of fertile ramulus; of two cells thus formed, the lower one, which is pigmented, is the basal cell of the spermatangial mother cell, and the upper one is the spermatangial mother cell (Fig. 8, B). From each spermatangial mother cell, one or two spermatangia arise terminally. The formation of the spermatangia is preceded by a slight elongation of the spermatangial mother cell towards the exterior of ramulus. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. The spermatangial protuberance is cut off by the gradual ingrowth of the wall, and the first spermatangium thus formed is an elongated body with protoplasmic contents, much swollen at one end and pulled out to a tail at the other. The mature spermatium is liberated through a narrow apical split in the wall. After an escape of the primary spermatium has been completed, the same spermatangial mother cell forms a secondary

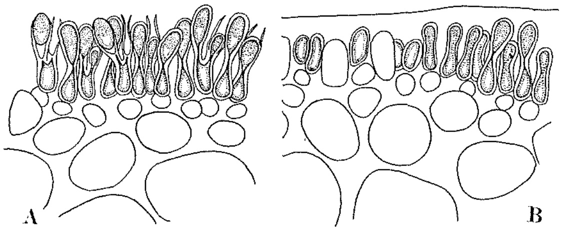

Fig. 8. Sections through spermatangial sori of *Delisea fimbriata* (LAMOUR.) MONT.; A, mature; B, young. A–B, ×800.

spermatangium by proliferation into the empty wall of the first formed one (Fig. 8, A).

Gelidium amansii LAMOUROUX

Pl. II, D; Fig. 9, A.

Material was gathered at Otaru, Hokkaido in September 1953.

This species is dioecious. The male frond is far smaller than both female and tetrasporic ones, and is conspicuous by the ultimate branches which are slightly dilated and flattened. These ultimate branches are covered with pale pink areas which are to be found behind the apex of them. The pale pink areas are spermatangial sori. The spermatangial mother cells are formed by an oblique division of superficial cells of the fertile area. The spermatangium is cut off from the spermatangial mother cell by the annular ingrowth of the wall, and the young spermatangium so formed is a cone in shape. The spermatangium, when fully ripen, is ellipsoidal in shape and about 2 μm by 3 μm in size. Through the apical split in the wall, the spermatium escapes into the surrounding water as a rounded cytoplasmic body.

Gelidium pacificum OKAMURA

Fig. 9, B.

Material was gathered at Ôhara, Chiba Prefecture in April 1956.

This species is dioecious. The male frond is smaller than both female and tetrasporic ones, and the ultimate branches, on which the male organ develops, are conspicuous by pale pink regions behind the tips of them. This region which is slightly dilated and flattened is a spermatangial sorus. The spermatangial mother cells and the spermatangia appear to be formed in the same manner as in those of *G. amansii*.

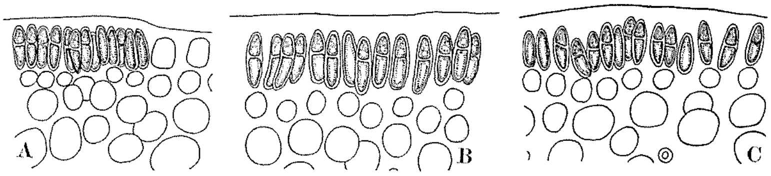

Fig. 9. Sections through spermatangial sori.
A. *Gelidium amansii* LAMOUR.
B. *Gelidium pacificum* OKAMURA.
C. *Gelidium subcostatum* OKAMURA.
A–C, ×800.

Gelidium subcostatum OKAMURA

Pl. II, E; Fig. 9, C.

Material was obtained from the drifts at Shichirigahama, Kanagawa Prefecture in April 1955.

This species is dioecious. Although the male frond is conspicuous by pale pink regions covering near the tips of pinnae, it is difficult to recognize the male specimens with the naked eye. The pale pink regions of pinnae are slightly dilated and flattened; within their regions the male organ develops. The spermatangial mother cells and the spermatangia are formed in the same way as in those of *G. amansii.*

Pterocladia densa OKAMURA

Pl. II, F; Fig. 10, A.

Material was gathered at Saga, Kôchi Prefecture in April 1956.

This species is dioecious. The male frond is conspicuous by the fertile ultimate branches with pale pink regions to be found near the tips of them. In the fertile region of the younger ultimate branch, the outmost layer of cortex is composed of the elongated and colourless cells. These cells are the spermatangial mother cells which are produced by an oblique division of superficial cells. The spermatangium is formed singly from a spermatangial mother cell in the same way as in *G. amansii.*

Pterocladia nana OKAMURA

Pl. II, G; Fig. 10, B.

Material was gathered at Mera, Chiba Prefecture in April 1956.

This species is dioecious. The male plants may be distinguished by pale pink regions over the ultimate branches which are slightly dilated and flattened. The

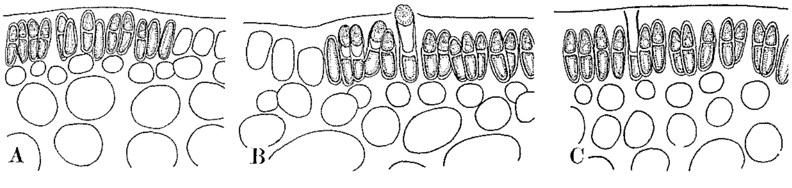

Fig. 10. Sections through spermatangial sori.

A. *Pterocladia densa* OKAMURA.
B. *Pterocladia nana* OKAMURA.
C. *Pterocladia tenuis* OKAMURA.
A–C, ×800.

pale pink regions are spermatangial sori. The spermatangial mother cells and the spermatangia are formed in the same way as in *G. amansii*.

Pterocladia tenuis OKAMURA

Pl. II, H; Fig. 10, C.

Material was gathered at Saga, Kôchi Prefecture in April 1956.

This species is dioecious. The male frond is conspicuous by the ultimate branches with the pale pink spermatangial sori. The outmost layer of the fertile region becomes the spermatangial mother cells which are formed by an oblique division of the superficial cells of cortex. The formation of spermatangia is the same way as those of *G. amansii*.

Dumontia incrassata (MUELLER) LAMOUROUX

Fig. 11, A.

Material was gathered at Otaru, Hokkaido in April 1954.

This species is dioecious. The male organ develops over almost the whole of the thallus with the exception of the base of the stipe. More often, however, sterile patches are left among the fertile sheets, dividing these into irregular sori, especially near the apex. The outmost cortical cells are cut off by walls which are parallel or somewhat perpendicular to the surface of the thallus. The cells so formed are spermatangial mother cells. These are colourless, oblong in shape and measure about 4 μm by 9 μm in size. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell and are cut off by an oblique annular ingrowth of the wall (Fig. 11, A). After the mature spermatium was liberated through a narrow apical split in the wall, the same spermatangial mother cell formed a secondary series by proliferation into the empty wall of the first-formed spermatangium. It is rarely the case that the new sper-

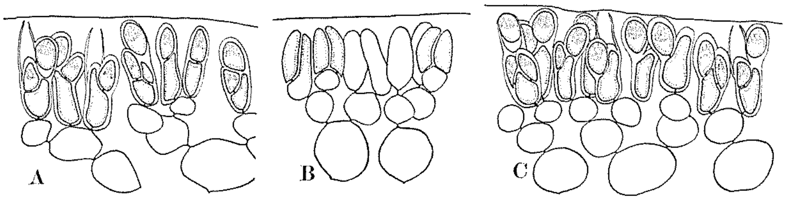

Fig. 11. Transverse sections of fronds through spermatangial sori.
A. *Dumontia incrassata* (MUELLER) LAMOUR., stages in development of spermatangia.
B–C. *Dumontia simplex* COTTON; B, formation of spermatangial mother cells; C, stages in development of spermatangia.
A–C, ×800.

matangium arises before the extrusion of the primary spermatium.

Dumontia simplex COTTON

Fig. 11, B-C.

Material was gathered at Otaru, Hokkaido in February and March 1954.

The plant is dioecious. The male thallus is a faintly purplish red in colour. The entire surface of the male thallus becomes fertile with the exception of its base. The production of the spermatangial mother cell is preceded by a division of an outer cortical cell (Fig. 11, B). The spermatangial mother cells are colourless, oblong in shape and measure about 5 μm by 9 μm in size. The development of spermatangia is the same way as those of *D. incrassata* (Fig. 11, C).

Hyalosiphonia caespitosa OKAMURA

Fig. 12, A-B.

Material was gathered at Otaru and Oshoro, Hokkaido in May and June 1954.

This species is dioecious. The male organ develops over the whole of the frond, but the lower portion of the main axis and the base of branches which are given off from the lower part of the plant remain sterile. More often, sterile patches are left among fertile areas, especially near the frond apex. The first step in the development of the male organ is a division of the outmost cortical cells. They are cut off by walls which are parallel or oblique to the frond surface. The cells so formed are spermatangial mother cells (Fig. 12, A), each of which bears one or two spermatangia. The spermatangial mother cell is colourless, oblong in shape and measures about 4 μm by 9 μm in size. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. Shortly the spermatangia are separated from the spermatangial mother cell by the

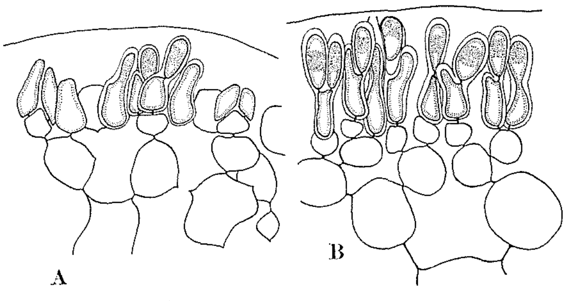

Fig. 12. *Hyalosiphonia caespitosa* OKAMURA.
A, formation of spermatangial mother cells in transverse section; B, formation of spermatangia in transverse section.
A-B, ×800.

gradual ingrowth of the wall (Fig. 12, B). The mature spermatangium is oblong in shape and measures about 3 μm by 7 μm in size.

Neodilsea yendoana TOKIDA

Fig. 13, A–C.

Material was gathered at Muroran, Hokkaido in October 1955.

The plant is dioecious. The male thallus is faint or yellowish red in colour. The male organ develops over almost the whole of the thallus. The outmost cortical cells are cut off by walls which are parallel or oblique to the thallus surface. The cells so formed are spermatangial mother cells (Fig. 13, C). The spermatangia appear as protuberances on the distal end of the spermatangial mother cell. Subsequently the spermatangium is cut off by an oblique annular ingrowth of the wall.

In the shape and size of the spermatangial mother cell and the spermatangium of this species the following two types are distinguishable. In one type, the spermatangial mother cell is oblong, measuring about 4 μm by 12 μm and the spermatangium is elliptic, measuring about 4 μm by 8 μm (Fig. 13, A). In the other type, the spermatangial mother cell is oblong, measuring about 3 μm by 6 μm and the spermatangium is elliptic, nearly spherical, measuring about 4 μm by 5 μm (Fig. 13, B) as in *N. tenuipes*. The spermatangial mother cell and the spermatangium of the latter type are smaller than those of the former type. The spermatangia of the latter type are more spherical than those of the former.

Neodilsea tenuipes YAMADA et MIKAMI

Fig. 13, D.

Material was gathered at Samani and Muroran, Hokkaido in August and October 1955.

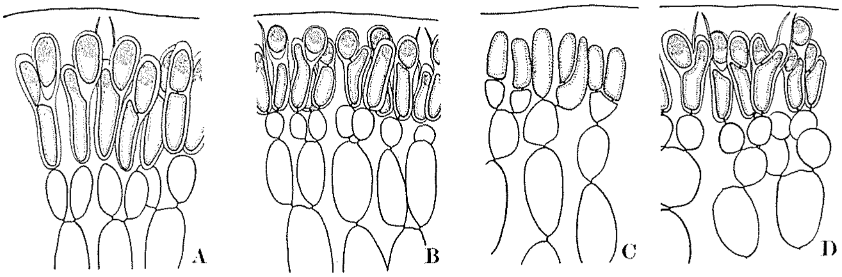

Fig. 13. Transverse sections of fronds through spermatangial sori. A–C. *Neodilsea yendoana* TOKIDA; A–B, showing two different types of spermatangium; C, formation of spermatangial mother cells. D. *Neodilsea tenuipes* YAMADA et MIKAMI. A–D, × 800.

The male thallus is faint or yellowish red in colour. The male organ is borne over almost the whole surface of the thallus. The development of the male organ is just the same as that described for *N. yendoana*. The spermatangial mother cell is oblong in shape and measures about 4 μm by 6 μm in size, and the spermatangium becomes nearly spherical in shape and attains about 4 μm in diameter.

Gloiopeltis furcata POSTLS et RUPRECHT

Fig. 14, A.

Material was gathered at Mera, Chiba Prefecture in April 1956.

This species is monoecious. The female organ is formed from the inner cortical cell, while the male one is from the superficial cell and develops over the whole surface of the frond (Fig. 14, A). The elongate cells formed the outer layer of the cortex give rise to the spermatangial mother cells by means of an apparently oblique division. Two spermatangia are formed subterminally and successively from the different sides of the spermatangial mother cell. The first spermatangium is formed as a protuberance surrounded by the wall of spermatangial mother cell. After the spermatangial protuberance has swollen increasing in size, the spermatangium is cut off by an oblique annular ingrowth of the wall. A second spermatangium develops by the side of the first at the apex of the spermatangial mother cell in the same way as the first one.

Gloiopeltis complanata (HARVEY) YAMADA

Pl. II, I; Fig. 14, B.

Material was gathered at Mera, Chiba Prefecture in April 1956.

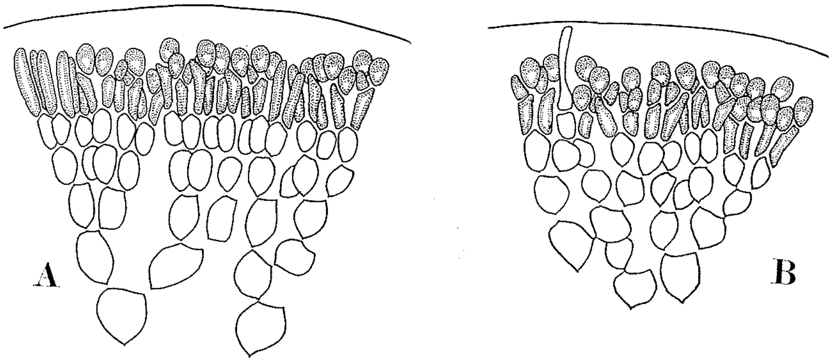

Fig. 14. Transverse sections through spermatangial sori.
A. *Gloiopeltis furcata* POST. et RUPR.
B. *Gloiopeltis complanata* (HARV.) YAMADA.
A–B, ×400.

This species is monoecious. The male organ is borne over the whole surface of branches. The formation of the male organ, however, is not found in the cortex occupied with the female organ. The male organ develops in the same way as in *G. furcata*. The spermatangial mother cell is produced by an oblique division of the last globose cell of outer cortical row. The spermatangia are cut off by an oblique annular ingrowth of the wall.

Desmia hornemanni MARTENS

Pl. IV, A; Fig. 15, D.

Material was gathered at Shichirigahama, Kanagawa Prefecture in April 1955.

This species is dioecious. The male organ is borne in the nemathecium which is recognizable as a pale and irregular cushion-like swelling on a branch of the frond. In a section of a branch through the male nemathecium it can be seen that the nemathecium is composed of colourless simple threads which grow out from the surface cells of the branch (Pl. IV, A). The first step in the development of the nemathecium is the formation of a cone-shaped initial cell of the nemathecial thread. This initial cell arises from the surface cell of the branch. The initial cell transversely divides to form a simple thread composed of several cells, usually five to six. The basal cell of the thread is oblong in shape and remains in sterile, while others are slightly spherical in shape and constitute the spermatangial mother cells which produce laterally one or two spermatangia (Fig. 15, D). The spermatangia first appear as protuberances which arise laterally from the spermatangial mother cells. After the spermatangial protuberances have developed, the spermatangia are cut off by an oblique annular ingrowth of the walls.

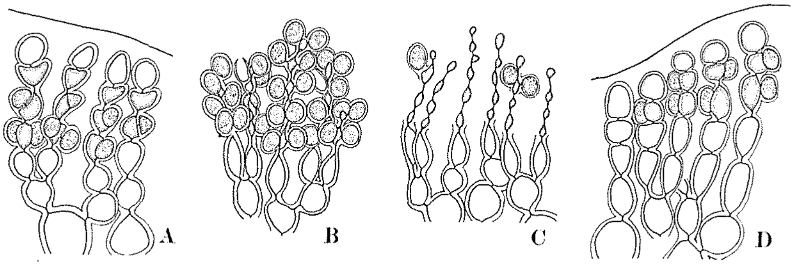

Fig. 15. Vertical sections of male nemathecia.

A–C. *Desmia japonica* HARV.; A, showing development of spermatangia; B. mature; C, showing threads of spermatangial mother cells after liberation of spermatia.

D. *Desmia hornemanni* MART., showing development of spermatangia. A–D, ×800.

Desmia japonica HARVEY

Fig. 15, A–C.

Material was gathered at Ôhara, Chiba Prefecture in May 1955.

This species is dioecious. The male organ is formed in the nemathecium which appears as a whitish pink and irregular cushion-like swelling on a branch of the frond. The male nemathecium is composed of a dense aggregate of fertile threads which grow out from the surface cells of the branch (Fig. 15, B–C). The spermatangial mother cells and the spermatangia are formed in the same way as in *D. hornemanni* (Fig. 15, A).

Rhodopeltis setchellii YAMADA

Fig. 16, A.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The plant is dioecious. The frond of this species is composed of three regions; an inner one consists of hyphal cells known as the medullary hypae, which on the exterior give rise to large cortical cells; the second region is the cortex consisting of four to five layers of the large cortical cells and being here strongly calcified; the last region consists of one or two layers of assimilative cells arising from the end cell of calcified cortex.

The male organ forms loose clusters on the outermost assimilative cells (Fig. 16, A). The first step in the development of the male organ is the formation of spermatangial mother cells. These appear as protuberances which become separated from the terminal cell of the assimilative cell row. The spermatangial mother

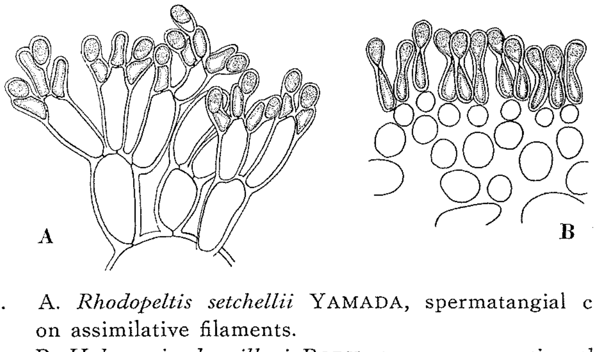

Fig. 16. A. *Rhodopeltis setchellii* YAMADA, spermatangial clusters on assimilative filaments.
B. *Halymenia durvillaei* BORY, transverse section through a spermatangial sorus, showing formation of spermatangia.
A–B, ×800.

cells thus formed are small bodies with dense protoplasmic contents. The formation of the spermatangia is preceded by a slight elongation of the spermatangial mother cells toward the exterior of the frond. From each of these elongated cells arise small protuberances. After the protuberances have developed, these are cut off by an annular ingrowth of the walls. The dense protoplasmic bodies thus formed are the spermatangia.

Halymenia durvillaei BORY

Fig. 16, B.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male specimen is yellowish red in colour and bears ramuli densely at the margins of branches. The male organ develops in sori covering the whole of the thallus with the exception of the lower portion. The formation of spermatangial mother cells may be preceded by a division of the cells of the outer layer. The spermatangium first appears as a protuberance which arises terminally from a spermatangial mother cell. The protuberance increases in size and is cut off from the spermatangial mother cell by the gradual ingrowth of the wall. Each spermatangial mother cell bears one spermatangium.

Grateloupia filicina (WULFEN) J. AGARDH

Fig. 17, A.

Material was gathered by Mr. Y. TSUJI at Sugashima, Mie Prefecture in April 1955.

This species is dioecious. The male frond is faint or yellowish red in colour. The male organ develops in sori covering the whole of the frond with the exception of the lower portion. Two spermatangial mother cells are borne by an oblique division of the terminal cell of cortical cell rows. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall. One or two spermatangia are borne on a spermatangial mother cell.

Grateloupia divaricata OKAMURA

Pl. III, A; Fig. 17, B.

Material was gathered at Otaru, Hokkaido in October 1953.

The male frond is faintly brownish or yellowish red in colour. The male organ develops in sori covering the upper regions of branchlets and the whole of

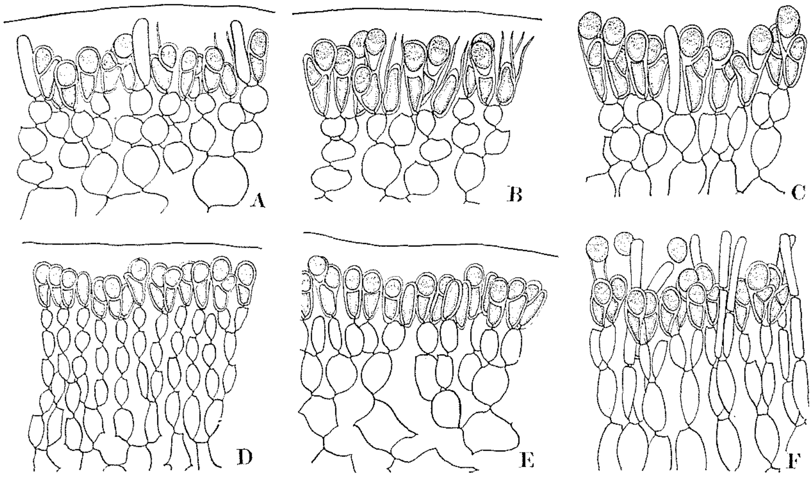

Fig. 17. Transverse sections through spermatangial sori.
A. *Grateloupia filicina* (WULFEN) J. AG.
B. *Grateloupia divaricata* OKAMURA.
C. *Grateloupia livida* (HARV.) YAMADA.
D. *Grateloupia okamurai* YAMADA.
E. *Grateloupia turuturu* YAMADA.
F. *Grateloupia imbricata* HOLMES.
A–F, ×800.

laterals which are pinnately arranged at the margins of branches. The spermatangial mother cells and the spermatangia are formed in the same way as in *G. filicina.*

Grateloupia livida (HARVEY) YAMADA

Fig. 17, C.

Material was gathered at Ashizuri-zaki, Kôchi Prefecture in April 1956.

The male frond is faintly purplish red in colour. The male organ is borne in the sorus covering almost the whole surface of the frond. In the fertile area the outmost cortical cells become spermatangial mother cells, each of which produces usually two spermatangia as protuberances budded off from its distal end. The spermatangial mother cells and the spermatangia are produced in the same way as in *G. filicina.*

Grateloupia okamurai YAMADA

Fig. 17, D.

Material was obtained at Shichirigahama, Kanagawa Prefecture in April 1955.

The male thallus is faint red in colour. The male organ is borne in the sorus covering almost the whole surface of the thallus. In a section of the thallus it can be seen that the cortical region consists of close-set cell rows extending perpendicularly to the periphery. Small celled chains of the cortex arise in pairs from the outer cells of widely separated stellate cells. The cortical cell rows of sterile portion of the thallus are terminated by a single rather elongated cell, while those of fertile portion end in a pair of spermatangial mother cells. The spermatangial mother cells and the spermatangia are produced in the same way as in *G. filicina*.

Grateloupia turuturu YAMADA

Fig. 17, E.

Material was gathered at Ôhara, Chiba Prefecture in May 1955.

The male thallus is faint red in colour. The male organ develops over almost the whole of the thallus with the exception of the lower portion. The outer cortex of the male thallus is composed of chains of a few globose cells, always terminating in two elongated cells. These elongated cells are the spermatangial mother cells, each of which produces usually two spermatangia as protuberances budded off from the distal end of it. The spermatangial mother cells and the spermatangia are produced in the same way as in *G. filicina*.

Grateloupia imbricata HOLMES

Fig. 17, F.

Material was gathered at Ashizuri-zaki, Kôchi Prefecture in April 1956.

The male organ develops over almost the whole of branches and branchlets of the frond. The outer cortex of the male frond is occupied by sterile and fertile threads, which grow out from the inner cortical cells. The sterile threads are terminated by a single elongated cell overtop the fertile ones, each of which is terminated by a pair of spermatangial mother cells. The spermatangial mother cells are produced by a oblique division of the last elliptical cells of fertile threads. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall.

As mentioned above, *G. imbricata* is different from the other members of *Grateloupia* in the structure of the cortex of the male thallus. In the former the outer cortex is composed of rather oblong sterile cells and globose fertile ones, whereas in the latter it is occupied by rows of the globose fertile cells. In this respect, *G. imbricata* is more closely related to the members of *Pachymeniopsis* than those of *Grateloupia*.

Pachymeniopsis elliptica (HOLMES) YAMADA

Fig, 18, A.

Material was gathered at Ashizuri-zaki, Kôchi Prefecture in April 1956.

The male organ develops over almost the whole of the thallus with the exception of the holdfast and around it. In a section of the male thallus the outer cortex shows a dense aggregate of cell rows which consist of small globose cells and oblong ones. The former cell row is always terminated by two spermatangial mother cells and the latter ends in a single elongated cell which overtops the former. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has devoloped, the spermatangium is cut off by an annular ingrowth of the wall.

Pachymeniopsis yendoi YAMADA

Fig. 18, B.

Material was collected by Dr. S. KAWASHIMA at Ôma, Aomori Prefecture in August 1956.

The male organ is borne over almost the whole surface of the thallus. The outer cortex of the male thallus is composed of rows of rather oblong cells and elliptical ones. The former cell row is terminated by a single oblong cell and the latter ends in a pair of small cells. These small cells are the spermatangial mother cells which bear one or two spermatangia. The spermatangia first appear as protuberaces which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall.

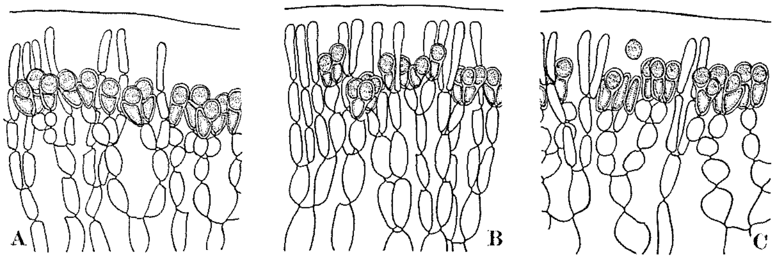

Fig. 18. Transverse sections through spermatangial sori.

A. *Pachymeniopsis elliptica* (HOLMES) YAMADA.
B. *Pachymeniopsis yendoi* YAMADA.
C. *Pachymeniopsis lanceolata* (OKAMURA) YAMADA.
A–C, ×800.

Pachymeniopsis lanceolata (OKAMURA) YAMADA

Fig. 18, C.

Material was gathered at Mera, Chiba Prefecture in April 1956.

The male organ develops over almost the whole of the thallus with the exception of the lower portion. The outer cortex of the male thallus is composed of two kinds of cell rows. One is the sterile threads which are composed of oblong cells and extend perpendicularly to the periphery. The other is the fertile ones which consist of small globose cells and grow out obliquely. The sterile threads overtop the fertile ones which terminate in a pair of the spermatangial mother cells. The spermatangial mother cells are produced by an oblique division of the outmost globose cortical cells. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed, the spermatangium is cut off an oblique annular ingrowth of the wall.

Phyllymenia sparsa (OKAMURA) KYLIN

Pl. III, B; Fig. 19, A.

Material was gathered at Ôarai, Ibaragi Prefecture in April 1955.

This species is dioecious. The male organ develops in sori which appear as small patches or as large irregular areas. Two spermatangial mother cells are formed by an oblique division of a superficial cell of the soral area. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall.

Carpopeltis affinis (HARVEY) OKAMURA

Fig. 19, B–E.

Material was gathered at Oshoro, Hokkaido in July 1953.

This species is dioecious. The male organ develops in sori covering on the upper part of the frond. The spermatangial sori are recognizable as pale yellow or pink and somewhat hyaline regions. Two spermatangial mother cells are borne by an oblique division of an outmost cell of each cortical cell row (Fig. 19, B, E). The formation of the spermatangia is preceded by a slight elongation of the spermatangial mother cells toward the exterior of the frond. From the surface of these elongated spermatangial mother cells the spermatangia first appear terminally as protuberances composed of an upward protoplasmic extension. After the spermatangial protuberance has developed, the spermatangium is cut off by

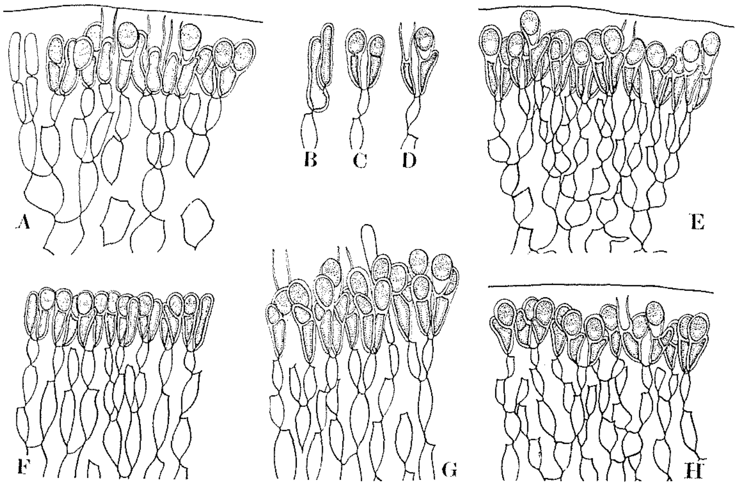

Fig. 19. Transverse sections through spermatangial sori.
A. *Phyllymenia sparsa* (OKAMURA) KYLIN.
B–E. *Carpopeltis affinis* (HARV.) OKAMURA; B–D, various stages in development of spermatangia.
F. *Carpopeltis divaricata* OKAMURA.
G. *Carpopeltis angusta* (HARV.) OKAMURA.
H. *Carpopeltis flabellata* (HOLMES) OKAMURA.
A–H, ×800.

an annular ingrowth of the wall (Fig. 19, C). The spermatium is liberated through an apical split in the elastic wall (Fig. 19, D). About the time when the first spermatangium matures, a second one develops laterally by the side of the first at the apex of the spermatangial mother cell; this grows up, ripens and liberates its contents in the same way as the first one (Fig. 19, D).

Carpopeltis angusta (HARVEY) OKAMURA

Pl. III, C; Fig. 19, G.

Material was gathered at Sirahama, Wakayama Prefecture in July 1957.

This species is dioecious. The male organ develops in sori over almost the whole of laterals of the frond, except for the margins of them (Pl. III, C). In the fertile region the outmost layer of the cortex becomes the spermatangial mother cells which are produced by an oblique division of the superficial cells of the outer cortex. The spermatangia are formed in the same way as in *C. affinis* (Fig. 19, G).

Carpopeltis divaricata OKAMURA

Fig. 19, F.

Material was gathered at Shichirigahama, Kanagawa Prefecture in April 1955.

This species is dioecious. The male organ develops in sori covering almost the whole of branches of the plant. The branches bearing the male organ are recognizable with the pale brownish red in colour. In the fertile area the outmost layer of the cortex becomes the spermatangial mother cells, each of which produces one or two spermatangia as protuberances budded off from it. The spermatangial mother cells and the spermatangia are formed in the same may as those of *C. affinis*.

Carpopeltis flabellata (HOLMES) OKAMURA

Fig. 19, H.

Material was gathered at Ashizuri-zaki, Kôchi Prefecture in April 1956.

This species is dioecious. The male organ develops in sori covering on the upper part of the thallus. The spermatangial sori are recognizable as whitish pink or pale yellow areas. In the fertile region the outmost layer of the cortex becomes the spermatangial mother cells which are produced by an oblique division of the terminal globose cell in each cortical cell row. The spermatangia are formed in the same way as in *C. affinis*.

Callophyllis adnata OKAMURA

Fig. 20, A.

Material was gathered at Sado Island in April 1956.

The male thallus is faint red in colour. The male organ is borne in sori covering the upper areas of branches of the frond. The spermatangial mother cell produced by a transverse or an oblique division of the outmost cortical cell is ellipsoidal in shape and measures about 3 μm by 5 μm in size. One or two spermatangia appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall. The mature spermatangium is ellipsoidal, nearly a spherical, in shape and measures about 3 μm by 4 μm in size.

Callophyllis crispata OKAMURA

Fig. 20, F.

Material was collected by Mr. Y. TSUJI at Shichirigahama, Kanagawa Prefecture in May 1955.

The male plant is faint red in colour. The male organ is borne in sori covering

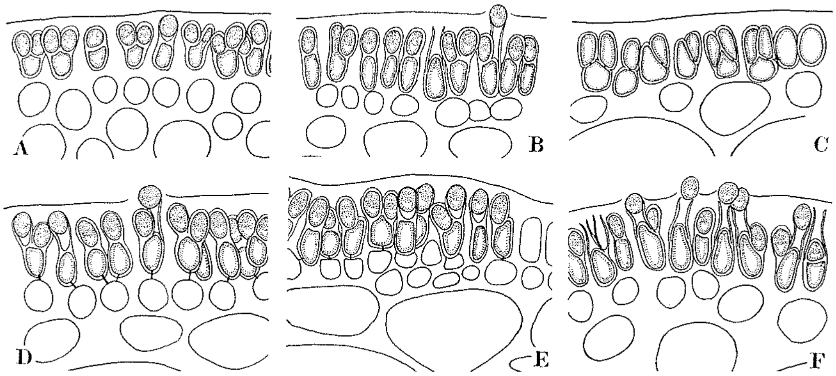

Fig. 20. Transverse sections through spermatangial sori.
A. *Callophyllis adnata* OKAMURA.
B–C. *Callophyllis japonica* OKAMURA, development of spermatangia (B) and mother cells (C).
D. *Callophyllis palmata* YAMADA.
E. *Callophyllis laciniata* (HUDS.) KUETZ.
F. *Callophyllis crispata* OKAMURA.
A–F, ×800.

the upper areas of branches. The spermatangial mother cells and the spermatangia are formed in the same way as in *C. adnata*. The spermatangial mother cell is oblong in shape and measures about 3 μm by 7 μm in size. The spermatangium arising from the distal end of the spermatangial mother cell is ellipsoidal in shape and measures about 3 μm by 5 μm in size.

Callophyllis japonica OKAMURA

Fig. 20, B–C.

Material was collected by Mr. Y. TSUJI at Shichirigahama, Kanagawa Prefecture in May 1955.

The male frond is faint red in colour. The male organ is borne in sori covering the upper areas of branches. The spermatangial mother cells (Fig. 20, C) and the spermatangia (Fig. 20, B) are formed in the same way as in *C. adnata*. The spermatangial mother cell is elliptical in shape and measures about 3 μm by 7 μm in size. The spermatangium is ellipsoidal in shape and measures about 3 μm by 5 μm in size.

Callophyllis laciniata (HUDSON) KUETZING

Pl. III, D; Fig. 20, E.

Material was gathered at Ochi-ishi, Hokkaido in June 1956.

The male plant is faint red in colour. The male organ develops in sori over almost the whole of branchlets. The spermatangial mother cells and the spermatangia are formed in the same way as in *C. adnata*. The spermatangial mother cell is elliptical in shape and measures about 3 μm by 6 μm in size. The spermatangium is elliptical in shape and measures about 3 μm by 5 μm in size.

Callophyllis palmata YAMADA

Fig. 20, D.

Material was obtained from the drifts at Matsushima, Miyagi Prefecture in April 1954.

The male thallus is faint red in colour. The male organ is borne in sori covering the upper areas of branches. The spermatangial mother cells and the spermatangia are formed in the same way as in *C. adnata*. The spermatangial mother cell is ellipsoidal in shape and measures about 4 μm by 7 μm in size. The spermatangium is elliptical in shape and measures about 3 μm by 5 μm in size.

Callymenia reniformis var. ***cuneata*** J. AGARDH

Pl. II, E; Fig. 21, A.

Material was obtained from the drifts at Ochi-ishi, Hokkaido in June 1956.

This species is dioecious. The male organ develops in sori covering the upper area of the thallus. The spermatangial sorus is recognizable as a faint or whitish red area. The inner cortex composes of usually two or three layers of spherical cells, and the outer one composes of usually one layer of ellipsoidal cells. The spermatangial mother cells are formed by an oblique or transverse division of the ellipsoidal cells of the outer cortex. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has been increased in size, the spermatangium is cut off by an annular ingrowth of the wall.

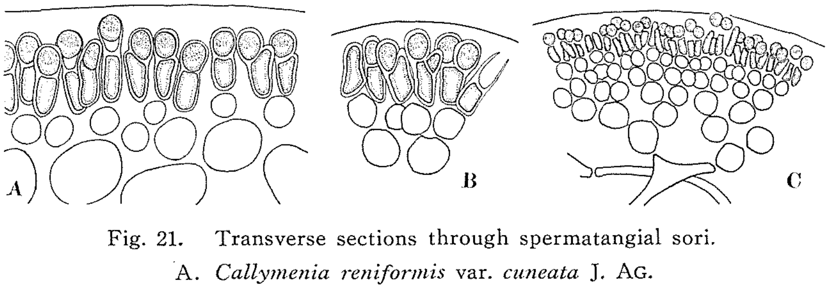

Fig. 21. Transverse sections through spermatangial sori.
A. *Callymenia reniformis* var. *cuneata* J. AG.
B–C. *Schizymenia dubyi* (CHAUVIN) J. AG.
A–B, ×800; C, ×400.

Schizymenia dubyi (CHAUVIN) J. AGARDH

Fig. 21, B-C.

Material was gathered at Matsushima, Miyagi Prefecture and Shichirigahama, Kanagawa Prefecture in April 1955.

The male thallus is faint or yellowish red in colour. The male organ develops in sori covering almost the whole surface of the thallus. The thallus composes of two regions; the inner one is formed with long hyphal cells known as the medulary hyphae; the outer one is the cortex which consists of anticlinal, dichotomously branched chains, whose cells are spherical in shape and are progressively smaller toward the exterior. The superficial cell of the cortex usually produces two spermatangial mother cells (Fig. 21, C). The spermatangium first appears as a conical projection from the distal end of the spermatangial mother cell. After the spermatangial projection has swollen increasing in size, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 21, B).

Gracilaria verrucosa (HUDSON) PAPENFUSS

Pl. III, G; Fig. 22, A-F.

Material was gathered at Akkeshi, Hokkaido in July 1954.

The male frond is mottled by pale small patches scattered on the main branch. The male organ develops within deep and cup-like cavities (Pl. III, G). The first step in the development of the male organ is the formation of an initial cell of fertile threads. The initial cell arises from the outer cell of the cortex increasing in size (Fig. 22, A), and divides to form the fertile threads (Fig. 22, B, C). As the fertile threads overgrow laterally and in the meantime, the neighbouring cortical threads grow out, they are sunk within the cortex (Fig. 22, D, E). Each cell of the fertile threads is the spermatangial mother cell. The spermatangial mother cells extend in the direction of the center of the cavity to give rise to spermatangia. The spermatangium first appears terminally from the surface of the elongated spermatangial mother cell as a protuberance composed of an upward protoplasmic extension. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall. The mature spermatium is liberated through a narrow apical split in the wall. After an escape of the primary spermatium has been completed, the same spermatangial mother cell forms a secondary spermatangium by proliferation into the empty wall of the first-formed one. Sometimes, the new spermatangium arises before the extrusion of the primary spermatium (Fig. 22, F).

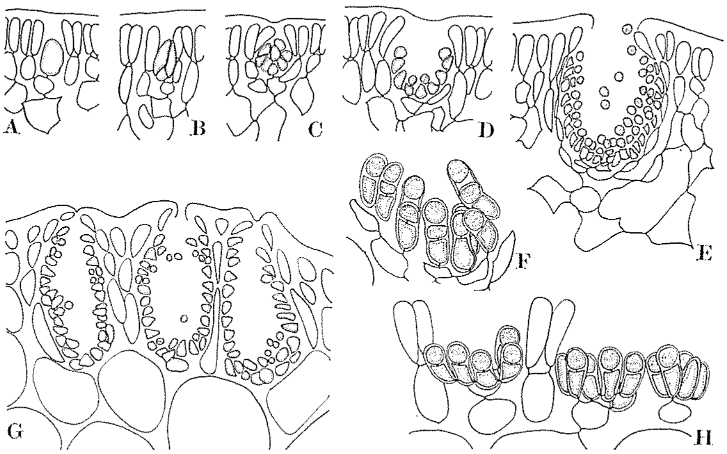

Fig. 22. Vertical sections of spermatangial conceptacles
A–F. *Gracilaria verrucosa*, (HUDS.) PAPENF.; A–E, various stages in development of spermatangial conceptacles.; F, development of spermatangia.
G. *Gracilaria arcuata* ZANARD.
H. *Gracilaria textorii* SUR., development of spermatangia.
A–E, G, ×400; F,H, ×800.

Gracilaria arcuata ZANARDINI

Pl. III, H; Fig. 22, G.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male frond is conspicuous by circular pale patches scattered on the branches. The male organ develops within deep and cup-like cavities. The inside layer of the cavity is composed of the threads of spermatangial mother cells. The male organ develops in the same way as in *G. verrucosa*.

Gracilaria textorii SURINGAR

Pl. III, F; Fig. 22, H.

Material was gathered at Usu, Hokkaido in July 1954 and at Shichirigahama, Kanagawa Prefecture in April 1955.

The male plants are easily recognizable by pale patches scattered on the whole of the thallus under a slight magnification with a hand-lens. The male organ develops within shallow saucer-like cavities. The first step in the development of the male organ is the formation of an initial cell of fertile threads which constitute a floor of the cavity. The initial cell transformed from the superficial cell of the thallus divides to form the fertile threads overgrown laterally, while the neighbouring cortical threads grow out in length. In the fertile region, therefore, the fertile threads are sunk within the cortex. Each cell of the fertile threads is a spermatangial mother cell. The formation of spermatangia is preceded by a slight elongation of the spermatangial mother cells toward the exterior of the thallus. From each of spermatangial mother cells a spermatangium is cut off by an annular ingrowth of the wall.

Hypnea boergesenii TANAKA

Pl. IV, B; Fig. 23, A, E.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male organ develops in sori covering almost the whole surface of the ultimate branchlets of the frond. The spermatangial mother cell is borne by an oblique division of the superficial cell of the cortex (Pl. IV, B; Fig. 23, A). The formation of the spermatangia is preceded by a slight elongation of the spermatangial mother cells toward the exterior of the ultimate branchlet. The spermatangia appear terminally from the surface of the spermatangial mother cell, as protuberances composed of an upward protoplasmic extension. After the spermatangial protuberance has developed, the spermatangium is cut off by an annular ingrowth of the wall. The mature spermatium is liberated through a narrow apical split in the wall. After an escape of the primary spermatium has completed, the same spermatangial mother cell forms a secondary spermatangium by proliferation into the empty sheath of the first-formed one; sometimes, the new spermatangium

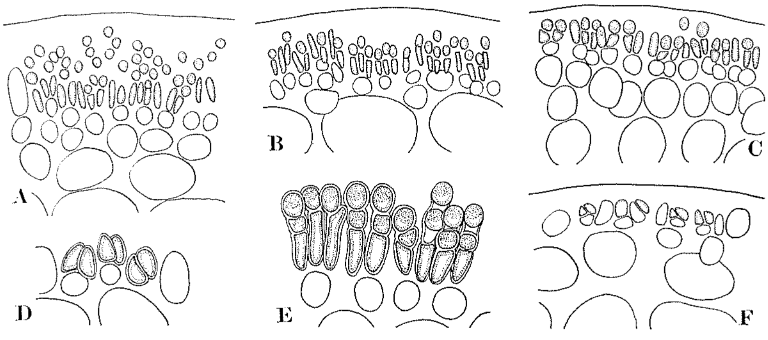

Fig. 23. Transverse sections through spermatangial sori.
A, E. *Hypnea boergesenii* TANAKA; E, development of spermatangia.
B, D. *Hypnea cervicornis* J. AG.; D, formation of spermatangial mother cells.
C, F. *Hypnea variabilis* OKAMURA; F, formation of spermatangial mother cells.
A–C, F, ×400; D–E, ×800.

arises before the extrusion of the primary spermatium (Fig. 23, E).

Hypnea cervicornis J. AGARDH

Fig. 23, B, D.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male organ develops in sori covering almost the whole surface of the ultimate branchlets. The superficial cells of the ultimate branchlet are cut off to form the spermatangial mother cells by a transverse or an oblique wall (Fig. 23, D). The spermatangia are formed in the same way as in *H. boergesenii* (Fig. 23, B).

Hypnea variabilis OKAMURA

Fig. 23, C, F.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male plant may be distinguishable on a close examination by the pale red regions over the ultimate branchlets. The pale red regions are spermatangial sori. The spermatangial mother cells (Fig. 23, F) and the spermatangia (Fig. 23, C) are formed in the same way as in *H. boergesenii.*

Chondrus crispus (L.) STACKHOUSE

Fig. 24, A.

Material was gathered at Kamoenai, Hokkaido in August 1954.

The male frond possesses flabellately dichotomous branches and is fringed with numerous leafy proliferations at the margin of the frond. The male organ develops in sori covering the upper part of the frond. The spermatangial mother

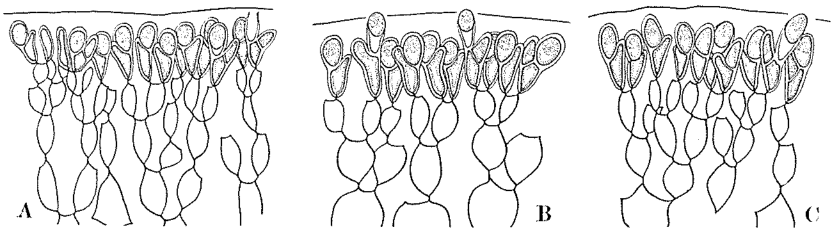

Fig. 24. Transverse sections through spermatangial sori.
A. *Chondrus crispus* (L.) STACK.
B. *Chondrus giganteus* YENDO.
C. *Chondrus pinnulatus* (HARV.) OKAMURA.
A–C, ×800.

cell is borne by an oblique division of a superficial cell of the cortex. The spermatangium arises from the distal end of the spermatangial mother cell as a narrow projection composed of an upward protoplasmic extension surrounded by the wall of the spermatangial mother cell. After the spermatangial projection has swollen increasing in size, the spermatangium is cut off by an oblique annular ingrowth of the wall.

Chondrus giganteus YENDO

Pl. IV, F; Fig. 24, B.

Material was gathered at Nakaminato, Ibaragi Prefecture in April 1955.

The male organ develops in sori covering almost the whole of the younger blades, except for the lower portion. The fertile blades are faint or yellowish red in colour. The spermatangial mother cells and the spermatangia are formed in the same way as in *C. crispus*.

Chondrus pinnulatus (HARVEY) OKAMURA

Pl. IV, G; Fig. 24, C.

Material was gathered at Muroran, Hokkaido in June 1953.

The male frond is subdichotomously branched and bears simple or once-forked proliferations which are pinnately arranged at the margins of branches. The male organ develops in sori covering the upper parts of the branches and often the whole of the proliferations. The spermatangial mother cells and the spermatangia are formed in the same way as in *C. crispus*.

Rhodoglossum japonicum MIKAMI

Pl. IV, D; Fig. 25, A.

Material was gathered at Otaru, Hokkaido in December 1953, and January and February 1954.

This species is dioecious. The male organ develops in sori covering almost the whole of the blades of the thallus. The fertile blades are faint or yellowish red in colour. The cortex of the fertile blade is composed of two or three layers of small ellipsoidal cells arranged in a perpendicular plane to the blade surface. Two spermatangial mother cells are produced by an oblique division of the last cell of a cortical cell row. The spermatangia appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has swollen and increased in size, the spermatangium is cut off by an oblique annular ingrowth of the wall. Through the apical split in the spermatangial wall, the spermatium escapes into the surrounding water. A second sper-

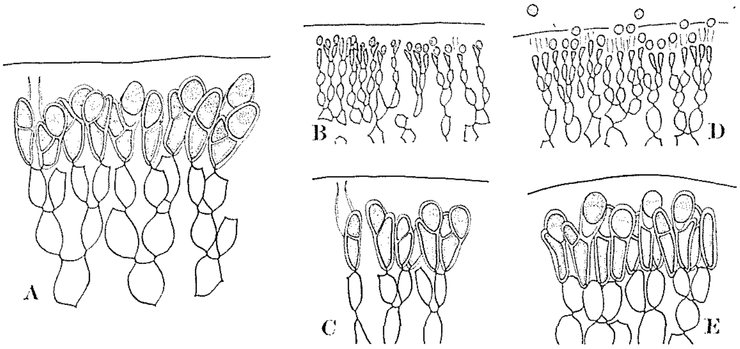

Fig. 25. Transverse sections through spermatangial sori.
A. *Rhodoglossum japonicum* MIKAMI.
B–C. *Gigartina intermedia* SUR.; C, various stages in development of spermatangia.
D–E. *Gigartina tenella* HARV.; E, various stages in development of spermatangia.
A, C, E, ×800; B, D, ×400.

matangium develops by the side of the first at the apex of the spermatangial mother cell; this grows up, ripens and liberates its contents in the same way as the first one.

Gigartina intermedia SURINGAR

Pl. IV, E; Fig. 25, B–C.

Material was gathered at Shichirigahama, Kanagawa Prefecture in April 1955.

This species is dioecious. The male organ is borne in sori covering almost the whole surface of branches. In a fertile area of the frond each cortical cell row is terminated by two narrow elongated cells (Pl. IV, E; Fig. 25, B). These cells are the spermatangial mother cells. The spermatangia are formed as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has swollen and increased in size, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 25, C).

Gigartina tenella HARVEY

Fig. 25, D–E.

Material was collected by Mr. Y. TSUJI at Sugashima, Mie Prefecture and Shichirigahama, Kanagawa Prefecture in April 1955.

This species is dioecious. The male organ develops in sori covering the upper parts of the branches and the whole of the branchlets issued from the upper portion of the frond. The spermatangial mother cells and the spermatangia are formed in the same way as in *G. intermedia.*

Chrysymenia wrightii (HARVEY) YAMADA

Fig. 26, A–B.

Material was gathered at Usu, Hokkaido in July 1954.

The male organ develops in sori occurring as isolated patches on the branches, or often covering the entire surface of branches. In a young male frond, the cortex consists of a single layer of ellipsoidal cells. The first step in the development of the male organ is the formation of the secondary cortical cells which arise subterminally from the primary cortical cell. From the secondary cortical cells, several spermatangial mother cells are borne by a transverse or an oblique division (Fig. 26, A). It is found often that the cell derived from the secondary cortical cell is again cut off into two or three spermatangial mother cells. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has swollen, the spermatangium is cut off by an annular ingrowth of the wall (Fig. 26, B).

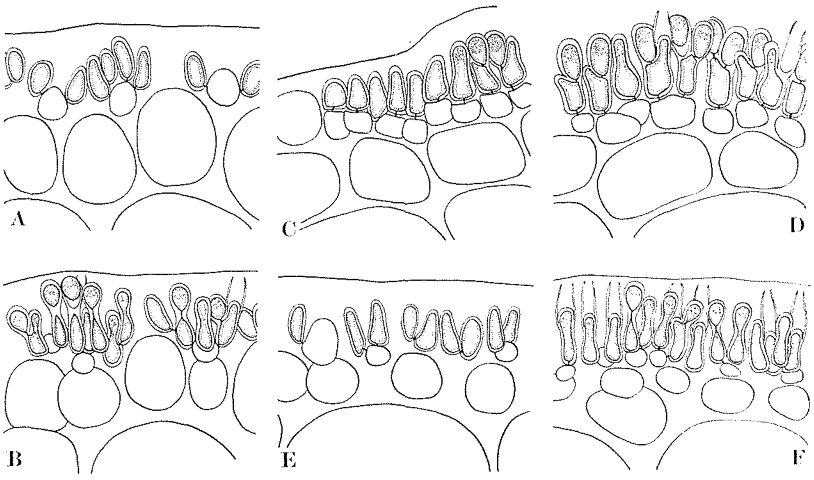

Fig. 26. Transverse sections through spermatangial sori.

A–B. *Chrysymenia wrightii* (HARV.) YAMADA, showing various stages in development of spermatangial mother cells (A) and spermatangia (B).

C–D. *Rhodymenia palmata* (L.) GREV.; C, young; D, mature.

E–F. *Rhodymenia pertusa* (POST. et RUPR.) J. AG.; E, young; F, mature.

A–F, ×800.

Rhodymenia palmata (L.) GREVILLE

Fig. 26, C–D.

Material was gathered at Otaru and Usu, Hokkaido in May 1954 and April 1955.

The male plant is mottled by pale patches scattered over the thallus. The pale patches are the spermatangial sori. The cortex of fertile region is composed of a single layer of small cells. The small cortical cells are cut off by transverse or oblique walls; of the two cells thus formed, the upper one is a colourless spermatangial mother cell, and the lower one, which is pigmented, is the basal cell of the former (Fig. 26, C). Each spermatangial mother cell produces one or two spermatangia. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has swollen, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 26, D). Although the younger region of the spermatangial sorus is covered by a common firm gelatinous membrane, the membrane peels off with the development of the spermatangial mother cells and the formation of the spermatangia.

Rhodymenia pertusa (POST. et RUPR.) J. AGARDH

Pl. IV, H; Fig. 26, E–F.

Material was gathered at Usu, Hokkaido in April 1955

The male plant may be distinguishable by faint red colour and thickness of the thallus. The male organ develops over the whole of the thallus with the exception of the base of the stipe. The cortex of the fertile region consists of one or two layers of small cells. On the formation of the spermatangial mother cells, the superficial cells of cortex are cut off by oblique or transverse walls. The spermatangial mother cells so formed are linked with the basal cells, which are transformed from the superficial cells of the cortex, by protoplasmic connections, rarely also with one other (Fig. 26, E). Each spermatangial mother cell produces one or two spermatangia. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell (Pl. IV, H; Fig. 26, F). After the spermatangial protuberance has increased in size, the spermatangium is cut off by the gradual ingrowth of the wall. The mature spermatium is liberated through a narrow apical split in the wall. After an escape of the primary spermatium has been completed, the secondary spermatangium is formed in the empty wall of the primary one (Fig. 26, F).

Lomentaria catenata HARVEY

Pl. IV, I; Fig. 27, A–B.

Material was gathered at Nakaminato, Ibaragi Prefecture, and Enoshima, Kanagawa Prefecture in April 1955.

The male organ develops in sori covering the bladder-like ramuli and the swelling of the upper parts of branchlets. In the fertile region, the cortex consists of a single layer of ellipsoidal cells. The first step in the development of the male organ is the formation of the secondary cortical cells. They arise subterminally from the primary cortical cells and develop into the basal cells of the spermatangial mother cells. From these basal cells, two or three spermatangial mother cells are borne by a transverse or an oblique division (Fig. 27, B). It is often found that the cell derived from the basal cell is again cut off into two or three spermatangial mother cells. The spermatangium first arises as a small protuberance at the distal end of the spermatangial mother cell. After the spermatangial protuberance has swollen, the spermatangium is cut off by the gradual ingrowth of the wall (Fig. 27, A). The spermatium is liberated through a narrow apical split in the wall. After a liberation of the primary spermatium has completed, the secondary spermatangium develops within the empty wall of the primary one.

Lomentaria hakodatensis YENDO

Fig. 27, C–D.

Material was gathered at Otaru and Muroran, Hokkaido in September 1953 and July 1954.

The male organ develops in sori scattered as small isolated patches on the

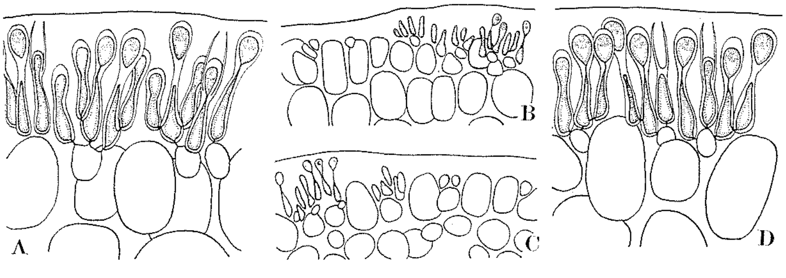

Fig. 27. Transverse sections through spermatangial sori.
A–B. *Lomentaria catenata* HARV.; A, development of spermatangia; B, young.
C–D. *Lomentaria hakodatensis* YENDO; C, young; D, development of spermatangia.
A, D, ×800; B–C, ×400.

upper region of the frond, but sometimes covers the entire surface of branchlets and ramuli. The developmental manner of the male organ of this species is exactly similar to that of *L. catenata*.

Champia parvula (AGARDH) J. AGARDH

Fig. 28, A-B.

Material was gathered at Otaru, Hokkaido in September 1953.

The male organ develops in sori which form girdle-shaped zones around the segments of the frond. In the fertile region, the cortex is composed of a single layer of the primary cortical cells. The first step in the development of the male organ is the formation of secondary cortical cells which arise laterally from the primary ones. The secondary cortical cells give rise to a system of branching threads which spread over the surface of the fertile region. Each cell of these branching threads is the spermatangial mother cells (Fig. 28, B). The spermatangial mother cells increase greatly in length, stretching upwards, and these, when fully developed, attain to as much as 10–15 μm in length. The spermatangial mother cell usually produces one or two spermatangia. The spermatangia are formed in the same way as in *Lomentaria catenata* (Fig. 28, A).

Binghamiella californica (FARLOW) SETCHELL et DAWSON

Fig. 28, C-D.

Material was a dried specimen preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male organ develops in sori covering the upper part of the thallus. The first step in the development of the male organ is the formation of fertile cells. They arise subterminally from the primary cortical cells and develop into the basal

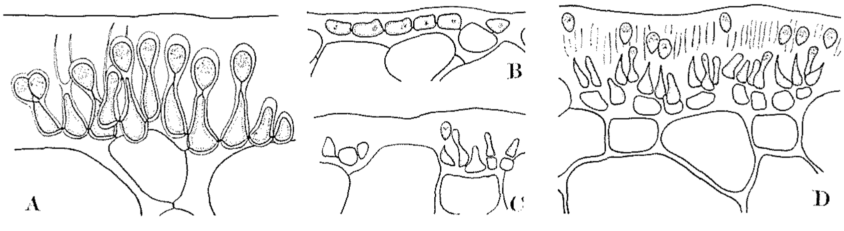

Fig. 28. Transverse sections through spermatangial sori.
A-B. *Champia parvula* (AG.) J. AG.; A, showing development of spermatangia; B, thread of spermatangial mother cells.
C-D. *Binghamiella californica* (FARL.) SETCHELL et DAWSON; C, young; D, mature.
A, ×800; B, ×400; C, D, ×600.

cells of the spermatangial mother cells. From these basal cells, two or three spermatangial mother cells are borne by a transverse or an oblique division (Fig. 28, C). It is found often that the cell derived from the basal cell is again cut off into two or three spermatangial mother cells. The spermatangium first appears as a protuberance which arises from the distal end of the spermatangial mother cell. After the spermatangial protuberance has swollen, the spermatangium is cut off a gradual ingrowth of the wall (Fig. 28, D).

Antithamnion nipponicum YAMADA et INAGAKI

Pl. V, A; Fig. 29, A–C.

Material was collected by Dr. S. KAWASHIMA at Ôma, Aomori Prefecture in August 1955.

This species is dioecious. The spermatangial stands are oppositely borne as spica-like bodies near the bases of the pinnae (Pl. V, A) and often appear on the adaxial sides of the pinnulae. They are usually sessile and often supported by a one-celled stalk (Fig. 29, C). The first step in the development of spermatangial stand is the formation of an erect cell row consisting of three or four cells (Fig. 29, A). The cell row is transformed into an axis of spermatangial stand. The spermatangial mother cells, concurrently with the formation of the axis, appear gradually from the lowest cell of the axis to the upper one (Fig. 29, B). Each of spermatangial mother cells puts out a protuberance which is cut off by an ingrowth of the wall, and the spermatangium thus formed is an ellipsoidal body with protoplasmic content.

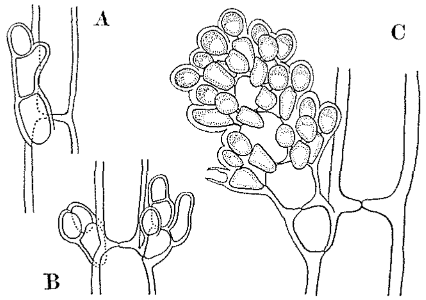

Fig. 29. *Antithamnion nipponicum* YAMADA et INAGAKI. A–B, showing development of spermatangial stands; C, mature spermatangial stand. A–C, ×800.

Ceramium cimbricum PETERSEN

Pl. V, B, D; Fig. 30, A.

Material was gathered at Akkeshi, Hokkaido in July 1955.

The formation of the male organ is confined to the corticated nodal regions (Pl. V, B), since the frond is zonately corticated only around the nodes. Further, it begins to occur on the adaxial sides of the nodes of branches and is always preceded by the continual divisions of cortical cells. The smaller superficial cells of the nodes are cut off in turn by walls which are parallel or somewhat perpendicular to the periphery. The cells so formed are spermatangial mother cells which are seen as an irregular layer covering the surface of the nodal regions of branches (Pl. V, D). The spermatangial mother cell usually produces one to three spermatangia. The formation of spermatangium is preceded by a slight elongation of the protuberance which arises from the distal end of the spermatangial mother cell. A common gelatinous sheath is pierced with the elongated protuberance, which is cut off by the gradual ingrowth of the wall forming spermatangia (Fig. 30, A). After the spermatium was liberated through a split in the apex of the spermatangial wall, the same spermatangial mother cell forms a secondary sper-

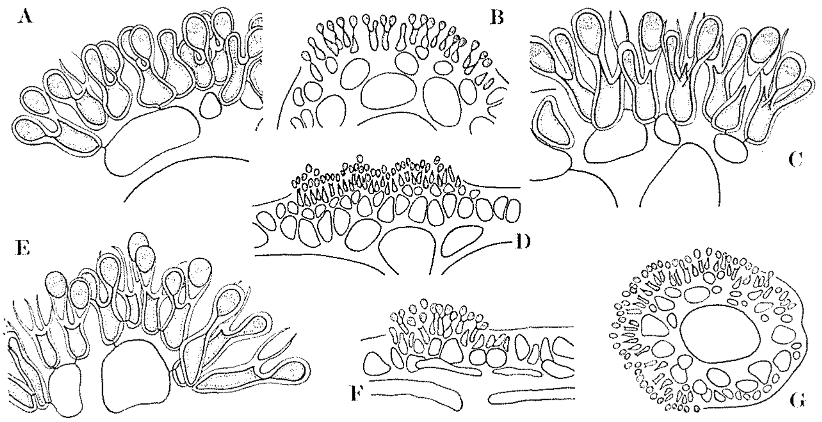

Fig. 30. A–E, G. Transverse sections of fronds through spermatangial sori.
A. *Ceramium cimbricum* PETERSEN.
B. *Ceramium paniculatum* OKAMURA.
C. *Ceramium kondoi* YENDO.
E, G. *Campylaephora hypnaeoides* J. AG.
D, F. Longitudinal sections of fronds through spermatangial sori.
D. *Ceramium japonicum* YENDO.
F. *Campylaephora crassa* (OKAMURA) NAKAMURA.
A, C, E, ×800; B, D, F, G, ×400.

matangium by proliferation into the empty sheath of the first formed one.

Ceramium paniculatum OKAMURA

Pl. V, C; Fig. 30, B.

Material was gathered at Nakaminato and Ôarai, Ibaragi Prefecture in April 1955.

The male organ is borne in cushion-like sori, as in *C. cimbricum*, on the corticated nodal regions (Pl. V, C). The spermatangial mother cells and the spermatangia are formed in exactly the same way as in *C. cimbricum* (Fig. 30, B).

Ceramium kondoi YENDO

Fig. 30, C.

Material was gathered at Muroran and Otaru, Hokkaido in June, September, and November 1953.

The male organ is borne in sori appearing as continuous cushion-like constructions on the branches. The spermatangial sorus first develops on the adaxial side of the upper branch and gradually spreads over the whole area of the frond. The branches bearing the spermatangial sori are fringed with a colourless edge. The male organ develops in the same way as in *C. cimbricum.*

Ceramium japonicum OKAMURA

Fig. 30, D.

Material was gathered at Muroran and Otaru, Hokkaido in June and September 1953.

The spermatangial sori first appear on the nodal portions (Fig. 30, D) and gradually spread over the whole area of the frond. The male organ develops in the same way as in *C. cimbricum.*

Campylaephora hypnaeoides J. AGARDH

Fig. 30, E, G.

Material was gathered at Usu, Hokkaido in July 1954.

The spermatangial sori, as in *Ceramium kondoi*, first appear as continuous cushion-like constructions on the adaxial sides of the upper branches and gradually spread over the whole area of the frond. In the upper portions of branches, practically every peripheral cell appears to give rise to spermatangial mother cells. The peripheral cells of the frond are cut off in turn by walls which are parallel or somewhat perpendicular to the periphery. The cells so formed are the spermatangial mother cells which are seen as an irregular layer covering the surface of the frond (Fig. 30, G). The developmental manner of the spermatangium is similar to that of *Ceramium* (Fig. 30, E).

Campylaephora crassa (OKAMURA) NAKAMURA

Pl. V, F; Fig. 30, F.

Material was gathered at Otaru, Hokkaido in October 1953 and at Ôhara, Chiba Prefecture in April 1956.

Thespermatangial sori are first borne on the adaxial sides of the upper branches and gradually spread over the whole area of the branches. The developmental manner of the male organ of this species is similar to that of *Ceramium*.

Microcladia elegans OKAMURA

Fig. 31, A–B.

Material epiphytic on *Carpopeltis* was gathered at Matsushima, Miyagi Prefecture in April 1955.

The male plants may be recognizable with the aid of a microscope. The spermatangial sori appear as cushion-like pale areas which are composed of smaller cells than sterile superficial ones. The spermatangial sori develop on the adaxial sides of the branchlets. The development of the male organ is preceded by a transverse or an oblique division of surperficial cells of the branchlet; of two cells thus formed, the upper one is the spermatangial mother cell and the lower one is

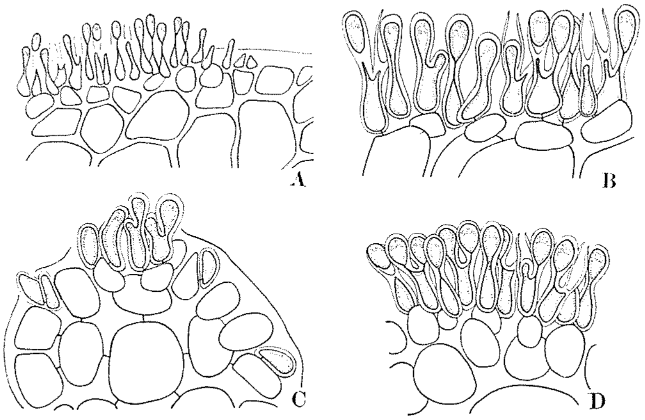

Fig. 31. Transverse sections through spermatangial sori.
A–B. *Microcladia elegans* OKAMURA; B, showing development of spermatangia.
C–D. *Reinboldiella schmitziana* (REINB.) DE TONI; D, showing development of spermatangia.
A, ×400; B–D, ×800.

the basal cell of the former. The formation of the spermatangium starts by a slight elongation of the protuberance which arises from the distal end of the spermatangial mother cell, piercing a common gelatinous sheath (Fig. 31, A). After the elongated protuberance has swollen, the spermatangium is cut off by the gradual ingrowth of the wall (Fig. 31, B). The spermatium is liberated through a split in the apex of the spermatangial wall. After an escape of the primary spermatium, the same spermatangial mother cell forms a secondary spermatangium by a proliferation into the empty wall of the first formed one.

Reinboldiella schmitziana (REINB.) DE TONI

Pl. V, G–H; Fig. 31, C–D.

Material epiphytic on *Grateloupia* was gathered at Saga, Kôchi Prefecture in April 1956 and at Koza, Wakayama Prefecture in July 1957.

The spermatangial sorus appears as a pale area which encloses a cylindrical ultimate branchlet (Pl. V, H). The outer cortical cell is cut off by an anticlinal wall; of the two cells thus formed, the upper one is the spermatangial mother cell, and the lower one is the basal cell of the former (Fig. 31, C). The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. The spermatangial protuberance is cut off by the ingrowth of the wall (Pl. V, G; Fig. 31, D).

Wrangelia argus MONTAGNE

Pl. V, E; Fig. 32, A–D.

Material was gathered at Shichirigahama, Kanagawa Prefecture in April 1955.

This species is dioecious. The male organ is borne as spherical clusters near the bases of whorled laterals (Pl. V. E). The cluster is surrounded by incurved enveloping threads. The first step in the development of the spermatangial stand is the formation of a short thread. This thread arises from the distal end of the cell near the bases of the whorled laterals and consists of two small cells; of the two cells thus formed, the lower one is a stalk cell of the spermatangial stand, and the upper one gives rise to the fertile region by divisions (Fig. 32, B, C). The first division occurs always by an oblique wall; as a result of this, the fertile region is now two celled. From these cells, several pericentral cells have been cut off all round, and these give rise, by further divisions, to numerous small cells which develop into the spermatangial mother cells (Fig. 32, A, D). The whole of this structure forms a single globular cluster enclosed in a common gelatinous sheath. The gelatinous sheath is pierced with the development of spermatangial protuberances. Concurrently with the development of the fertile region, enveloping threads

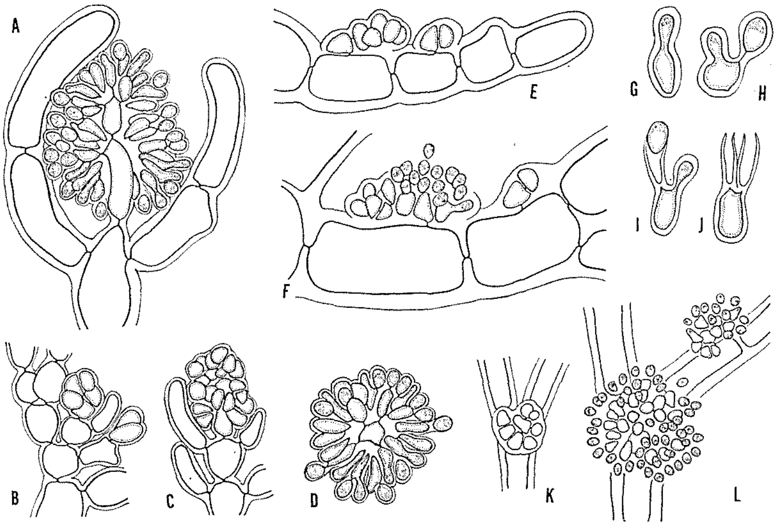

Fig. 32. A–D. *Wrangelia argus* MONT.; A, D, longitudinal (A) and transverse (D) sections of spermatangial stands; B–C, showing development of spermatangial stands.
E–J. *Callithamnion callophyllidicola* YAMADA; D–E, showing development of spermatangial stands; G–J, showing the formation of spermatangia.
K–L. *Callithamnion corymbosum* (SMITH) LYNGB.; K, young spermatangial stand; L, two spermatangial stands.
A–F, K–L, ×400; G–J, ×800.

which surround the fertile region, are formed from the distal end of the stalk cell (Fig. 32, B–C). The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has increased in size, the spermatangium is cut off by an annular ingrowth of the wall.

Callithamnion corymbosum (SMITH) LYNGBYE

Fig. 32, K–L.

Material epiphytic on *Sargassum* was gathered at Sado Island in April 1956.

This species is dioecious. The spermatangial stands are borne as more or less hemispherical bodies on the adaxial sides of the upper branchlets (Fig. 32, L); each of them is singly produced from the distal end of a segmental cell of the branchlet, but occasionally two adjoining clusters become confluent with each other, forming a bush of fertile cells. The first step in the development of the spermatangial stand is the formation of a dome-shaped initial cell of fertile threads. The initial cell appears near the distal end of a segmental cell of the branchlet and then divides to form a system of branching threads which spread in every direction over the surface of the segment cell (Fig. 32, K). The terminal cells of the threads are able to function as the spermatangial mother cells. The whole of this structure is enclosed in a common gelatinous sheath which, sooner or later, is pierced with the development of spermatangial protuberances. The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed, the spermatangium is cut off by the ingrowth of the wall.

Callithamnion callophyllidicola YAMADA

Pl. VI, A; Fig. 32, E–J.

Material epiphytic on *Callophyllis* and *Cladophora* was gathered at Nakaminato, Ibaragi Prefecture in April 1955 and at Mera, Chiba Prefecture in April 1956.

The spermatangial stands are borne as crowded bushes of fertile cells on the upper sides of the ultimate branchlets (Pl. VI, A). The younger spermatangial stands are singly situated on each segment of the branchlets, but the mature ones become confluent with one another, forming large bushes. The male organ of this species develops in exactly the same manner as in that of *C. corymbosum* (Fig. 32, E–F). The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells (Fig. 32, G). After the spermatangial protuberance has developed, the spermatangium is cut off by the ingrowth of the wall (Fig. 32, H–I). The mature spermatium is set free by escaping through a split which is formed at the tip of the spermatangium (Fig. 32, I–J). The production of spermatangia is repeated usually two (rarely three) times on the same spermatangial mother cell (Fig. 32, H–I).

Neomonospora yagii (OKAMURA) YAMADA

Pl. VI, B; Fig. 33, A–C.

Material epiphytic on *Gelidium* was gathered at Ôhara, Chiba Prefecture in April 1956.

This species is dioecious. The spermatangial stands are borne as cylindrical bodies on the upper parts of branchlets (Pl. VI, B). The first step in the development of spermatangial stand is the formation of a short thread, which consists of four or five cells. The basal cell of the thread is larger than others and is transformed into the monosiphonous stalk of the spermatangial stand (Fig. 33, A). The other cells are transformed into a main axis and each of them cuts off several pericentral cells. The pericentral cell produces small cells which are able

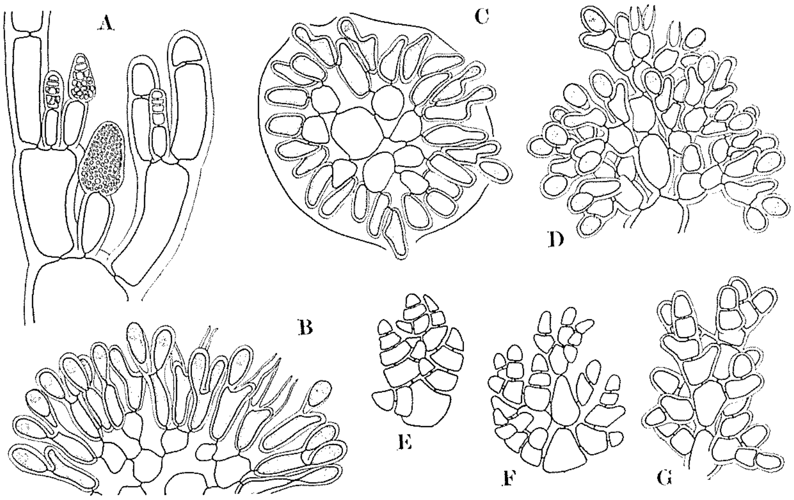

Fig. 33. A–C. *Neomonospora yagii* (OKAMURA) YAMADA; A, part of branchlet with spermatangial stands of different stages; B, portion of mature spermatangial stand in transverse section; C, transverse section of a young spermatangial stand, showing development of spermatangia.
D–G. *Griffithsia japonica* OKAMURA; D, portion of mature spermatangial stand; E–G, showing development of spermatangial stands.
A, ×147; B, D, ×800; C, ×400; E–G, ×467.

to function as the spermatangial mother cells (Fig. 33, C). The whole of this structure is enclosed in a common gelatinous sheath derived from the vegetative cell. The gelatinous sheath is pierced with the development of spermatangial protuberances. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has increased in size, the spermatangium is cut off by an annular ingrowth of the wall (Fig. 33, B).

Griffithsia japonica OKAMURA

Pl. VI, G; Fig. 33, D–G.

Material was gathered at Nakaminato, Ibaragi Prefecture in April 1955 and at Saga, Kôchi Prefecture in April 1956.

This species is dioecious. The male organ is visible as colourless areas encircling the upper constrictions of articulations, forming a striking contrast to the otherwise deep red colour of the plant (Pl. VI, G). The male organ consists of densely branched threads and is surrounded by incurved enveloping cells. The branched thread is a spermatangial stand. The first step in the development of the spermatangial stand is the formation of a single cell. From this, several cells one above the other are cut off, more or less in a straight row, forming the axis of the spermatangial stand. Around each of the axial cells a number of pericentral cells are cut off in every direction. From the pericentral cells are cut off a further series of cells, many of which grow out into short branches (Fig. 33, E–G) bearing at their apices spermatangial mother cells. Occasionally the spermatangial mother cells may be found growing out from central, pericentral or higher orders of cells (Fig. 33, D). The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall. The spermatium is liberated through a narrow apical split in the wall (Flg. 33, D).

Ptilota pectinata (GUNN.) KJELLMAN

Pl. VI, D–E; Fig. 34, F–G.

Material was gathered at Otaru and Shirikishinai, Hokkaido in May 1954 and April 1955.

This species is dioecious. The male organ usually develops in clusters on the laterals of compound pinnae (Pl. VI, D), sometimes also on the serrations of simple pinnae (Pl. VI, E). The central cells of the lateral of the compound pinna or the serration of the simple one develop into the main axis of the spermatangial cluster (Fig. 34, G). From each segment cell of the main axis, the axes of the second degree are pinnately branched (Fig. 34, F, G). Small cells, which are homologous with cortical cells of sterile laterals and serrations, arise from the segment cells of the secondary axis. These small cells divide to form spermatangial mother cells. Each spermatangial mother cell gives rise to two or three spermatangia. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. Subsequently the spermatangium is cut off by an annular ingrowth of the wall. The spermatium is liberated through a split in the apex of the spermatangial wall. After an escape of the primary spermatium has been completed, the same spermatangial mother cell forms a secondary spermatangium by proliferation into the empty wall of the first formed one.

Neoptilota asplenioides (TURN.) KYLIN

Pl. VI, F; Fig. 34, H.

Material was gathered at the Cape of Nosappu, Ochi-ishi, and Akkeshi, Hokkaido in July 1955.

This species is dioecious. The male plants are distinguished by pale regions

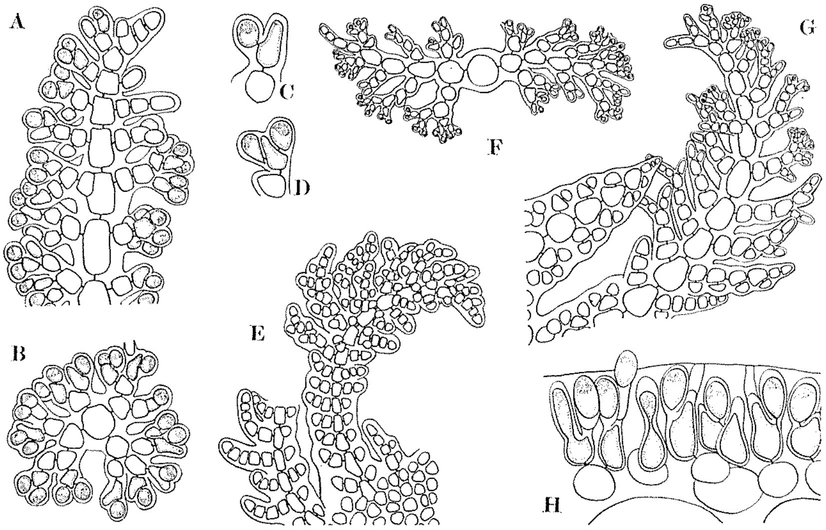

Fig. 34. A–E. *Psilothallia dentata* (OKAMURA) KYLIN: A, portion of a spermatangial cluster; B, transverse section of the same; C–D, showing development of spermatangia; E, young spermatangial cluster.
F–G. *Ptilota pectinata* (GUNN.) KJELLM.; F, transverse section of a spermatangial cluster; G, young spermatangial cluster formed on a serration of simple pinnae.
H. *Neoptilota asplenioides* (TURN.) KYLIN, showing development of spermatangia in vertical section.
A–B, ×480; C–D, H, ×800; E–G, ×243.

covering the surface of simple and compound pinnae. These pale areas are the spermatangial sori. The fertile pinnae are larger and thinner than the sterile ones. In sterile region, the outer layer of an pinna consists of a single layer of cortical cells containing pigments. The development of the male organ is preceded by an oblique or a transverse division of cortical cells; of two cells thus formed, the upper one is the spermatangial mother cell and the lower one is the basal cell of the former. From each spermatangial mother cell, one or two spermatangia arise terminally. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has increased in size, the spermatangium is cut off by an annular ingrowth of the wall.

The genus *Neoptilota* established on the basis of *Ptilota californica* by KYLIN (1955) includes four species; *N. californica*, *N. densa*, *N. asplenioides*, and *N. hypnoides*. In these species the male plant is known only in *N. californica* (*Pterota californica*). According to C. CRAMER (1863), the male organ of this species occurs in small clusters on the fine branchlets, as in *Ptilota pectinata*. As mentioned above, the structure and the development of the male organ of *N. asplenioides* are cleary different from those described for *N. californica*.

Psilothallia dentata (OKAMURA) KYLIN

Pl. VI, G; Fig. 34, A–E.

Material was gathered at Ôarai, Ibaragi Prefecture and Ôhara, Chiba Prefecture in April 1955.

This species is dioecious. The male organ develops in clusters on the compound pinna which appears in the axil of the simple pinna (Pl. VI, G). The spermatangial cluster possesses an axis which was developed from central cells of the lateral of the compound pinna (Fig. 34, E). Around each of the axial cells, short branched threads are formed in every direction (Fig. 34, B). The apical cells of the threads are spermatangial mother cells (Fig. 34, A), each of which usually gives rise to two spermatangia. The spermatangia first appear as protuberances which arise terminally or laterally from the spermatangial mother cells (Fig. 34, C). After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 34, D).

Laingia pacifica YAMADA

Pl. VII, A, D; Fig. 35, A–B.

Material was gathered at Akkeshi, Hokkaido in June 1956.

The male blade possesses a midrib and distinct lateral veins, and on the midrib of it leaf-like proliferations are formed. The blade is polystromatic, consisting of three to five layers of cells, but the proliferation is monostromatic except the midrib and lateral veins. The male organ is borne in sori covering both surfaces of the blades and proliferations except the midrib, the vein and the marginal area. The younger sori are found as separate minute spots, but mature ones become confluent with one another, forming irregular large sori.

In the leaf-like monostromatic proliferation, the formation of the male organ is preceded by cell divisions parallel to the surface on both sides of the proliferation. The proliferation is now three layered in the fertile region (Pl. VII, A). Each of these cells of outer layers is divided by a vertical wall and then by the second vertical wall at right angles to the first, thus giving rise to a group of four cells in a single layer, sometimes each of these is again divided by an additional vertical wall giving eight cells in a single layer. In the fertile areas, therefore, the original thallus cells are clothed on either surface with groups of four or eight small cells (Pl. VII, D). These small cells are the spermatangial mother cells.

In the polystromatic blades, the male organ is formed from superficial cells.

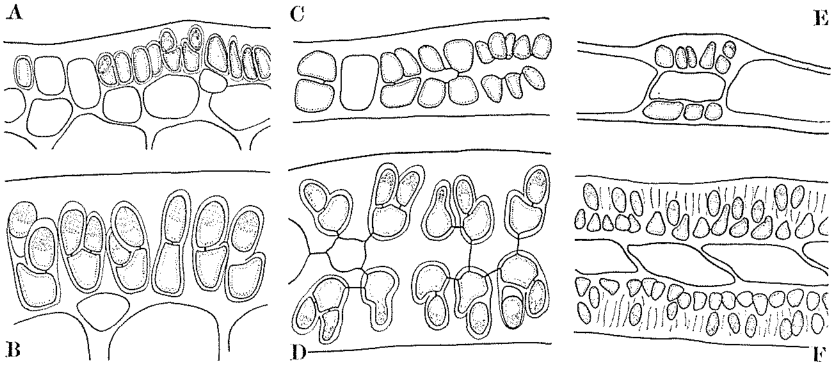

Fig. 35. Vertical sections through spermatangial sori.
A–B. *Laingia pacifica* YAMADA; A, early stage in formation of spermatangial sorus; B, showing development of spermatangia.
C–D. *Delesseria violacea* (HARV.) KYLIN; C, early stage in formation of spermatangial sorus; D, showing development of spermatangia.
E–F. *Vanvoorstia coccinea* J. AG.; early (E) and later (F) stages in formation of spermatangial sori.
A, C, E, F, ×400; B, D, ×800.

On the formation of the male organ the superficial cells are divided by intersecting vertical walls giving four cells, or are cut off by a vertical wall giving two cells. The cells so formed are the spermatangial mother cells (Fig. 35, A). The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has increased in size, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 35, B).

Delesseria violacea (HARVEY) KYLIN

Pl. VII, G–H; Fig. 35, C–D.

Material was gathered at Otaru, Hokkaido in April and May 1954.

The male organ is borne in sori covering both surfaces of the wings of blades which are composed of one layer of cell except the veins and the margin (Pl. VII, H). On the development of the male organ, cells of the wing are cut off by a wall parallel to the surface giving two layers of cells (Fig. 35, C), and in some parts, they give rise to three layers of cells dividing two parallel walls. The cells so formed are divided by vertical walls giving two to eight small cells in a single layer (Pl. VII, G; Fig. 35, D). These small cells are the spermatangial mother cells. The spermatangia first appear as beak-like projections which arise from the distal ends of the spermatangial mother cells. After the spermatangial projection has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 35, D). The spermatium is liberated through a narrow apical split in the wall.

Vanvoorstia coccinea J. Agardh

Fig. 35, E–F.

The genus *Vanvoorstia,* according to Kylin (1956), includes three species, *V. spectabilis, V. benettiana,* and *V. coccinea.* For the *Vanvoorstia*-species which is called "Karagoromo" in Japanese, the name of *V. spectabilis* was adopted by Okamura (1936), however, this alga was identified by Segawa (1939) with *V. coccinea.*

The developmental manner and structure of the male organ in the genus *Vanvoorstia* was described by Papenfuss (1937) for *V. spectabilis.* According to him, the male organ of this species is formed in sori on both surfaces of the ultimate blades, which have not yet anastomosed, and the regions bearing it are always three layers of cells. The many small spermatangial mother cells are formed by anticlinal division of the cortical cells, which are cut off from the primary cells.

The following account is based on *V. coccinea,* of which material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University under the name of *V. spectabilis.*

The male organ is borne in sori which occur on both surfaces of the ultimate blades. Whereas the ultimate blades before developing the male organ consist of a single layer of cell and remain flat, the sterile blades become greatly corticated and assume a cylindrical shape. The first step in the development of the male organ is the formation of cortical cells on both surfaces of the blade. The male blade is now three layered in the fertile region. Each of the cortical cells divides into a number of small cells by walls which are more or less perpendicular to the blade surface (Fig. 35, E). The cells so formed are the spermatangial mother cells. The spermatangia are first produced as protuberances which arise from the distal ends of the spermatangial mother cells. Subsequently each of them may be cut off by an annular ingrowth of the wall (Fig. 35, F).

Erythroglossum pinnatum Okamura

Pl. VII, B, E; Fig. 36, A–B.

Material was collected by Dr. S. Kawashima at Ozaki Point, Iwate Prefecture in August 1952.

The middle portion of the male thallus is polystromatic consisting of several layers of cells, but the marginal portion remains monostromatic. The male organ is borne in oblong sori which occur on both surfaces of the monostromatic region near the upper part of the thallus. On the formation of the male organ, cells of the region of single layer cut off one small cell on each side by a wall parallel

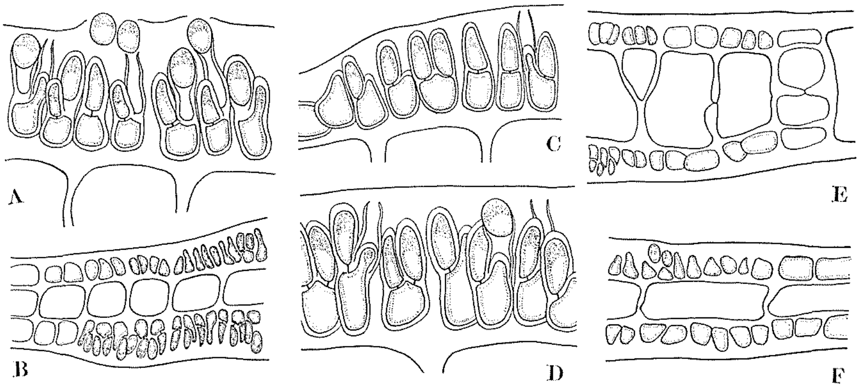

Fig. 36. Vertical sections through spermatangial sori.
A–B. *Erythroglossum pinnatum* OKAMURA; A, showing development of spermatangia.
C. *Nienburgia japonica* (YAMADA) KYLIN, showing development of spermatangia.
D–E. *Acrosorium polyneurum* OKAMURA; D, showing development of spermatangia; E, young spermatangial sorus.
F. *Cryptopleura membranacea* YAMADA, early stage in formation of spermatangial sorus.
A, C, D, ×800; B, E, F, ×400.

to the surface of the thallus. Each small cell divides by a vertical wall and then by the second vertical wall at right angles to the first, thus giving rise to a group of four cells in a single layer. Each of these is divided by two additional intersecting vertical walls giving finally sixteen cells in a single layer. In the fertile areas, therefore, the original thallus cells are clothed on either surface with groups of sixteen small cells. Each of the small cells is the spermatangial mother cell (Pl. VII, E; Fig. 36, B). The spermatangia first appear as narrow beak-like protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has increased in size, the spermatangium is cut off by an oblique annular ingrowth of the wall (Pl. VII, B; Fig. 36, A). Each spermatangial mother cell forms two or three spermatangia, each member of which being at a different stage of development. The mature spermatium is liberated through a narrow apical split in the spermatangial wall. After the liberation of the primary spermatium, the same spermatangial mother cell forms a secondary spermatangium by proliferation into the empty sheath of the first formed one (Fig. 36, A).

Nienburgia japonica (YAMADA) KYLIN

Pl. VII, C, F; Fig· 36, C.

Material was obtained from the drifts at Ôhara, Chiba Prefecture in April 1956.

The male plants of this species are exactly similar in outward appearance to both female and tetrasporic ones, but they may be distinguished on close examination by pale band-like areas seen on both surfaces of the blades. These colourless areas are the spermatangial sori.

The male thallus of *N. japonica* is composed of a single layer of cells except the midrib and veins, whereas that of other members of *Nienburgia* (*N. andersoniana* and *N. borealis*) consists of several layers of cells.

In *N. japonica* the spermatangial sori are always borne in the region of a single layer and are laid as vaguely parallel bands between the veins, but never crossing the veins. On the formation of the male organ, cells of the region of a single layer cut off one small cell on each side, by walls parallel to the surface of the thallus. The thallus is now three layered in the fertile regions. Each of the small cells divides by several vertical walls giving twelve cells in a single layer. In the fertile areas, therefore, the original thallus cells are clothed on either surface with groups of twelve small cells (Pl. VII, C, F). Each of these small cells is the spermatangial mother cell. The spermatangia first appear as beak-like protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 36, C). The mature spermatium is liberated in turn through the apical split in the spermatangial wall. After the escape of the primary spermatium has been completed, the secondary spermatangium appears to be formed within the empty wall of the first formed one, developing in the same way as in the first one.

In *N. andersoniana*, KYLIN (1924) described as follows: "Die Mutterzellen der Spermatangien nicht unmittelbar aus den Zentralzellen des fertilen Thallusteiles entwickeln, sondern dass einige Zellschichten (1 bis 3) zwischen den Mutterzellen und Zentralzellen eingeschaltet werden."

As above mentioned, in the structure of the fertile area, *N. japonica* is rather similar to the members of the genus *Phycodrys* (KYLIN, 1923; ROSENVINGE, 1923–1924) than *N. andersoniana*; in *Phycodrys* the fertile region becomes three layered on the formation of the male organ, but spermatangial sori are laid as bands parallel to the margin of the thallus.

Acrosorium polyneurum OKAMURA

Pl. VIII, A–B; Fig. 36, D–E.

Material was gathered at Nakaminato, Ibaragi Prefecture and Ôhara, Chiba Prefecture in April 1955 and 1956.

The male frond possesses rich lobes and bears small proliferations at the margin. The thallus and the proliferations are composed of a single layer of cells except the veins consisting of three layers and the thallus base composed of one or two layers of cortical cells. The male organ is formed in irregular sori near the apical part of the lobes or on the proliferations. On the formation of the male organ, cells of a single layer cut off one cell on each side by walls parallel to the thallus surface. The lobe is now three layered in the fertile regions. Each of the surface cells is cut off by several divisions which are perpendicular to the surface (Fig. 36, E). In the fertile areas, therefore, original thallus cells are clothed on either surface with groups of sixteen to thirty-two small cells (Pl. VIII, B); these cells are the spermatangial mother cells. The spermatangia first appear as elongate protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has swollen, the spermatangium is cut off from the spermatangial mother cell by an oblique annular ingrowth of the wall (Pl. VIII, F; Fig. 36, D). The spermatium is liberated through a narrow apical split in the wall. After the liberation of the primary spermatium, the spermatangial mother cell forms a secondary spermatangial protuberance into the empty wall of the first formed spermatangium.

Cryptopleura membranacea YAMADA

Pl. VIII, C–D; Fig. 36, F.

Material was dried specimens preserved in the Herbarium of the Faculty of Science, Hokkaido University.

The male plant of this species consists of palmate branches, each of which possesses rich lobes. The male organ is formed in small sori covering both surfaces of lobes or laying along the margins of branches. The regions bearing the spermatangial sori are always composed of a single layer of cells. The first step in the development of the male organ is a division of these cells, giving rise to three layers of cells which are quadrate or rectangular in surface veiw. The quadrate surface cell divides by a vertical wall and then by a second wall, also vertical, at right angles to the first, thus giving rise to a group of four small cells in a single layer (Fig. 36, F). On the other hand, the rectangular surface cell is successively cut off by two walls which are perpendicular to the surface and parallel with each other, giving rise to a group of three small cells in a single layer. Each of these four or three small cells is divided by two additional intersecting vertical walls. In the fertile areas, therefore, the original thallus cells are clothed on either surface with groups of sixteen or twelve small cells (Pl. VIII, C). These cells are the spermatangial mother cells. The spermatangia first arise terminally from the spermatangial mother cells as beak-like projections (Pl. VIII, D). Soon, they may be cut off from the spermatangial mother cell by the gradual ingrowth of the wall.

Dasya collabens HOOKER et HARVEY

Fig. 37, A-E.

Material was gathered at Otaru, Hokkaido in August 1954.

The male organ occurs in the spermatangial stands borne on the pseudolaterals. The spermatangial stand is formed as a polysiphonous lateral with a stalk and a short sterile tip which is composed of one or two cells (Fig. 37, C-D). The first step in the development of the spermatangial stand is the formation of an erect cell row consisting of several cells (Fig. 37, A). The basal and apical portion of this cell row remain monosiphonous and sterile (Fig. 37, B). Each cell of the intervening segments is an initial for the fertile axis. From each of these initials, five or six cells are cut off as pericentral cells constituting a single layer. Subsequently the pericentral cells formed in each segment undergo a transverse or an oblique division to produce a compact layer of spermatangial mother cells (Fig. 37, D-E). In the fertile region so developed, each cell of the axis of spermatangial

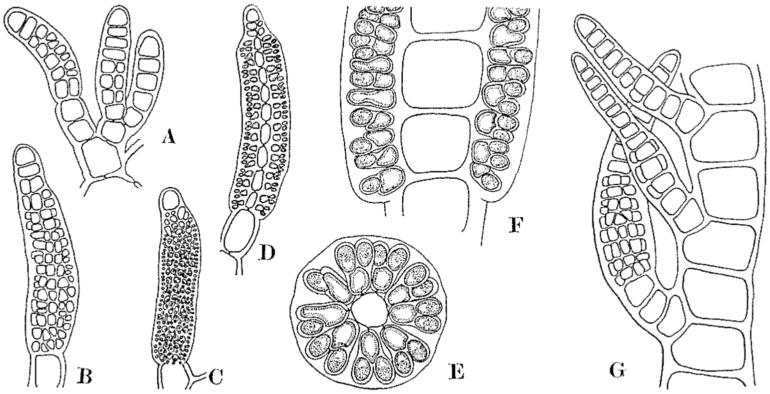

Fig. 37. Spermatangial stands.
A-E. *Dasya collabens* HOOK. et HARV.; A-C, different stages in development; D, longitudinal and E, transverse.
F-G. *Heterosiphonia pulchra* (OKAMURA) FALKENB.; F, portion of longitudinal section; G, showing various stages in development.
A-B, D, F, ×400; C, G, ×240; E, ×800.

stand is encircled by ten to fifteen spermatangial mother cells. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 37, E). The spermatium is liberated through a narrow apical split in the wall.

Dasya sessilis YAMADA

Pl. IX; F.

Material was collected by Dr. S. KAWASHIMA at Asamushi, Aomori Prefecture in July 1956.

The spermatangial stands arise laterally from the pseudolaterals (Pl. IX, F) and are situated in the same position as that of the stichidia in the tetrasporic frond. The spermatangial stand is formed as a polysiphonous lateral supported by one- or two-celled stalk and terminated by a short (one- or two-celled) or long (five- or six-celled) sterile tip. The male organ develops in exactly the same manner as in *Dasya collabens*.

Heterosiphonia pulchra (OKAMURA) FALKENBERG

Pl. IX, G; Fig. 37, F–G.

Material epiphytic on *Sargassum* was gathered at Sado Island in April 1956.

The male organ is formed in spermatangial stands, each of which is supported by a two- or three-celled stalk and terminated by a long sterile tip composed of six to twelve cells. The first step in the development of the spermatangial stands is the formation of pseudolaterals which arise adaxially from every other segment of monosiphonous ultimate branches (Pl. IX, G; Fig. 37, G). The pseudolaterals develop into cell rows consisting of ten to twenty segments in length. The basal (two- or three-celled) and upper (five- to eight-celled) segments of the fertile pseudolaterals remain monosiphonous and sterile. Each cell of the intervening segments is an initial for the fertile axis. From each of these initials, four cells are cut off as pericentral cells to produce a compact layer of spermatangial mother cells. In the fertile region so developed, each cell of the axis of spermatangial stand is encircled by a number of spermatangial mother cells (Fig. 37, F). The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 37, F). The spermatium is liberated through a narrow apical split in the wall.

Polysiphonia GREVILLE

In seven species of this genus studied, the male organ is borne in the spermatangial stands. The spermatangial stand arises usually as a branch of the trichoblast which is situated near the apex of the polysiphonous lateral (Fig. 38, A–C). It is commonly furnished with a two-celled stalk and a sterile tip composed of 1–2 or several cells. The upper stalk-cell usually forms a sterile branch which may be further ramified. In *P. senticulosa* and *P. morrowii*, however, the spermatangial stand is formed as a simple trichoblast. The spermatangial stand is represented by the peculiar form according to the species.

The first step in the development of the spermatangial stand is the formation of a trichoblast consisting of several cells (Fig. 38, A). The basal and apical cells of the trichoblast remain sterile. The intervening segments are subsequently divided into a central and several pericentral cells. The pericentral cells divide copiously to form a compact layer of spermatangial mother cells, each of which gives rise to two or three spermatangia (Fig. 38, D–E).

The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 38, D–E). The spermatangium is liberated through a narrow apical split in the wall.

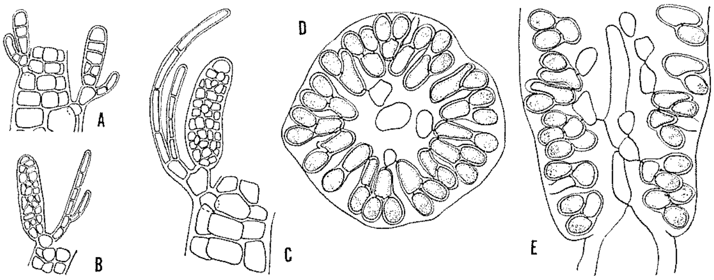

Fig. 38. Spermatangial stands of *Polysiphonia*.
A–C, different stages in development; D, transverse and E, longitudinal section.
A. *P. codiicola*. B, D, E. *P. tapinocarpa*. C. *P. novae-angliae*.
A–C, ×243; D, E, ×800.

Polysiphonia codiicola ZANARDINI

Pl. VIII, F; Fig. 39, A–E.

Material was gathered at Otaru, Hokkaido in September 1954.

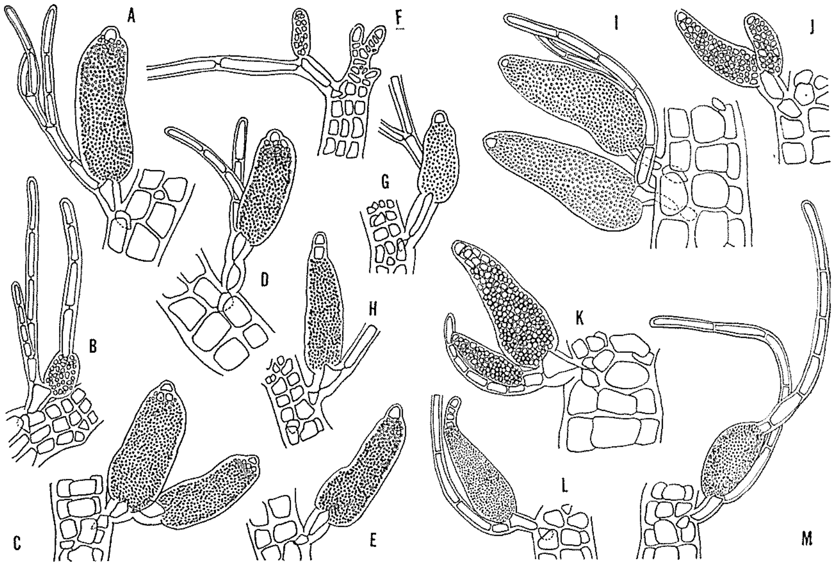

Fig. 39. Spermatangial stands of *Polysiphonia*.
A–E. *P. codiicola* ZANARD.
F–H. *P. harlandii* HARV.
I–M. *P. japonica* HARV.
A–H, J, K, ×147; I, L, M, ×70.

In general the spermatangial stand is cylindrical or spindly in shape, measuring 60–70 μm by 120–150 μm in size. The fertile region is provided with a 1–2-celled sterile tip and a 2- (rarely 3-) celled stalk. The upper stalk cell forms usually a ramified sterile branch (Pl. VIII, F; Fig. 39, A, D). Sometimes, one or two spermatangial stands are produced on a trichoblast devoid of the sterile branch (Fig. 39, C, E). The spermatangial stand is rarely globular, measuring about 30 μm in diameter and is terminated by a long sterile tip composed of several elongate cells (Fig. 39, B).

Polysiphonia harlandii HARVEY

Fig. 39, F–H.

Material was collected by Prof. Y. YAMADA at the Island of Hachijô in October 1952.

In general, the spermatangial stand is lanceolate or cylindrical in shape, measuring 65–90 μm by 150–200 μm in dimension. It is provided with a 1–2-celled sterile tip and a 2-celled stalk (Fig. 39, G–H). The upper stalk cell forms a sterile branch which is ramified. A dwarf type of the spermatangial stand which measures about 25 μm by 50 μm in dimension was observed (Fig. 39, F).

Polysiphonia japonica HARVEY

Pl. VIII, H; Fig. 39, I–M.

Material was gathered at Otaru, Hokkaido in August 1953 and at Enoshima, Kanagawa Prefecture and Matsushima, Miyagi Prefecture in April 1954.

In general, the spermatangial stand is lanceolate in shape, measuring 50–80 μm by 200–250 μm in dimension (Pl. VIII, H). It is provided with a one (often several) celled sterile tip and a two celled stalk (Fig. 39, I, L, M). The upper stalk cell usually forms a ramified sterile branch and often does not (Fig. 39, J). Sometimes one or two spermatangial stands are produced on the same trichoblast (Fig. 39, J, K).

Polysiphonia novae-angliae TAYLOR

Pl. VIII, G; Fig. 40, A–B.

Material was gathered at Otaru, Hokkaido in October 1953.

In general, the spermatangial stand is cylindrical or lanceolate in shape (Pl. VIII, G; Fig. 40, A), measuring 60–65 μm by 160–170 μm in dimension. The sper-

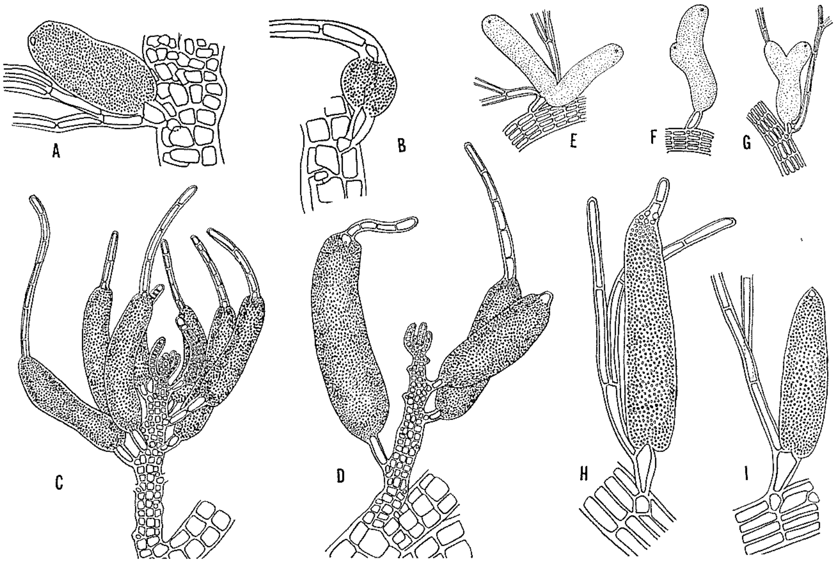

Fig. 40. Spermatangial stands of *Polysiphonia*.
A–B. *P. novae-angliae* TAYLOR.
C. *P. morrowii* HARV.
D. *P. senticulosa* HARV.
E–I. *P. tapinocarpa* SUR.
A, B, H, I, ×147; C–G, ×70.

matangial stand is terminated by a sterile tip composed of one or two cells and is supported by a two-celled stalk. The upper stalk cell forms a sterile branch which is ramified. An unusual type of the spermatangial stand was rarely observed; it is globular in shape, measuring about 25 μm in diameter (Fig. 40, B) and is terminated by a long sterile tip composed of five to ten elongate cells.

Polysiphonia tapinocarpa SURINGAR

Pl. IX, A; Fig. 40, E–I.

Material was collected by Prof. Y. YAMADA at Shichirigahama, Kanagawa Prefecture in April 1954.

In general, the spermatangial stand is lanceolate or cylindrical in shape (Pl. IX, A), measuring 40–50 μm by 140–200 μm. It is terminated by a short sterile tip composed of one cell and is supported by a two-celled stalk. The upper stalk cell forms a sterile branch which is ramified (Fig. 40, I). Sometimes the fertile region is terminated by a comparatively long sterile tip composed of two elongate cells (Fig. 40, H). Further, the fertile region possesses a protuberance in the middle part (Fig. 40, F). It is forked in the middle part (Fig. 40, G) or at the base (Fig. 40, F).

Polysiphonia morrowii HARVEY

Fig. 40, C.

Material was gathered at Sado Island in April 1956.

The spermatangial stand is first formed as a simple trichoblast on a polysiphonous lateral which arises endogenously from a branch. The spermatangial stand is cylindrical in shape and slightly bends toward the adaxial side, attaining 40–55 μm by 200–300 μm in size. It is provided with a long sterile tip composed of a few elongate cells at the apex and is supported by a simple two-celled stalk (Fig. 40, C).

Polysiphonia senticulosa HARVEY

Pl. IX, C; Fig. 40, D.

Material was gathered at Otaru, Hokkaido in April 1954.

The spermatangial stand is first formed as a simple trichoblast on the upper part of a polysiphonous lateral which arises endogenously from the fork of a branch (Fig. 40, D). The fertile region is cylindrical in shape and slightly bends toward the adaxial side, measuring 80–110 μm by 300–400 μm. It is supported by a two-celled stalk which is devoid of the sterile branch, and is terminated by a short (one- or two-celled) or a long (five- or six-celled) sterile tip.

An unusual spermatangial stand was rarely observed; the male organ is formed in a cluster covering the upper portion of the lateral which arises endogenously from the branch (Pl. IX, C).

Benzaitenia yenoshimensis YENDO

Pl. VIII, E; Fig. 41, A–D.

Material parasitic on *Chondria crassicaulis* was gathered at Sado Island in April 1956.

This species is dioecious. The male frond was found as a yellow mass on *Chondria crassicaulis*. The spermatangial stands are borne as a small and narrow swelling on the surface of the frond (Pl. VIII, E). The first step in the development of the spermatangial stand is the formation of an initial cell on the terminal of the row of hyaline cells starting from the medulla. This initial cell is cut off to give a row of several cells forming an axis of a spermatangial stand (Fig. 41, A), and each of these is cuts off five to seven pericentral cells. The pericentral cells formed in each segment undergo the transverse and oblique divisions to produce a compact layer of the spermatangial mother cells (Fig. 41, B–C). The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed,

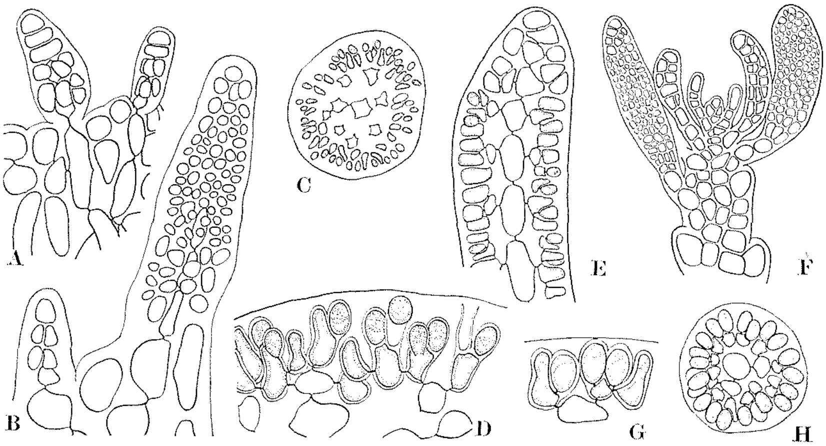

Fig. 41. Spermatangial stands.

A–D. *Benzaitenia yenoshimensis* YENDO; A–B, various stages in development; C, transverse section; D, part of the same, showing development of spermatangia.
E. *Symphyocladia linearis* (OKAMURA) FALKENB., longitudinal section.
F. *Symphyocladia marchantioides* (HARV.) FALKENB., apex of a free lateral with young spermatangial stands.
G–H. *Symphyocladia latiuscula* (HARV.) YAMADA; G, showing development of spermatangia; H, transverse section.

A–B, ×267: C, F, ×243; D, G, ×800; E, H, ×400.

the spermatangium is cut off by an oblique annular ingrowth of the wall. The spermatium is liberated through a narrow apical split in the wall (Fig. 41, D).

Symphyocladia FALKENBERG

There was no difference in the development of the spermatangial stands among three species of this genus as far as examined by the writer. The spermatangial stands are formed as simple trichoblasts which are situated near the apex of the free polysiphonous laterals. The male trichoblast commonly consists of a two- or three-celled stalk surmounted by the fertile region. The fertile region is terminated by a short sterile tip composed of one or two cells. The first step in the development of the spermatangial stand is the formation of a trichoblast consisting of several cells. The basal and apical cells of the trichoblast remain monosiphonous and sterile (Fig. 41, F). Each cell of the intervening segment is an initial cell for the fertile axis. From each of the initial cells, four or five cells are cut off as pericentral cells constituting a single layer. Subsequently, the pericentral cells formed in each segment undergo transverse and oblique divisions to produce spermatangial mother cells (Fig. 41, E, H). The spermatangia first appear as protuberances which arise from the distal ends of the spermatangial mother cells. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 41, G). The spermatium is liberated through a narrow apical split in the wall.

Symphyocladia marchantioides (HARVEY) FALKENBERG

Pl. IX, D; Fig. 41, F.

Material was collected by Mr. Y. TSUJI at Ôhara, Chiba Prefecture in April 1955.

The spermatangial stands of this species are formed on the upper part of the free lateral which appears along the margin of the flat thallus (Pl. IX, D). The free polysiphonous lateral consists of many segments with usually six pericentrals and each segment of its upper part bears the simple trichoblast which commonly consists of a two-celled stalk surmounted by the fertile region. The fertile region is lanceolate or cylindrical in shape.

Symphyocladia linearis (OKAMURA) FALKENBERG

Pl. IX, B; Fig. 41, E.

Material was gathered at Ôhara, Chiba Prefecture in April 1956.

The spermatangial stands of this species are situated in the same position as in *S. marchantioides* (Pl. IX, B). The free laterals arise from the adaxial sides of the serrate lobes which appear along the margin of the flat thallus. The free lateral consists of many segments with usually six pericentrals, and the segments of its upper part form the simple trichoblasts, each of which commonly consists of a two-celled stalk surmounted by the fertile region. The fertile region is lanceolate or spindly in shape and measures 55–60 μm by 170–200 μm in size.

Symphyocladia latiuscula (HARVEY) YAMADA

Pl. IX, E; Fig. 41, G–H.

Material was gathered at Muroran and the Cape of Erimo, Hokkaido in July and August 1954.

The spermatangial stands of this species are situated in the same position as in *S. marchantioides* and *S. linearis* (Pl. IX, E). The free laterals are recognizable on the growing margin of the branchlet, and the segments of their upper part produce the simple trichoblasts, each of which commonly consists of a two-celled stalk surmounted by the fertile region. The spermatangial stand is lanceolate or cylindrical in shape and measures 50–60 μm by 180–200 μm in size.

Rhodomela larix (TURN.) C. AGARDH

Pl. X, C; Fig. 42, A–E.

Material was gathered at Muroran, Hokkaido in April 1953.

The spermatangial stands arise usually as simple trichoblasts on the upper part of the ramulus which is situated in the axil of a lateral (Pl. X, C; Fig. 42, A), sometimes on the apical part of a lateral (Fig. 42, C). It is commonly furnished a two-celled stalk surmounted by the fertile region. The fertile region is cylindrical in shape and measures 80–120 μm by 180–250 μm in size.

The first step in the development of the spermatangial stand is the formation of a trichoblast consisting of several cells (Fig. 42, B–C). The basal cells of the trichoblast remain monosiphonous and sterile, and the other cells are the initial cells for the fertile axis. From each of the initial cells, several cells are cut off as pericentral cells constituting a single layer (Fig. 42, E). The pericentral cells divide copiously to form a compact layer of spermatangial mother cells. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 42, D). The spermatium is liberated through a narrow apical split in the wall.

Rhodomela gracilis YAMADA et NAKAMURA (non HARVEY)

Pl. X, B; Fig. 42, G–I.

Material was gathered at Muroran and Shirikishinai, Hokkaido in May 1954

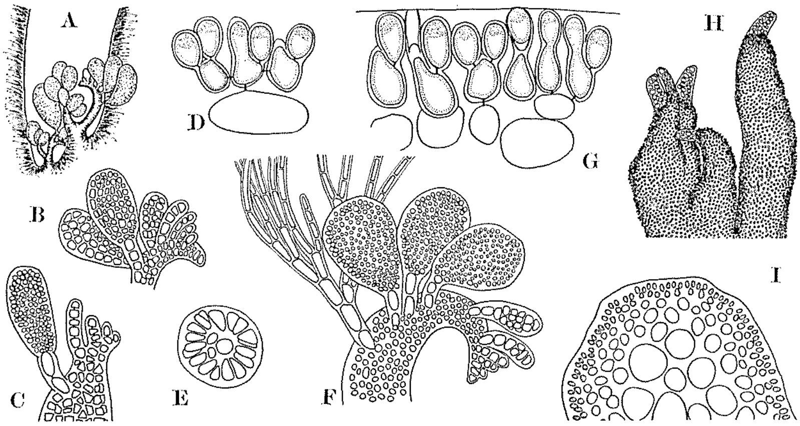

Fig. 42. Spermatangial stands.
A–E. *Rhodomela larix* (TURN.) C. AG.; A, fertile ramuli situated in an axil of a lateral; B–C, young ones formed on the fertile ramulus (B) and lateral (C); D, development of spermatangia; E, transverse section of young one.
F. *Rhodomela subfusca* OKAMURA (non C. AG.), formed on a lateral.
G–I. *Rhodomela gracilis* YAMADA et NAKAMURA (non. HARV.); G, transverse section, showing development of spermatangia; H, a portion of surface view; I, transverse section.
A; ×70; B–C, F, ×148; D, G, ×800; E, ×400; H, ×80; I, ×247.

and 1955.

The male plant of this species agrees fairly well with OKAMURA's illustration of *Rhodomela subfusca* from Shimushu Island and Muroran, Hokkaido (Icon. Jap. Alg., 4 (8), Pl. 186, Figs. 1–2).

The spermatangial stands arise as polysiphonous and irregularly ramified laterals which are situated on the apical parts of branchlets (Pl. X, B; Fig. 42, H). Early stages in the development of the spermatangial stand agree well with those of the growing apex of a sterile branchlet. Several, usually five to seven pericentral cells are formed from a central cell in each segment. Subsequently a parenchymatous cortex is formed by outgrowth of a group of cortical cells which originate from the pericentral cells. Each surface cell divides copiously to form the spermatangial mother cells (Fig. 42, I), each of which gives rise to two or three spermatangia. The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 42, G). The spermatium is liberated through a narrow apical split in the wall. After liberation of the primary spermatium, the same spermatangial mother cell produces a secondary spermatangium by proliferations into the empty sheath of the first formed one.

The shape and structure of the spermatangial stands are similar to those of European *R. subfusca* (WOODW.) C. AGARDH, described by FALKENBERG (1901) and ROSENVINGE (1903).

Rhodomela subfusca OKAMURA (non C. AGARDH)

Pl. X. A; Fig. 42, F.

Material was gathered at Matsushima, Miyagi Prefecture in April 1954, and at Shizunai, Hokkaido in May 1955.

The alga which is called by the Japanese name "Itofujimatsu" has long been passed among us under the name of *Rhodomela subfusca* (WOODW.) C. AGARDH since OKAMURA's identification in 1921. The male plants investigated by the writer agree fairly well with OKAMURA's illustration of *R. subfusca* from Iwaizaki, Miyagi Prefecture (Icon. Jap. Alg., 4 (8), Pl. 186, Fig. 4).

The spermatangial stand arises usually as a simple trichoblast on the upper part of a lateral (Pl. X, A). It is commonly provided with a two- or three-celled stalk surmounted by the fertile region (Fig. 42, F), which is cylindrical in shape and measures 80–100 μm by 150–200 μm in size. The spermatangial stand develops in the same way as in *R. larix* (Fig. 42, F).

The spermatangial stands of the male plant investigated by the writer agree fairly well with the description and illustration of OKAMURA's *R. subfusca* (non C. AGARDH), but they are clearly different from those of European *R. subfusca* (WOODW.) C. AGARDH described by FALKENBERG (1901) and ROSENVINGE (1903).

Odonthalia corymbifera (GMELIN) J. AGARDH

Fig. 43, A–B.

Material was gathered at Muroran, Hokkaido in July 1954.

This species is dioecious. The male plants are conspicuous by the pale purplish red and by flat laterals arising from the edges of branches. The male organ develops in sori occurring as irregular patches on the surface of the flat lateral which consists of a pseudoparenchymatous structure. The spermatangial mother cells are borne by a transverse or an oblique division of superficial cells of the fertile lateral (Fig. 43, A). The spermatangium arises from the distal end of the spermatangial mother cell as a narrow beak-like protuberance. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 43, B). Through the apical split of the spermatangial wall, the spermatium escapes into the surrounding water as a rounded cytoplasmic body.

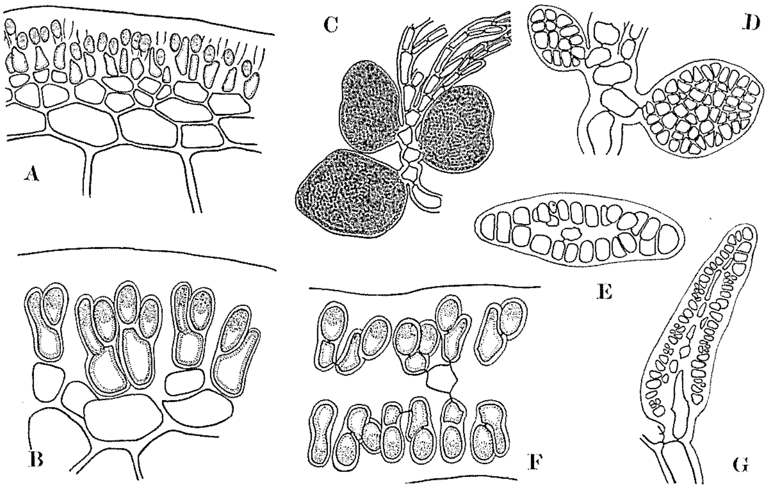

Fig. 43. A–B. *Odonthalia corymbifera* (GMEL.) J. AG.; A, transverse section through a spermatangial sorus; B, part of the same, showing development of spermatangia.
C–G. *Chondria dasyphylla* (WOODW.) C. AG.; C, three spermatangial stands on a trichoblast; D, two young ones; E, transverse and G, longitudinal section of young ones; F, part of transverse section, showing development of spermatangia.
A, ×400; B, F, ×800; C, ×80; D, E, G, ×240.

Chondria dasyphylla (WOODW.) C. AGARDH

Pl. IX, H; Fig. 43, C–G.

Material was collected by Dr. Y. SAKAI at Matsushima, Miyagi Prefecture in April 1954.

The male organ is formed in the spermatangial stand occupying the lowest lateral of a trichoblast which is lodged in an apical depression of a ultimate branchlet (Pl. IX, H; Fig. 43, C). The spermatangial stand is a biconvex disc in shape, the edge of which is occupied by the enlarged and sterile cells. The first step in the development of the spermatangial stand is the formation of an initial cell of the axis. The initial cell appears laterally from the segmental cell of the lowest part of the trichoblast and then divides to form a branching system which progresses in the branched axis of the spermatangial stand. The branching system forms a biconvex disc like mass (Fig. 43, D). The individual branchlets of the branched axis are terminated with sterile apical cells; the remaining cells of the branchlets cut off, on either surface, pericentral cells which produce a continuous layer of globular spermatangial mother cells (Fig. 43, E, G). The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall (Fig. 43, F). The spermatium is liberated through a narrow apical split of the wall.

Laurencia composita YAMADA

Pl. X, E; Fig. 44, A.

Material was gathered at Shichirigahama, Kanagawa Prefecuture in April 1955.

The male fronds can easily be distinguished by means of their swollen pinna tips, due to the presence of embedded conceptacles with dense yellow contents. The male organ is borne on axis lining the conceptacle. The conceptacles have been shown by KYLIN (1923) for *L. pinnatifida* to be formed by rapid growth of groups of cells around the apical cell of a pinna, the latter ceasing to function and becoming carried down into a concave depression. At the same time, there is carried down a group of hairs which develop from the outer layer of cells at the apex of each fertile pinna, and these line densely the whole internal wall and even the ostiole of the conceptacle. The uppermost cell of the fertile trichoblast remains sterile, while the remainder form the axes around which the spermatangial mother cells and the spermatangia are borne (Pl. X, E).

Each cell of the upstanding axes cuts off a few pericentral cells, and these divide again several times so that the whole axis is densely clothed with a number of pericentral cells. Each of these becomes a spermatangial mother cell (Fig. 44, A). The spermatangia first appear as protuberances which arise from the distal end of the spermatangial mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall. The spermatium is liberated through a narrow apical split in the wall.

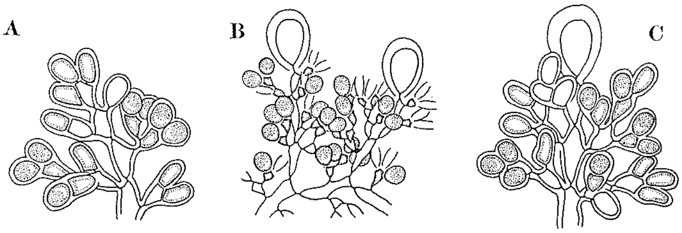

Fig. 44. Spermatangial stands.

A. *Laurencia composita* YAMADA.
B. *Laurencia glandulifera* KUETZ.
C. *Laurencia pinnata* YAMADA.
A, C, ×800; B, ×400.

Laurencia pinnata YAMADA

Pl. X, D, G; Fig. 44, C.

Material was gathered at Shichirigahama, Kanagawa Prefecture in April 1955.

The male fronds can easily be distinguished by means of their swollen pinna tips, owing to the presence of embedded conceptacles with dense pale contents. The male organ is borne on richly branched trichoblasts developed in a conceptacle. Each branch of the fertile trichoblasts becomes the axes, around which the spermatangial mother cells and the spermatangia are borne (Pl. X, D), and it is terminated by a sterile giant cell (Pl. X, G). The spermatangial mother cells and the spermatangia develop in the same way as in those of *L. composita* (Fig. 44, C).

Laurencia glandulifera KUETZING

Pl. X, F; Fig. 44, B.

Material was gathered at Otaru, Hokkaido in June 1954.

The male plants are recognizable under a slight magnification with a hand-lens, by the cup-like hollows at the apex of the swollen ultimate pinna, which are embedded with pale trichoblasts. The trichoblasts give rise to the spermatangial mother cells and the spermatangia; the fertile trichoblasts are made up of branching rows of long narrow cells. On these cells the spermatangial mother cells are borne, the earliest formed appearing near the base of the axis; a progressive development therefore takes place both in the spermatangial mother cells and the spermatangia, the base of the axis often being fully fertile while the apex shows no sign of spermatangia; the axis is terminated by a swollen giant cell, but this does not invariably occur. The spermatangial mother cells and the spermatangia are borne in the same way as in those of *L. composita.*

Conclusion

1. The structure of the male reproductive organ.

The sexual plants of the Florideae are usually dioecious, but the following species are monoecious: *Nemalion vermiculare, Liagora robusta, L. japonica, L. ceranoides, L. orientalis, L. setchellii, L. pinnata, Gloiopeltis furcata,* and *G. complanata.*

The male plant usually resembles the female or tetrasporic plant in external appearance. Occasionally, however, as in some members of *Gelidium* and *Rhodymenia,* it is smaller or has a more ephemeral existence than the female, and in *Dumontia* it is thought to die after discharging spermatia.

The arrangement or grouping of the spermatangia on the thallus is varied.

In some species of Helminthocladiaceae, the spermatangia form small clusters on the assimilative filaments. In major species of Gelidiaceac, Dumontiaceae, Endocladiaceae, Grateloupiaceae, Callymeniaceae, Nemastomaceae, Hypneaceae, Gigartinaceae, Rhodymeniaceae, Lomentariaceae, Delesseriaceae, and some species of Ceramiaceae, the spermatangia form superficial sori. The sorus is usually enclosed by a gelatinous cuticle.

In some species of Ceramiaceae, Dasyaceae, and Rhodomelaceae, the spermatangia are formed in the spermatangial stands which are not incorporated in the thallus tissue. The spermatangial stands of *Laurencia* and *Griffithsia* are composed of a system of richly branched threads ; in *Polysiphonia* and *Rhodomela,* etc., they are polysiphonous.

The spermatangia of *Desmia* are formed in nemathecia which form irregular cushion-like swellings on the thallus. In section the male nemathecia show a dense aggregate of fertile threads which grow out from the surface cells of the thallus.

In *Galaxaura* and *Gracilaria* the spermatangia are formed in conceptacles which are sunk in the thallus.

2. The position of the male reproductive organ.

In the majority of cases, the spermatangia develop on male plants in the same position as that in which the procarps and tetraspores are borne, but in some species of *Laurencia* the spermatangia resemble the procarps in position, differing in this respect from the asexual ones. In others, such as *Ceramium* and *Dasya,* the procarps occur in a different position from the spermatangia and tetraspores, while in the members of *Polysiphonia* and *Symphyocladia,* the position of the spermatangia does not resemble that of either the tetraspores or the procarps.

The position of the male reproductive organ on the thallus is very varied. In *Nemalion, Helminthocladia, Liagora* and *Dermonema,* the spermatangia are scattered indiscriminately on the whole of the thallus. In *Dumontia* and *Grateloupia,* etc., the spermatangia are formed over almost the whole of the thallus, while in *Gelidium* and *Callophyllis,* etc., the spermatangia are formed in sori which are localized in certain parts of the thallus ; the apical regions (*Callophyllis* and *Lomentaria,* etc.), the margin of the thallus (*Cryptopleura* and *Erythroglossum*), the ultimate branches (*Gelidium* and *Hypnea,* etc.), the proliferations (*Acrosorium polyneurum*), and the special laterals (*Odonthalia corymbifera*). In *Polysiphonia* and *Chondria,* etc., the spermatangial stands are borne on simple or branched trichoblasts situated near the apex of branchlets, while in *Dasya* and *Heterosiphonia* they occur laterally on pseudolaterals.

The position of spermatangial groups can be summed up in the following scheme :

A. Spermatangia formed on the whole thallus.

a) Spermatangia formed over almost the whole of thallus.

Dumontia spp.
Neodilsea spp.
Gloiopeltis spp.
Grateloupia spp.
Pachymeniopsis spp.
Ceramium spp.
Campylaephora spp.
Hyalosiphonia caespitosa.
Halymenia durvillaei.
Schizymenia dubyi.
Chondrus giganteus.
Rhodoglossum japonicum.
Rhodymenia pertusa.

b). Spermatangia scattered on the whole of thallus.

Nemalion spp.
Helminthocladia spp.
Liagora spp.
Galaxaura spp.
Gracilaria spp.
Dermonema frappieri.
Scinaia hormoides.
Rhodopeltis setchellii.
Phyllymenia sparsa.
Rhodymenia palmata.

B. Spermatangia localized in certain parts of thallus.

a). Spermatangia formed in superficial sorus.

1). Sorus on an upper region of thallus.

Desmia spp.
Callophyllis spp.
Lomentaria spp.
Binghamiella californica
Nienburgia japonica
Carpopeltis flabellata
Callymenia reniformis
Chrysymenia wrightii
Champia parvula
Chondrus crispus

2). Sorus at a margin of thallus.

Erythroglossum pinnatum
Cryptopleura membranacea

3). Sorus on an ultimate branch.

Gelidium spp.
Pterocladia spp.
Carpopeltis spp.
Hypnea spp.
Gigartina spp.
Vanvoorstia coccinea
Delisea fimbriata
Grateloupia divaricata
Microcladia elegans
Reinboldiella schmitziana
Neoptilota asplenioides

4). Sorus on a difinite lateral or a proliferation.

Chondrus pinnulatus
Psilothallia dentata
Acrosorium polyneurum
Ptilota pectinata
Laingia pacifica

5). Sorus on a specially developed lateral.

Odonthalia corymbifera

b). Spermatangia formed in a spermatangial stand.

1). Stand on the whole of thallus.

Benzaitenia yenoshimensis

2). Stand on an upper part of branch.

Neomonospora yagii *Griffithsia japonica*
Rhodomela gracilis

3). Stand on a definite side of branch.

Callithamnion spp.

4). Stand on a definite lateral.

Asparagopsis spp. *Antithamnion nipponicum*
Dasya spp. *Wrangelia argus*
Heterosiphonia pulchra

5). Stand on a trichoblast.

Polysiphonia spp. *Symphyocladia* spp.
Rhodomela spp. *Laurencia* spp.
Chondria dasyphylla

3. The development of the spermatangial mother cell.

The spermatangia in the Florideae are always developed from a cell which is known as the spermatangial mother cell. The mother cells are the terminal cells of a branch-system and are invariably uninucleate. They commonly possess reduced chromatophore and are sometimes colourless. In a few of the more primitve Florideae (*Batrachospermum* and *Nemalion*) the mother cells are not differentiated from the vegetative cells.

Concerning the development of the spermatangial mother cell, the following types can be classified:

A. Mother cell transformed from a vegetative cell (Fig. 45, A).

Nemalion vermiculare

B. Mother cell formed by division of a vegetative cell.

1). Mother cell formed as a protuberance budded off from a vegetative cell (Fig. 45, B_1).

Helminthocladia spp. *Nemalion pulvinatum*
Liagora spp. *Dermonema frappieri*

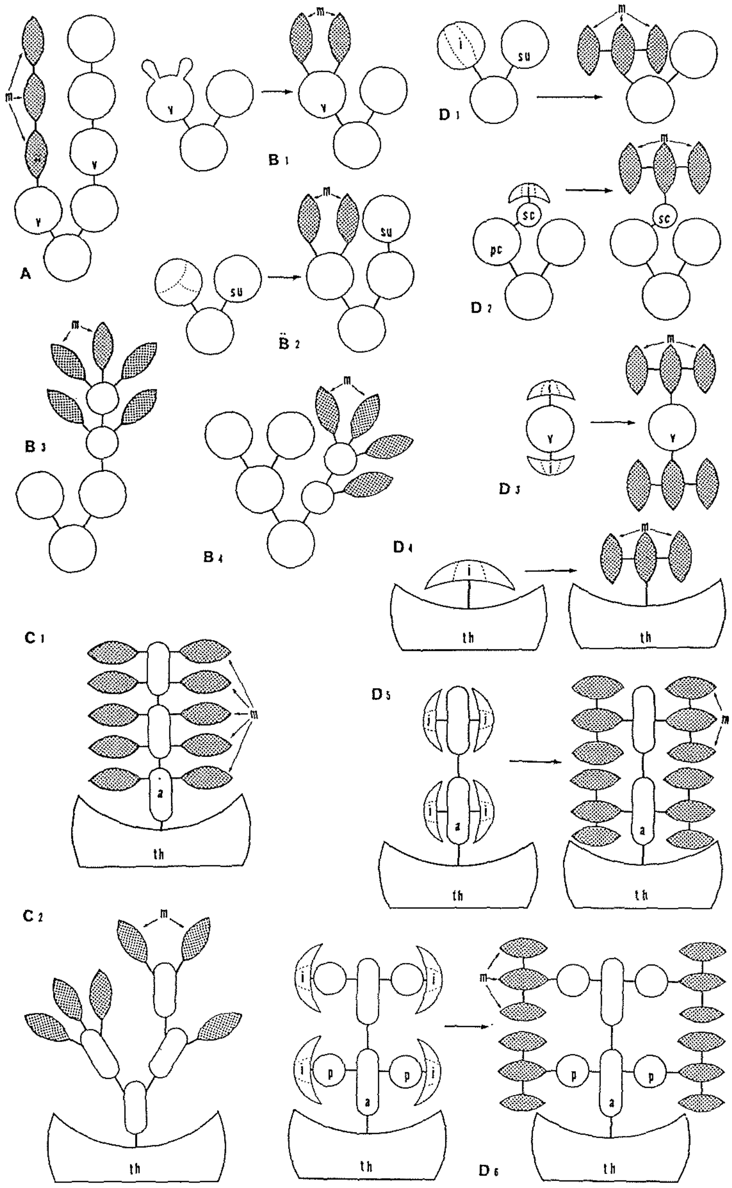

Fig. 45. Diagrams of various types in development of the spermatangial mother cell.

a, axial cell of spermatangial stand; i, initial cell of spermatangial mother cell; m, spermatangial mother cell; p, pericentral cell; pc, primary cortical cell; sc, secondary cortical cell; su, superficial cell of thallus; v, vegetative cell.

2). Mother cell formed from a superficial cell of thallus (Fig. 45, B_2).

Asparagopsis spp.
Gelidium spp.
Pterocladia spp.
Dumontia spp.
Neodilsea spp.
Gloiopeltis spp.
Grateloupia spp.
Pachymeniopsis spp.
Carpopeltis spp.
Callophyllis spp.
Hypnea spp.
Chondrus spp.
Gigartina spp.
Ceramium spp.
Delisea fimbriata
Hyalosiphonia caespitosa
Halymenia durvillaei
Phyllymenia sparsa
Callymenia reniformis
Schzymenia dubyi
Rhodoglossum japonicum
Microcladia elegans
Reinboldiella schmitziana
Neoptilota asplenioides
Rhodomela gracilis
Odonthalia corymbifera
Rhodymenia spp.
Campylaephora spp.

C. Mother cell formed in a special structure, not incorporated in a thallus tissue.

1). Mother cell formed pericentrally from an axial cell of the spermatangial stand (Fig. 45, C_1).

Antithamnion nipponicum

2). Mother cell formed as an end cell of a branch-system (Fig. 45, C_2).

Laurencia spp.
Griffithsia japonica

3). Mother cell formed as an end cell of a branch-system developing from an outer cell of thallus (Fig. 45, B_3).

Ptilota pectinata
Psilothallia dentata

4). Mother cell formed as an end cell of a branch-system developing from an internal cell of thallus (Fig. 45, B_4).

Galaxaura spp.
Scinaia hormoides

D. Mother cell formed by repeated division of an initial cell.

1). Initial cell transformed from a vegetative cell (Fig. 45, D_1).

Desmia spp.
Gracilaria spp.
Delesseria violacea

2). Initial cell formed from a secondary cortical cell (Fig. 45, D_2).

Lomentaria spp.
Binghamiella californica
Champia parvula

3). Initial cell formed pericentrally from a vegetative cell (Fig. 45, D$_3$).

Laingia pacifica
Erythroglossum pinnatum
Acrosorium polyneurum
Vanvoorstia coccinea
Nienburgia japonica
Cryptopleura membranacea

4). Initial cell formed as a special cell, not incorporated in a thallus tissue (Eig. 45, D$_4$).

Callithamnion spp.

5). Initial cell transformed from a pericentral cell of a special structure, not incorporated in a thallus tissue (Fig. 45, D$_5$).

Dasya spp.
Heterosiphonia pulchra
Wrangelia argus
Chondia dasphylla

6). Initial cell formed from a pericentral cell of a special structure, not incorporated in a thallus tissue (Fig. 45, D$_6$).

Polysiphonia spp.
Benzaitenia yenoshimensis
Symphyocladia spp.
Rhodomela spp.

4. The development of the spermatangium and spermatium.

The spermatangia of the Florideae are spherical or oblong, unicellular structures, producing a single male gamete which is known as the spermatium, from the entire contents. As a general rule the spermatangia first appear as protuberances, which usually arise subterminally and successively from different sides of the mother cell. After the spermatangial protuberance has developed, the spermatangium is cut off by an oblique annular ingrowth of the wall.

The spermatium is liberated through a narrow apical split in the elastic wall. After the liberation of the primary spermatium, the same mother cell produces a secondary spermatangium by a proliferation into the empty membrane of the first formed one.

In *Gracilaria* and *Hypnea*, the spermatangia arise terminally and sometimes form short rows, dividing by transverse septum.

5. Classification of the Florideae on the basis of the male reproductive organ.

The classification of the Florideae based on the male reproductive organ has been published by N. E. Svedelius (1908) and V. M. Grubb (1924). The writer drew up the following scheme based on the developmental types of spermatangial mother cells, and the position and structure of spermatangial groups:

I). Mother cell not differing a vegetative cell either in form or contents.

Nemalion vermiculare

II). Mother cell differentiated from a vegetative cell.

A). Spermatangia expansive.

i). Spermatangia formed over almost the whole of thallus; the mother cell formed by division of the outer cortical cell of thallus.

Dumontia incrassata
Dumontia simplex
Hyalosiphonia caespitosa
Neodilsea yendoana
Neodilsea tenuipes
Gloiopeltis furcata
Gloiopeltis complanata
Halymenia durvillaei
Grateloupia filicina
Grateloupia livida
Grateloupia okamurai
Grateloupia turuturu
Grateloupia imbricata
Pachymeniopsis elliptica
Pachymeniopsis lanceolata
Pachymeniopsis yendoi
Schizymenia dubyi
Chondrus giganteus
Rhodoglossum japonicum
Rhodymenia pertusa
Ceramium cimbricum
Ceramium paniculatum
Ceramium kondoi
Ceramium japonicum
Campylaephora hypnaeoides
Campylaephora crassa

ii). Spermatangia scattered on the whole of thallus.

a). Mother cell formed as a protuberance budded off from a vegetative cell; spermatangia formed in the clusters.

Nemalion pulvinatum
Helminthocladia australis
Helminthocladia macrocephala
Helminthocladia yendoana
Dermonema frappieri
Rhodopeltis setchellii
Liagora robusta
Liagora japonica
Liagora boninensis
Liagora ceranoides
Liagora orientalis
Liagora setchellii
Liagora farinosa
Liagora pinnata

b). Mother cell formed from the outer cortical cell of thallus.

Phyllymenia sparsa
Rhodymenia palmata

c). Mother cell formed as the end cell of a branch-system, developing from the internal cell of thallus.

1). Spermatangia formed in the cluster covering the surface of thallus.

Scinaia hormoides

2). Spermatangia formed within the conceptacle sunk in thallus.

Galaxaura elegans
Galaxaura hystrix
Galaxaura falcata
Galaxaura papillata

d). Mother cell formed by repeated division of the initial cell transformed from the cortical cell; spermatangia formed within the conceptacle sunk in thallus.

Gracilaria verrucosa
Gracilaria textorii
Gracilaria arcuata

B). Spermatangia localized in certain parts of thallus.

i). Spermatangia formed in the superficial sorus.

a). Mother cell formed from the superficial cell of thallus.

1). Sorus on the upper region of thallus.

Callymenia reniformis var. *cuneata*
Carpopeltis flabellata
Chondrus crispus
Chrysymenia wrightii
Callophyllis adnata
Callophyllis crispata
Callophyllis japonica
Callophyllis laciniata
Callophyllis palmata

2). Sorus on the ultimate branch.

Delisea fimbriata
Gelidium amansii
Gelidium pacificum
Gelidium subcostatum
Pterocladia nana
Pterocladia densa
Pterocladia tenuis
Grateloupia divaricata
Carpopeltis affinis
Carpopeltis angusta
Carpopeltis divaricata
Hypnea boergesenii
Hypnea cervicornis
Hypnea variabilis
Gigartina intermedia
Gigartina tenella
Microcladia elegans
Reinboldiella schmitziana
Neoptilota asplenioides

3). Sorus on the difinite lateral or the proliferation.

Chondrus pinnulatus

4). Sorus on the specially developed lateral.

Odonthalia corymbifera

b). Mother cell formed as the end cell of a branch-system developing from the outer cell of thallus.

Ptilota pectinata
Psilothallia dentata

c). Mother cell formed by repeated division of the initial cell.

α). Initial cell transformed from a vegetative cell.

Delesseria violacea

β). Initial cell formed from the secondary cortical cell.

Lomentaria catenata *Champia parvula*
Lomentaria hakodatensis *Binghamiella californica*

γ). Initial cell formed pericentrally from a vegetative cell.
1). Sorus on the upper region of thallus.

Nienburgia japonica

2). Sorus at the margin of thallus.

Erythroglossum pinnatum *Cryptopleura membranacea*

3). Sorus on the ultimate branch.

Vanvoorstia coccinea

4). Sorus on the definite lateral or the proliferation.

Laingia pacifica *Acrosorium polyneurum*

ii). Spermatangia formed in the nemathecium swelling on the surface of thallus; the mother cell formed by repeated division of the initial cell transformed from the cortical cell.

Desmia hornemanni *Desmia japonica*

iii). Spermatangia formed in the spermatangial stand.
a). Mother cell formed from the superficial cell.

Asparagopsis hamifera *Rhodomela gracilis*
Asparagopsis taxiformis

b). Mother cell formed pericentrally from the axial cell of the spermatangial stand.

Antithamnion nipponicum

c). Mother cell formed as the end cell of a branch-system.
1). Stand on the upper part of branch.

Griffithsia japonica

2). Stand on the trichoblast.

Laurencia composita *Laurencia pinnata*
Laurencia glandulifera

d). Mother cell formed by repeated division of the initial cell.
α). Initial cell formed as the special cell on the definite side of branch.

Callithamnion corymbosum
Callithamnion callophyllidicola

β). Initial cell transformed from the pericentral cell of the spermatangial stand.

1). Stand on the definite lateral.

Wrangelia argus
Heterosiphonia pulchra
Dasya sessilis
Dasya collabens

2). Stand on the trichoblast.

Chondria dasyphylla

γ). Initial cell formed from the pericentral cell of the spermatangial stand.

1). Stand on the whole of thallus.

Benzaitenia yenoshimensis

2). Stand on the upper part of branch.

Neomonospora yagii

3). Stand on the trichoblast.

Polysiphonia codiicola
Polysiphonia harlandii
Polysiphonia japonica
Polysiphonia novae-angliae
Polysiphonia tapinocarpa
Polysiphonia morrowii
Polysiphonia senticulosa
Symphyocladia marchantioides
Symphyocladia linearis
Symphyocladia latiuscula
Rhodomela larix
Rhodomela subfusca

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PLATE I

A–C. Spermatangial clusters

A. *Dermonema frappieri* (MONT. et MILL.) BOERGESEN, ×495.

B. *Scinaia hormoides* SETCHELL, ×495.

C. *Helminthocladia australis* HARVEY, ×672.

D–F. Vertical sections of spermatangial conceptacles

D. *Galaxaura elegans* TANAKA, ×125.

E. *Galaxaura falcata* KJELLMAN, ×188.

F. *Galaxaura hystrix* KJELLMAN, ×152.

[TAZAWA] PLATE I

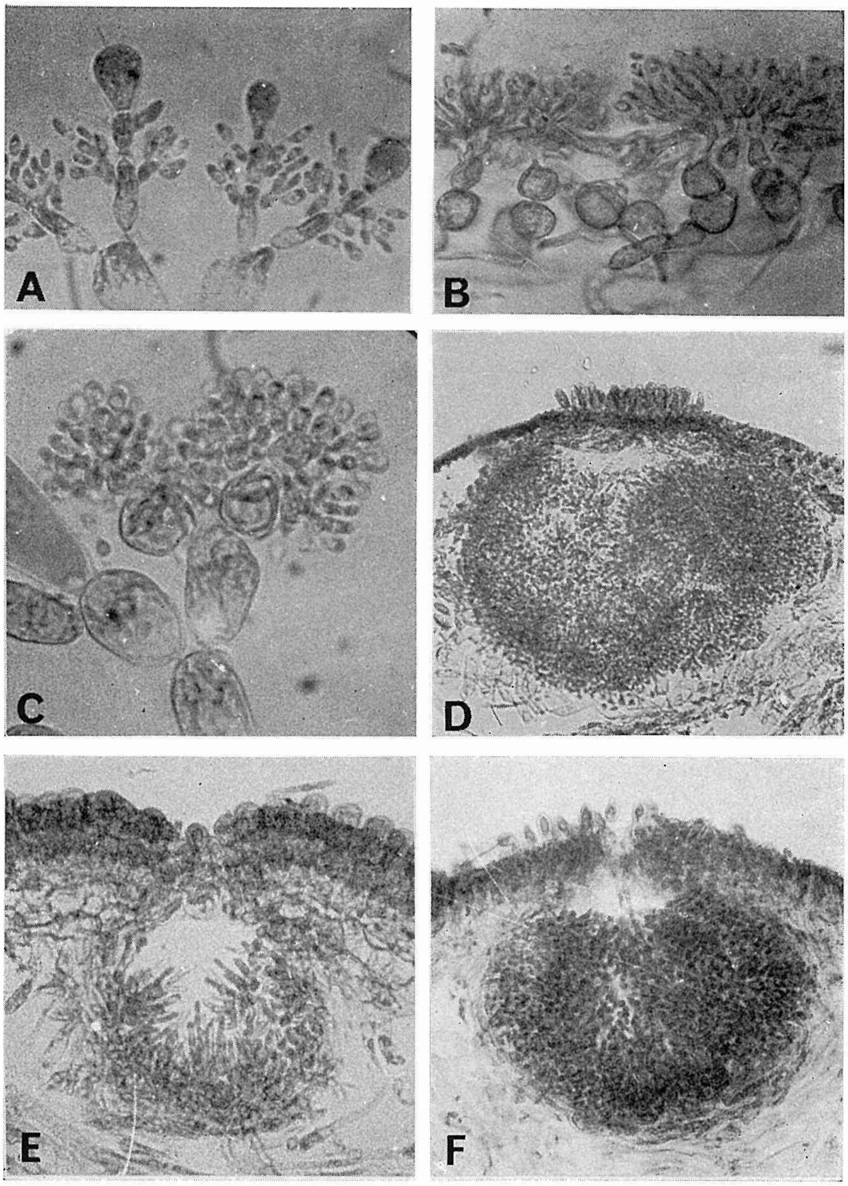


PLATE II

A. *Nemalion vermiculare* SURINGAR, spermatangial cluster, ×672.

B. *Asparagopsis hamifera* (HARIOT) OKAMURA, spermatangial stands, ×31.

C. *Delisea fimbriata* (LAMOUR.) MONTAGNE, ramulus with spermatangial sorus, ×24.

D–J. Sections through spermatangial sori

D. *Gelidium amansii* LAMOUROUX, ×806.

E. *Gelidium subcostatum* OKAMURA, ×806.

F. *Pterocladia densa* OKAMURA, ×707.

G. *Pterocladia nana* OKAMURA, ×806.

H. *Pterocladia tenuis* OKAMURA, ×806.

I. *Gloiopeltis complanata* (HARVEY) YAMADA, ×707.

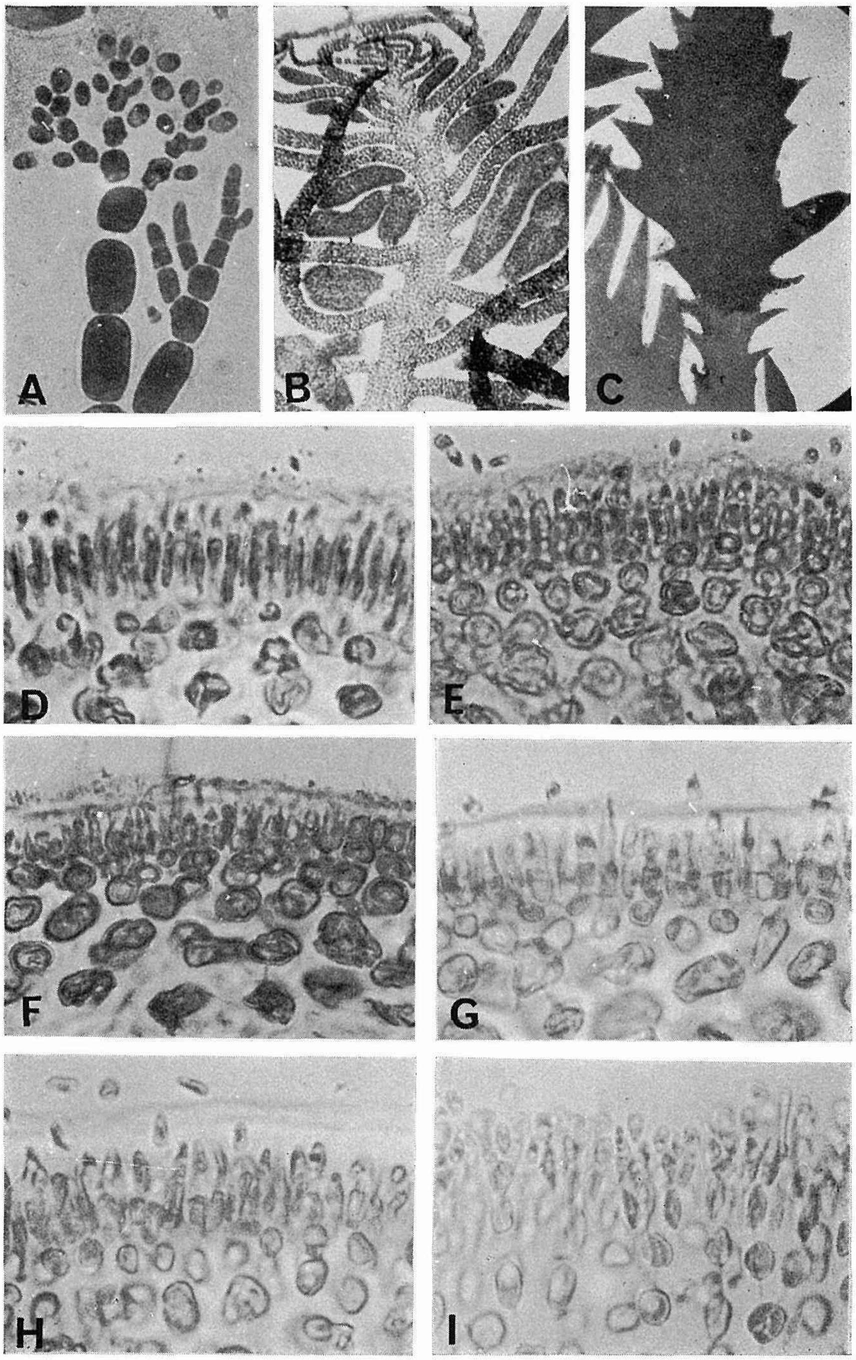

A
B
C
D
E
F
G
H
I

PLATE III

A–E. Sections through spermatangial sori

A. *Grateloupia divaricata* OKAMURA, ×707.
B. *Phyllymenia sparsa* (OKAMURA) KYLIN, ×707.
C. *Carpopeltis angusta* (HARVEY) OKAMURA, ×160.
D. *Callophyllis laciniata* (HUDSON) KUETZING, ×707.
E. *Callymenia reniformis* var. *cuneata* J. AGARDH, ×707.

F–H. Vertical sections of spermatangial conceptacles

F. *Gracilaria textorii* SURINGAR, ×707.
G. *Gracilaria verrucosa* (HUDSON) PAPENFUSS, ×601.
H. *Gracilaria arcuata* ZANARDINI, ×601.

[TAZAWA] PLATE III

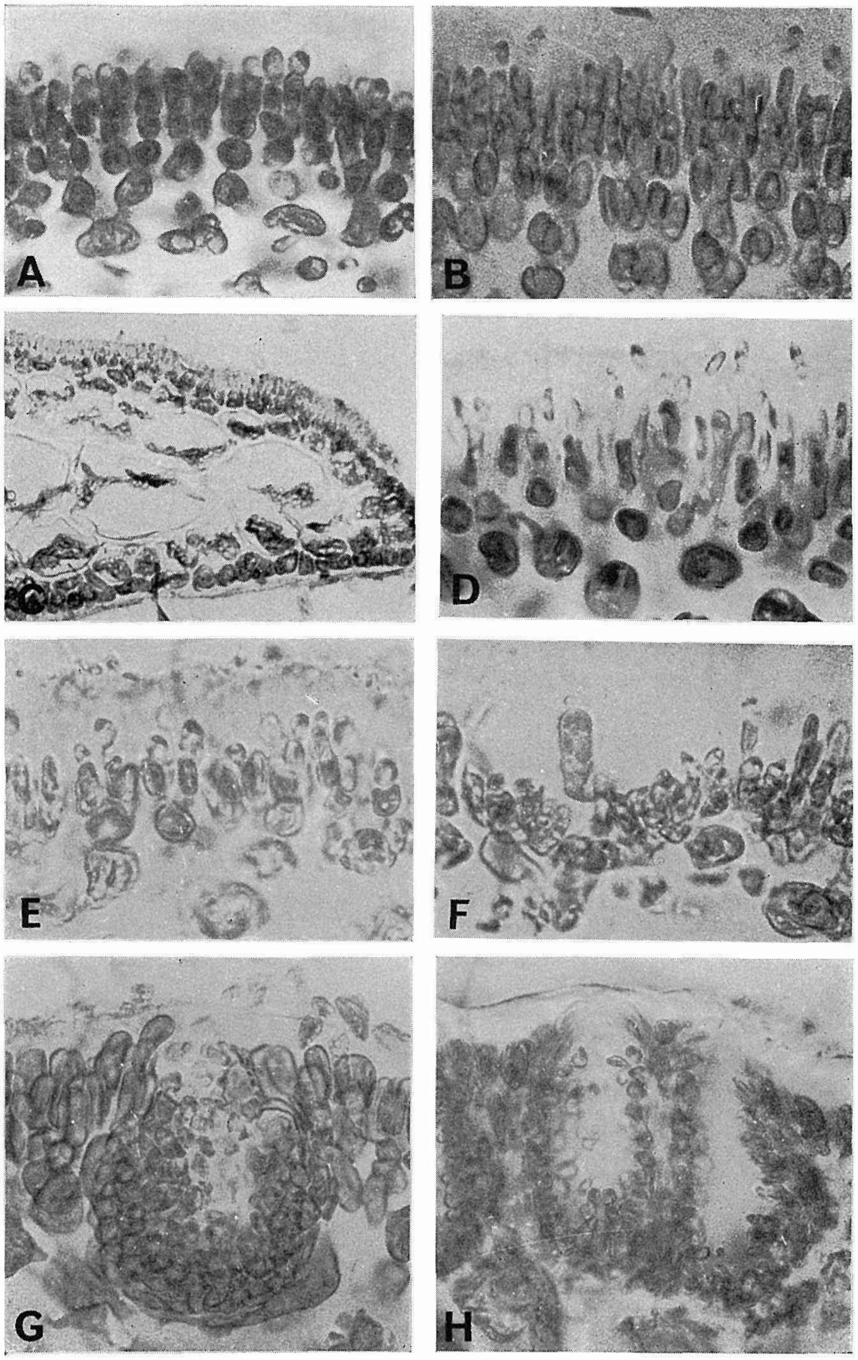


PLATE IV

A. Section of a male nemathecium of *Desmia hornemanni* MARTENS.

B–I. Sections through spermatangial sori

B. *Hypnea boergesenii* TANAKA.

C. *Carpopeltis affinis* (HARVEY) OKAMURA.

D. *Rhodoglossum japonicum* MIKAMI.

E. *Gigartina intermedia* SURINGAR.

F. *Chondrus giganteus* YENDO.

G. *Chondrus pinnulatus* (HARVEY) OKAMURA.

H. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH.

I. *Lomentaria catenata* HARVEY.

A–I. ×707.

[TAZAWA] PLATE IV

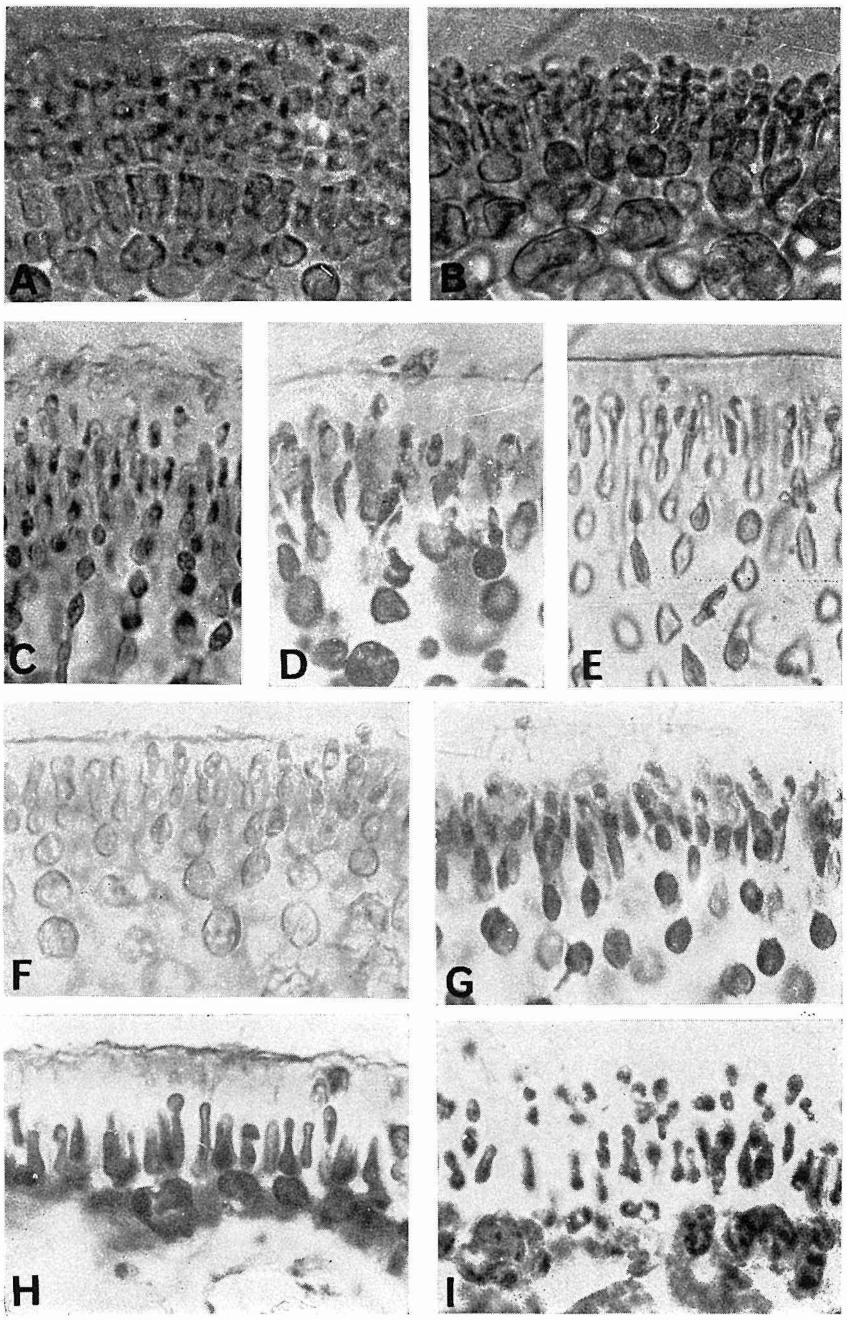


PLATE V

Portions of fronds with spermatangial stands (A–C, E) and sori (H)

A. *Antithamnion nipponicum* YAMADA et INAGAKI, ×80

B. *Ceramium cimbricum* PETERSEN, ×106.

C. *Ceramium paniculatum* OKAMURA, ×86.

E. *Wrangelia argus* MONTAGNE, ×89.

H. *Reinboldiella schmitziana* (REINB.) DE TONI, ×78.

D, F, G. Sections through spermatangial sori

D. *Ceramium cimbricum* PETERSEN, ×707.

F. *Campylaephora crassa* (OKAMURA) NAKAMURA, ×707.

G. *Reinboldiella schmitziana* (REINB.) DE TONI, ×707.

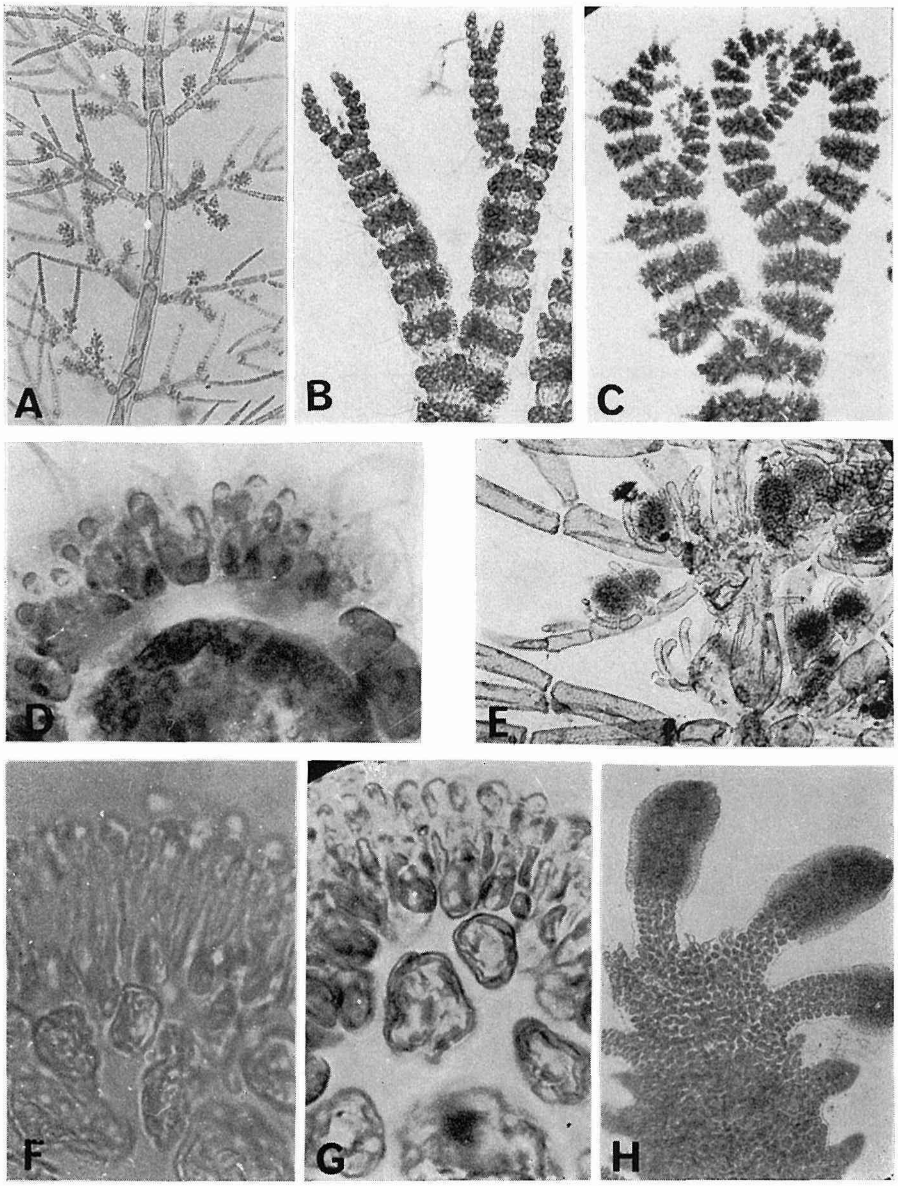

A
B
C
D
E
F
G
H

PLATE VI

Portions of fronds with spermatangial stands (A–C) and clusters (D, E, G)

A. *Callithamnion callophyllidicola* YAMADA, ×86.

B. *Neomonospora yagii* (OKAMURA) YAMADA, ×91.

C. *Griffithsia japonica* OKAMURA, ×33.

D–E. *Ptilota pectinata* (GUNN.) KJELLMAN. D, ×28, E, ×86.

F. *Neoptilota asplenioides* (TURN.) KYLIN, section through a spermatangial sorus, ×707.

G. *Psilothallia dentata* (OKAMURA) KYLIN, ×68.

[TAZAWA] PLATE VI

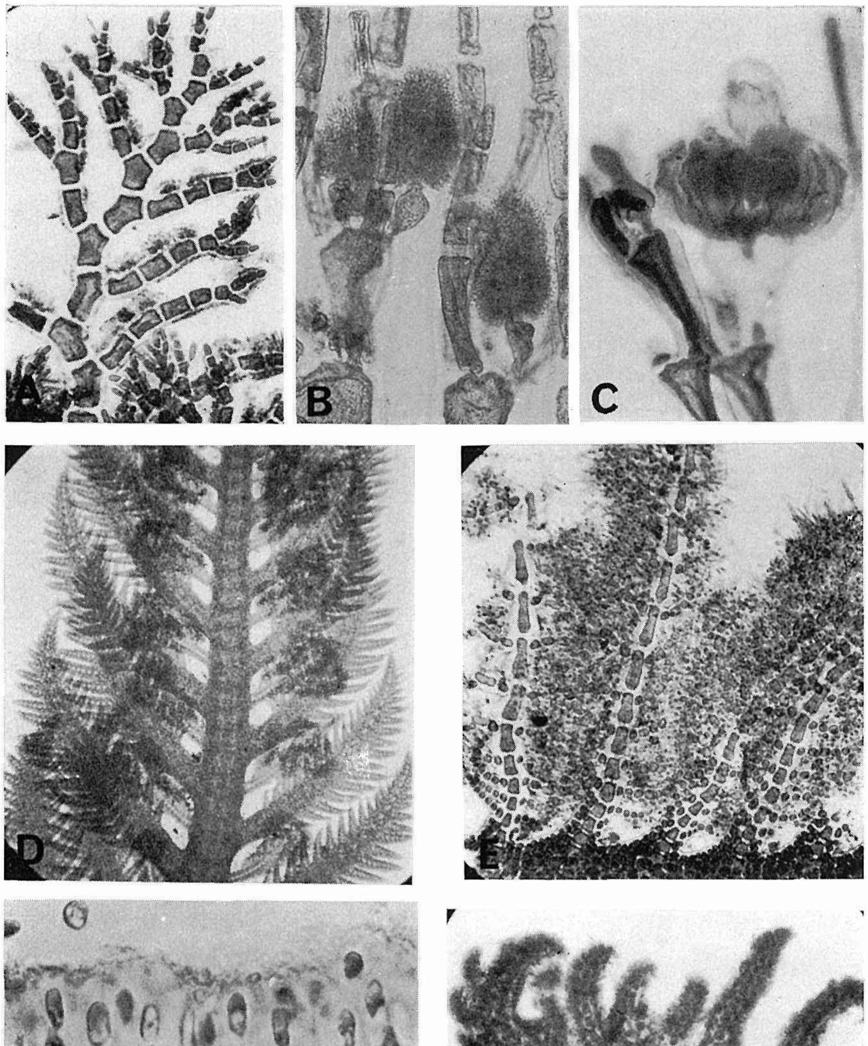


PLATE VII

Side (A–C, G) and surface (D–F, F) views of spermatangial sori

A, D. *Laingia pacifica* YAMADA.
B, E. *Erythroglossum pinnatum* OKAMURA.
C, F. *Nienburgia japonica* (YAMADA) KYLIN.
G–H. *Delesseria violacea* (HARVEY) KYLIN.

A–G. ×530, H. ×86.

[TAZAWA] PLATE VII

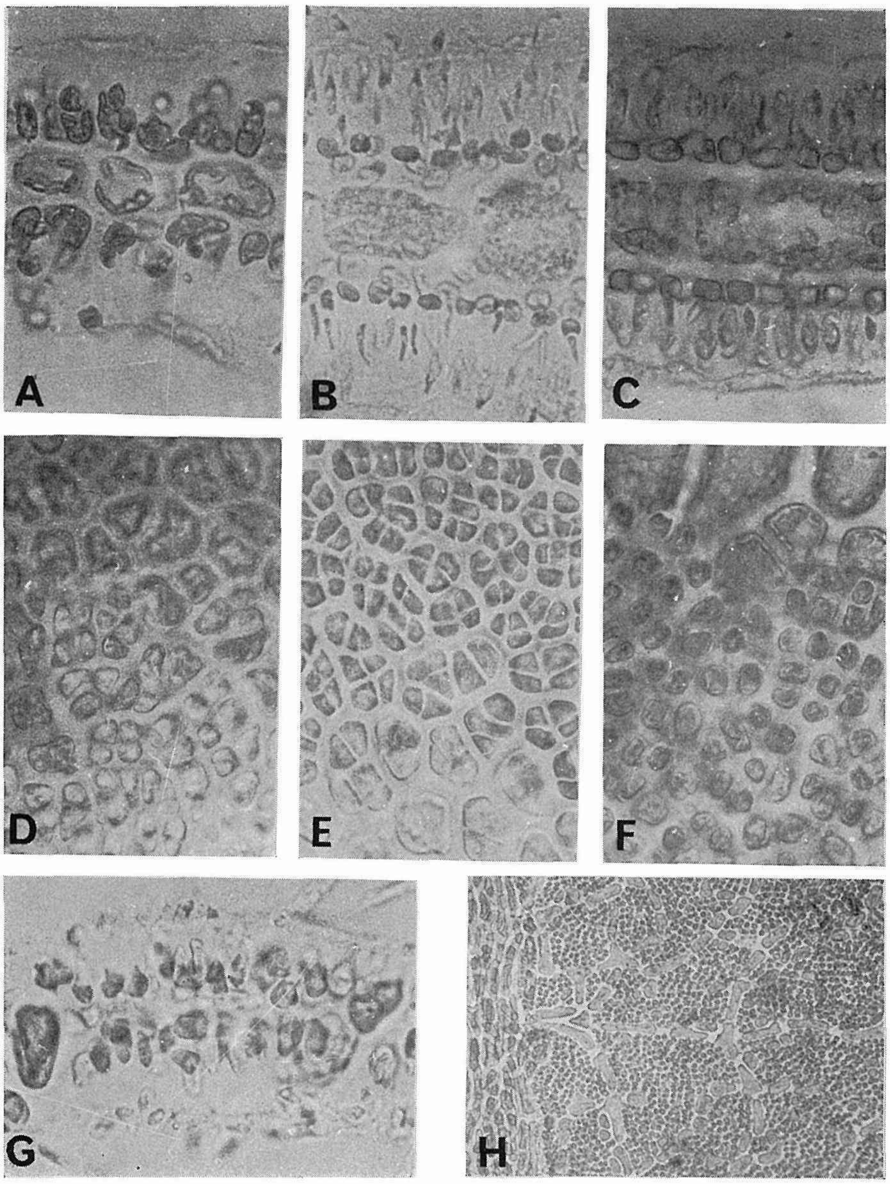


PLATE VIII

Side (A, D) and surface (B, C) views of spermatangial sori

A–B. *Acrosorium polyneurum* OKAMURA, ×530.

C–D. *Cryptopleura membranacea* YAMADA, ×530.

Portion of a frond with spermatangial stands

E. *Benzaitenia yenoshimensis* YENDO, ×616.

F. *Polysiphonia codiicola* ZANARDINI, ×108.

G. *Polysiphonia novae-angliae* TAYLOR, ×114.

H. *Polysiphonia japonica* HARVEY, ×81.

[TAZAWA] PLATE VIII

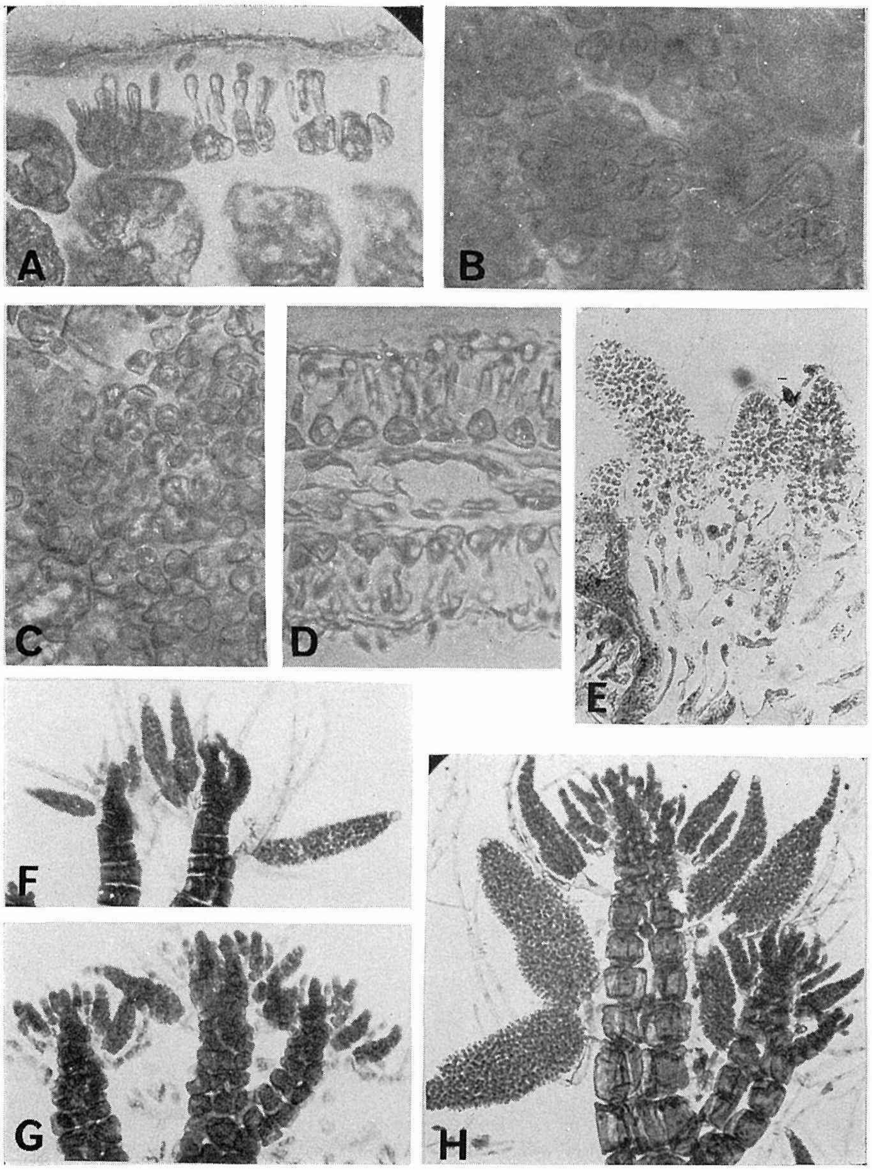


PLATE IX

Portions of fronds with spermatangial stands

A. *Polysiphonia tapinocarpa* SURINGAR, ×91.
B. *Symphyocladia linearis* (OKAMURA) FALKENBERG, ×91.
C. *Polysiphonia senticulosa* HARVEY, ×114.
D. *Symphyocladia marchantioides* (HARVEY) FALKENBERG, ×91.
E. *Symphyocladia latiuscula* (HARVEY) YAMADA, ×91.
F. *Dasya sessilis* YAMADA, ×228.
G. *Heterosiphonia pulchra* (OKAMURA) FALKENBERG, ×52.
H. *Chondria dasyphylla* (WOOD.) C. AGARDH, ×30.

[TAZAWA] PLATE IX

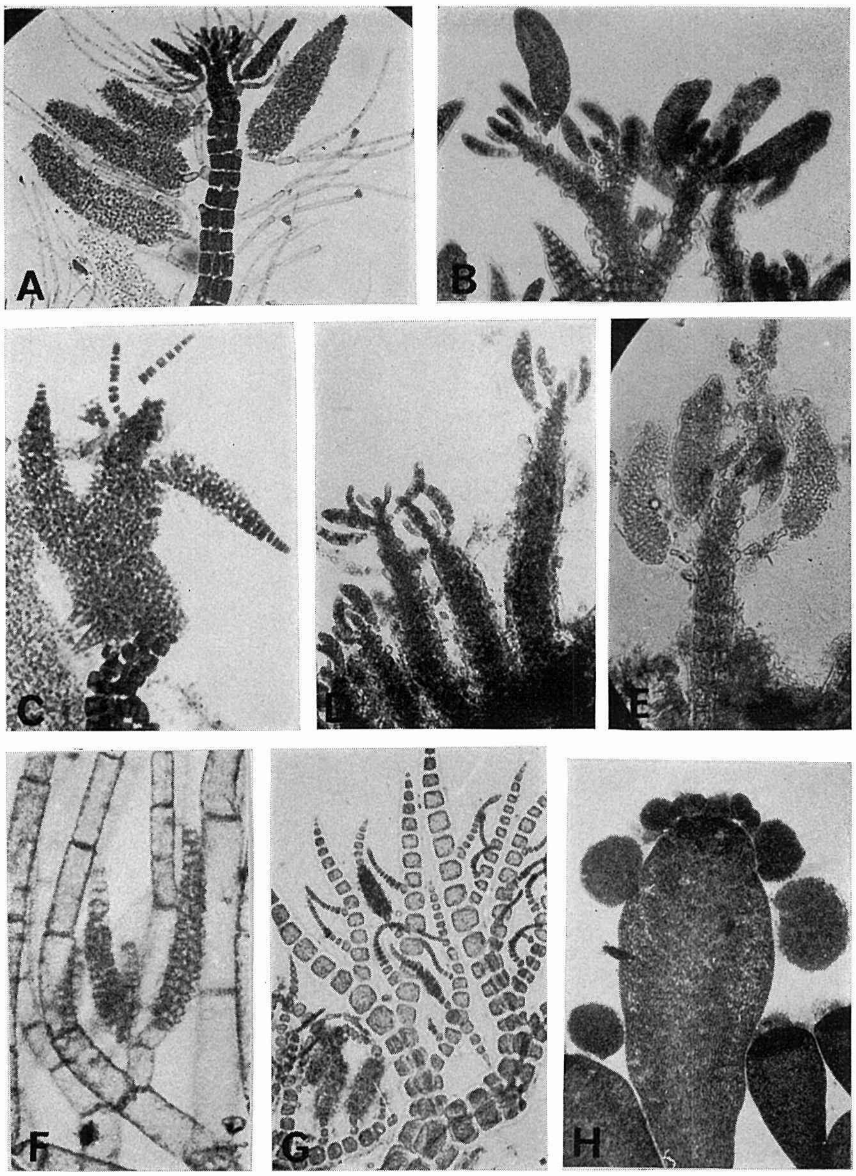


PLATE X

Spermatangial stands

A. *Rhodomela subfusca* OKAMURA (non C. AGARDH,), ×30.

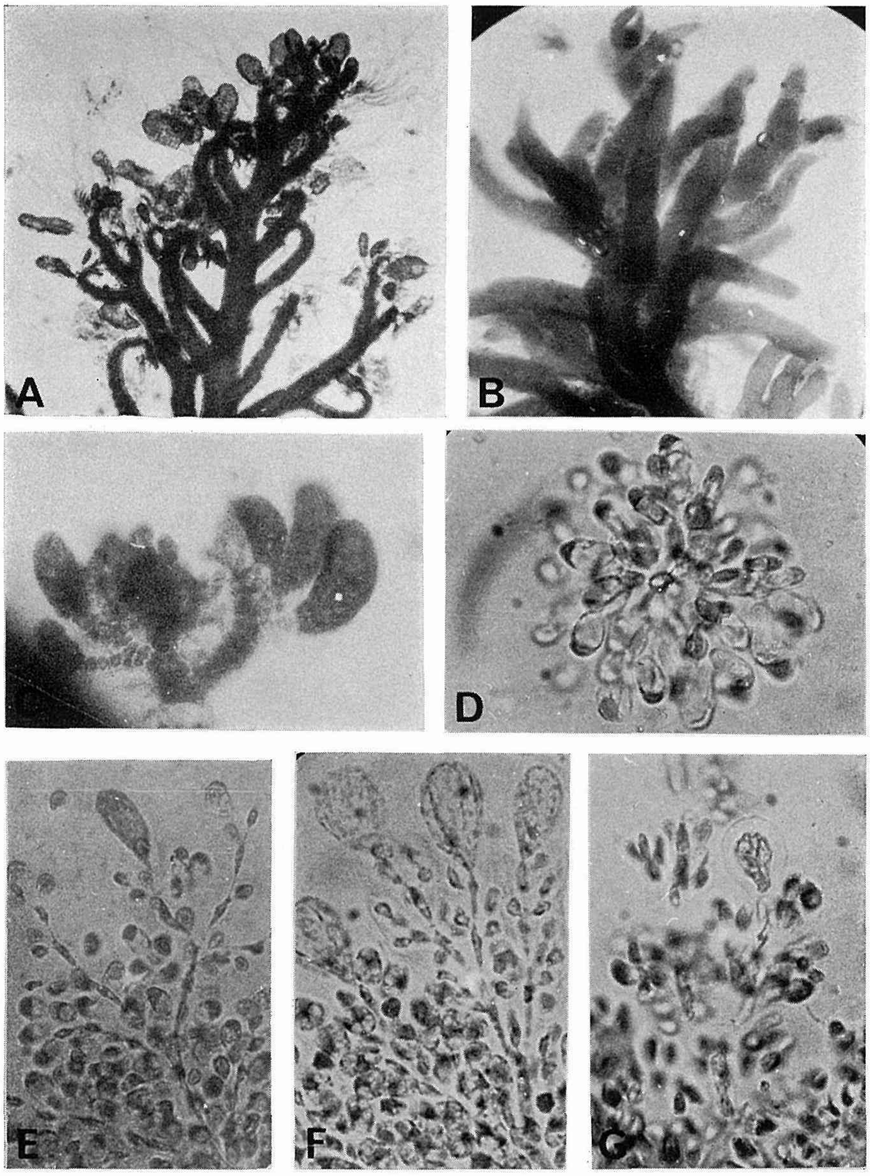
B. *Rhodomela gracilis* YAMADA et NAKAMURA (non HARVEY), ×30.

C. *Rhodomela larix* (TURN.) C. AGARDH, ×148.

D, G. *Laurencia pinnata* YAMADA. D, Transverse section, ×524; G, ×577.

E. *Laurencia composita* YAMADA, ×524.

F. *Laurencia glandulifera* KUETZING, ×577.


A
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